SOME EFFECTS OF TREEFALL-INDUCED SOIL DISTURBANCE ON UNDERSTOREY VEGETATION DEVELOPMENT FOLLOWING THE STORM OF 1987

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Summary

The development of vegetation surrounding the root plates of trees downed in the Great Storm was examined at three semi-natural woodlands in Kent: Blean Woods NNR, Wye Downs NNR and Ham Street Woods NNR. In the sixth growing season following the storm, vegetation centred around selected root plates was examined in contiguous quadrat grids and analysed using TWINSPAN and frequency testing procedures.

This revealed important differences between root pit and root plate positions and their surroundings. Although the adjacent woodland vegetation rapidly colonised much of the disturbed area from plant fragments and via lateral spread, the freshly bared and litter-free surfaces presented opportunities for both adventive species and those germinating from the soil seed bank. In particular, the adaxial surfaces of the root plates represented one of the few places where open-ground species could compete and survive. Root pits provided shadier and wetter conditions which appeared to benefit more hydrophilic species and ferns (*Dryopteris* species). Soil shedding from both root plate surfaces continued to be a significant factor, creating further secondary disturbances and colonisation opportunities.

The regeneration of trees and shrubs was prolific at all sites. Some species were more successful at root plate locations but others were most abundant in undisturbed areas. The evidence suggests that composition of the eventual canopy will be determined by a number of factors, particularly gap size, the availability of regeneration from different tree species, and the persistence of the crowns on fallen trees. These factors are discussed in relation to patterns of damage caused by the Great Storm.

Long-term studies are now needed not only to assess the significance of storm damage in altering and determining canopy composition, but also to determine whether the microsite variation continues to determine understorey vegetation diversity in future years.

Introduction

The uprooting of trees has long been seen as a natural forest process, especially in North America, where the ecological significance of periodic woodland disturbance from severe storms and hurricanes is clearly recognised (eg Lutz 1940; Stephens 1956): indeed such work has been instrumental in focusing attention on the developing subject of patch dynamics in ecology (Pickett & White 1985).

Storm damage in woodland can be viewed at several diminishing scales: the landscape scale, including the overall area of canopy affected, the pattern of damage (whether as small gaps, groups, or devastated swathes of forest), and the frequency of disruption; the scale of an individual canopy gap, including factors such as gap size, shape, regeneration of fallen tree crowns, presence of understorey trees and the zonation of existing ground vegetation; and the significance of surface disturbance within an individual gap, as affected by tip-up mounds and pits created by fallen trees, including the presence of logs and rotting wood on the forest floor.

Although this paper is primarily concerned with the smallest scale of disturbance, this cannot be separated from larger-order factors such as storm frequency and gap size. Moreover the vegetation on the ground prior to storm damage may itself be a consequence of a past disturbance, whether natural or man-induced.

Pattern and frequency of gap formation

The incidence of tropical cyclones (hurricanes) and intense windstorms along the eastern coast of the USA and Canada is well documented, especially their effects on forest structure and dynamics (Stephens 1956; Henry & Swan 1974; Foster 1988a, b). Meteorological records and historical and vegetation studies in the region suggest a pattern of hurricane strike every 20-40 years, with catastrophic storms like those of 1635, 1788, 1815 and 1938 occurring every 100-150 years (Foster 1988a). This has given rise to a characteristically hummocky micro-relief ('pit and mound topography') in forested land along the eastern seaboard, for example affecting over 90% of Appalachian forests (Beke & McKeague 1984).

Although not of hurricane force, storms causing catastrophic windthrow of trees and forests typically occur in some part of the UK every 15 years or so (Miller 1985; Hopkins 1994). Prior to 1987 the three previous events were in NE Scotland (31 January 1953), Central Scotland (15 January 1968), and mid-Wales and the Midlands (3 January 1976). However the 1987 storm not only blew down more timber than all three of its predecessors put together, but it occurred in south-east England where the return period for a storm of this magnitude is estimated at over 200 years (Burt & Mansfield, 1988). It also severely affected coppice woods, many overgrown and unmanaged since the Second World War, creating pits and mounds which would previously have been lacking for perhaps hundreds or thousands of years (Evans & Barkham 1992).

Effects of gap size

The responses of forest herbs to canopy gaps have been comprehensively reviewed by Collins *et al.* (1985). Gap size is of primary importance, since this affects both light level and quality, with larger gaps being not only lighter (Minckler & Woerheide 1965), but receiving a higher proportion of filtered light in red to far-red wavelengths, thus affecting physiological processes such as flowering (Mitchell & Woodward 1988). Some understorey species may not be able to colonise, or respond to open conditions if the gaps are too small; in particular, narrow and elliptical gaps are less efficient than isodiametric gaps in promoting light-demanding species (Collins *et al.* 1985). Invaders and light-demanding woody species are normally associated with larger gaps (Metzger & Schultz 1981); for herbaceous species Falinski (1978) demonstrated how sun herbs were able to spread in gaps in naturally self-thinning stands in Bialowieza forest, Poland.

Vegetation may also respond to higher daytime, and lower night-time temperatures in gaps (Ash & Barkham 1976), and to lower soil moisture and higher vapour pressure deficits. Not only is seed production and seed dispersal of understorey species likely to be affected by all these physical factors, but the extent will also be largely determined by gap size.

The significance of soil disturbance

Estimates of the amount of soil disturbance created by downed trees in wind-damaged stands vary according to factors such as the frequency and intensity of storms, the structure of the crop, the canopy species and the historical perspective of the observer. In the last case, estimates of observers concerned with a single windthrow event have generally been low, of the order of a few percent of the ground surface, whereas pits and mounds created over successive disturbances in time can account for much larger areas (Table 1).

Table 1. Estimates of surface soil disturbance created by treefalls by different observers in semi-natural forests

Author	Site conditions	% area disturbed
Putz (1983)	Pits and mounds in tropical rain forest on Barro Colorado Island, Panama	0.1%
Brewer & Merritt (1978)	Pits and mounds created by the severe storm of 1975 in beech-maple, Michigan	0.26%
	Estimate for disturbance over 25 years	0.66%
Thompson (1980)	Root pits in upland streamside and prairie grove forests in East-Central Illinois	<1%
Falinski (1978)	Root pits in Tilio-Carpinetum in Bialowieza Forest, Poland, over a ten-year period	2%
Spurr (1956)	Central New England forests following the 1938 hurricane	8%
Stephens (1956)	Pits and mounds in Havard Forest, estimated over a period of 500 years	14%
Lyford & MacLean (1966)	Pits and mounds over several centuries in forests in northeastern USA	20-50%

For example, Putz (1983), working in tropical rainforest, found only small areas of soil perturbation, probably because rainfall erosion and litter accumulation, respectively, rapidly levelled the mounds and pits, compared with Stephens' (1956) temperate forest site in New England which still exhibited microrelief created by treefalls 500 years earlier. Stephens' work implies that periods of 3000-4000 years would be required to obtain complete turnover of temperate forest soils, similar to estimates of 3500-5000 made for beech-maple woods in Michigan (Brewer & Merritt 1978).

This 'arbroturbation' is important in the development and rejuvenation in forested soils (Beke & McKeague 1984). Pits and mounds under forested land in Novia Scotia were characterised by discontinuous horizons, showing increased pH values in the pit and thicker B horizons on the mound. Higher pH values in tree pits were also found under maple-beech forest in New York State, with lower nutrient status, lower CEC and less organic matter in the mounds (Beatty 1984). Mounds were also drier and, being litter-free, were more prone to freezing (Federer 1973).

The physical and chemical differences between pits and mounds might be expected to influence patterns of vegetation development. Wetter conditions in tree pits in Bialoweiza Forest favoured non-forest species including aquatic, silt and mud therophytes as well as *Carex remota* and *Rumex sanguineus*, while *Asarum canadense* and *Hydrophyllum appendiculatum* occurred in these positions in three Illinois forest preserves (Thompson 1980). Beatty (1984) found a very strong differentiation between pits and mounds in her maple-beech plots, with species such as *Aster divaricatus* and *Erythronium americanum* being prominent on the former and *Allium tricoccum* and *Dryopteris spinulosa* in the latter.

Contrasting vegetation communities on mounds and pits are not necessarily the result of differing soil conditions. Depending on the age of the disturbance, freshly bared soil surfaces may be subject to different rates of colonisation from *in situ* sources, such as the adjacent vegetation, the buried seed bank, or dispersal via wind, insects and animals. Tree pit perimeters are easily colonised vegetatively (Thompson 1980), while plants may be more likely to reach the interior via seed dispersal. Animal movements around fallen trees and selective herbivory between different microsite types could also account for vegetation differences.

Finally, although not considered here, fallen logs occupy potentially much larger areas of the forest floor than pits and mounds, and may provide an important substrate for vegetation colonisation, especially as they rot and accumulate humus layers.

Experimental sites and methods

Plant distributions associated with the root plates of trees downed in the Great Storm of 1987 were investigated at three wooded National Nature Reserves in Kent: Wye Downs NNR, Ham Street Woods NNR and Blean Woods NNR, in the early summer of 1993 (Table 2).

Table 2. Study sites used for root-plate recording

Site	Soil type	Canopy	Ground flora
Blean Woods NNR TR 114606	Drift over London clay: WICKHAM 4 (711h) Association	Singled beech with birch, oak and hornbeam	Dominated by *Pteridium aquilinum, Rubus fruticosus* and *Lonicera periclymenum,* with occasional *Holcus mollis, Hyacinthoides non-scripta, Melampyrum pratense* and *Lamiastrum galeobdolon. Crataegus laevigata* abundant in shrub layer. NVC group W10/15
Ham Street Woods NNR TR 007344/017341	Weald clay: WICKHAM 1 (711e) Association	Oak and occasional birch standards, hornbeam and sweet chestnut coppice	*Hyacinthoides non-scripta, Rubus fruticosus* and mosses (eg *Mnium hornum* and *Atrichum undulatum*), with the ferns *Dryopteris affinus* and *D. dilatata.* NVC group W10e.
Wye Downs NNR TR 074457	Rendzina over chalk: very steep Andover/ Upton Series	Ash and beech standards with hazel coppice and 'chalk' scrub	Dominated by *Mercurialis perennis* and *Rubus fruticosus*, with *Fragaria vesca* and *Veronica chamaedrys.* Plentiful ash and sycamore seedlings. NVC group W12.

Wye Downs NNR

The area examined was at Pickersdane Scrubs, a steep chalk scarp slope with thin rendzina soil profiles. Part of the site was secondary woodland, but contained pockets of older ash *Fraxinus excelsior* and beech *Fagus sylvatica* woodland with an understorey of *Mercurialis perennis, Rubus fruticosus* and chalk shrubs such as *Viburnum lantana, Ligustrum vulgare, Rhamnus cathartica* and *Euonymus europaeus.*

The vegetation surrounding root plates was described for 11 fallen individuals (six beech, three ash and two oak *Quercus robur*), seven of which were still alive (Appendix 1). One of these, a fallen beech with a bole 76 cm in diameter at breast height, was present in a very large gap surrounded by sparse ash saplings 15-20 years old. Younger sycamore *Acer pseudoplatanus* and ash saplings dominated the undisturbed area around the root plate, which measured approximately 3.5 m high by 6 m wide, with a corresponding pit covering an area of 23 m^2. For this individual, Domin estimates of vegetation cover were made of the pit, mound and the surrounding area in a contiguous 10 x 10 m grid of 1m^2 quadrats. On the vertical root plate an equivalent area was sampled on the adaxial surface and plate crest; the abaxial face supported no vegetation.

Ham Street Wood NNR

The woodland area examined at Ham Street consisted predominantly of oak standards over mixed hornbeam *Carpinus betulus* and sweet chestnut *Castanea sativa* coppice, on base-poor soils derived from Weald Clay. Understorey vegetation was relatively species-poor, with large areas dominated by *Hyacinthoides non-scripta, Rubus fruticosus,* mosses and ferns. Canopy damage in the wood was relatively light, with most fallen trees occurring in small gaps which were partly shaded by surrounding trees.

Notes were made on ten fallen boles in Little Carter Wood (Appendix 2) and one large individual, an overgrown chestnut coppice stool in Compartment 8 of the main wood, was examined in detail. This consisted of five main stems, each up to 40 cm at breast height, the upper ones of which had regenerated vigorous vertical shoots. The resulting canopy gap was partly overstood by adjacent overmature hornbeam coppice, partly shading the root plate (2.25 m high by 4 m wide) and pit (occupying about 5 m^2). A contiguous grid of 6 x 6 m, 1 m^2 quadrats was used to record the vegetation.

Blean Woods NNR

Much of Blean Woods consists of oak standards and hornbeam/sweet chestnut coppice on London Clay, but the area selected for study was an area dominated by beech standards, including some singled from old coppice stools, where small canopy gaps had been created by the storm. As at Ham Street the soils were relatively base-poor surface-water gleys; under the beech canopy the vegetation was sparse, consisting predominantly of *Pteridium aquilinum, Rubus fruticosus* and *Lonicera periclymenum* and *Hedera helix.*

Ten canopy gaps of different sizes were examined for the study (Bolas 1993), in which three distinct investigations were carried out, aimed at different scales of disturbance.

a. Four of the ten canopy gaps were mapped in detail and in these the percentage cover of understorey vegetation was recorded in contiguous grids of 2 m x 2 m quadrats. Comparative control areas were also recorded in adjacent, intact woodland, separated by a distance corresponding to at least the long axis of the gap.

b. The vegetation of root plates and their corresponding pits was recorded from one fallen tree in each of the ten canopy gaps, using contiguous 0.5 x 0.5 m quadrats located across each pit and on each face of the root plate. Quadrats were extended to a similar area to cover undisturbed vegetation surrounding the pit.

c. Soil was collected in May 1993 from representative root plates in six canopy gaps, located in four areas: the abaxial side of the plate; the adaxial side; the undisturbed area around the root plate, and intact woodland surrounding the gap.

Bulked soil samples were taken to 15 cm depth, placed in seed trays in an unheated polythene tunnel, and the number and species of seedlings germinating recorded over a period of thirteen weeks.

Results

Vegetation distribution in treefall gaps in the Blean

Treefall gaps at Blean were generally small, consisting of 1-7 blown individuals (Table 3). Typically they were elliptical and orientated north-east/south-west, with diameter: height ratios of less than 1 with the largest measuring 44 x 25 m (0.11 ha), and the smallest only 8 x 8 m. Of the 26 uprooted individuals only two had died and one other had been windsnapped: most of the remainder were actively regenerating new canopies, which in the sixth growing season occupied 30-80% of the gaps. Very little vegetation survived under these positions and they were excluded from the survey.

