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Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain

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Summary

- 1. The amount of dead wood, particularly as fallen dead wood and standing dead trees, in British forests is attracting attention from forest managers as part of their interest in increasing biodiversity within forests managed for timber. Existing levels of dead wood in managed and unmanaged forests were assessed to provide a basis for what might be considered high or low amounts of dead wood under present conditions.
- 2. Estimates of fallen dead wood, derived from line-intersect sampling, were collated for 63 sites (87 stands) in Britain. The values obtained ranged from virtually zero in recently cut coppie to 60–140 m³ ha⁻¹ in stands largely undisturbed over at least the last 80 years. The highest values (from unmanaged stands) overlap with estimates for the volumes of fallen logs in old-growth broadleaved forests in North America and continental Europe. Forests currently managed for timber had less than 20 m³ ha⁻¹ of fallen logs.
- 3. In unmanaged stands, localized accumulation of fallen material was often associated with exceptional events such as the 1976 drought or the 1987 great storm. Following the 1987 storm the amounts of fallen dead wood in unmanaged forests in eastern England appear to have doubled from about $10 \, \mathrm{m}^3 \, \mathrm{ha}^{-1}$ to $23 \, \mathrm{m}^3 \, \mathrm{ha}^{-1}$.
- **4.** Large standing dead trees (snags), > 40 cm diameter, were rarely recorded in the forests surveyed because most forests in Britain have been cut over at least once this century and any large timber removed.
- 5. The following, based on the range of values found in this survey, are proposed as provisional benchmarks for amounts of dead wood in British broadleaved forests: low $<20 \,\mathrm{m^3\ ha^{-1}}$ fallen dead wood, 0–10 snags ha⁻¹ (all below 10 cm diameter); medium 20–40 m³ ha⁻¹ fallen dead wood, 11–50 snags ha⁻¹ (of which some are more than 10 cm diameter); high $>40 \,\mathrm{m^3\ ha^{-1}}$ fallen dead wood, more than 50 snags ha⁻¹ (of which some are more than 40 cm diameter).
- **6.** Further work on assessing the dead wood resource in British forests is needed.

Key-words: broadleaved woodland, forest management, survey, transect.

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Introduction

Dead wood plays a variety of roles in woodland systems through its influence on biological, physical and chemical processes (Harmon *et al.* 1986; McMinn & Crossley 1993; Samuelsson *et al.* 1994). Directly or indirectly it provides a substrate or host for a wide range of organisms, particularly fungi and invertebrates; cavities formed by rot are used as nesting sites or shelter by many vertebrates; and decaying logs may act as safe sites for seedling germination or for the growth of bryophytes away from the competition of

the woodland ground flora. Fallen logs may create bare soil patches and crush or shade out the ground vegetation; they may slow soil and water movement on slopes. Soil nutrient levels are likely to be higher around or under dead wood and thus affect the ground flora at that point (Falinski 1986).

Dead wood has, thus, long been recognized as important in British forests by ecologists (e.g. Elton 1966; Stubbs 1972; Warren & Key 1991; Kirby & Drake 1993). More recently, forest managers have accepted its value as a contribution to maintaining forest biodiversity (e.g. Ratcliffe 1993) and man-

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agement may be altered to maintain or to increase the amounts of dead wood present (Hodge & Peterken, in press). There have, however, been few estimates of how much dead wood there is in British forests and little knowledge of how it is affected by different forest management practices.

TYPES OF DEAD WOOD

Dead wood may be grouped into fallen material, standing dead trees, stumps, and dead wood on or in living trees (Ferris-Kaan *et al.* 1993). In this paper we concentrate on fallen wood and standing dead trees. These are the components that are most obvious to, and most easily influenced by, forest managers, who may choose to leave some areas with much dead wood undisturbed or to leave standing dead trees uncut, and who decide how much fallen or felled timber is removed (Kirby 1992).

