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Long-term studies in British woodland

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We would like to dedicate this volume to two former members of the Oxford Forestry Department, Colyear Dawkins and Eustace Jones and their pioneering works at Wytham and Lady Park Wood respectively.

PREFACE

The papers in this volume were presented at the British Ecological Society symposium held in the Oxford Forestry Institute on 13 July 1999. Our aim was to bring together examples of different types of long-term monitoring. The papers and posters presented explore changes in British woods over periods ranging from five to 50 years in trees and shrubs, ground flora, invertebrates and birds. The work described deals both with natural processes such as stand dynamics, population cycles, phenology and interactions of plant host and invertebrates; and with human-induced effects - woodland management, air pollution and climate change.

As important as the results of the studies themselves are the common threads that emerge with respect to the establishment and maintenance of long-term studies; the archiving and publishing of results so that others may continue the work; and the tension between trying to design systems that might be useful to future researchers, but are also simple enough that they do survive to be picked up by those (hypothetical) researchers.

We hope that these papers will provide inspiration and encouragement for those who are struggling with potential long-term studies of their own.

ACKNOWLEDGEMENTS

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Recent English Nature and JNCC publications relevant to British woodland studies

English Nature Research Reports

43. PARKER, S.J. & WHITBREAD, A.M. 1993. Re-recording storm damaged woods in Kent and Sussex.

143. KIRBY, K.J., THOMAS, R.C. & DAWKINS, H.C. 1995. Changes in the structure and composition of the tree and shrub layers in Wytham Woods (Oxfordshire), 1974-1991.

175. KIRBY, K.J. & BELL, J. 1996. Changes in abundance of six ground flora species in Wytham Woods (1974-1991).

270. MOUNTFORD, E.P. & PETERKEN, G.F. 1998. Monitoring natural stand change in Monks Wood National Nature Reserve.

301. SOLLY, L., KIRBY, K.J. & SODEN, N, D. 1999. National sample survey of SSSI woodland.

302. MOUNTFORD, E.P., PETERKEN, G.F. & BURTON, D. 1998. Long-term monitoring and management of Langley Wood.

320. KIRBY, K.J. & THOMAS, R.C. 1999. Changes in the ground flora in Wytham Woods, southern England, 1974-1991, and their implications for nature conservation.

324. KIRBY, K.J. 1999. Woodland surveillance and monitoring - a discussion paper.

340. HOPKINS, B. 1999. The effect of shade and weather on daffodils *Narcissus pseudonarcissus* in West Dean Woods, West Sussex.

346. MOUNTFORD, E.P. & PETERKEN, G.F. 2000. Natural developments at Scords Wood, Toy's Hill, Kent since the Great Storm of October 1987.

348. MOUNTFORD, E.P., PAGE, P.A. & PETERKEN, G.F. 2000. Twenty-five years of change in a population of oak saplings in Wistman's Wood, Devon.

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23. KIRBY, K.J. & BUCKLEY, G.P. 1994. Ecological responses to the 1987 Great Storm in the woods of south-east England.

34. KIRBY, K.J. & MORECROFT, K.D. 2000. Long term studies in British woodland (this volume).

JNCC Reports

295. HALL, J.E., KIRBY, K.J. & MORECROFT, M.D. 1999. Minimum intervention woodlands and their use for ecological research in Great Britain.

298. PURDY, K.M. & FERRIS, R. 1999. A pilot study to examine the potential linkage between and applications of multiple woodland datasets: a GIS based approach.

300. BUNCE, R.G.H. & HIRST, N. 2000. Woodland change 1971-1988 in north-west England and south-west Scotland - a trial survey.

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PREFACE

ACKNOWLEDGEMENTS

THE HUMAN ELEMENT IN LONG TERM WOODLAND STUDIES

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Summary

Experience with a number of long-term studies is summarized and key differences between these and short-term research projects are identified. If new studies are to survive to become long-term they must be designed around human limitations, with as much attention paid to archiving and institutional memory as to ecology and research design.

Introduction

Long-term ecological studies are not like ecological research that lasts, say, less than five years (Taylor 1989). Short-term research projects are presented as studies that started with an hypothesis, continued with observations or experiments carefully designed to falsify that hypothesis, reached a conclusion, then stopped. Long-term studies on the other hand last much longer, by definition, tend to proceed by observation and inference, and remain open-ended. Almost invariably, short-term studies remain closely under the control of the initiators, but long-term studies are inevitably subject to the vagaries of changing institutional and personal interests and priorities, and must eventually be relinquished by those who started them.