Table 3. Details of the ten canopy gaps surveyed at Blean Woods NNR, showing gap dimensions and the fate of the fallen trees

Gap	Compt	Size (m) and orientation (^{o})		Fallen species	Orientation of fallen species (^{o})		Type of damage	Condition of fallen species	Regenerating canopy (total % of gap)	Height of surrounding canopy (m)	D:H ratio
1	22b	22	NE-SW	Beech	NE	50	U	CR	50	23	0.7
		8	NW-SE	Oak	NE	50	S				
2	22b	44	NE-SW	Beech	NE	78	U	CR	30	26	1.3
		25	NW-SE	Beech	N	0	U	CR			
				Beech	N	0	U	CR			
				Beech	NE	40	U	CR			
				Beech	NE	70	U	CR			
				Beech	NE	40	U	CR			
				Beech	NE	22	U	CR			
3	22b	12	NE-SW	Beech	N	10	U	CR	40	20	0.4
		5	SW-NE								
4	23fg	13	N-S	Beech	NE	20	U	CR	40	17	0.6
		7	E-W	Beech	NW	340	U	CR			
5	33	12	NE-SW	Beech	NE	30	U	CR	40	21	0.6
		12	SW-NE	Beech	NE	30	U	CR			
				Sweet chestnut	NE	13	U	CR			
6	33	8	NE-SW	Sweet chestnut	NE	17	U	D		23	0.3
		8	SW-NE								
7	33	19	NE-SW	Sweet chestnut	NE	28	U	CR	80	19	0.8
		10	NW-SE	Sweet chestnut	NE	20	U	CR			
				Sweet chestnut	NE	20	U	CR			
				Beech	NE	20	U	CR			
8	22b	21	NE-SW	Beech	NE	60	U	CR	30	24	0.6
		7	NW-SE	Beech	NE	80	U	CR			
				Oak	NE	72	U	A			
9	23fg	30	N-S	Beech	NE	30	U	CR	30	28	0.8
		12	E-W	Beech	NE	30	U	CR			
				Beech	NE	22	U	CR			
10	23ef	11	N-S	Beech	NE	68	U	D		17	0.9
		19	E-W								

Compt	=	compartment	A	=	alive but no canopy
U	=	uprooted	D	=	dead
S	=	snapped	D:H	=	mean diameter of gap:mean height of adjacent intact canopy
CR	=	regenerating to give canopy			

Table 4. **Species cover (Domin values) recorded in the field layer at Blean Woods in canopy gaps and adjacent intact woodland, respectively.**

	Canopy Gaps										Intact Woodland									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<u>Herbs</u>																				
Ajuga reptans	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anemone nemorosa	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-
Calluna vulgaris +	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex pilulifera *+	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chamerion angustifolium	-	1	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Cytisus scoparius	-	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Dryopteris dilatata	1	1	1	-	1	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-
Dryopteris filix-mas	-	1	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Hedera helix	2	1	4	-	1	-	-	1	2	1	1	1	2	-	1	-	-	1	1	1
Holcus mollis	-	-	1	-	1	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-
Hyacinthoides non-scripta	1	1	1	-	1	-	-	-	-	-	1	1	-	-	2	-	-	1	-	-
Hypericum pulchrum +	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus effusus *+	-	1	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Lamiastrum galeobdolon	-	-	-	-	1	-	1	-	-	1	1	1	-	-	1	-	-	-	-	2
Lonicera periclymenum	2	1	1	-	5	-	2	1	-	1	2	1	3	-	2	-	-	-	-	1
Luzula pilosa	-	1	-	-	-	1	-	-	-	1	1	-	-	-	1	-	-	-	1	1
Melampyrum pratense	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Melica uniflora	-	-	-	-	-	-	1	-	-	1	-	1	1	-	1	-	-	-	-	1
Milium effusum	-	1	1	1	1	-	-	-	1	-	-	1	1	-	1	-	-	-	-	1
Pteridium aquilinum	2	3	3	1	1	-	-	1	1	2	1	-	1	1	1	-	-	-	1	-
Rosa arvensis	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-
Rubus fruticosus agg.	5	4	4	1	5	-	8	3	4	8	2	4	8	-	2	1	1	2	2	6
Ruscus aculeatus	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scrophularia nodosa *+	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solidago virgaurea	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Teucrium scorodonia	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Viola seedling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<u>Shrubs</u> (seedlings only)																				
Betula pendula	-	1	-	1	1	-	1	-	2	1	-	-	-	1	-	-	-	-	1	-
Carpinus betulus	-	1	1	-	-	1	1	1	-	1	-	-	-	-	1	-	-	-	-	1
Corylus avellana	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crataegus laevigata	-	-	1	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Fagus sylvatica	-	1	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Ilex aquilinum	1	1	-	-	-	-	-	1	-	1	1	-	1	1	-	-	-	1	-	-
Malus sylvestris	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus spp.	-	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Sorbus torminalis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Moss spp.	1	1	1	3	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
<u>Mosses</u> (gaps only)																				
Atrichum undulatum *+	1	1	-	1	1	1	1	-	1	-										
Campylopus introflexus *+	1	1	-	1	1	-	1	-	1	-										
Dicranella heteromalla *+	1	1	1	1	1	1	1	1	1	1										
Dicranum scoroparium *	-	1	-	1	-	-	-	1	-	-										
Hypnum spp. *+	1	1	-	1	1	-	1	-	1	-										
Isothecium myosuroides *+	-	-	-	1	1	-	-	1	-	-										
Mnium hornum *+	1	-	-	1	1	1	-	-	-	-										
Polytrichum formosum *+	1	1	-	-	1	-	1	1	1	-										

* Species found only in root pits   + Species found only on root plates   *+ Species found only on root pits and root plates

Fisher Exact frequency testing of all canopy gaps and their adjacent areas showed species such as *Chamerion angustifolium* ($p<0.001$), *Juncus effusus* ($p<0.05$) and *Dryopteris dilatata* ($p<0.05$) to favour canopy gaps, although others (*Cytisus scoparius, Betula pendula, Rubus fruticosus* and *Pteridium aquilinum*) had a similar tendency (Table 4). *Betula* and *Chamerion* both have wind-dispersed seeds and a high ability to colonise freshly-disturbed mineral soil. *Dryopteris* and *Juncus* may also benefit from the disturbance but perhaps as important are the moist conditions provided by root pits and rotting wood. *Rubus* and *Pteridium* are both capable of responding rapidly to open conditions, the former typically forming thickets from buried seed or via lateral spread from existing plants, while in *Pteridium* vegetative spread and spore production is much greater than in unshaded habitats (Grime *et al.* 1988).

In the largest of the canopy gaps (gap 2, Table 3) seven beech trees had been uprooted, falling at angles between 0-70^0 (N-NE) and were regenerating to form a low, and in places dense, canopy. Several young beech trees, once part of the understorey, were present in the gap, as were standards of beech, wild service and oak (Figure 1). TWINSPAN analysis of the 2 x 2 m quadrats showed concentrations of *Chamerion, Betula,* and *Rubus* in areas A and C, representing the most disturbed and open areas of the gap. Seedlings of birch varied in height from <1 m - 2.5 m but were largest in areas A and C; a few small seedlings of beech, oak, hornbeam and sweet chestnut were also present.

The zonation of vegetation found in gap 2 contrasted strongly with smaller gaps, where TWINSPAN analysis failed to produce meaningful groupings of species. In gap 5, for example, the canopies of the three fallen trees covered 80% of the area, the remainder being occupied by *Rubus* and *Lonicera periclymenum.*

<u>Wye Downs root plates</u>

Some plates were wide and thin (commonly in beech), up to 3-5 m high, but with only poorly developed pits less than 0.5 m deep. Other plates were smaller (2-3 m high) but made deeper pits, ranging from 0.5 - 1 m depending on the depth of the soil and the nature of the root system. Typical root plate morphology is illustrated in Figure 2. The abaxial faces of the root plates were virtually pure mineral chalk and were usually unvegetated, but the adaxial faces retained a soil covering, some of which was shedding. Small piles of soil and chalk rubble accumulated around the base of the plates on both sides, including accumulation on the tree bole. There was also soil slippage from the root plate crests into the pits, some of which had recently occurred, as well as soil creep at the pit edges.

Because of soil shedding the adaxial surfaces were poorly vegetated, but supported plants originating from buried, or newly arrived seeds, together with pre-existing vegetation, including sapling trees. On the larger plates the horizontal crests represented a distinct zone where vegetation was less subject to soil erosion. The pits themselves were dry, often consisting almost entirely of chalk rubble, but were relatively well vegetated. Small pits were sometimes completely overgrown by *Rubus* and *Clematis vitalba*, precluding entry of other species.

TWINSPAN analysis of plant cover data from the large root plate surveyed in detail showed clear divisions, the major split distinguishing the root plate crest and adaxial face (Group 1: Figure 3). Here a sparse cover comprising *Reseda lutea, Senecio jacobaea, Veronica arvensis* and *Poa annua* replaced *Mercurialis* and *Rubus* which were dominant in the surrounding vegetation. A second group (2) corresponded to the mineral soil of the pit itself and was characterised by *Chamerion angustifolium* (especially on debris cones beneath the plate) and scramblers such as *Ranunculus repens, Solanum dulcamara, Fragaria vesca* and *Clematis vitalba.* Dominance of *Mercurialis* was reduced in this zone, which still contained much bare ground, but *Rubus* was abundant despite the lack of soil. The third group (3) was similar, but was associated with disturbance around the pit perimeter. *Mercurialis* and seedlings of ash and sycamore were more abundant, but there was still sufficient open ground allowing *Geum urbanum, Epilobium parviflorum, Poa trivialis, Scrophularia nodosa* and *Prunella vulgaris* to persist together with *Cirsium arvense, C. vulgare, Picris echioides* and *Myosotis arvense.*

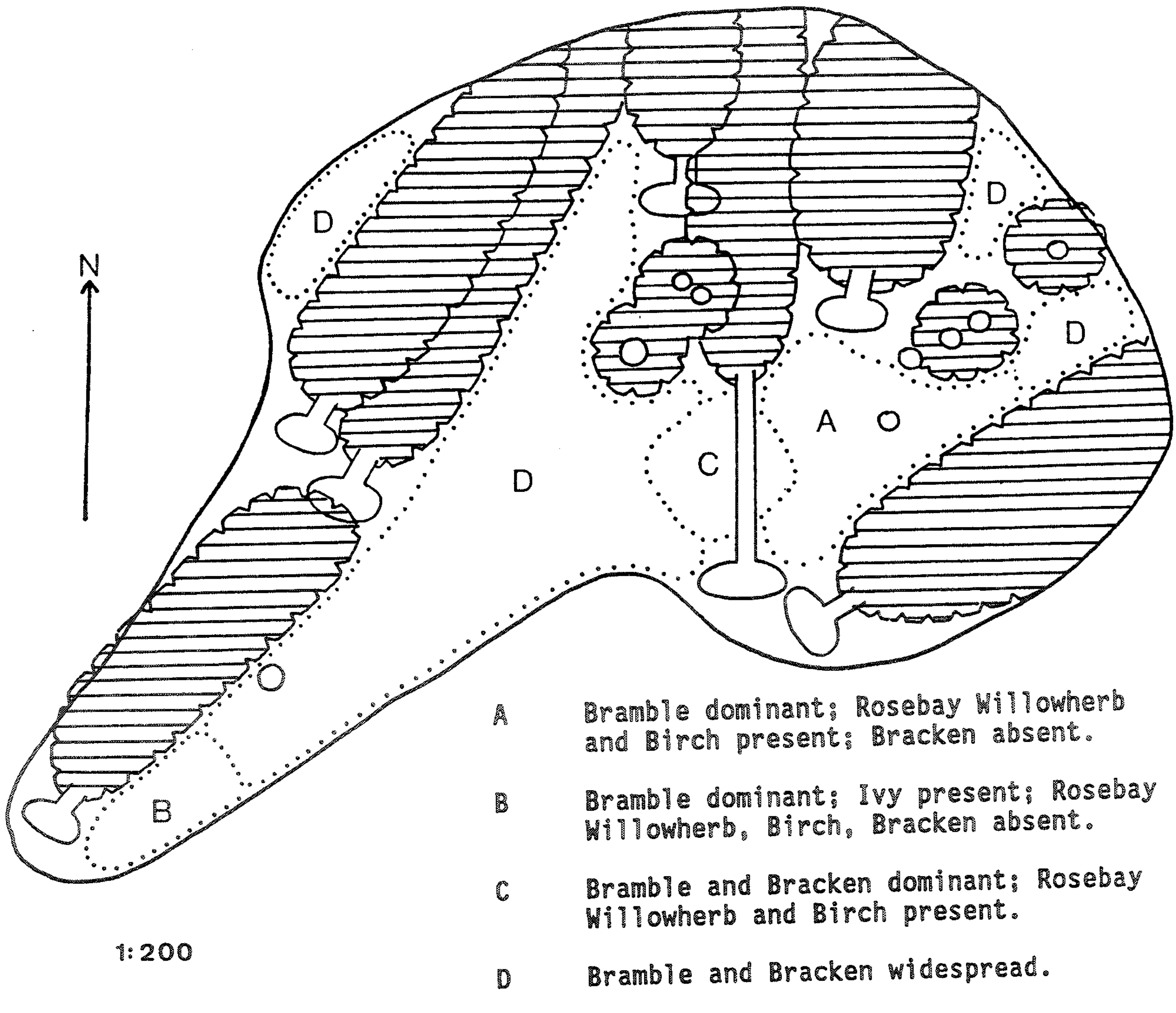
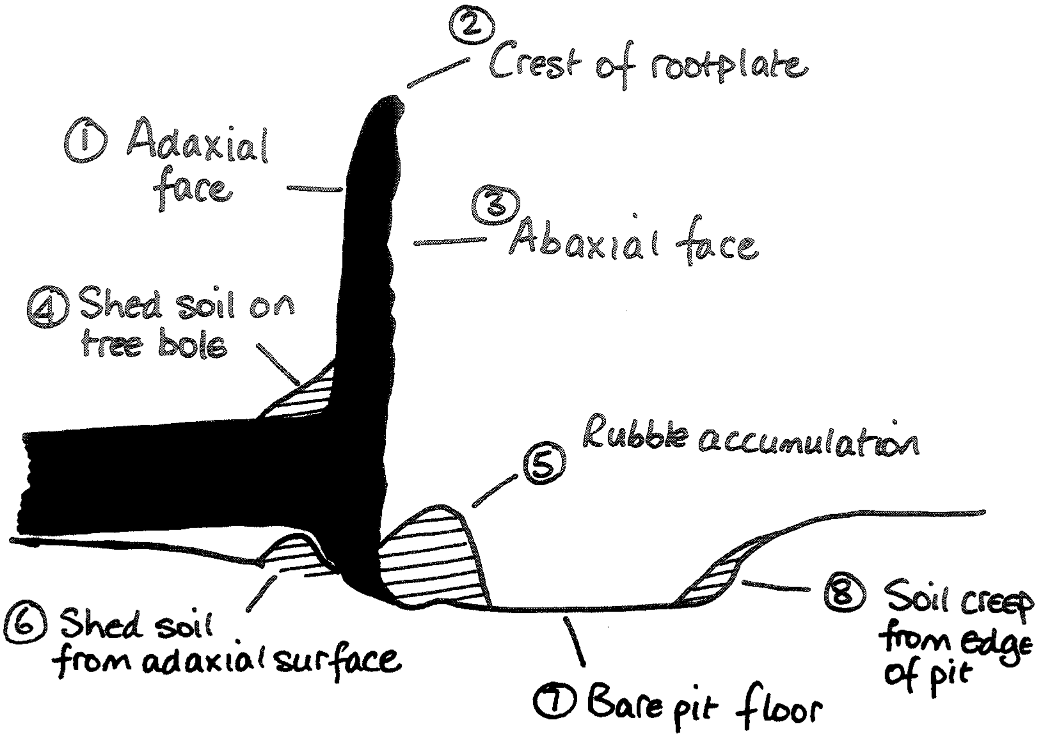