Fallen material includes dead twigs, branches and trunks. Twigs and small branches of less than 5 cm diameter have been classed as part of woodland litter and are relatively rapidly broken down to produce undifferentiated organic matter on or in the soil. Such small branchwood has its own distinctive invertebrate fauna (Paviour-Smith & Elbourn 1993; Alexander 1994) but it is not considered further in this paper.

Trunks and branchwood of greater than 5 cm diameter form the bulk of the dead wood resource on the ground. Some is alive when it falls, e.g. branches ripped off in the wind or left on site after felling. Other branches may have died while still attached in the canopy and their decay is well-advanced before they reach the ground. Standing dead trees (snags) include large individuals killed by disease, lightning strikes, drought, water logging, or pollution as well as smaller trees killed by shading during the early growth of densely stocked stands.

VARIATIONS IN THE AMOUNT OF DEAD WOOD IN THE FOREST

Input of small dead wood from branches and small trees, and internal decay in trees is fairly steady from year to year, but the addition of large pieces of dead wood (trunks and major branches) to the ground and the death of whole trees is irregular and may be episodic (Onega & Eickmeier 1991). In old-growth stands that escape catastrophic disturbance about 1% of canopy trees may die annually (Runkle 1985). Storms, droughts and disease can, however, kill many trees in a short period, generating a pulse of large dead wood. In Britain between 1970 and 1980 many elms Ulmus spp. were killed by Dutch elm disease; the 1976 drought killed much of the beech Fagus sylvatica in Lady Park Wood (Peterken & Jones 1987); and in southern England large numbers of trees were brought down by the exceptional storms of 1987 and 1990 (Kirby & Buckley 1994). Dead wood disappears

through transport off-site (by people and in streams), through fire and biological and physical decay.

Within natural forests the distribution of dead wood is usually patchy (Muller & Liu 1991). Variation at the landscape scale depends on the history and pattern of catastrophic disturbances. Within stands, dead wood tends to be most abundant in and around gaps. The total amount declines during regeneration (as decay proceeds and little new material is added), with minimum levels reached during the mid-thicket phase (Bormann & Likens 1979). Thereafter there is a gradual increase as new material is added until the stand is again disturbed.

In managed forests the dead wood created by felling is largely removed [although there may sometimes be a temporary abundance of small branches left behind (Tritton 1980)]. Stand disturbances, the silvicultural operations, are more regularly distributed in time and usually occur before the stands reach the old-growth/veteran stage. Disturbances are also more evenly distributed in space so that it is unlikely that any stand will not be felled before it reaches the veteran stage.

AIMS

We provide estimates of the amount of fallen dead wood and frequency of standing dead trees in a range of British woods and compare them with those in other, particularly temperate broadleaved, forests in Europe and North America. A simply survey technique is described that can be used by forest managers to determine whether their site contains high or low amounts of dead wood in a British context. Preliminary conclusions are drawn on the effects of different management regimes and of the severe storms in 1987 and 1990 (Kirby & Buckley 1994) on dead wood abundance in British forests.

Methods

LINE-INTERCEPT SAMPLING FOR FALLEN WOOD

Since 1988, line-intercept sampling has been widely used in Britain to measure fallen dead wood. If a transect line is set down in a stand of trees then the length of fallen logs in that stand can be estimated from the following equation (Warren & Olson 1964; Van Wagner 1968; Brown 1974):

$$L = \pi \ 10^4 \ N \ (2t)^{-1}$$

where N is the number of intersections, t is the transect length (metres), and L is the total length of fallen wood per hectare (metres). The conversion factor of 10^4 is needed to change the results to metres per hectare rather than per metre-square. In the surveys undertaken in this study, 5-10 transects were recorded in each stand; the transects were 25 or $50 \,\mathrm{m}$ long depending on the frequency with which logs were

Fallen dead wood in British forests encountered in different sites; and the lower size limit for logs to be recorded was 5 cm diameter at the point of intersection with the transect line.