This paper is based on several studies of change in the composition and structure of unmanaged semi-natural woods in Britain. These include both studies we initiated in the 1980s, and others started decades before by other ecologists (Peterken & Backmeroff 1988). Their survival and achievements have been limited by human failings of various kinds, which are likely to remain a factor even in the modern era of recording and data storage. Recognition of the limitations, however, many help those who design long-term studies in the future.

Woodland processes *v* human time scales

It may be helpful to compare the rate and duration of woodland processes with human spans. Dominant trees, such as oak *Quercus* spp., beech *Fagus sylvatica* and lime *Tilia* spp., may live for 300-500 years. The intervals between major natural disturbances may be decades or centuries. For example, the great storm of 1987 in south-east England was said to be the most severe since 1703. When a managed mixed-deciduous wood is allowed to develop naturally, gap formation may start within decades, but dead wood volumes will probably take 100 years or so to build up to natural levels.

Admittedly, significant changes can take place quickly. For example, mature stands may be levelled by a storm within an hour or so. The colonisation of Monks Wood NNR by muntjac deer *Muntiacus reevesii* resulted in profound changes in stand structure and ground flora composition within a decade (Crampton *et al.* 1998). The 1976 drought in Lady Park Wood killed many beech within a year or two, and stopped the survivors from growing for perhaps 8 years (Peterken & Mountford 1996). Disease killed most adult elm trees *Ulmus glabra* within five years (Peterken & Mountford 1998). However, in all these instances, the consequences of the short-term event could only be appreciated against a background of long-term observations, including records of prior condition and subsequent responses, which may need to be made over periods of at least 20 years.

Contrast woodland processes with human time-spans. Research grants last for about 3 years, and funding for any project rarely lasts longer than 5 years. Ecologists tend to change their jobs every 5-10 years. Even if individuals stay in one job, their interests and priorities tend to change over a decade. A career in ecology lasts for 25-35 years. Even if an individual maintains an interest throughout a career, institutional priorities change, and institutions themselves are regularly re-organised. For example, my own 23-year career as a specialist woodland ecologist for the Government's nature conservation organisation involved working successively for the Nature Conservancy, Natural Environment Research Council, Institute of Terrestrial Ecology, Nature Conservancy Council, English Nature and the Joint Nature Conservation Committee, three changes of location and six changes of office (which is when old records are easily lost), all without once changing the character of my work.

The mis-match between human and woodland timescales extends beyond individuals and institutions. Ecology has only been recognised as a distinct science for about a century. Modern forestry dates back further, but it was rare - but not unknown - for early foresters to record observations that are valuable to ecologists today, eg in Boubinsky Prales (Peterken 1981). Moreover, intellectual fashion changes in decades, or quicker. Any woodland study that has endured for 50 years will have been maintained against a background of loss of confidence in the concept of succession to a stable climax, and the rise in consciousness of the importance of natural disturbances.

How long does it take before studies become 'long-term'?

It is rarely worth re-recording studies of stand change in less than 10 years. Change is usually fairly slow, and errors in tree measurement are large in relation to growth over a few years. However, by 10 years, for example, significant relationships between growth rates and size can be detected, for example at Langley Wood (Mountford *et al.* 1998) and Craigellachie birchwood (Mountford and Peterken, unpublished data). On this basis, a decade is required to measure initial rates and directions of change, and 20 years is needed for a third recording, which allows any changes in rates and direction to be measured.

Even in 20 years, one is 'lucky' to observe a disturbance. At Clairinsh a hurricane passed seven years after the first recording (Backmeroff & Peterken 1989), and in Denny Wood regeneration ceased about a decade after observations started (Mountford *et al.* 1999), but in Lady Park Wood the first substantial events, the elm disease outbreak of about 1971 and the drought of 1976, occurred 26 years and 31 years respectively after the first records (Peterken & Jones 1987). The cessation of regeneration at Denny only became obvious nearly 30 years after recording started. On the basis that over the last 50 years a majority of the woods that I have helped to study have sustained a major event, such as a blowdown, severe drought, disease outbreak or major change in grazing pressure, a long-term study has an even chance of observing a major event in, perhaps, 35-40 years.

A general threshold of 25 years seems appropriate. If a study endures for longer than that, it can reasonably be described as 'long-term'.