Figure 1 Plan view of treefall gap 2 at Blean Woods NNR, showing the location of species associations identified by TWINSPAN

a) ELEVATION



b) PLAN

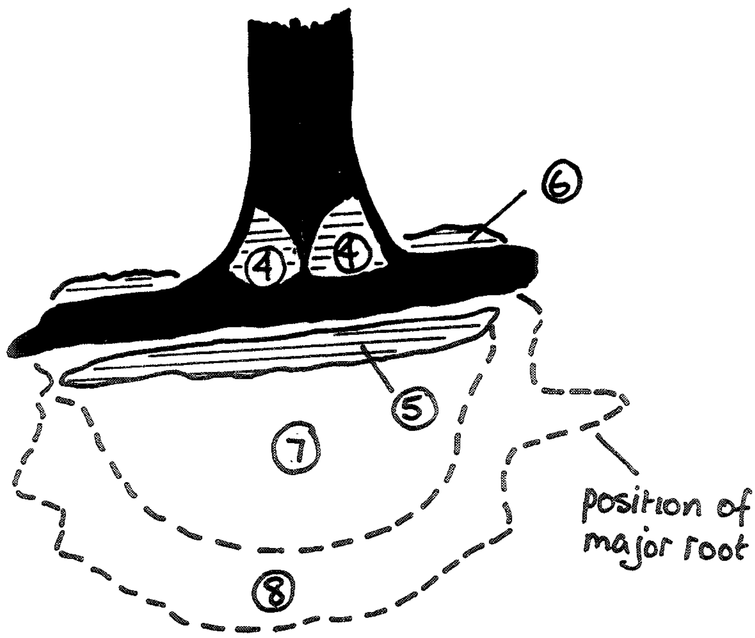


Figure 2. Typical root plate morphology, shown in plan and elevation, from observations at the Wye Downs NNR

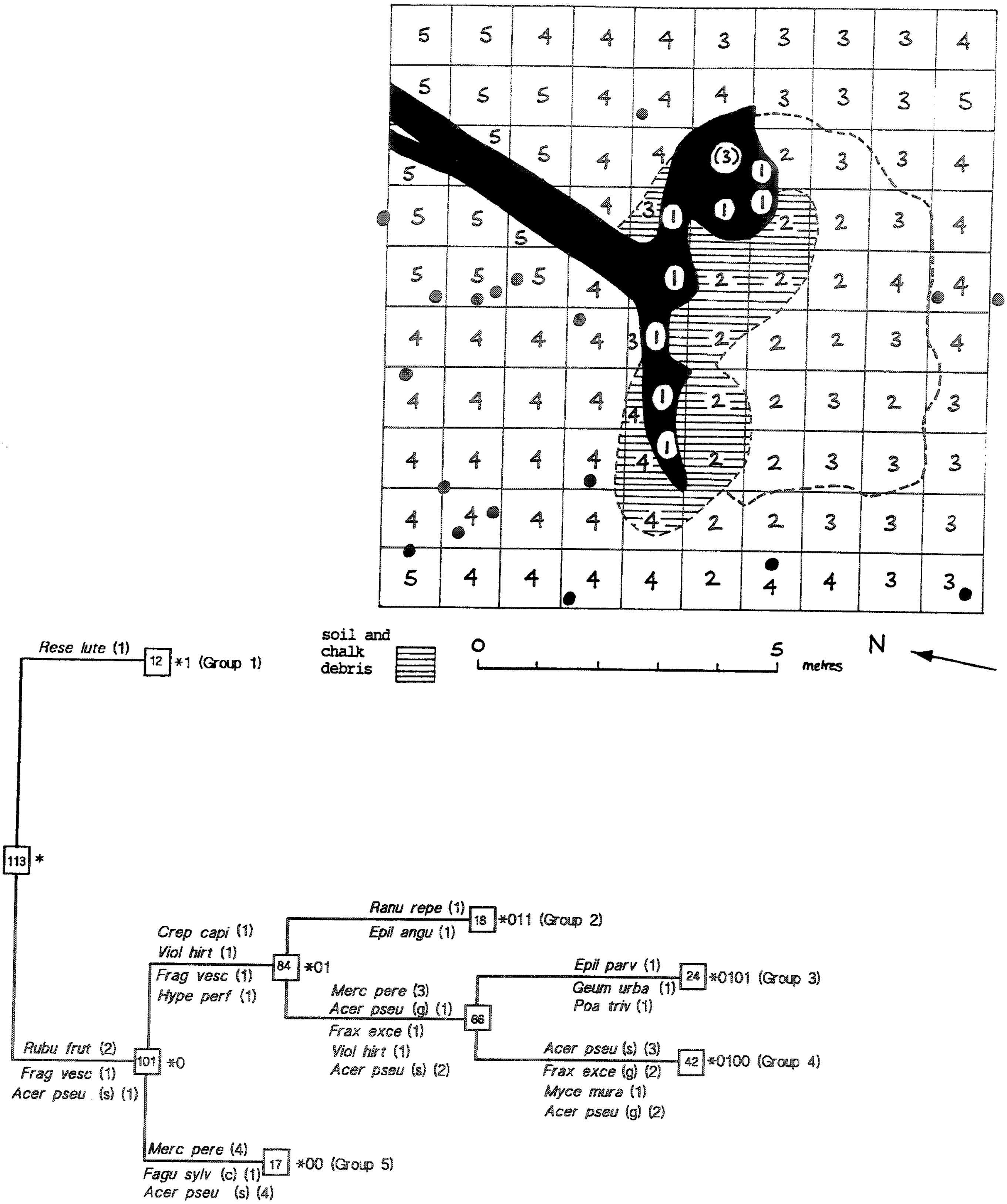


Figure 3. Vegetation groups classified by TWINSPAN, shown as a dendrogram and in relation to the area around the beech root plate surveyed at Wye Downs NNR. (Figures after species names refer to pseudospecies levels; c=canopy, s=scrub layer, g=seedlings. Black dots refer to prominent *Acer pseudoplatanus* saplings.)

Groups 4 and 5 represented a much less disturbed area surrounding the root plate and pit. Group 4, the largest, was distinguished by the dominants *Mercurialis*, *Rubus* and abundant tree and shrub seedlings, but also contained *Fragaria vesca, Viola hirta, Hypericum perforatum, Veronica chamaedrys, Crepis capillaris* and other species more typical of less shaded habitats. This distinguished it from group 5 which was *Mercurialis*- dominated and was strongly associated with the fallen bole and its surviving canopy.

To summarise, the root plate crest was distinguished by adventives arriving on a shedding soil surface (eg *Senecio*) or short-lived species suited to dry sites such as *Veronica arvensis* and *Reseda*; these last two may have germinated from a persistent seed bank or were introduced by wind or animal dispersal. The chalk rubble of the root pit also appeared to be a hostile environment, being poorly vegetated after six growing seasons, but containing a wider representation of the surrounding vegetation, including *Mercurialis*, fragments or seeds of which may have slipped down from above. There was some evidence that the interior of the pit adjacent to the abaxial surface was more likely to be colonised by scramblers or wind-dispersed seeds than the perimeter, where competition from established vegetation growing on organic soil layers had a colonising advantage.

Most sapling regeneration occurred on the less disturbed areas rather than on the root plate or pit: chi-squared testing showed that *Acer pseudoplatanus, Fraxinus excelsior* and *Ligustrum vulgare* were much less abundant on the root plate and in the root pit (Groups 1 and 2) than elsewhere (Table 5). Regeneration of *Viburnum lantana* and *Sambucus nigra* was most prolific to the north of the root plate (Groups 4 and 5), where the shadier and more humid conditions may have benefited seedling development. Only *Rhamnus cathartica* was significantly more frequent in the root pit (Group 2) than in the area immediately adjacent to the beech bole (Group 5).

Further description of root plate vegetation at Wye is provided by Russell (1993).

Table 5. Percentage frequencies of tree and shrub species, present as seedlings and saplings, in relation to TWINSPAN vegetation groupings around the beech root plate at Wye Downs NNR (see Figure 3)

	Group 1	Group 2	Group 3	Group 4	Group 5	Total
Number of occurrences (n)	(12)	(18)	(24)	(42)	(17)	(113)
Fraxinus excelsior	17	22	66	88	82	65
Acer pseudoplatanus	17	22	54	57	59	47
Viburnum lantana	0	11	21	33	23	22
Ligustrum vulgare	0	0	29	33	23	22
Sambucus nigra	0	5	4	14	35	12
Crataegus monogyna	0	0	12	21	0	11
Rhamnus cathartica	0	22	4	7	0	7
Rosa canina	8	11	8	5	0	6
Corylus avellana	0	0	4	11	5	6
Cornus sanguineus	0	0	0	7	7	5
Euonymus europaeus	0	0	8	9	0	5
Fagus sylvatica	0	0	0	2	18	3
Salix caprea	0	5	0	0	0	<1
Sorbus aucuparia	0	0	0	<1	0	<1
Prunus spinosa	0	0	0	<1	0	<1

Ham Street Woods root plates

More than half of the fallen trees recorded in Little Carter Wood were birch, with the remainder oak and hornbeam (Appendix 2). The root plates were mostly smaller, and the corresponding pits relatively deeper than those on the Wye Downs: despite recent heavy rain none contained water. Soil shedding appeared to be less than at Wye on the adaxial surfaces, possibly due to the clay substrate. In this respect a moss cover of *Mnium hornum, Atrichum undulatum* and *Dicranum* and *Dicranella* species (which occurred around the tree bases and lower bole of many standing trees) may have played a part in protecting the surface from raindrop erosion. The area recorded in detail around the chestnut root plate was very species-poor, with only 10 vascular species recorded in 40, 1 m^2 quadrats.

The main vegetation consisted of *Hyacinthoides non-scripta* and *Rubus fruticosus*, with occasional *Oxalis acetosella, Carpinus betulus* seedlings and the ferns *Pteridium aquilinum* and *Dryopteris dilitata*. There was little bare ground, except on the vertical face of the root plate; leaf litter and moss cover were abundant.

TWINSPAN analysis grouped the quadrats according to the presence of *Carpinus*, as overhead canopy or seedlings, together with *Oxalis* at the southern edge of the area (Figure 4). The second division picked out quadrats largely present in the tree pit or on the adaxial face of the root plate, characterised by *Dryopteris affinis*, mosses and reduced *Hyacinthoides* and *Rubus* cover (Group 1), from the area surrounding the root pit (Group 2). The other major vegetation group lay to the north and west on the edge of a canopy gap, but partly shaded by the regenerating chestnut stool. In the lightest areas *Pteridium* grew particularly well.

This vegetation pattern suggests little invasion of species not already present in the immediate area in contrast to Wye. *Hyacinthoides* and most other species survived well on the root plate but were also found in the pit, possibly due to soil slippage. Initially the pits may have provided litter-free and damp surfaces suitable for the colonisation of *Oxalis* (Grime *et al.* 1988) and hornbeam seedlings, which may also have been beneficial for the development of *Dryopteris affinis*. Moss cover was also extensive in these areas and particularly on the adaxial plate, which was virtually free of leaf litter.

Blean Woods root plates

The root pits created by fallen trees at Blean were generally well vegetated, but the plates were once again bare on the abaxial surfaces, with vegetation cover on the adaxial side mainly concentrated on the crest. Only seven out of ten root plates and pits studied (Appendix 3) produced sufficient data for TWINSPAN analysis, the other three being either too small or too sparsely vegetated. In most cases the indicator species for the root pits and the surrounding vegetation was *Rubus*, while that for the adaxial root plates were mosses such as *Dicranella heteromalla*. There were no important divisions of quadrats located in the surrounding areas and the root pits.

For three canopy gaps vegetation data was available for comparison from 0.5 m x 0.5 m quadrats in the surrounding undisturbed vegetation. In these cases Fisher Exact frequency testing showed that both *Juncus effusus* and *Dryopteris dilatata* were commoner in areas disturbed by root plates, with *Juncus* almost exclusively present in root pits. The data for all seven gaps showed that *Rubus* was also significantly more frequent in root pits than on plates. The mosses *Polytrichum formosum* and *Atrichum undulatum* were much more common on disturbed ground associated with root plates than their surroundings, although not at a significant level because of their patchy occurrence on the root plate crests. *Betula* and *Chamerion angustifolium* were present in a number of root pits and on the occasional root plate, but showed no particular concentration in these areas.