Estimates of fallen log length per unit area were converted to volumes using the diameter of the logs at the point of intersection with the transect line and assuming a circular cross-section for all logs. Log intersections were assigned to diameter classes and the mean cross-sectional area for that class was calculated. The total volume for each diameter class then equals the length for that class multiplied by the cross-sectional area, that is:

$$V = nd^2 \pi^2 10^4/8t$$

where V is the total volume of fallen logs of diameter class d (the diameter being measured at the intersection with the transect line), n is the number of intersections for logs of diameter d, and t is the total length of transect as before. For the stand as a whole the volume per hectare is the sum of the volumes for each diameter class.

Fallen logs are unlikely to be randomly distributed or orientated (Falinski 1978). Observers were therefore careful to avoid bias in selecting starting points and line orientation that might just include or just avoid particular logs (especially large ones).

MEASUREMENTS OF STANDING DEAD AND LIVING TREES

Information about standing dead trees (snags) was recorded in some of the surveys from a plot running 2 m either side of the transect line. The centre of the tree had to be within the plot to count. The diameter at breast height (d.b.h.) was measured for trees more than 5 cm d.b.h.

THE SITES

Estimates of the volume of fallen dead wood were available for 63 sites across Britain, for the most part collected by the authors, but including results from some other surveys which had used the same methods (Kirby et al. 1991; Kirby 1992; Reid 1994; Reid et al. 1996; Crampton 1996; Green & Peterken, in press; and unpublished surveys by M. King and F.B. Goldsmith for the Forestry Commission in East Anglia, by A. Maier and J. Dagley in Epping Forest, and by English Nature site managers on National Nature Reserves across England). The sites were distributed from East Anglia to Wales and from the New Forest in the south to the north of Scotland. They include mixed deciduous woodland, limestone forests, western oak forests, oak high forest, native pinewoods and some conifer plantations. All sites were ancient woodland, but their past management varied, some being former coppice woods, others wood-pastures. A listing of results for individual sites is available from the first author.

Usually only a part of the wood was sampled, mostly semi-natural stands of between 2 and 10 ha. There are 87 separate estimates in total because there was more than one sample for some sites. For 60 samples, information on the length of fallen wood as well as the volume per hectare was provided; and for 37 samples details from the individual transects in the set of five or 10 could be used to estimate standard error terms for the volume figure. Information on densities of standing dead trees was similarly only available for 37 sites.

The sites are not a structured survey. Therefore comparisons have been restricted to a few broad-scale comparisons. Samples were classified according to whether they were from broadleaved or coniferous forests, and to whether they were managed or unmanaged for wood production. The conifer areas were divided on the basis of their known history and structure into plantations (managed) and unmanaged seminatural stands. The broadleaved areas were divided among the following five management regimes: managed coppice (i.e the trees were still young enough to be within the rotation age (5–30 years) and coppice was being cut somewhere in the wood); unmanaged coppice (stands that retained a coppice structure, but

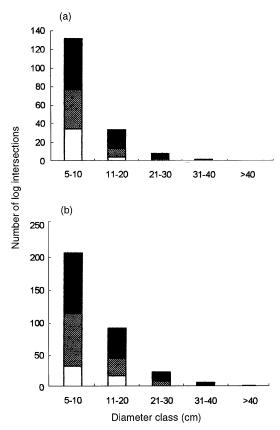


Fig. 1. Diameter distribution and decay class for fallen logs from (a) Monks Wood, and (b) the New Forest. Well-decayed = solid part of bar; part rotten = hatched; still solid logs = open. (The 'still solid' category combines decay classes 1 and 2 from Table 1).

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had not been cut for at least 50 years); managed high forest (stands with single-stemmed trees either planted or naturally regenerated, and managed for timber by thinning and felling); unmanaged high forest (stands with predominantly single-stemmed trees, but which showed no signs of felling or thinning in the last ≈ 80 years); and unmanaged wood-pasture (stands which contained scattered old pollard trees among younger maiden stems).