How do studies become long-term ?

If any woodland study is to become long-term it must survive at least one transition from initiator to successors. It must achieve this without guaranteed funding, against a background of changing concepts and institutions. It will only do this if:

- the record is understandable by a successor who will probably not have access to the initiator;
- the record itself survives and can be understood;
- someone knows the record survives;
- the study site itself survives in a state that is worth studying; and
- present-day ecologists think the study is worth maintaining and recording.

In other words, if someone is planning to establish a new long-term study, they have to pay attention to (i) recording clearly and completely the methods used, (ii) archiving, (iii) the institutional memory, (iv) site management, and (v) they will also have to record features which have enduring value for their successors.

These points may be obvious, but many potentially long-term studies have failed because one of these conditions was not fulfilled, and those that have survived have been vitiated by partial failures. The history of five studies that had endured for at least 25 years was told by Peterken and Backmeroff (1988), and since then the tale of human failings in these studies has continued, as exemplified by the study in Denny Wood (Mountford *et al.* 1999). Since 1988 the entire original record of the Denny transect (started 1956) was lost when someone moved jobs: fortunately in this instance the record had been copied to another institution. Moreover, it has lately become clear that a recording in the 1970s has been completely lost, and that this would have been extremely valuable for estimating the effect of the 1976 drought. On the other hand, a second transect, which had last been recorded in 1964, was relocated in 1999 after many years of searching. At Wistmans Wood a complete copy of the records (started 1922) was lost within an NCC office, and the archive now survives as a single copy kept in a box in my loft. In the Black Wood of Rannoch one of the five plots initiated in 1948 by the Forestry Commission was accidentally partially 'overprinted' by an exclosure paid for from a research allocation which I controlled. At Lady Park Wood, the value of the 55-year observations is being compromised by excessively high deer populations: what had been a study of near-natural woodland is becoming a study of conversion from high forest to wood-pasture.

One of the key features of records that have survived to be understood and useful is simplicity. Simple measurements of tree presence and size (girth) become valuable in the long-term in much the same way that one pound, invested at average rates of interest, would become extremely valuable within 100-200 years. Elaborate codified observations (eg of canopy stratification) become unintelligible if the code is lost, and useless if successors have no faith in the code. For our studies, we favour transects over random or grids of plots, even though separate plots may be statistically superior, partly because transects are more easily found and reconstructed by successors after a period of apathy, whereas lost plots tend to be lost for ever.

Perception of long-term studies

In addition to the accidents of recording, data storage, etc, two other factors have, I think, made long-term studies unpopular amongst professionals. The results are often perceived as boring, predictable, and answering the questions posed several decades ago, which reduces their scientific status. Even if they are regarded as valuable, patience is required, yet most ecologists want to move on to other interesting topics or into senior management.

The predictability criticism has some force. Thus, after 10 years, the second recordings in Craigellachie, Black Wood of Rannoch, Denny Wood, Glen Tanar, Lady Park Wood and Langley Wood all showed patterns of growth and thinning in undisturbed stands that were entirely predictable. If Wistmans Wood had been recorded again after 10 years, it would hardly have changed at all. Even where a significant change occurred within the first 10 years (eg the invasion of Monks Wood by muntjac), the permanent plot records merely quantified changes that were already obvious.

Nevertheless, with the passage of time and the completion of a third recording, it becomes possible to measure changes in the rates of processes, such as growth or mortality. The chance that a formative event will take place within the period of observation increases with time. Furthermore, as time passes, stands approach old-growth, and the chance that a particular event will have a significant impact will increase. Thus, for example, the incidence of disturbances within the old-growth stands at Lady Park Wood has increased over the 55 years of observation, not because the wood has lately been more closely observed, but because the stand is more mature and vulnerable to disturbance.

Table 1. Significant events in studies lasting more than 35 years, and the time that has elapsed between the start of the study and the time when the event or the impact became obvious

Wistmans Wood (started 1921)	Grazing change and period of regeneration, ended *c*1965 (44 years). Rowan de-barking during prolonged snow cover, 1962/3 (41 years). Heavy snow storm, 1977/8 (56 years). Increasingly vigorous growth, which may or may not reflect climatic change (*c*60 years).
Lady Park Wood (started 1945)	Instability of large trees on slope (2 weeks). Grey squirrel impacts (14 and 38 years). Dutch elm disease (25-30 years). Severe drought (32 years). Late spring snowfall (39 years). Catastrophic vole damage to regeneration (40 years). Impact of excessive fallow deer populations (45 years).
Black Wood of Rannoch (started 1948)	Storm damage (*c*20 years).
Denny Wood (started 1955)	Stress due to wet and dry summers (5 years). Effects of increased grazing/browsing on regeneration (10-20 years). Severe drought (22 years). Grey squirrel damage becomes severe (c25 years). Storm impacts (32 years).
Clairinsh (started 1961)	Hurricane impacts (7 years).