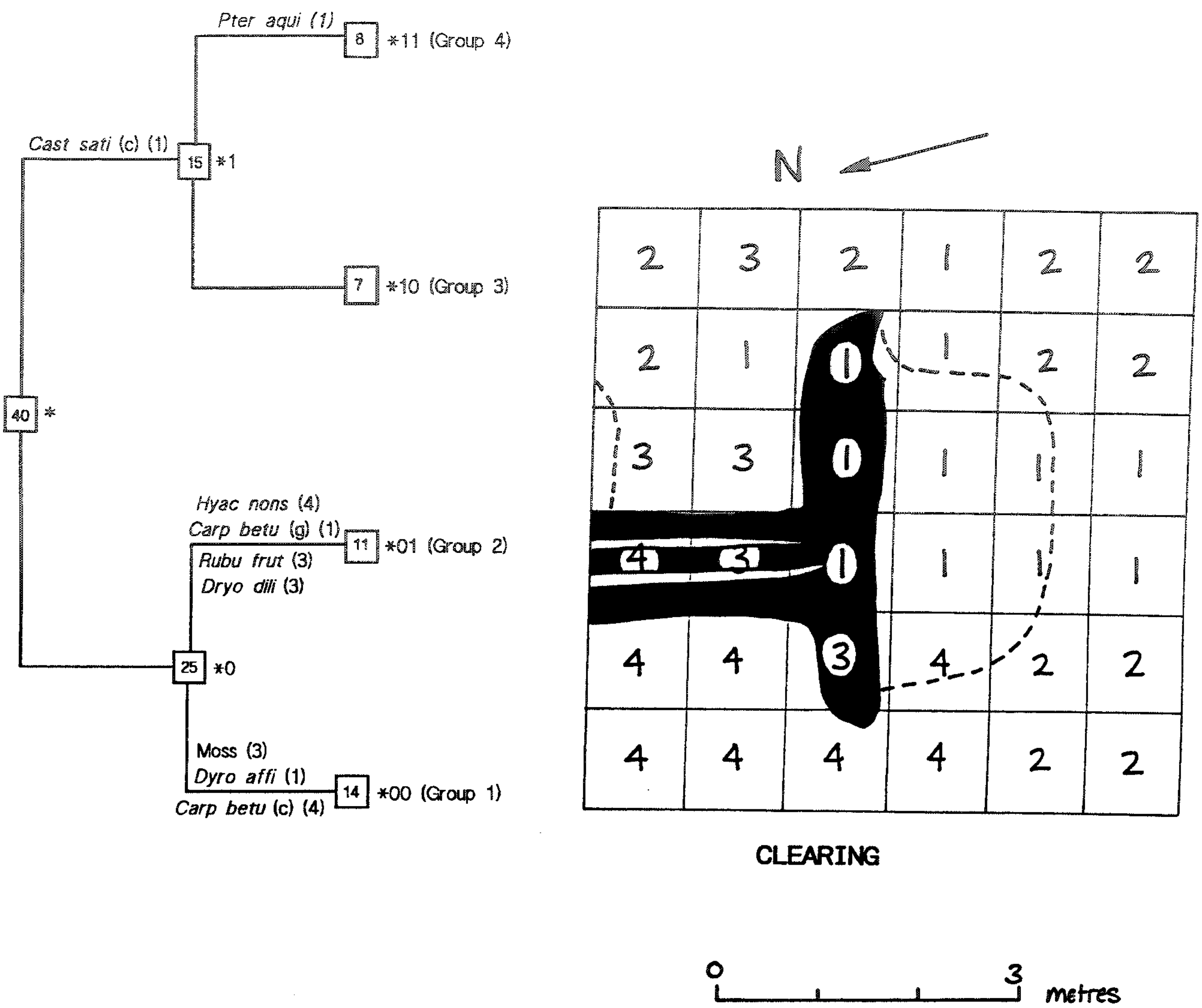


Figure 4. Vegetation groups classified by TWINSPAN in the vicinity of a sweet chestnut root plate at Ham Street Woods NNR

Seeds germinated in soil samples collected from the undisturbed ground, the adaxial root plates and intact woodland adjacent to the gaps, but not from subsoil removed from the abaxial faces (Table 6). The most abundant species were *Betula* and *Juncus*, but *Rubus* and *Hypericum pulchrum* were also common. The presence of *Calluna vulgaris* and *Cytisus scoparius* in samples taken from compartment 22b suggest a heathland origin to this part of the stand: the former was found growing on the crest of one root plate. The low numbers of seeds in samples taken from adaxial plate positions was probably due to soil shedding.

Table 6. Numbers of seedlings germinating from soil samples gathered from six root plate replicates at Blean Woods NNR

	Adaxial face	Abaxial face	Adjacent area	Woodland control
Juncus effusus	20	0	10	57
Betula pendula	1	0	26	35
Rubus fruticosus	1	0	9	8
Hypericum pulchrum	3	0	3	8
Cytisus scoparius	0	0	1	3
Scrophularia nodosa	1	0	2	0
Luzula pilosa	0	0	1	1
Veronica officinallis	1	0	0	1
Calluna vulgaris	1	0	1	0
Carex sp.	0	0	0	1

Discussion

Microsite variation and vegetation pattern

Differences between the undisturbed vegetation of the forest floor and areas disturbed by the root plates were relatively small, but species distributions attributable to the different microenvironments resulting from root plate and root pit positions were found at all three sites, confirming previous literature (Thompson 1980; Beatty 1984).

The most obvious common factor was the absence of vegetation on near-vertical abaxial faces, partly due to soil shedding, but also to the lack of a buried seed bank in the exposed subsoil. Soil shedding was also an important factor on the adaxial faces, except where stabilised by moss cover, which in turn may have benefited from the predominantly north-facing aspects of these surfaces (due to the direction of tree-fall) and to the absence of litter.

The adaxial surface and its crest represented one of the few places where buried seed could germinate safely, free from the competition of woodland herbs and often in high light conditions, but this environment was also limited by soil shedding and desiccation. The crest supported species of more open habitats: *Reseda lutea, Poa annua, Senecio jacobaea* and *Veronica arvensis* at Wye; *Calluna vulgaris* at Blean). Soil, subsoil and rubble provided a bare mineral surface for colonisation on either side of the root plates for adventive species such as *Epilobium* spp. and *Cirsium* spp. but addition of fresh material from above, together with competition from scrambling species such as *Rubus, Clematis* and *Fragaria* meant that some of these debris cones were only temporarily available to "ruderal" type species.

The root pit itself was initially free from litter and competition, conditions which appeared to benefit the establishment of the ferns *Dryopteris dilatata* at Blean and *D. affinis* at Ham Street, possibly by providing suitably damp and shady sites for spore germination and gametophyte development. Similar, moist conditions also appeared to promote *Juncus effusus, Rubus fruticosus* and *Betula pendula* at Blean, *Oxalis acetosella* and *Carpinus* seedlings at Ham Street and *Rhamnus* at Wye.

The spread of surrounding woodland vegetation into the pits was rapid, although the presence of thick beech leaf litter at Blean may have influenced species composition. In the long term these depressions will be expected to resemble more closely their surroundings as they fill with soil, subsoil and litter and colonising species are out-competed. The plates themselves will begin to collapse and their ephemeral vegetation will enter the seed bank, or disperse, as the canopy closes and more shade-tolerant vegetation becomes established. However, it is unlikely that complete uniformity will result. Major changes to the soil physical structure and persistent, but subtle variation in microtopography are capable of influencing plant species patterns for decades or hundreds of years (Thompson 1980; Beatty 1984). Indeed, continued disturbance through windthrow is probably fundamental to the organisation and evolution of forest herb communities, by breaking up monospecific patches and increasing heterogeneity (Collins *et al.* 1985).

The significance of root plates as sites of tree seedling regeneration

In none of the three sites was there any lack of tree and shrub regeneration. Around the Wye root plate a shrub cover of young sycamore and ash was well established after six years, with frequencies of 47% and 65% respectively in 1 m^2 quadrats. Even the low frequencies of the beech seedlings present (3%) were capable of restoring the gap created by the original tree, together with a wide variety of shrubby species. At Ham Street the canopy was partly overstood, but 57% of the quadrats contained hornbeam seedlings. At Blean, the commonest sapling species in two of the largest gaps was birch (61% and 20% respectively), together with occasional oak and beech.

Although forest succession appears to be assured in these windthrow gaps, there is only circumstantial evidence to suggest that soil disturbance directly influenced the pattern of tree regeneration. Birch and hornbeam both appear to be associated with gaps, at Blean and Ham Street respectively, possibly because these species require litter-free, bare mineral surfaces. Small, light seeds such as birch are exacting as to surface conditions and are vulnerable to desiccation and competition (Kinnaird 1974; Buckley 1984): the seed also germinates most freely in canopy gaps. Other pioneer species may have difficulty in penetrating litter mats, or are subject to litter leachates (Putz 1983).

In contrast, neither litter nor soil disturbance appeared to be important factors at Wye, where ash and sycamore saplings occurred frequently on undisturbed soils: physical conditions on the root plate and pit were generally less suitable for germination and seedling establishment in these locations.

Broader effects of gap dynamics on vegetation

Despite an apparently devastating storm, the understorey vegetation of the three study areas survived well, while a replacement canopy quickly began to close over the gaps created. Gap size, which does not appear to have been closely examined in post-Storm studies, will play a crucial role in determining vegetation development. It will influence recruitment to the canopy, increasing the proportion of pioneer species in larger gaps, as observed at the Blean and Wye sites, where birch and sycamore and ash, respectively, have begun to replace a predominantly beech canopy. Management factors or other events, such as grazing, will determine whether this represents a permanent, or temporary change. In the meantime lighter conditions in the understorey will certainly influence the field layer.

Gap size is in turn linked to the amount of soil disturbance taking place; large gaps which result from windthrow are more likely to increase the proportion of soil disturbance compared with smaller gaps caused by crown snap, or the natural disintegration of individuals *in situ* (Putz 1983). In Blean Wood, for example, the gaps were not only narrow, but their orientation, along a north-east/south-west axis meant that the disturbed soil of the rootplates was often situated in the southern, shadiest edge of the gap.

The available colonisation surface was further reduced by crown regeneration on the fallen boles, an important feature of the study sites, where 81% of the downed trees were still alive (see also Thomas *et al.* 1994). In a broadleaved stand in Bialowieza Forest 78% of downed trees survived initially (Falinski 1978) but there is little literature suggesting whether this is likely to be more than a temporary phenomenon. Some fallen trees are developing vertical shoots which are capable of replenishing the canopy and under these relatively little change in vegetation may be expected. Partial canopy regrowth may favour the recruitment of shade-tolerant tree seedlings, bypassing a pioneer canopy. As Rackham (1990) remarks, "a horizontal tree - alive or dead - is at least as good a habitat as an upright one". If the fallen trees do eventually die, their rotting limbs may also provide sites for tree and shrub regeneration; however no post-Storm accounts have yet described this.

The maintenance of canopy diversity by 'normal', endemic windthrow of individuals or small tree groups appears unlikely: in unmanaged forests, it is only exceptional storms which can restore diversity to the canopy in the long term (Brewer & Merritt 1978). Although the pattern of damage resulting from the storm was skewed towards single tree gaps and small groups in semi-natural stands (Davies & Pritchard 1994), large swathes of damage were created by turbulent wind-lines in local cases (Lamb 1989). These swathes may be the most effective in breaking the monopoly of centuries of species selection and uniform management practices such as coppicing, creating a patchiness in the canopy and below it, at microsite level, and establishing more 'natural' conditions in future.

References

ASH, J.E. AND BARKHAM, J.P. 1976. Changes and variability in the field layer of a coppiced woodland in Norfolk, England. *Journal of Ecology* **64**, 697-712.

BEATTY, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* **65**, 1406-1419.

BEKE, G.J. AND MCKEAGUE, J.A. 1984. Influence of tree windthrow on the properties and classification of selected forested soils from Novia Scotia. *Canadian Journal of Soil Science* **64**, 195-207.

BOLAS, M.J. 1993. *The effects of the 1987 Storm on the ground flora of Blean Woods National Nature Reserve, Kent.* Wye College, University of London (Unpublished M.Sc Report).

BREWER, R. AND MERRITT, P.G. 1978. Wind throw and tree replacement in a climax beech-maple forest. *Oikos* **30**, 149-152.

BUCKLEY, G.P. 1984. The uses of herbaceous companion species in the establishment of woody species from seed. *Journal of Environmental Management* **18**, 309-322.

BURT, S.D. AND MANSFIELD, D.A. 1988. The Great Storm of 15-16 October 1987. *Weather* **43**, 90-108.

COLLINS, B.S., DUNN, K.P. AND PICKETT, S.T.A. 1985. Responses of forest herbs to canopy gaps. In *The ecology of natural disturbance and patch dynamics,* edited by S.T.A. PICKETT & P.S. WHITE, pp 217-234 Orlando, Academic Press.

DAVIES L. & PRITCHARD, C. 1994. An assessment of post-storm woodland action centred on two areas surrounding Sevenoaks and Canterbury in July 1990. In *Ecological responses to the 1987 Great Storm in the woods of south-east England*, edited by K.J. KIRBY and G.P. BUCKLEY pp 13-23, Peterborough English Nature (English Nature Science 23).

EVANS, M.N. AND BARKHAM, J.P. 1992. Coppicing and natural disturbance in temperate woodlands -a review. In *Ecology of coppice management*, edited by G.P. BUCKLEY, pp 79-98, London, Chapman and Hall.

FALINSKI, J.B. 1978. Uprooted trees, their distribution and influence on the primeval biotope. *Vegetatio* **38**, 175-183.

FEDERER, C.A. 1973. Annual cycles of soil and water temperatures at Hubbard Brook. *United States Forest Service Northeastern Forest Experiment Station Research Note NE-167.*

FOSTER, D.R. 1988a. Disturbance history, community organisation and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, USA. *Journal of Ecology* **76**, 105-134.

FOSTER, D.A. 1988b. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* **76**, 135-151.

GRIME, J.P., HODGSON, J.G. & HUNT, R. 1988. *Comparative plant ecology.* London, Unwin Hyman.

HENRY, J.D. & SWAN, J.M.A. 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. *Ecology* **55**, 772-783.

HOPKINS, B. 1994. The storm. In *Ecological responses to the 1987 Great Storm in the woods of south-east England*, edited by K.J. KIRBY & G.P. BUCKLEY pp 1-11, Peterborough, English Nature (English Nature Science 23).

KINNAIRD, J.W. 1974. Effect of site conditions on the regeneration of birch (*Betula pendula* Roth and *B. pubescens* Ehrh.). *Journal of Ecology* **62**, 467-472.

LAMB, J. 1989. *The ecological effects of the Great Storm of October 1987.* Peterborough Nature Conservancy Council (CSD Report 937).

LUTZ, H.J. 1940. Disturbance of forest soil resulting from the uprooting of trees. *School of Forestry Bulletin* **45**, Yale University.

LYFORD, W.H. & MACLEAN, D.W. 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper 15*, Harvard University.

METZGER, F. & SCHULTZ, J. 1981. Understorey response to 50 years of management of a northern hardwood forest in Upper Michigan. *American Midland Naturalist* **112**, 209-23.

MILLER, K.F. 1985. Windthrow hazard classification. *Forestry Commission Leaflet 85*, London HMSO.

MINCKLER, L.S. & WOERHEIDE, J.D. (1965). Reproduction of hardwoods 10 years after cutting as affected by site opening and size. *Journal of Forestry* 63, 103-7.

MITCHELL, P.L. & WOODWARD, F.I. 1988. Responses of three woodland herbs to reduced photosynthetically active radiation and low red to far-red ration in shade. *Journal of Ecology* 76, 807-25.

PICKETT, S.T.A. & WHITE, P.S. 1985. *The ecology of natural disturbance and patch dynamics.* Orlando, Academic Press.

PUTZ, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64, 1069-1074.

RACKHAM, O. 1990. *Trees and woodland in the British landscape.* London, Dent.

RUSSELL, R. 1993. *The vegetation of selected root plates and associated pits.* Unpublished report, Wye, English Nature.

SPURR, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* **37**, 443-451.

STEPHENS, E.P. 1956. The uprooting of forest trees: a forest process. *Soil Science Society of America Proceedings* **20**, 113-116.

THOMAS, R.C., KIRBY, K.J. & COOKE, R.J. 1994. The fate of storm-damaged trees in Ham Street National Nature Reserve, Kent. In *Ecological responses to the 1987 Great Storm in the woods of south-east England*, edited by K.J. KIRBY and G.P. BUCKLEY, pp 65-80 Peterborough, English Nature (English Nature Science 23).