Data collected by the authors from the eight stands in the New Forest, Hampshire (a wood-pasture site), and three stands at Monks Wood, Cambridgeshire (an unmanaged coppice), are used to illustrate the distribution of the fallen logs among different size categories and decay classes (Table 1).

Twenty-three samples from East Anglia (all but one unmanaged coppice stands) recorded fallen wood in 1989 that had apparently been brought down by the exceptional storm in 1987, as distinct from that which appeared to have been there for longer (M. King and F.B. Goldsmith, unpublished data).

Results

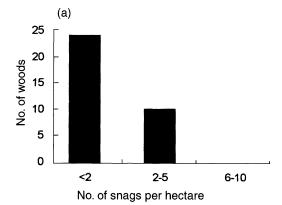
The length of fallen dead wood per hectare (data available for 60 stands) ranged from less than 500 m to more than 6000 m, with 50% of the stands containing less than 2000 m ha⁻¹. Dead wood volumes per hectare (from 87 stands) ranged from 0.3 to 139 m³ with 48% containing 20 m³ or less. Where a standard error for the volume estimate could be calculated (37 stands) the coefficient of variation was generally between 30 and 50%. Most of the fallen wood encountered was small (less than 20 cm diameter) and in decay classes 3 and 4 (partially rotten or well-decayed) as is illustrated for the data from Monks Wood and the New Forest (Fig. 1).

Standing dead trees (snags) were scarce in broadleaved woods (less than 50 ha⁻¹ of all sizes) and were for the most part small (less than 20 cm diameter) (Fig. 2), in contrast to their contribution to the dead wood resource in pinewoods (Reid *et al.* 1996). An exception was in Great Monk Wood, Essex, where 8 out of 10 snags recorded were over 20 cm diameter

 Table 1. Subjective decay classes used in dead wood surveys

 using line-intersect transects

Class	Description (assessed at point of intersection with the transect line)			
1	Fresh fallen (previous 6 months), bark still on			
2	Older material, most of the bark still attached,			
	little evidence of rotting			
3	Bark partly detached, partially rotten, but log still reasonably intact			
4	Rot well-advanced; log well-decayed and likely to collapse if pressure is applied			



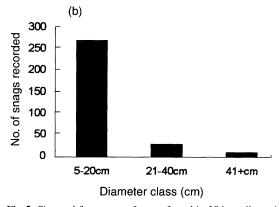


Fig. 2. Size and frequency of snags found in 37 broadleaved stands for which there was consistently recorded information: (a) frequency of occurrence of snags; (b) size distribution for all snags encountered in these woods.

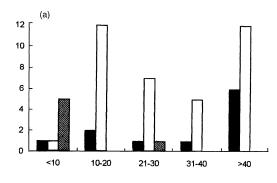
and the estimated volume of snags was $43.5 \,\mathrm{m}^3 \,\mathrm{ha}^{-1}$ (J Dagley, personal communication).

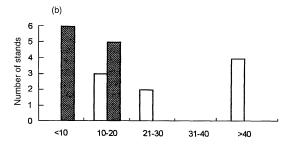
EFFECTS OF WOODLAND TYPE AND MANAGEMENT REGIME

Unmanaged coppice (37 stands) had 10–60 m³ ha⁻¹ fallen dead wood, the results overlapping with those from the 10 unmanaged high forest stands (Fig. 3), most of which are derived from coppice last cut 80–100 years ago. Worked coppice (6 stands) and actively managed high forest (11 stands) contained very little fallen dead wood (mostly less than 20 m³ ha⁻¹). Five of the wood-pasture stands contained very high levels of fallen wood (>60 m³ ha⁻¹) (Fig. 3). However, for three of the New Forest stands the amount recorded (10–15 m³ ha⁻¹) was less than that found in many neglected coppice woods.

The six conifer plantations contained less fallen wood than the six semi-natural stands, but the values for fallen wood in the semi-natural pinewoods were not particularly high (13–21 m³ ha⁻¹) in comparison to neglected broadleaved woods, even in stands left undisturbed as nature reserves (Fig. 3).