In practice, projects that have survived for 25 years or more have all sustained significant events, none of which were predictable at the outset (Table 1). Yet the impacts of the events have only become apparent many years later, eg the cessation of regeneration in Denny Wood about 1964. Even where the immediate impacts were very obvious, the response of the stand may still not be complete after 20 years (eg beeches in Lady Park Wood are still dying from the 1976 drought in 1999). On the other hand, the impact of the 1968 hurricane at Clairinsh has turned out to be small, though at the time it looked at least locally devastating.

The scientific value of long-term studies has been elaborated elsewhere (Strayer *et al.* 1986). Rare and unpredictable events can be studied, eg the arrival of elm disease in Lady Park Wood (Peterken & Mountford 1998). The significance of short-term phenomena can be seen, eg the four-hour late-April snow-lie that has permanently altered the form of limes in Lady Park Wood and would have increased their rate of vegetative reproduction if deer had not been reaching epidemic proportions. Hypotheses and assumptions can be put to the test. Thus, understandings of long-term ecological change derived from models or chronosequence studies, can be checked against reality. Assumptions of stability can also be tested. Thus, in Lady Park Wood it has been possible to demonstrate the fluctuations in the balance between beech, ash and lime, and thereby to recognise that there is no single 'correct' structure and composition to which this (or any other) woodland reserve should aim.

Scientific standards of long-term studies

Records inherited from the initiators of long-term studies are generally incomplete in some important sense, and they rarely conform to modern design and statistical standards. Analyses are thus often restricted, and editors may not be inclined to make allowances. More fundamentally, long-term studies may be criticised for lacking an hypothesis. This happened to us when we submitted a 50-year study of demographic change in a population of wych elm (Peterken & Mountford 1998). My reply was that I did not know if the initiator had an hypothesis about elm, and that there was no sign that he anticipated the 1970s elm disease outbreak. We could have written the account as if there had been an hypothesis, but that would have misrepresented the study.

An increasing flow of long-term studies indicates that perceptions may be improving. More ecologists seem to appreciate the need to observe what actually happens on the ground, which enables us to test models of development and assumptions about conservation objectives and methods.

Assumptions and experience in the design of long-term studies

Those who today are designing studies that they intend to become long-term will probably assume (i) that clear objectives are required, (ii) that these objectives will be sustained in the long-term to generate predictable research outcomes, (iii) that the design must meet the highest scientific standards, (iv) that detailed records must be made, (v) that regular, frequent recording must be planned and achieved, (vi) therefore, that funding will be regular and predictable, and (vii) that databases must be electronic.

These assumptions can be challenged. Experience from our stand studies shows that objectives will probably change, that outcomes are unpredictable, that simple, practical design layouts may last longer than statistically-correct layouts, that funding is irregular, that regular recording may be less cost-effective than opportunistic recording, and that computer databases may be less durable and accessible than paper records. Clear objectives, correct design and precise plans may be necessary to gain initial approval and funding, but the realistic researcher should see these more as pretexts than predictions

Of course, other kinds of long-term study may be predictable and plannable. Massive undertakings, such as the Hubbard Brook studies (Bormann & Likens 1989), achieve a higher standard of design and record. However, the general experience of other kinds of long-term study is that simplicity is the key, combined with sustained interest by the initiator (Taylor 1989).

A broad view of long-term studies

It is worth recognising that long-term studies may emerge from observations that were not intended to be long-term. Thus, some existing long-term studies started as a single survey, with no intention of repeating the observations. They became long-term because (i) the record survived, (ii) the observations could be relocated on the ground, and (iii) someone was interested in repeating the observations. For example, the plot recorded by Worth in 1921 to describe Wistmans Wood was relocated and re-recorded by Proctor *et al.* (1980) and thus became a long-term study.