THOMPSON, J.N. 1980. Treefalls and colonisation patterns of temperate forest herbs. *American Midland Naturalist* **104**, 176-184.

Appendix 1 Descriptions of root plates at Wye Down NNR

	Species Lists not complete			
Plate description	**Adaxial surface**	**Abaxial surface**	**Pit**	**Other**
Beech, tree dead. 2 m high. Plate lies NW-SE 0.5 - 1 m deep it. Open canopy	*Rubus fruticosus, Fraxinus* seedling, *Senecio jacobea, Viburnum lantana* seedling. *Clematis vitalba, Galium aparine, Mycelis muralis, Veronica chamaedrys, Fragaria vesca.*	Bare	Covered by trailing bramble	
Ash, tree living. 2 m high plate. NE-SW 0.5 m pit. Surrounded by 5-6 m sycamore regeneration	Mostly bare, shedding soil. Sycamore sapling from before storm surviving on plate	Bare	*Fraxinus excelsior* seedling. *Rubus fruticosus, Viola riviniana, Primula veris, Fragaria vesca, Mercurialis perennis*	*Reseda* on crest, with some *Glechoma* (the latter probably pre-existing)
Beech, dead. 3 m high plate NE-SW. 0-0.5 m deep	Fairly bare. Some *Glechoma hederacea, Veronica chamaedys, Veronica officinalis.* More on bole mound (*Sonchus, Poa annua*) *Rubus* and sycamore from before storms	Bare	*Poa trivialis*, beech regeneration. Ash regeneration. *Fragaria vesca, Rubus fruticosus, Cirsium arvense, Mycelis muralis, Mercurialis perennis, Sonchus oleraceous*	*Reseda* on crest
Ash, live. Plate 2-3 m high, N-S. Pit 0.5-1 m deep. Open canopy	Dense scramble of bramble and some elder completely hides face	Bare chalk	*Mercurialis perennis, Cirsium vulgare, Urtica dioica, Sambucus nigra, Rubus fruticosus, Stachys sylvatica*	
Oak, live. Plate 3 m across, but only partly lifted so pit is cave like. 0.5-1.0 m deep. Small canopy gap 10-15 m across	Overrun by bramble with some *Clematis, Mercurialis, Sambucus, Fraxinus excelsior* (seedling)	Bare chalk	Only vegetated at edge. *Rubus fruticosus. Prunus spinosa. Urtica dioica*	
Oak, live. 2 m high plate, E-W. 0.5-1.0 m deep pit	*Rubus fruticosus, Fraxinus excelsior, Viburnum lantana, Ligustrum vulgare, Brachypodium sylvaticum, Arctium minus, Stachys sylvatica*	Bare chalk	Some bramble and brash pushed into pit, partly filling it	

Species Lists not complete				
Plate description	**Adaxial surface**	**Abaxial surface**	**Pit**	**Other**
Beech, live. Plate 2 m across. Pit over 1 m deep. Plate has slipped back, partly filling pit.	Much bare soil. Ash regeneration. Sycamore regeneration. *Viburnum lantana* regeneration. *Veronica chamaedrys, Cirsium vulgare, Rubus fruticosus, Brachypodium sylvaticum*	Bare chalk		*Reseda* on crest
Ash, tree alive. 4 m high thin plate. E-W. Under 20-30 m canopy gap	Largely bare, much soil shed. Privet, elder and *Senecio jacobea* on bole ledge	Bare chalk	Densest vegetation cover in strip closest to the plate. *Leontodon hispidus, Viburnum lantana, Rubus fruticosus, Urtica dioica, Arctium minus, Poa trivalis, Fragaria vesca, Geum urbanum*	*Sonchus oleraceus* on plate crest
Beech, dead. East-west plate. 3 m high. Pit 0.5-1.0 m deep	Virtually bare	*Senecio jacobea, Reseda lutea, Moehringia trinervia*	Pit more or less covered by scrambling bramble and *Clematis*. Occasional *Epilobium hirsutum*	
Beech, dead. 4 m high plate running east-west. Open canopy over pit and base	Virtually bare. Bole ledge with *Myosotis, Epilobium montanum, Poa trivalis, Galium aparine*	Bare	Much bramble, sycamore and ash regeneration	*Reseda* and *Verbascum* on crest
Beech, live in part. SE-NW plate. 4-5 m high, 0-0.5 m deep pit	Some shedding of soil but much *Poa trivalis, Fragaria vesca, Inula conyza, Crepis capillaris, Veronica chamaedrys, Sonchus oleraceus, Rubus*, ash and sycamore regeneration	Bare chalk	*Rubus fruticosus, Ajuga reptans, Hypericum hirsutum, Epilobium hirsutum, Sambucus nigra, Urtica dioica*	

Appendix 2 Descriptions of root plates at Ham Street NNR

	Species Lists not complete			
Plate description	**Adaxial surface**	**Abaxial surface**	**Pit**	**Other**
Oak, alive. Plate NW-SE, 1.5 m high, pit 0.5 m deep, 70% canopy cover over plate	Some soil shedding. 60% moss cover on crest and adaxial face. *Pteridium aquilinum, Rubus fruticosus*. Weak oak regrowth from bole base	Bare clay	Bracken on edge. *Dryopteris dilatata*	
Birch, multi-stemmed, alive. Plate N-S, 1.0 m high, pit less than 0.5 m, 70% canopy cover.	60% moss, *Hyacinthoides, Pteridium*. Little soil shedding	Bare clay	Bracken in middle moss, *Hyacinthoides* on edge	
Birch, dead. Plate 1.5 m, pit less than 0.5 m. 80% canopy cover. N-S plate	70% moss. *Hyacinthoides, Pteridium,* particularly on crest. Pre-existing holly seedling. Little soil shedding	Bare clay	Largely bare. Occasional *Hyacinthoides, Luzula pilosa,* moss	
Oak, multi-stemmed, plate 1 m high, pit 0.5 - 1.0 m deep. Plate N-S. 100% canopy cover	Patchy soil shedding 70% moss cover. Oak shoots (weak) from roots. *Hyacinthoides*	Some bramble, but mainly bare clay. Crest collapsing on to abaxial side	Bracken-bluebell slippage into pit	
Birch, dead. Plate 1.5 m, NW-SE. Pit 0.5 m. 80% canopy cover	40% moss cover. *Hyacinthoides, Rubus fruticosus, Dryopteris dilatata*	Bare	*Pteridium, Hyacinthoides,* sparse moss	
Birch, alive. Plate N-S, 1 m high, less than 0.5 m deep 50% canopy cover	Some soil shedding. 40% moss cover	Bare	Bare except where moss slumped in from edge	
Hornbeam, alive. Plate 1 m high, N-S, less than 0.5 m deep	20% moss cover. Much slumping	50% moss cover, where crest slumping down abaxial side	Bare	
Birch, live. Plate SE-NW, 1 m high. Pit 0.5-1 m. 80% canopy cover	Sparse *Hyacinthoides*. Little moss. Litter shed but little soil	Bare	Bare	

Species Lists not complete				
Plate description	**Adaxial surface**	**Abaxial surface**	**Pit**	**Other**
Birch, dead. Plate 2 m, N-S. Pit 0.5-1.0 m. 60% canopy cover (but gap to south)	Moss on tree bole. Occasional *Hyacinthoides* and moss	Bare	*Hyacinthoides, Pteridium.* Hornbeam seedling	
Oak, alive. Plate 1.5 m high, NW-SE. Only partly lifted out (or rather has slumped back into pit). Pit 0.5-1.0 m deep. 100% canopy cover	Sparse moss, slightly denser on crest. Occasional *Hyacinthoides*	Bare	*Pteridium*	

Appendix 3 Characteristics of root plates and pits studied in treefall gaps at Blean Woods NNR

Gap	Fallen Species	Orientation of fallen species (^{0})	Depth of pit (m)	Size of plate		Angle of plate (^{0})
				Height (m)	Width (m)	
1	Beech	NE 50	0.5	2.2	3.7	85
2	Beech	NE 0	0.6	2	3.2	85
3	Beech	N 10	0.3	2.2	4.5	105
4	Beech	NW 340	0.5	1.6	3.6	85
5	Beech	NE 30	0.6	3.5	2	85
6	Sweet chestnut	NE 17	0.5	1.5	2.7	85
7	Sweet chestnut	N 20	0.5	2.5	4	80
8	Beech	NE 60	0.25	1	2	80
9	Beech	NE 30	0.5	1.2	2.4	85
10	Beech	NE 68	0.5	2.6	6	95

THE REDISCOVERY OF STARVED WOOD-SEDGE *CAREX DEPAUPERATA* CURTIS EX WITH. AT GODALMING, SURREY AFTER THE GREAT STORM OF 1987.

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Summary

Starved wood-sedge *Carex depauperata* Curtis ex With. is a very rare plant in the British Isles and in north west Europe. It has been lost from most of its localities in England, and by the mid 1970s was only known from one site in Somerset. It was rediscovered in an old site near Godalming, Surrey in 1992. The Surrey population had probably originally declined due to lack of regeneration under dense woodland shade, and the final plant was probably lost to a landslide in the early 1970s. In 1992 one plant was rediscovered directly under a gap in the canopy caused by loss of a big branch during the Great Storm of 1987. The disturbance and increased light had probably caused buried seed to germinate. PLANTLIFE are carrying out conservation work at the site.

Introduction

Starved wood-sedge *Carex depauperata* Curtis ex With. is a very rare plant in Britain, and is protected under the Wildlife and Countryside Act, 1981. It is also regarded as endangered in north west Europe.

Starved wood-sedge has been recorded from a total of 11 sites in Britain and Ireland (Table 1). In England, it had become extinct at three sites by 1900, and was lost from another during the Second World War. Three other sites have not been confirmed, and no details of the Welsh site at Holyhead are known. The tenth site near Godalming, Surrey was thought to have gone extinct in the early 1970s, leaving a sole English population in Somerset which consisted of only five plants. This site received some conservation work under the English Nature 'Recovery' programme (Birkinshaw 1990) and is currently stable. In 1973, it was discovered in Ireland in County Cork by T O'Mahony, and 15 tussocks were present in 1992.

Table 1. Summary of starved wood sedge records in the British Isles (after Birkinshaw 1990)

Site	First record	Last record
Effingham Chalk Pit, Surrey	1874	1881
Charterhouse, Surrey	1843	1938
Frith Hill, Surrey	c. 1842	1891
Ockford Wood (Westbrook), Surrey	1843	1994
Charlton Wood, Kent	1787	1830
Axbridge, Somerset	1860	1994
Leigh Woods, Somerset*	1888	1888
Templecombe, Somerset*	Late 19th Century	Late 19th Century
Holyhead, Anglesey	1936	1967
Wimbourne, Dorset*	1920s	1920s
Co Cork, Republic of Ireland	1973	1994

*one unconfirmed record only

As part of PLANTLIFE's 'Back from the brink' project which is aimed at saving critically endangered plant species, the old site at Godalming was visited in 1992 to assess the potential of the site for active conservation work. One new tussock of starved wood-sedge was found in the old locality, probably resulting from the opening of the canopy in the 1987 storm.

History of starved wood-sedge at Godalming

Starved wood-sedge has been recorded from at least three sites in the Godalming area. The Charterhouse site "copse near Hurtmore Cottages" was first found in c.1843 by C.E. Salmon. Lousley (1976) records that he last saw this site in 1938 but that it disappeared during the war (probably after timber extraction). A site at Frith Hill was first reported in c.1842 by C.E. Salmon, seen again by A. Bennett in 1852, and by many botanists between 1875 and 1891.

The third site, usually referred to incorrectly as "Westbrook Copse" was always the best of the populations in the Godalming area. It was first reported by Jno. D. Salmon in 1843. E.C. Wallace photographed the plant on an open flowery bank on 13 June 1936. The photograph shows a smallish clump with 6 or 7 flowering spikes on an open platform about 1 m wide in a carpet of bramble and grass, rising to a steeper bank with hazel behind. Plants associated with the starved wood-sedge which are clearly identifiable include cleavers *Galium aparine*, dewberry *Rubus caesius*, wood sedge *Carex sylvatica*, creeping buttercup *Ranunculus repens* and rough meadow-grass *Poa trivialis*. In the 1940s, the plant was locally frequent in the wood, both along the track side, on the bank, at the top of the bank and on the slopes above (F. Rose, personal communication 1992). J.E. Lousley saw "five fine plants by lane" in 1949, but Mrs B. Welch saw only one on 12 June 1949. R.W. David and O. Polunin saw five plants "one plant in gutter, two on bank above, and two more just into the wood at the top of the bank and 10 yards downhill" on 2 June 1961. There were numerous reports up to the 1960s when it became scarcer. J. Gardener photographed one robust healthy plant in 1968 on the distinct shelf beside the track associated with red campion *Silene dioica*, hogweed *Heracleum sphondylium*, bush vetch *Vicia sepium*, a small amount of ivy *Hedera helix*, false brome *Brachypodium sylvaticum* and a little bramble *Rubus fruticosus*. By 1970, only one plant remained on the edge on the shelf, and Mrs J.E. Smith and W.E. Warren took measures to prevent the bank being undermined by the small stream running along the gutter on the north side of the track. F. Rose and E.C. Wallace last saw one vegetative plant inside the wood in 1972. The last plant seems to have disappeared from the site about this time as a result of a landslide (Mrs J.E. Smith, personal communication 1992).

J.E. Lousley and Mrs J.E. Smith searched all the known sites in 1973 (Lousley 1976) without success, and in 1975 the Surrey Flora Committee searched all the old localities and advertised in a local paper with a picture of the sedge in case it lurked in some copse or garden (one wood sedge *Carex sylvatica* was the only response). R.W. David failed to find the plant in 1974. Thorough searches by Mrs J.E. Smith, A. Byfield and Lady R. Fitzgerald in December 1986, and by Lady R. Fitzgerald, J.R. Akeroyd, Mrs J. Leslie and A. Leslie in June 1987 of many suitable areas around Godalming failed to find any plants, and it was regarded as extinct.

During the Great Storm of October 1987, a number of trees and branches on the site were blown down, which opened up the canopy and disturbed the ground. Mrs J.E. Smith hoped that this might stimulate buried seed to germinate, and organised a number of unsuccessful searches of this and neighbouring woods. Searches by C. Birkinshaw in 1989, whilst working on the plant at Cambridge Botanic Garden, also failed to find the species.

Then in 1992 one plant was found, a small tuft with a fountain of leaves about 10 cm across at the base, with 26 flowering branches. Fruit set looked promising. The remains of the previous year's flowering branches were found suggesting that the plant was in at least its third year. The plant was in exactly the same area in which it had been seen before, though the site was very much more overgrown with ivy and brambles than it had been. A large branch of one of the big lime *Tilia x vulgaris* trees directly above the plant had been blown down in the 1987 storm, and the canopy above was open. This probably stimulated buried seeds to germinate.