Fallen dead wood in British forests





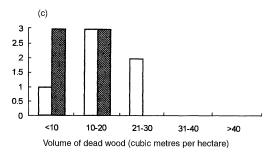


Fig. 3 Volumes of dead wood found in stands with differing management histories: (a) wood-pasture (solid bars), managed (hatched bars) and unmanaged coppice (open bars); (b) managed (hatched bars) and unmanaged (open bars) broadleaved high forest; (c) conifer plantations (hatched bars) and semi-natural (open bars) conifer stands.

INPUT OF FALLEN WOOD FOLLOWING EXCEPTIONAL STORMS

In Sheephouse Wood, Buckinghamshire, there was no significant difference (comparison of means using ttest) between the mean results from two independent surveys, based on 10 transects each, taken 7 years apart [21 m³ ha⁻¹ in 1988 and 11 m³ ha⁻¹ in 1995 (standard errors 7 and 4 m³ ha⁻¹, respectively)] (Kirby, Webster & Antczak 1991). In Great Monk Wood, however, the amount recorded went from $27 \,\mathrm{m}^3 \,\mathrm{ha}^{-1}$ in 1989 to 95.3 $\mathrm{m}^3 \,\mathrm{ha}^{-1}$ in 1996. This stand (unlike Sheephouse Wood) was badly affected by severe storms in January 1990, which blew over some large beeches (Fagus spp.) and broke off major branches (J. Dagley, personal communication). A very high value for fallen wood (139 m³ ha⁻¹) from a Cotswold stand was similarly from an area of old beechwood badly affected by the 1990 storm (English Nature, unpublished results).

Large increases in fallen dead wood following

exceptional storms are also suggested by the results from 23 woods recorded in 1989 in East Anglia (M. King & F.B. Goldsmith, personal communication). Fallen logs that pre-dated the 1987 storm were estimated at a mean of $10.1 \,\mathrm{m^3}$ ha⁻¹ whereas the mean volume rose to $23.0 \,\mathrm{m^3}$ ha⁻¹ (standard errors 2 and $3 \,\mathrm{m^3}$ ha⁻¹, respectively) when those brought down by, or post-dating this storm were included.

Discussion

COMPARISON OF BRITISH DEAD WOOD VALUES WITH THOSE IN MORE NATURAL FORESTS

Estimates of the amount of dead wood in virgin forests in Britain cannot be made because such forests no longer exist. However, some estimates are available for the amounts of fallen wood and snags from the old-growth forests in eastern North America and near-natural old-growth stands in continental Europe. Such stands typically contain 50–150 m³ ha⁻¹ of fallen wood (Table 2). The least disturbed parts of unmanaged forests such as Monks Wood, Cambridgeshire, Lady Park Wood (Wye Valley), Skoska Wood, North Yorkshire and some old wood-pasture stands have built up levels that overlap this range. The second component of the dead wood resource that was recorded was the number of standing dead trees (snags). Even in old-growth stands the majority of snags may be small (McComb & Muller 1983), and in the British sites standing dead trees larger than 40 cm were rare even in stands currently unmanaged (Fig. 2).

The scarcity of fallen dead wood and standing dead trees (particularly in the larger size categories) is because there are few sites in Britain which have been left undisturbed over the last 100 years, so as to allow trees to grow large and die without being harvested for timber. Even if there is no timber harvesting there may be firewood collection in some unmanaged forests. This is one reason for the low levels of fallen dead wood in some New Forest stands (Wilson 1986). Dead and dying trees or branches may also be removed because they are considered dangerous or unsightly in areas that have a high recreational use (Kirby et al. 1995).