Extending this idea, it is worth recognising old photographs as informal long-term studies. Photographs preserve unedited information, which may provide good qualitative information on unforeseen developments. Repeat photographs and sustained fixed-point photography (eg Gruell *et al.* 1982) may afford a greater general appreciation of change than careful, quantitative records.

Organisation of long-term studies

Long-term studies tend to change hands, from initiator to successors, and from one institution to another. For example, the Denny transect has been the responsibility of Southampton University (Botany department), is now largely the responsibility of Ed Mountford and myself, and may soon become the responsibility of Forest Enterprise as part of its monitoring programme for the New Forest. This, however, can lead to problems of "ownership". For example, the plots in the Black Wood of Rannoch, which were started by the Forestry Commission in 1948, were saved by local staff of the Nature Conservancy Council through recording and re-marking in 1984, and extended by new transects established in 1986. In the 1990s, the Forestry Commission resumed interest, but just when Ed Mountford and myself obtained an EU grant under which we would have re-recorded both the plots and the transects. A similar accident has recently happened with a 1961 plot established by the Nature Conservancy in Coed Cymerau NNR.

Clearly, there is a case for some co-ordination. Ideally, perhaps, a single archive should be established as an Ecological Archive Office. Failing that, it would be valuable to establish a clearing-house, which holds information on which projects exist, where the record is held, and who is for the time-being responsible.

The value of an Ecological Archive Office as a simple repository should not be underestimated. Almost every study that has become long-term has survived a period of apathy. This usually happens between the time when the initiator loses interest (say, 10 years), and the time when changes become interesting (say, 25 years). Furthermore, ecologists die, and executors will probably not be ecologists. Even those who appoint specialist executors only half solve the problem. For example, I hold records bequeathed by Eustace Jones (Lady Park Wood and other sites) and Molly Spooner (Wistmans Wood), but the records survive only because I remain interested. I still hold many box files on 1960s records originally made by Richard Steele and others. But for me, they would have been thrown out when he retired as Director-General of NCC in the 1980s. We need somewhere to place material which may be of long-term value.

Conclusions

No doubt this view of long-term studies in woodland is unduly coloured by the particular kind of study with which I have been involved. Perhaps studies of other elements of woodlands, such as invertebrates or physical attributes, can effectively become long-term rather sooner than 25 years. However, even here one must distinguish between short-term fluctuations and long-term trends, and be prepared to observe unexpected changes (eg Likens 1985). If we value long-term observations and wish to increase the chance that new studies will become long-term, we must adopt an approach which is alien to short-term researchers, by (i) designing them around human limitations, and (ii) paying as much attention to archiving and the institutional memory as to ecology and research design.

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LONG-TERM STAND CHANGE IN A NEAR-NATURAL OAKWOOD ON CLAIRINSH ISLAND, SCOTLAND

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Summary

Changes in unmanaged semi-natural stands at Clairinsh were quantified by means of two permanent transects recorded in 1961, 1986 and 1998. The island was treated as coppice-with-standards up until 1913, when it was last felled to leave a shelterwood of mainly oak. The composition of the wood remains strongly influenced by pre-1913 treatment, and, to a lesser extent, by continued control of non-native invasive tree species. Nevertheless, during the past 85 years the wood has developed structures and processes that are typical of natural temperate woodland.

In gaps left after the 1913 felling, regeneration established in which seedlings of shade-intolerant trees, especially birch (*Betula* spp.) and shrub species were common. After the gaps infilled, a period of stem-exclusion prevailed and only a few dominant trees remained vigorous. Losses were high amongst the post-1913 recruits, which became overtopped by the promoted canopy oaks *Quercus* spp. Only a few young birch, oak, ash *Fraxinus excelsior* and alder *Alnus glutinosa* managed to sustain vigorous growth and recruit into the canopy. An understorey re-initiation phase began a few decades after the stand had closed. Below the canopy, shade-tolerant holly *Ilex aquifolium* and rowan *Sorbus aucuparia* developed strongly. By 1998 the pattern of growth, mortality and gap creation had shifted. Most of the surviving dominant oaks had peaked in diameter growth and mortality had decreased, becoming increasingly associated with storm-damage. The canopy had started to open up, but gaps remained too small, scattered and ephemeral, to provide substantial opportunities for the regeneration of new light-demanding trees or shrubs. The potential long-term composition of woodland is discussed.