Following this rediscovery, Mrs J.E. Smith again searched other sites around Godalming in 1992 without success.

Habitat requirements of starved wood-sedge

The plant usually occurs in dry, deciduous woodland (Birkinshaw 1991). The soils range from acid podzols to calcareous brown earths. The plant is often associated with tracks ranging in size from small animal tracks to rough vehicle tracks, probably because it prospers in conditions of semi-shade and disturbance. Lousley (1976) reported starved wood-sedge as being "... sometimes fairly plentiful after the woods had been felled or coppiced". At Fontainebleau (one of the best sites in NW Europe), the plant was formerly abundant in woods near the River Seine. It declined to a handful of plants until the French Forestry Department felled the Beech trees and churned up the soil, after which hundreds reappeared (F. Rose, personal communication 1992). Heavily shaded plants are often sterile.

The population of starved wood-sedge at Godalming probably declined overall due to the absence of regeneration due to the documented increase of dense undergrowth of ivy and bramble, and the lack of coppicing or other disturbance. The opening of the canopy due to the 1987 storm created suitable conditions for seeds to germinate. Birkinshaw (1990) noted that germination is erratic, and may take up to 18 months.

Conservation work

In 1992, a three point action plan was drawn up to manage the site. The work involved preservation of the genotype, opening the canopy and recruitment of a local PLANTLIFE member to keep a regular eye on the plant.

A licence to collect material to place in the Royal Botanic Garden Kew Seed Bank at Wakehurst Place was granted by English Nature, and material was collected in 1992 and deposited at Wakehurst Place; of the eight fruits collected on one inflorescence branch, only six contained well-formed seeds. Plants have been grown on with a view to providing material for possible restocking of nearby sites.

The owner of the land, Mr Peter Stovold, kindly gave permission to carry out some active conservation work on the site. A small project grant was obtained from English Nature under the Species Recovery Programme to thin out the canopy, coppice some of the hazel bushes, thin the holly hedge on the south side, remove brambles and ivy, and generally disturb the site. This was carried out in November 1992. A 40 m section of the lane centred on the area in which the sedge occurred was cleared to the top of the embankment, some large branches taken off the limes, hazel stools re-coppiced and hollies removed. The large lime branch was cut up and mostly removed from site. Throughout great care was taken not to damage the existing plant.

A local PLANTLIFE member, Mrs A. Fairbrother, has been recruited to keep an eye on the plant - PLANTLIFE's first 'Minder'.

On 12 September 1994 four young plants and two possible seedlings were found adjacent to the existing single plant. These were on the uphill side and probably grew from buried seed rather than being offspring of the original plant.

The precise site is being kept secret, and people are requested not to visit it as it is very sensitive.

Acknowledgements

I am grateful to Francis Rose, Anne Fairbrother, Peter Marren, Dagmar Junghanns, Lynne Farrell, Ro Fitzgerald and Joyce Smith for help and information. This work was funded by PLANTLIFE, with a grant for the clearance work from English Nature's Species Recovery Programme. We are also grateful to Peter Stovold for permission to carry out the clearance work.

References

BIRKINSHAW, C.R. 1990. *The ecology of Carex depauperata and its reinforcement at Cheddar Wood, Somerset.* Peterborough, Nature Conservancy Council, CSD Report No. 1152.

BIRKINSHAW, C.R. 1991. The habitat preferences of *Carex depauperata* Curtis ex With.. *Bulletin of the British Ecological Society* **22**, 26-31.

LOUSLEY, J.E. 1976. *Flora of Surrey.* Newton Abbot, David & Charles.

RESPONSES OF WOODLAND BIRDS TO STORMS, WITH PARTICULAR REFERENCE TO THE STORM OF 1987

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Summary

The potential direct (mortality, forced dispersal) and indirect (changes in food supply and habitat) effects of storms on woodland birds are briefly reviewed. Comparison of changes in breeding bird populations in samples of damaged and undamaged woods in south-east England suggested that any changes in bird numbers that arose from the Great Storm of 1987 were short-lived. Distribution of breeding birds was examined within four storm-damaged woods in Suffolk and Sussex. There was considerable variation amongst the woods in the apparent responses of birds to the creation of treefall gaps. Warblers had strongly colonised some treefall gaps; this seems to be a general feature where there has been vigorous regeneration and bramble growth. There was also an indication that wrens select some treefall areas but that tits may avoid them. Large-scale clearance of windblown pine in Aldewood Forest, Suffolk, has created large areas of new habitat for nightjars and woodlarks. As a result the nightjar population more than doubled in this forest between 1987 and 1992.

Introduction

There has been little research on the effects of storms on terrestrial birds. This paper presents information on the effects of the Great Storm of 1987 on woodland birds in south-east England. This exceptional storm, with winds reaching hurricane force, passed across south-east England on the night of 15/16 October 1987 causing widespread damage to woodlands in the region. We analyse population trends of woodland birds in south-east England and examine the numbers and distribution of breeding birds within four storm-damaged woods. The results from these studies are considered alongside other more general observations on the effects of the storm on birds.

Storm damage in woodlands can have both direct and indirect effects on birds. Direct, relatively short-term effects are those where birds are killed or forcibly displaced by storms, disrupting established social systems. Perhaps the best documented example is the impact of a storm in January 1990 on a population of crested tits (scientific names of birds are given in the appendix) in Belgium (Lens & Dhondt 1992). This storm uprooted approximately 25% of the trees in a pinewood where the birds had been individually colour-ringed. There was major dispersal of birds up to 5.5 km from the wood, and more than half the individuals were not resighted after the storm. The subsequent breeding population was reduced by at least 50%. There is also increasing evidence that hurricanes in North America can have profound impacts on the population structure and habitat distribution of birds (Engstrom & Evans 1990; Dunning & Watt 1991). Another direct effect, with longer-term consequences, is the destruction, or reduction in quality, of habitat for birds. This may force individuals to abandon their previous haunts and may lead to increased mortality or the occupancy of sub-optimal habitat. On the other hand, strong site-fidelity may cause some individuals to remain faithful to sites, even though their quality has deteriorated (Wiens 1989). New habitats may also be created. For example where windblown woodland is cleared and replanted the change in the age structure of the woodland may benefit species dependent on young growth, such as nightjar. The effects of storm damage on bird populations can also be indirect, altering the available habitats or food resources in the longer-term.

Table 1. **Three scales of storm damage in woodland and their possible indirect effects on birds. See text for definition of isolated treefall, canopy damage and treefall gap.**

1. **Isolated treefall**

Localised increase in low foliage and dead wood may create rich feeding sites for some species of birds.

The scale of the canopy opening is probably insufficient to have much influence on bird distribution. However, wrens will use the root plates of isolated fallen trees as nest sites, and there is some suggestion that in primeval Polish forest pied flycatchers prefer to nest in areas with quite small canopy gaps (L. Tomiałojć pers. comm.).

2. **Extensive canopy damage**

Increased light penetration through the canopy may lead to denser foliage in the field and shrub layers; bramble in particular may spread. This may improve habitat quality for species that depend on low foliage, eg wren and several warblers.

With damage to twigs and buds there may be a reduction in foliage insects in the canopy. This could act to reduce overwinter survival or breeding success of birds such as blue tit which feed mainly on canopy insects.

There will be a greater amount of dead wood in the canopy, presumably leading to an increase in saproxylic insects that make use of small-diameter dead wood. This may increase canopy food supplies for some birds eg lesser spotted woodpecker.

3. **Large treefall gap**

Depending on the size and shape of the gap, and the grazing pressure, a large area of impenetrable low dense foliage can develop. This can form a suitable nesting and feeding site for several insectivorous species, which may be scarce in closed-canopy areas. During the breeding season in the primeval forest of Białowieża National Park, Poland, tree pipit, dunnock, garden warbler, blackcap and chiffchaff are strongly associated with treefall gaps (R.J. Fuller unpublished). Other species which may be expected to respond positively to gaps in Britain include wren and nightingale. In North American forests, migrating insectivorous birds have been shown to make heavy use of gaps because they support concentrations of foliage insects (Blake & Hoppes 1986; Martin & Karr 1986).

A substantial concentration of dead wood and associated insects is formed which may benefit hole-nesters (though availability of nest sites may not always be a factor limiting populations of these species) and woodpeckers which forage for wood-boring invertebrates (Virkkala *et al.* 1991; Carlson & Aulén 1990). A huge number of insects live in dead or decaying wood, and a high proportion of these utilise dead wood for only a part of their life cycle; at other times they may be available as food to a much wider range of bird species. Therefore, many insectivorous birds, not just woodpeckers, could benefit from a substantial increase in the total amount of dead wood. In this connection Nilsson (1979) found that variations between eight forest areas in the overall bird densities and numbers of species were best accounted for by the proportion of standing timber that was dead or moribund.

Availability of fruits is likely to be much greater in treefall gaps than under closed-canopy forest, or in isolated treefalls or under areas of canopy damage. Hence, treefall gaps can provide major food resources for frugivorous birds (Blake & Hoppes 1986; Martin & Karr 1986).

In the absence of any major post-storm management, three scales of storm damage can be identified within temperate woodland. These are:

1. **isolated treefalls** in which individual trees fall down at widely spaced intervals, creating small canopy gaps;

2. **canopy damage** where the trees remain standing but there has been major loss, often extensive, of twigs and boughs;

3. **treefall gaps** where several trees in close proximity have fallen to create a substantial canopy gap.

Canopy damage can cover extensive areas and, therefore, its effects on woodland ecology may be less localised than those of isolated treefalls. The potential indirect effects on birds are summarised in Table 1, although those for canopy damage and isolated treefalls should be treated as hypotheses waiting to be tested. For treefall gaps, however, there is evidence, both from North America and Europe, that these can lead to changes in bird community composition within woodland, and also provide major concentrations of resources - notably dense low foliage, fruits and dead wood - which can be exploited by certain birds (Table 1). Treefall gaps can contribute substantially to the richness of bird communities in forest habitats because several species may find a preferred habitat within them. However their size, shape, and the numbers and characteristics of living trees that remain standing are likely to influence the responses of different birds to them.

Study areas and methods

Population Changes

Information from the BTO's Common Birds Census (CBC) was used to indicate trends in sizes of breeding populations for individual species holding territory on census plots in south-east England before and after the storm. Bird numbers are estimated from maps compiled by volunteers using a territory mapping method (Marchant *et al.* 1990). Observers make several visits to their census plot throughout the breeding season and they record all birds seen or heard on a large-scale map. These individual records are termed 'registrations'. The maps from the different visits are subsequently used to compile separate maps for each species, and the registrations are used to estimate numbers and locations of territories. Year-to-year population changes can be indexed from an arbitrary base year when the index is set at 100, by chaining the percentage changes in subsequent pairs of consecutive years.

Immediately following the storm, all CBC fieldworkers were asked to record on large-scale maps the extent and severity of damage to their census plots. This information was used to identify which woodland census plots had suffered damage and which had not. Damaged plots were defined as those where at least a fifth of the plot area had been severely damaged by the storm and where no substantial effort had been made to clear up the debris. Canopy damage alone was insufficient for a plot to be classified as damaged; there had to be extensive treefall. A total of 13 damaged plots was identified in south-east England. Population trends on these plots were compared with those on an equal number of undamaged plots in the same region. Individual plots in the two samples could not be matched directly according to habitat types, but care was taken to ensure that the samples were similar with respect to the balance of broadleaved and coniferous plots they contained and also in terms of the general structure of their stands. The mean areas of the plots in the two samples were: damaged 23.5 ha, undamaged 30.4 ha. The sample of damaged plots was probably not representative of the more severe levels of damage to woodland that occurred as a result of the 1987 storm.

Case studies in two Suffolk woods

The territory mapping method used on woodland CBC plots theoretically made it possible to assess whether there was any evidence of changes in spatial distribution of birds within the woodland census plots in relation to storm damage. In practice this analysis proved difficult to perform because in many damaged plots it was not possible to define clearly the boundaries of damaged areas, and often the damage was widely dispersed. However, two sites with reasonably discrete areas of storm damage were identified, Hollesley Heath and Newbourn Springs, both Suffolk Wildlife Trust reserves.

Hollesley Heath included approximately 10.5 ha of mature Scots pine *Pinus sylvestris* of which nearly half was blown down. The undamaged area has a dense canopy with little understorey and sparse bracken growth which contrasts with the storm-damaged area where there is a far denser growth of low vegetation, especially bracken. A small amount of subsequent clearance was carried out but the site was mostly left alone after the storm. Newbourn Springs is a damp woodland with much alder *Alnus glutinosa*. Approximately 5 ha of the 17 ha census plot were severely damaged by the storm. There is vigorous growth of shrubs within the damaged area but it is uncertain whether this low foliage is appreciably thicker now than before the storm. Within these two plots the spatial distribution of birds was examined across the period 1986 to 1992. Fourteen species of songbirds were selected, including both resident species and summer visitors. The numbers of registrations of birds within the damaged and the undamaged areas of woodland were counted separately for each year. The proportions of total registrations recorded in the damaged area were then calculated for each year. By plotting these numbers and proportions of registrations against year it was possible to make a visual assessment of whether any species might have changed its distribution in relation to the windblow.

Case studies in two Sussex woods

Ebernoe Common and The Mens are two ancient wood-pastures in West Sussex, dominated by mature oak *Quercus* spp. and beech *Fagus sylvatica*. The 1987 storm created several treefall gaps within each wood (Whitbread & Montgomery 1994). Both woods are Sussex Wildlife Trust reserves and neither has been cleared since the storm.

A grid of 40 points was established in 1988 within each wood with a minimum of 100 m between points. Some points were in gaps, others in closed-canopy areas. A five-minute point count was conducted at each of these points at least three times in each breeding season (April to June from 1988 to 1990). All birds seen or heard within a 50 m radius of the point were recorded. The highest count was taken for each species at each point separately for each year. In 1990 the woodland structure and tree species composition were estimated at each point in terms of the following variables: number of tree and shrub species, tree diversity (% dominance of the most abundant species), numbers of trees in different size categories, canopy cover, ground cover, standing dead trees, fallen trees, density of the shrub layer.

Regression analysis was used to explore relationships between the habitat variables and the abundances of birds at each point. Separate analyses were conducted for each wood in each year. There was a high level of correlation between the habitat variables. Therefore, the habitat measurements for each point were subjected to a principal components analysis (PCA) with the aim of reducing the habitat variables to a relatively small number of new variables or descriptive components. These components were interpreted in terms of gradients of habitat structure or tree species composition. The first three components, which together accounted for 63% and 64% of the variance in the habitat variables for Ebernoe Common and The Mens respectively, could be interpreted as habitat gradients (Table 2). In each wood one component represented the amount of storm damage; PC3 at Ebernoe Common and

PC1 at The Mens. The first three components were entered as independent variables in regression analyses in which the total counts of birds (log. transformed) in three families were the dependent variables. The three families, warblers (Sylviidae), thrushes (Turdidae), and tits (Paridae), are useful ecological indicators in that the warblers are associated mainly with open areas with dense undergrowth, the thrushes are mainly ground feeders, and the tits are hole-nesters.