The importance of occasional catastrophic events on the levels of fallen dead wood in unmanaged stands has been illustrated. Fallen dead wood is relatively scarce in the oak stands in Sheephouse Wood (Buckinghamshire) (>22 m³ ha⁻¹). These have been left alone for \approx 130 years, and so far have escaped the major disturbances (droughts and storms) that have recently affected the similarly aged beech stands in Lady Park Wood (Peterken & Jones 1987), Great Monk Wood and the Cotswolds site (67–139 m³ ha⁻¹). The approximate doubling of fallen dead wood in East Anglian woods following the 1987 storm was also found for forests in the same part of the country

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		Volume of fallen wood	
Location	Type of woodland	$(m^3 ha^{-1})$	Source
USA	Fagus-Betula	82	Harmon <i>et al.</i> (1986)
USA	Quercus mixed	46	Macmillan (1981)
USA	Quercus mixed	94	Harmon et al. (1986)
USA	Quercus prinus	132	Harmon et al. (1986)
USA	Quercus mixed	54	Muller & Liu (1991)
USA	Acer-Fagus	78	Gore (1986)
USA	Acer	86	Hardt & Swank (1997)
USA Hemlock-hardwood		55	Tyrell & Crow (1994a)
USA Acer-Fagus		137*	Tritton 1980
USA	Quercus mixed	76*	Lang & Forman (1978)
Poland Bialowieza Forest	Tilio-Carpinetum	60-71	Falinski 1978
Poland Bialowieza Forest	Tilio-Carpinetum	75	Kirby et al. (1991)
Poland Bialowieza Forest	Tilio-Carpinetum	94	Kirby et al. (1991)

^{*} From biomass figures assuming a specific gravity of 0.28.

by Smith (1994) who used circular plots rather than line transects to make his estimates. In the parts of Monks Wood where the highest values of fallen wood were recorded (31–53 m³ ha⁻¹), much of this appeared to be birch (*Betula* spp.) which suffered considerable mortality during recent droughts (Crampton 1996), so again a relatively concentrated input of material has occurred.

DEAD WOOD IN MANAGED FORESTS IN BRITAIN

Managed forests in this survey contained very much less fallen dead wood than unmanaged ones. This is likely to be true also for dead branches in the canopy and dead wood within the trunks of living trees, although there may be more stumps in managed than in unmanaged stands. The scarcity in Britain of many invertebrates that are dead wood specialists, and their high representation among species known to have gone extinct in the last few thousand years, probably reflects the effects of past and present management in reducing the amounts of dead wood left in the forest (Buckland & Dinnin 1993; McLean & Speight 1993).

There is, as yet, no direct evidence from Britain that the proposals by foresters (Hodge & Peterken, in press) to increase the amounts of fallen dead wood left in managed forests will increase the diversity of these forests, but this seems likely given the wide variety of ecological functions that fallen wood can fulfil (Harmon *et al.* 1986; McMinn & Crossley 1993; Samuelsson *et al.* 1994). In Scandinavian forests, a direct relationship has been found between the amount of fallen dead wood and the richness of that site for some fungal groups (J. Stokland, personal communication).

There is also a need to explore through structured surveys other aspects that might affect the amounts of fallen dead wood, such as geographical location, stand age and tree species composition, that could not be addressed through the current unbalanced set of data. Line-intersect transects (with accompanying plots for standing dead and living trees) may be useful in such surveys as well as in providing forest managers with a relatively quick way of assessing whether their forest rates as having high or low amounts of dead wood (Table 3), based on studies to date.

Line-intersect sampling is useful for quick, broadscale surveys, but other approaches need to be considered in parallel (e.g. Tyrrell & Crow 1994b; Harmon & Sexton 1996). These include the recording (on maps or by photographs) of individual large trees or fallen pieces of wood (>60 cm diameter) that usually

Table 3. Provisional benchmarks for dead wood in British forests (based on data collated to date)

Level of dead wood	Volume of fallen wood (m³ ha ⁻¹)	No. of standing dead trees (ha ⁻¹)	Size distribution of standing dead trees	Comment
Low Medium	< 20 20–40	0–10 11–50	All < 10 cm d.b.h. Some > 10 cm d.b.h.	Typical values for managed forests Common in unmanaged forests that
High	>40	> 50	Some > 40 cm d.b.h.	have not been cut for about 50 years Uncommon, stands likely to be long (>70 years) unmanaged and/or to
				have been affected by major disturbance, such as a storm

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occur too infrequently to be detected in the transects or associated plots. Research sites are also needed where more detailed monitoring of dead wood in both managed and unmanaged stands is linked to the study of other species or features that are expected to respond to changes in dead wood abundance.