Introduction

Increasing interest is being shown in long-term monitoring in minimum intervention reserves (Peterken 1996; Parviainen *et al.* 1999). In Great Britain, a national programme of studies on long-term change in unmanaged semi-natural woodland based on permanent transects/plots was initiated in the mid-1980s under the general supervision of Dr. George Peterken of the Nature Conservancy Council (Peterken & Backmeroff 1988). Other long-term woodland monitoring studies have since been formalised or initiated (Hall, Kirby & Morecroft 1999). This paper reports on changes following a third recording in one of these minimum-intervention reserves. It follows on from a recording made in 1986 (Backmeroff & Peterken 1989), and extends the monitoring to almost four decades.

Site details

Clairinsh (national grid reference NS 413 899) is a 6ha island located in the southern part of Loch Lomond, Central Scotland (Backmeroff & Peterken 1989). It is part of the Loch Lomond National Nature Reserve and is maintained by Scottish Natural Heritage.

W11 *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland (Rodwell 1991) covers most of the island, with oak, *Quercus petraea, Q. robur* and hybrids and a few downy birch *Betula pubescens* growing over an understorey of mainly rowan *Sorbus aucuparia*, holly *Ilex aquifolium* and hazel *Corylus avellana*. A marginal low-lying base-rich area to the north-east of the island has much ash *Fraxinus excelsior*, oak and downy birch, growing over a mixed understorey. At the opposite end of the island, another marginal area with base-poor soils has mostly alder *Alnus glutinosa*, birch, and oak, growing over rowan, holly and hazel. These marginal stands correspond to types of W7 *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland, and towards the shoreline they grade into W2 *Salix cinerea-Betula pubescens-Phragmites australis* woodland (Rodwell 1991).

The island lies within a zone naturally dominated by oak woodland (McVean & Ratcliffe 1962; Birks 1988), but has been influenced by human activity for many centuries (Tittensor 1969, 1970; Placido 1986; Backmeroff & Peterken 1989). Parts have been cleared, but there is no evidence of cultivation (Placido 1986). The wood was managed from at least the 17th century, when coppice-with standards treatment prevailed; oak was generally promoted, and several species were planted in. The island was last coppiced in 1913, when the underwood was cut and a shelterwood of oak was left by retaining standard trees and singling the oak stools. The wood has been left unmanaged since, apart from the felling of some non-native trees during 1970-71 (beech *Fagus sylvatica*, larch *Larix* spp. and rhododendron *Rhododendron ponticum*) and in 1998 (western red cedar *Thuja plicata*).

Recording

Ken Wallace working for the Nature Conservancy made the baseline records for Clairinsh. During 1960-2, he made an assessment of the make up and structure of the wood because it exhibited interesting features, such as mixed age composition and continuing natural regeneration, not found in other oakwoods (Wallace 1962). Two transects were established, each 11 yards (10m) wide, and covering 190 yards (174m) and 396 yards (362m) length. Within them all trees and dense holly groves were mapped, and measurements made of stem girths and heights. In addition, three profile diagrams, each covering three sections length, were drawn for three separate parts of the transects, and twenty oaks were aged by taking stem cores.

Christa Backmeroff, working for the Nature Conservancy Council, undertook a second recording of the transects during June 1986 (Backmeroff 1986). To standardise the recording, new 20m-wide transects were recorded following the approximate centre line of the earlier transects. Virtually all the ground covered by the earlier transects was included, and all trees attaining 1.3m height were mapped and girths measured.

All the ground recorded in the 1986 transects was recorded again during April 1998. Trees attaining 1.3m height were mapped. Girths were measured and each stem was allocated to a canopy layer. In addition, canopy gaps, established seedlings, and areas covered by low-growing holly suckers were mapped.

Analysis

Full details of the precise analysis methods and statistical tests applied are available from the author. The data set provided information on 4154 stems. Change was examined in the combined area of the core and marginal stands and within both the Wallace and Backmeroff transects. The core stand dominates the central free-draining higher part the island, whilst the marginal base-rich and base-poor stands respectively occupy adjacent low-lying areas to the north and south. The Wallace transect covered 0.484ha or 9% of the island area, and the Backmeroff transect covered 0.950ha or 18% of the island area. Comparisons were constrained by different thresholds used at each recording. Statistical procedure followed Zar (1984) and tests were carried out using Microsoft Excel Version 7.0a and Statistica Release 4.5 computer packages. Although most individual stems were confidently re-identified, a few errors, omissions, misidentifications, and problems caused by changes in the recording methodology had to be 'adjusted' for.