Results

Population Changes

For 12 species there were sufficient samples to construct an index of population changes between 1987 and 1988 on the damaged and undamaged plots (Figure 1). Species occurring on fewer than seven plots in any year in either sample were excluded. Most species declined on damaged plots relative to undamaged plots. Only wren showed any indication of increasing on damaged relative to undamaged plots. These results are consistent with the hypothesis that the storm caused short-term population declines.

Longer-term population changes on the damaged and undamaged plots for six species of songbirds (Figure 2) however indicate that, in general, population trends in the two samples of plots do not differ greatly. Indeed, population trends of wren and robin show almost identical patterns, whilst population declines in blackbird and chaffinch were evident in both samples. These results suggest that, at least on these study plots, any changes in woodland bird populations that were a direct result of storm damage were only short-lived. Only in the case of willow warbler was there any indication that population trends diverged on damaged and undamaged plots (Figure 2). This applied only for the years 1988 to 1990 when numbers on the damaged plots were in steep decline, in contrast to the undamaged plots. Since 1990 willow warblers have been in decline on both types of plot.

Case studies in two Suffolk woods

There was no clear evidence that the storm greatly affected the distribution or numbers of birds within Newbourn Springs. This wood has a complex structure and was generally rich in birds, probably because there was a well developed field and shrub layer throughout much of the census plot. Warblers and nightingales, for example, (species one might expect to benefit from the creation of treefall gaps - see Table 1) were present in both the damaged and undamaged areas, before and after the storm. The distribution of these birds showed no marked changes following the storm, perhaps because the storm did not generate a substantial change in the foliage profile within the damaged areas, at least in the structure of the low foliage.

At Hollesley Heath, numbers of blackcaps, chiffchaffs and willow warblers increased in years following the storm (Figure 3), the first two most strongly in the damaged area. The contrasting results from the two woods suggests that responses of breeding birds to creation of treefall gaps will be most pronounced in woods with a sparse understorey.

Table 2. **Interpretation of components derived from a principal components analysis of habitat variables in Ebernoe Common and The Mens.**

Those habitat features most strongly correlated (eigenvectors larger than 0.3) with each component are listed; the strongest associations (>0.4) are underlined. A summary of the likely gradient represented by the component is given in parentheses. Eigenvalues are given as percentages of variance in parentheses.

Ebernoe Common

PC1 32% Many tree and shrub species; closed canopy.
(Gradient of tree species richness)

PC2 18% Few trees; open canopy; high ground cover.
(Gradient from open areas with few trees to closed areas with many trees)

PC3 13% Many standing dead and fallen trees; low tree diversity.
(Gradient from storm-damaged to undamaged areas)

The Mens

PC1 34% Closed canopy; few standing dead and fallen trees; high number of tree and shrub species; little ground cover.
(Gradient from closed-canopy areas to treefall gaps)

PC2 17% Large numbers of shrub and tree species; high ground cover; few large trees.
(Gradient from areas rich in tree and shrub species to areas that are species-poor)

PC3 13% Low tree diversity; many large trees; few medium-sized trees.
(Gradient from areas characterised by massive trees, probably of one species, to areas that are more diverse in structural terms)

Table 3. **Relations of the abundance of warblers, thrushes and tits to habitat variables in the form of principal components.**

Only those regressions which were significant at $P<0.05$ are summarised. The sign of the relationship is indicated after the component. Adjusted R^2 values are given as the % of the variance explained by the relationship.

	Group	Year	Component	P	R^2
Ebernoe Common	Warblers	1988	PC2 (+)	<0.05	8%
	Warblers	1989	PC2 (+)	<0.01	14%
	Thrushes	1988	PC1 (–)	<0.01	16%
	Tits	1988	PC2 (–)	<0.05	9%
The Mens	Warblers	1988	PC1 (–)	<0.01	15%
	Warblers	1989	PC1 (–)	<0.02	11%
	Warblers	1990	PC1 (–)	<0.01	18%
	Thrushes	1990	PC2 (+)	<0.02	13%
	Tits	1989	PC1 (+)	<0.001	24%

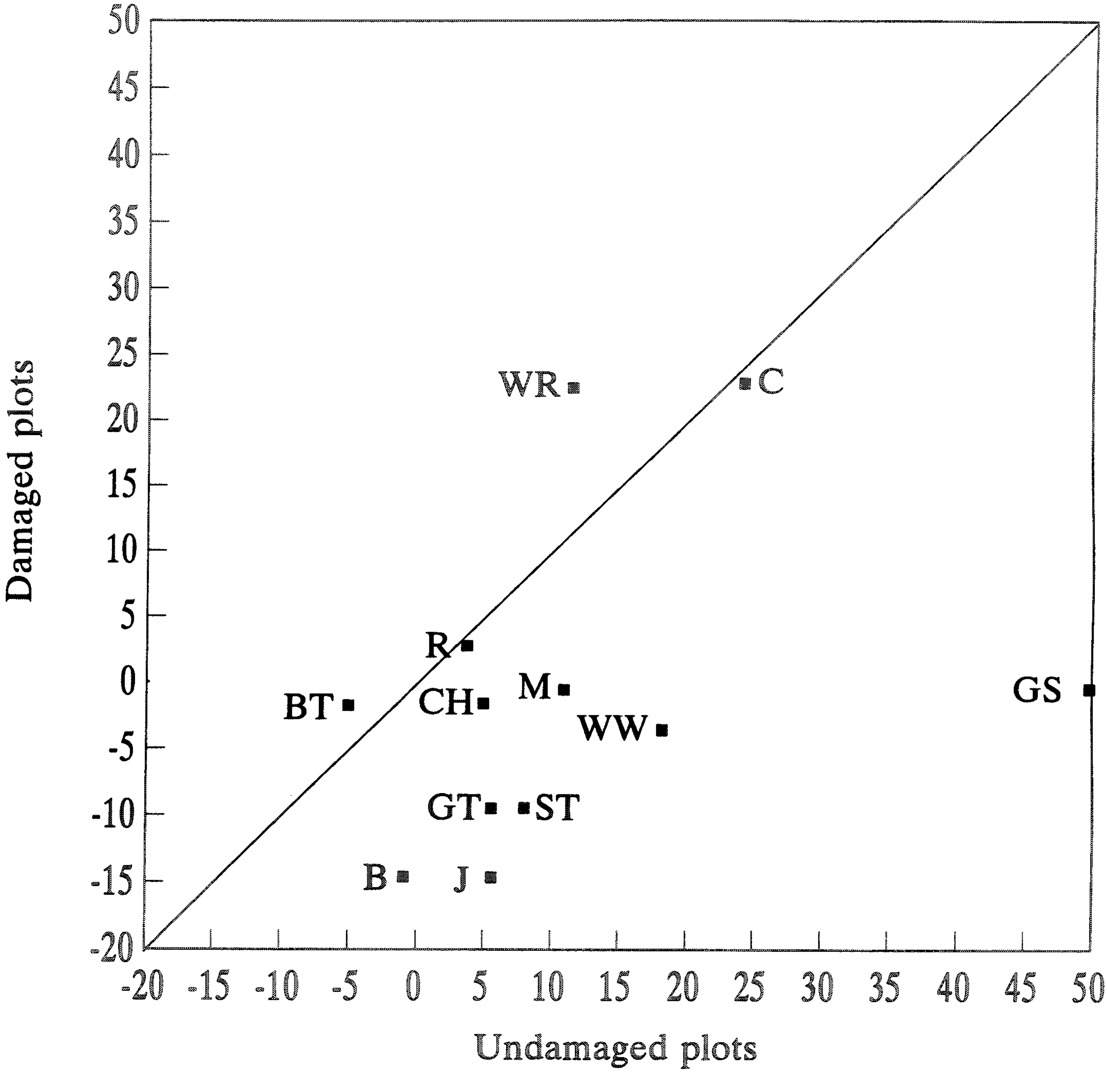

Figure 1 Percentage changes in the breeding populations of 12 bird species between 1987 and 1988 on damaged and undamaged woodland census plots in south-east England. Species codes: GS great spotted woodpecker, WR wren, R robin, B blackbird, ST song thrush, M mistle thrush, WW willow warbler, BT blue tit, GT great tit, J jay, C carrion crow, CH chaffinch.

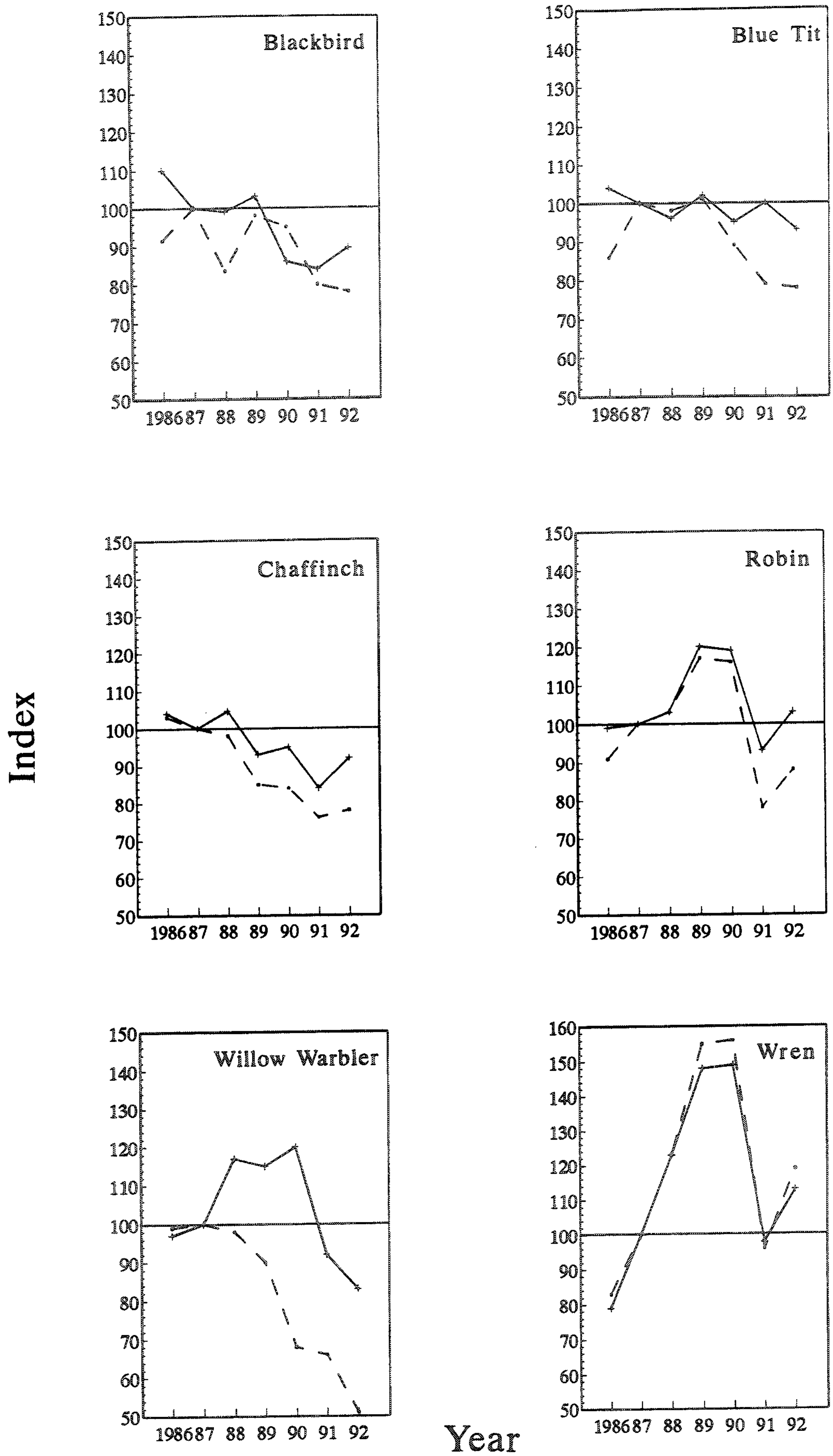

Figure 2 Population trends of six bird species on damaged (- - -) and undamaged (----) woodland census plots in south-east England.

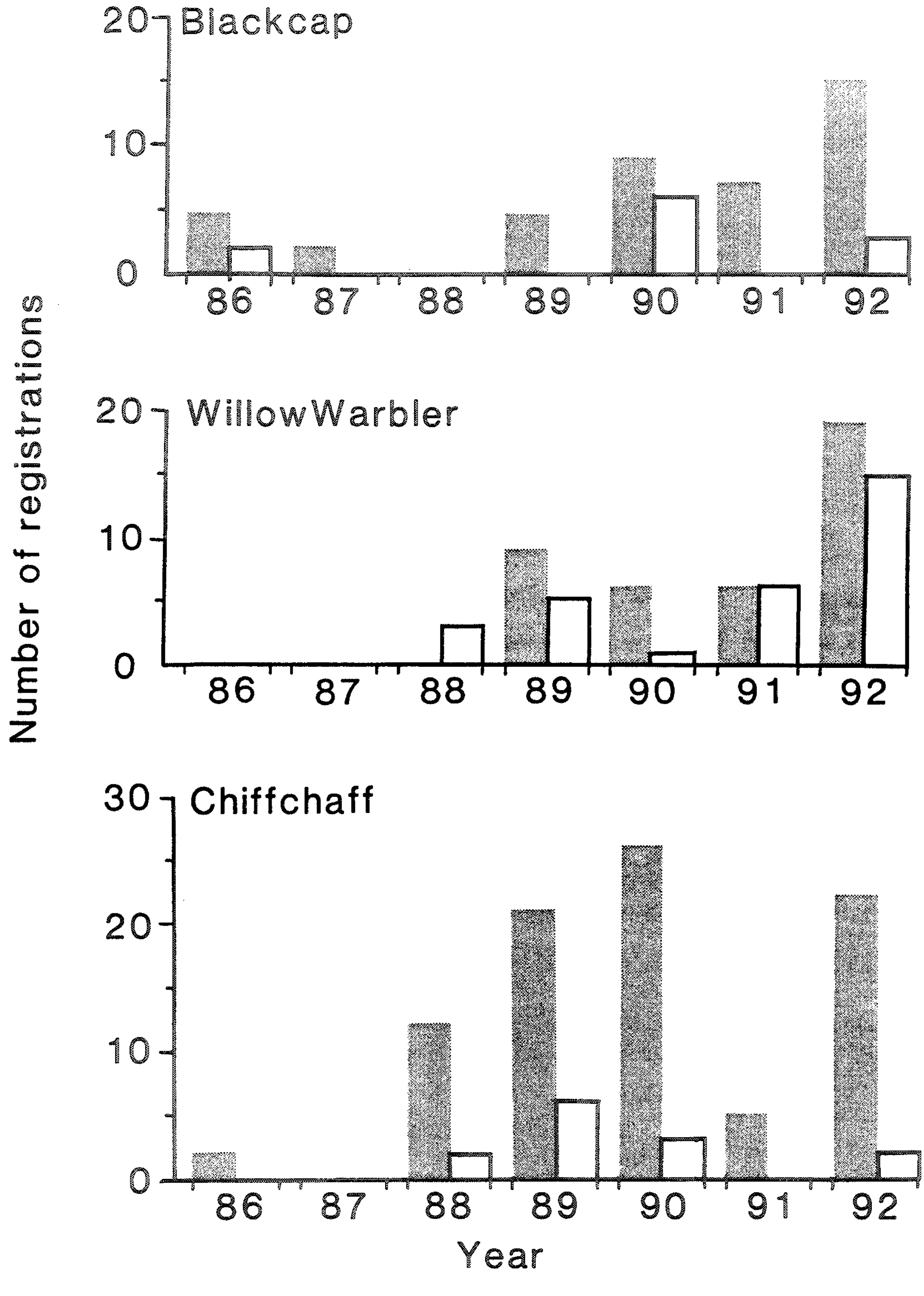

Figure 3 Numbers of census registrations for three species of warblers at Hollesley Heath, Suffolk in areas damaged (hatched bars) and undamaged (open bars) by the storm in October 1987. The damaged and undamaged areas were of similar area.