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References

- Alexander, K.N.A. (1994) The use of freshly downed timber by insects following the 1987 storm. *Ecological Responses* to the 1987 Great Storm in the Woods of South-East England (eds K.J. Kirby & G.P. Buckley), pp. 134–150. English Nature (English Nature Science 23), Peterborough.
- Bormann, F.H. & Likens, G.E. (1979) Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.
- Brown, J.K. (1974) *A handbook for inventorying downed woody material*. USDA Forest Service (General Technical Report INT-16), Ogden, Utah.
- Buckland, P.C. & Dinnin, M.H. (1993) Holocene woodland—the fossil insect evidence. *Dead Wood Matters* (eds K.J. Kirby & C.M. Drake), pp. 6–20. English Nature (English Nature Science 7), Peterborough.
- Crampton, A.B. (1996) Monks Wood NNR: an insight into the stand structure and dynamics of an ash-oak woodland. MSc thesis, University of Oxford, Oxford.
- Elton, C.S. (1966) The Pattern of Animal Communities. Methuen, London.
- Falinski, J.B. (1978) Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetatio*, **38**, 175–183.
- Falinski, J.B. (1986) Vegetation Dynamics in Temperate Lowland Primeval Forests. Junk, The Hague.
- Ferris-Kaan, R., Lonsdale, D. & Winter, T. (1993) *The conservation management of dead wood.* Forestry Commission (Research Information Note 241), Farnham.
- Gore, J.A. (1986) Small mammals and habitat structure in an old-growth northern hardwoods forest. PhD thesis, University of Massachusetts, Amherst.
- Green, P. & Peterken, G.F. (in press) Variation in the amounts of dead wood in the woodland of the Lower Wye Valley. Forest Ecology & Management.
- Hardt, R.A. & Swank, W.T. (1997) A comparison of structural and compositional characteristics of southern Appalachian young second-growth, maturing and old-growth stands. *Natural Areas Journal*, 17, 42–52.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. & Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133–302.
- Harmon, M.E. & Sexton, J. (1996) Guidelines for measurements of woody detritus in forest ecosystems. LTER Network Publication 20, Seattle.