Results

Stand development before 1961

Backmeroff and Peterken (1989) give details of stand change to 1961. The core and marginal base-poor stands had closed over and remained intact, whereas the marginal base-rich stand had remained somewhat open. The combined stem size-class distribution in 1961 revealed a scatter of larger trees retained in 1913 and abundant regeneration since.

Oaks dominated the canopy in 1961 (Table 1), largely due to the retention of existing oak standards and coppice stools that were either promoted by singling or simply left uncut in 1913. By 1961 most of these were >10m high, >75cm g.b.h., and in the canopy layer.

Most post-1913 recruits were overtopped and shaded by 1961. Oak recruits included both stems from coppice stools and maidens. Virtually all of these were in the understorey, and coppice individuals had thinned to one or a few stems per stool. Oak regeneration was especially poor in the marginal base-rich stand, despite abundant gaps and seed-bearing standards. Recruitment of birch, mostly from seed, was abundant apart from in the marginal base-rich stands. Very few oak and birch recruits had sustained rapid growth and these were associated with larger gaps. Ash recruitment was largely restricted to the marginal base-rich stand. It was most abundant as coppice growth on the open ground immediately above the shoreline, whilst elsewhere only one maiden had developed into a vigorous tree below a gap. Most alder were apparently from coppice stools and most had recruited into the marginal base-poor stand, where a few large individuals had developed into canopy or sub-canopy trees below an original large gap.

By 1961, a shade-tolerant understorey of rowan and holly had established in the core and marginal base-poor stands (Table 1). Most individuals were small and appeared have recently seeded in under the closed canopy, but a few may have been coppiced or retained in 1913. Hazel formed a minor part of the understorey as scattered individuals and aggregated groups. Several large individuals that appeared to be coppice from 1913 remained in reasonable vigour, but others shaded by oak standards were in decline. A few small individuals may have been recent recruits. In contrast the more open-canopied marginal base-rich stand had a diverse shrub layer. These, ranked in abundance, were hawthorn *Crataegus monogyna*, rose *Rosa* spp., broom *Sarathamnus scoparius*, blackthorn *Prunus spinosa*, guelder rose *Viburnum opulus*, hazel, and rowan. These helped infill some of the gaps in the main stand and formed a low-growing scrub with the ash coppice stools on the ground immediately above the shoreline.

Table 1: Density and basal area of large and small individuals in the core and marginal stands in 1961, 1986 and 1998. In the Wallace transect large individuals had the largest stem ≥0cm g.b.h., small individuals had the largest stem <10cm g.b.h. in 1961 and 5-9.5cm g.b.h. in 1986 and 1998; and basal area was based on large individuals and only the largest stem on multi-stemmed individuals. In the Backmeroff transect large individuals had the largest stem ≥10cm g.b.h., small individuals had the largest stem <10cm g.b.h., and basal area was based on all stems ≥5cm g.b.h.

	Large individuals (n ha $^{-1}$)					**Small individuals (n ha $^{-1}$)**					**Basal area (m^2 ha $^{-1}$)**				
	Wallace transect			**Backmeroff transect**		**Wallace transect**			**Backmeroff transect**		**Wallace transect**			**Backmeroff transect**	
	1961	**1986**	**1998**	**1986**	**1998**	**1961**	**1986**	**1998**	**1986**	**1998**	**1961**	**1986**	**1998**	**1986**	**1998**
Oak	227	190	178	178	163	10	12	4	11	4	17.9	23.5	25.6	22.5	24.0
Birch	207	122	101	157	131	33	12	6	14	7	2.1	2.0	2.1	2.5	2.6
Rowan	140	211	227	194	194	110	81	50	72	59	0.6	1.0	1.4	1.5	1.8
Hazel	76	33	39	31	39	31	41	48	93	96	0.2	0.1	0.1	0.3	0.4
Holly	72	322	364	310	350	233	244	186	256	233	0.5	1.4	2.1	2.0	3.0
Ash	37	31	31	31	29	2	4	-	4	-	0.7	0.4	0.5	0.6	0.7
Alder	33	21	12	16	12	-	2	-	1	-	0.5	0.5	0.3	0.6	0.5
Hawthorn	14	17	10	13	12	4	2	2	11	6	0.2	0.1	<0.1	0.2	0.1
Beech	2	2	2	2	2	-	-	2	-	3	<0.1	<0.1	<0.1	<0.1	<0.1
Blackthorn	2	12	19	21	25	8	10	19	75	83	<0.1	<0.1	<0.1	0.1	0.1
Larch	2	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
Pine	2	2	2	1	1	-	-	-	-	-	0.1	0.3	0.5	0.2	0.2
Yew	-	6	6	8	9	6	-	4	2	4	-	<0.1	0.1	<0.1	0.1
Cedar	-	2	2	1	1	-	-	-	-	-	-	<0.1	<0.1	<0.1	<0.1
Guelder rose	-	2	-	1	-	10	-	4	9	22	-	<0.1	-	<0.1	<0.1
Rose	-	-	2	-	1	14	10	19	25	20	-	-<0.1	<0.1	<0.1	<0.1
Crab apple	-	-	-	2	2	-	-	-	-	-	-	-	-	<0.1	<0.1
Willow	-	-	-	1	-	-	-	-	-	-	-	-	-	<0.1	-
Bird cherry	-	-	-	-	-	-	-	-	2	2	-	-	-	<0.1	<0.1
Broom	-	-	-	-	-	25	2	-	2	9	-	-	-	<0.1	-
Total	769	930	950	928	936	473	409	320	490	444	23.1	29.3	32.7	30.4	33.5