Case studies in two Sussex woods

Data were available for a total of 16 gaps and an equivalent number of nearby closed-canopy sites in the two woods combined. Numbers of birds recorded at gaps and closed sites were compared for warblers (all counts of Sylviidae combined), tits (all counts of *Parus* species combined), and for wren and robin. Wilcoxon tests were used to test whether gaps and closed points differed in numbers of birds. In 1988 and 1989, far fewer tits were recorded in gaps than in closed areas ($P<0.001$ in both cases). Wren was more abundant in gaps than closed areas in 1989 ($P=0.02$). There was a suggestion that warblers were more abundant in gaps in 1990 ($P=0.08$). Robins showed no evidence of selection or avoidance of gaps.

Regression of components (Table 3) produced for Ebernoe Common no significant relationships between the amount of storm damage (PC3) and bird numbers. Warblers at Ebernoe Common were more strongly associated with open areas with few trees, rather than with treefall areas. At The Mens, however, the abundance of warblers in each year was related to storm damage (PC1) (low scores on PC1) with more warblers in treefall areas. In one year, 1989, numbers of tits in The Mens were lower in treefall areas than in closed-canopy areas.

Discussion and conclusions

The Great Storm of 1987 may have caused very short-lived effects at a population level for several species in woods in south-east England, but there was no evidence of any major or consistent population changes amongst species that could be linked to the storm. Unfortunately the sample of CBC plots available for analysis was not representative of the most severely damaged woods and, locally, many bird populations must have been greatly disrupted in ways similar to those described by Lens and Dhondt (1992). We are unaware however of any similar such study using individually-marked birds, in relation to the 1987 storm.

There is firmer evidence for widespread indirect effects, in that the composition of breeding bird communities in some woods appears to have changed substantially following the storm. Warblers have strongly colonised treefall gaps in some woods as might be expected because these migratory birds are generally associated with early successional stages (Helle & Fuller 1988; Fuller 1992). There is also weaker evidence that wrens selectively use gaps while tits may avoid them.

There has been much variation from one wood to another in the responses of birds to the creation of treefall gaps. Differences in the pre-storm structure of woods may be significant in that woods with dense undergrowth, may show fewer changes in bird communities than woods with little undergrowth. In the latter cases the storm is more likely to introduce new types of habitat. The indirect effects on birds are likely to have been greatest where large gaps are created, but will also differ according to shading, soil productivity, deer browsing etc. Many of the woods in the extreme south-east have low densities of deer at present, which has allowed more vigorous regeneration than would have been the case if the storm had passed further to the north. With heavy pressure from deer, treefall gaps might not develop the type of vegetation structure preferred by many warblers.

Observations of responses of birds to treefalls in Essex and Kent

In north Essex, nightingales moved into some areas of damaged sweet chestnut *Castanea sativa* coppice in 1988 and have held territory in these places every year since (R Leavett pers. comm.). Initially the birds were using the prostrate canopies of fallen live trees, but the subsequent development of dense bramble in the treefall areas has probably also benefited the birds. No other bird species has become so strongly associated with the treefalls in these north Essex woods.

In Kent, large areas of old coppice and some areas of mature beech were brought down by the storm leading to substantial changes in the bird communities of several woods (B Watmough pers. comm.). At Larkey Valley Wood near Canterbury, nightingales and warblers have colonised dense areas of vigorous regeneration and bramble growth in cleared and uncleared windblown areas. These changes appear similar to those which occur after cutting in coppiced woods (Fuller 1992; Fuller & Henderson 1992).

Observations from cleared woodland

Following the 1987 storm, large areas of windblown woodland in south-east England were cleared and replanted. Several species of birds are strongly associated with the establishment stage of young plantations, including tree pipit, grasshopper warbler and whitethroat and local increases in these birds are suspected as a result.

The best documented example of a response in a bird population to woodland clearance is that of nightjars in Aldewood Forest (comprising Rendlesham and Tunstall Forests), coastal Suffolk (Figure 4). These pine plantations cover approximately 3000 ha and the 1987 storm destroyed 78% of the standing mature pine. Virtually all of this fallen pine was cleared and the area replanted. Young plantations, up to some 12 years of age, form a major habitat of the nightjar in Britain (Ravenscroft 1989; Bowden & Hoblyn 1990; Morris *et al.* 1994). In Aldewood Forest, the population of nightjars had been slowly increasing during the 1980s in response to the felling of first-generation stands. Between 1987 and 1992, however, the nightjar population more than doubled as a result of the creation of a huge area of new habitat following the clearance. It is doubtful whether the nightjars would have found the uncleared windblown pines such a suitable habitat. Woodlarks benefited in a similar way to the clearance in Aldewood Forest (R. Hoblyn pers. comm.).

No data are available to compare changes in bird communities in areas that were left uncleared with those that were cleared and replanted. In uncleared areas the prostrate trees immediately create an effective shrub layer, especially where the canopies are still in leaf. This appears to benefit nightingales (see above). On the other hand, some species such as woodlark (Bowden 1990), may avoid the dense tangle of woody debris that occurs within uncleared gaps, perhaps because they require a more open habitat or bare ground for feeding. In woodland in north Essex, whitethroats appear to have colonised cleared areas but not uncleared treefall gaps (R Leavett pers. comm.).

Concluding thoughts

The results presented here relate only to counts of breeding birds. Studies of marked individuals would tell us more accurately how birds respond to treefall gaps. Do gaps provide food resources for birds that are otherwise scarce in much mature woodland? Do birds nesting in adjacent closed-canopy woodland use gaps for feeding? Do birds on migration make more use of gaps than closed-canopy areas in European woods, which is the situation in North America (Blake & Hoppes 1986; Martin & Karr 1986)? How similar are the bird communities of man-made openings (young plantations and coppice) and natural gaps? Are the food resources and microhabitats offered by these various open and young-growth habitats the same?

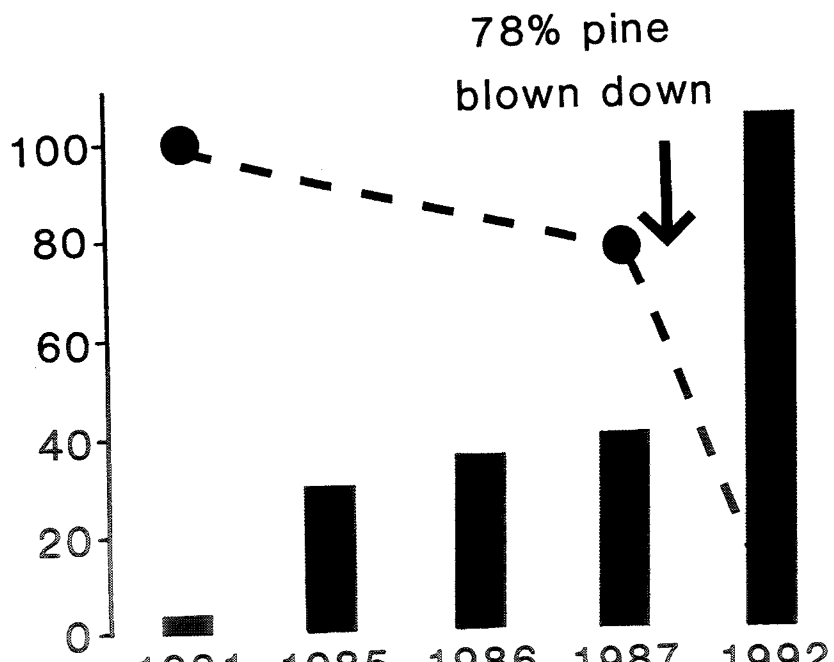

Figure 4 Numbers of churring male nightjars (shaded bars) in Aldewood Forest, Suffolk, in relation to the % of the area covered by pole-stage pine plantation (broken line). (Based on information from Morris *et al.* 1994). The scale is the same for both % cover by mature pine and for number of nightjars. In 1992 the estimated population was 104 male nightjars.

Acknowledgements

The enthusiasm and commitment of the late Stuart Hughes was a driving force behind the work in Ebernoe Common and The Mens. The bird counts there were carried out by Frank and Madelaine Dougherty, Stuart Hughes, Leonard and June Manns, Molly and Dennis Pooley. We are also grateful to Alf and Iris Simpson, and to Carolyne Ray who helped in various ways with the Sussex project. Thanks also to all those who have contributed to the woodland CBC. Hollesley Heath has been censused since 1986 by Alan Miller, Newbourn Springs by Brian Thompson. Ron Hoblyn, Russell Leavett and Brian Watmough provided helpful information. Charlotte Collins and Ruth Fuller helped prepare the data, Sophie Foulger and Julie Sheldrake the manuscript and Su Gough the figures. This paper is based on work partly funded by the Joint Nature Conservation Committee (on behalf of English Nature, the Countryside Council for Wales and Scottish Natural Heritage) and by a contract with the Department of the Environment, Northern Ireland.

References

BLAKE, J.G. & HOPPES, W.G. 1986. Influence of resource abundance on use of treefall gaps by birds in an isolated woodlot. *Auk* **103**, 328-340.

BOWDEN, C.G.R. 1990. Selection of foraging habitats by woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology* **27**, 410-419.

BOWDEN, C. & HOBLYN, R. 1990. The increasing importance of restocked conifer plantations for woodlarks in Britain: implications and consequences. *RSPB Conservation Review* **4**, 26-31.

CARLSON, A. & AULÉN, G. (eds.) 1990. *Conservation and management of woodpecker populations*. Uppsala, Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 17.

DUNNING, J.B. & WATT, B.D. 1991. Habitat occupancy by Bachman's sparrow in the Francis Marion National Forest before and after Hurricane Hugo. *Auk* **108**, 723-725.

ENGSTROM, R.T. & EVANS, G.W. 1990. Hurricane damage to red-cockaded woodpecker (*Picoides borealis*) cavity trees. *Auk* **107**, 608-610.

FULLER, R.J. 1992. Effects of coppice management on woodland breeding birds. In *Ecology and Management of Coppice Woodlands,* edited by G.P. BUCKLEY, pp.169-192. London, Chapman & Hall.

FULLER, R.J. & HENDERSON, A.C.B. 1992. Distribution of breeding songbirds in Bradfield Woods, Suffolk, in relation to vegetation and coppice management. *Bird Study* **39**, 73-88.

HELLE, P. & FULLER, R.J. 1988. Migrant passerine birds in European forest successions in relation to vegetation height and geographical position. *Journal of Animal Ecology* **57**, 565-579.

LENS, L. & DHONDT, A.A. 1992. The effect of a severe storm on a population of crested tits *Parus cristatus* in Belgium. *Bird Study* **39**, 31-33.

MARCHANT, J.H., HUDSON, R., CARTER, S.P. & WHITTINGTON, P.A. 1990. *Population Trends in British Breeding Birds.* Tring, British Trust for Ornithology/Nature Conservancy Council.

MARTIN, T.E. & KARR, K.R. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scandinavica* **17**, 165-174.

MORRIS, A., BURGES, D., FULLER, R.J., EVANS, A.D. & SMITH, K.W. 1994. The status and distribution of the nightjar *Caprimulgus europaeus* in Britain in 1992. *Bird Study* **41**, 181-191.

NILSSON, S.G. 1979. Density and species richness of some forest bird communities in south Sweden. *Oikos* 33, 392-401.

RAVENSCROFT, N.O.M. 1989. The status and habitat of the nightjar *Caprimulgus europaeus* in coastal Suffolk. *Bird Study* 36, 161-169.

VIRKKALA, R., HEINONEN, M. & ROUTASUO, P. 1991. The response of northern taiga birds to storm disturbance in the Koilliskaira National Park, Finnish Lapland. *Ornis Fennica* 68, 123-126.

VOOUS, K.H. 1977. *List of recent Holarctic bird species.* London British Ornithologists' Union.

WIENS, J. 1989. *The ecology of bird communities.* 2 Volumes. Cambridge, Cambridge University Press.

WHITBREAD, A. & MONTGOMERY H.A.C. 1994. Storm damage in The Mens. In *Ecological responses to the 1987 Great Storm in the woods of south-east England*, edited by K.J. KIRBY and G.P. BUCKLEY, pp 50-55 Peterborough English Nature (English Nature Science 23).

APPENDIX 1

A list of the scientific names of bird species appearing in the text. Species are listed following Voous (1977)

Nightjar	*Caprimulgus europaeus*
Great spotted woodpecker	*Dendrocopos major*
Lesser spotted woodpecker	*Dendrocopos minor*
Woodlark	*Lullula arborea*
Tree pipit	*Anthus trivialis*
Wren	*Troglodytes troglodytes*
Dunnock	*Prunella modularis*
Robin	*Erithacus rubecula*
Nightingale	*Luscinia megarhynchos*
Blackbird	*Turdus merula*
Song thrush	*Turdus philomelos*
Mistle thrush	*Turdus viscivorus*
Grasshopper warbler	*Locustella naevia*
Whitethroat	*Sylvia communis*
Garden warbler	*Sylvia borin*
Blackcap	*Sylvia atricapilla*
Chiffchaff	*Phylloscopus collybita*
Willow warbler	*Phylloscopus trochilus*
Pied flycatcher	*Ficedula hypoleuca*
Crested tit	*Parus cristatus*
Blue tit	*Parus caeruleus*
Great tit	*Parus major*
Jay	*Garrulus glandarius*
Carrion Crow	*Corvus corone*
Chaffinch	*Fringilla coelebs*