- Hodge, S.J. & Peterken, G.F. (in press) Dead wood in British forests: priorities and a strategy. *Forestry*.
- Kirby, K.J. (1992) Accumulation of dead wood a missing ingredient in coppicing? *Ecology and Management of Cop*pice Woodland (ed. G.P. Buckley), pp. 99–112. Chapman and Hall, London.
- Kirby, K.J. & Buckley, G.P. (1994) Ecological responses to the 1987 great storm in the woods of south-east England. English Nature (English Nature Science 23), Peterborough.
- Kirby, K.J. & Drake, C.M. (1993) Dead Wood Matters. English Nature (English Nature Science 7), Peterborough.
- Kirby, K.J., Thomas, R.C., Key, R.S., McLean, I.F.G. & Hodgetts, N. (1995) Pasture woodland and its conservation in Britain. *Biological Journal of the Linnean* Society, 56 (Suppl.) 135–153.
- Kirby, K.J., Webster, S.D. & Anctzak, A. (1991) Effects of forest management on stand structure and the quantity of fallen dead wood: some British and Polish examples. Forest Ecology and Management, 43, 167–174.
- Lang, G.E. & Forman, R.T.T. (1978) Detritus dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. *Ecology*, 59, 580–595.
- MacMillan, P.C. (1981) Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. American Midland Naturalist, 106, 335–344.
- McComb, W.C. & Muller, R.N. (1983) Snag densities in old growth and second growth Appalachian forests. *Journal of Wildlife Management*, **47**, 376–382.
- McLean, I.F.G. & Speight, M.C.D. (1993) Saproxylic invertebrates: the European context. *Dead Wood Matters* (eds K. J. Kirby & C.M. Drake), pp. 21–32. English Nature (English Nature Science 7), Peterborough.
- McMinn, J.W. & Crossley, D.A. (1993) *Biodiversity and Coarse Woody Debris in Southern Forests*. USDA Southern Research Station, Athens, GA.
- Muller, R. N. & Liu, Y. (1991) Coarse woody debris in an old growth deciduous forest on the Cumberland Plateau, south-eastern Kentucky. *Canadian Journal of Forest Research*, **21**, 1567–1572.
- Onega, T.L. & Eickmeier, W.G. (1991) Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. *Bulletin of the Torrey Botanical Club*, **118**, 52–57.
- Paviour-Smith, K. & Elbourn, C.A. (1993) A quantitative study of the fauna of small dead and dying wood in living trees in Wytham Woods near Oxford. *Dead Wood Matters* (eds K.J. Kirby & C.M. Drake), pp. 33–57. English Nature (English Nature Science 7), Peterborough.
- Peterken, G.F. & Jones, E.W. (1987) Forty years of change in Lady Park Wood: the old growth stands. *Journal of Ecology*, **75**, 477–512.
- Ratcliffe, P.A. (1993) *Biodiversity in Britain's forests*. Forestry Commission, Edinburgh.
- Reid, C.M. (1994) The effects of management on dead wood resources of Caledonian pine forests. MSc thesis, University of Oxford, Oxford.
- Reid, C.M., Foggo, A. & Speight, M. (1996) Dead wood in the Caledonian pine forest. *Forestry*, **69**, 275–279.
- Runkle, J.R. (1985) Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A Pickett & P.S. White), pp. 17–33. Academic Press, London.
- Samuelsson, J., Gustafsson, L. & Ingelög, T. (1994) Dying and dead trees: a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala.
- Smith, K. (1994) The effects of the 1987 and 1990 storms on great spotted woodpecker *Dendrocopus major* numbers and nest site selection in two Hertfordshire woods. *Ecological Responses to the 1987 Great Storm in the Woods of South-East England* (eds K.J. Kirby & G.P. Buckley), pp.

- 124–133. English Nature (English Nature Science 23), Peterborough.
- Stubbs, A. (1972) Wildlife conservation and dead wood. Journal of Devon Trust for Nature Conservation, 4 (supplement), 169–182.
- Tritton, L.M. (1980) Dead wood in the northern hardwood forest ecosystem. PhD thesis, Yale University, Connecticut.
- Tyrell, L.E. & Crow, T.R. (1994a) Structural characteristics of old growth hemlock–hardwood forests in relation to age. *Ecology*, **75**, 370–386.
- Tyrell, L.E. & Crow, T.R. (1994b) Dynamics of dead wood in old-growth hemlock—hardwood forests of northern Wisconsin and northern Michigan. *Canadian Journal of Forest Research*, **24**, 1672–1683.

- Van Wagner, C.E. (1968) The line intersect method in forest fuel sampling. *Forest Science*, **14**, 20–26.
- Warren, M.S. & Key, R.S. (1991) Woodlands: past, present and future potential for invertebrates. *The Conservation of Insects and Their Habitats* (eds M. Collins & J. Thomas), pp. 155–211. Academic Press, London.
- Warren, W.G. & Olsen, P.E. (1964) A line intersect technique for assessing logging waste. *Forest Science*, **10**, 267–276.
- Wilson, P. (1986) *The dead wood resource of New Forest unenclosed woodlands*. Unpublished report, Nature Conservancy Council, Lyndhurst.

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