Table 2: Mortality, reduction and recruitment of large individuals in the core and marginal stands between 1961-86 and 1986-98. Large individuals had the largest stem ≥10cm g.b.h.

	Wallace transect										**Backmeroff transect**			
	1961		**1961-86**		**1986**	**1986-98**					**1986**	**1986-98**		
	No. alive	**No. died**	**No. reduced to <10cm g.b.h.**	**No. recruited & <10cm g.b.h. or not recorded in 1961**	**No. alive**	**No. died**	**No. reduced to <10cm g.b.h.**	**No. recruited & ≥ 10cm g.b.h. in 1961 & <10cm g.b.h. in 1986**	**No. recruited & <10cm g.b.h. in 1961 & 1986**	**No. recruited & <10cm g.b.h. or not recorded in 1986**	**No. alive**	**No. died**	**No. reduced to <10cm g.b.h.**	**No. recruited & <10cm g.b.h. or not recorded in 1986**
Oak	110	21	-	3	92	6	-	-	-	-	169	13	-	-
Birch	100	44	2	5	59	10	-	-	-	-	149	25	-	-
Rowan	68	10	2	46	102	1	3	-	8	4	184	11	4	15
Hazel	37	14	10	3	16	1	1	3	2	-	29	1	2	11
Holly	35	1	1	123	156	3	6	-	3	26	294	5	6	49
Ash	18	3	-	-	15	1	-	-	-	1	29	3	-	2
Alder	16	5	1	-	10	4	-	-	-	-	15	4	-	-
Hawthorn	7	2	-	2	7	3	-	-	-	-	1	4	-	4
Beech	1	1	-	1	1	-	-	-	-	-	2	-	-	-
Larch	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Pine	1	-	-	-	1	-	-	-	-	-	1	-	-	-
Blackthorn	1	-	1	6	6	-	1	-	-	4	20	3	1	8
Yew	-	-	-	3	3	-	-	-	-	-	8	-	-	1
Crab apple	-	-	-	1	1	1	-	-	-	-	3	1	-	-
Cedar	-	-	-	1	1	-	-	-	-	-	1	-	-	-
Rose	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Guelder rose	-	-	-	1	1	-	1	-	-	-	1	-	1	-
Willow	-	-	-	-	-	-	-	-	-	-	1	1	-	-
Total	395	102	17	195	471	30	12	3	14	36	917	72	14	91

Table 3: Mortality, growth and recruitment of small individuals in the core and marginal stands between 1961-86 and 1986-98. Small individuals in the Wallace transect had the largest stem <10cm g.b.h. in 1961 and 5-9.5cm g.b.h. in 1986 and 1998. Small individuals in the Backmeroff transect had the largest stem <10cm g.b.h.

	Wallace transect												**Backmeroff transect**				
	1961	**1961-86**					**1986**	**1986-98**					**1986**	**1986-98**			
	No. alive	**No. died**	**No. grown to ≥ 10cm g.b.h.**	**No. reduced to <5cm g.b.h.**	**No recruited & ≤10cm g.b.h. in 1961**	**No. recruited & <5cm g.b.h. or not recorded in 1961**	**No. alive**	**No. died**	**No. grown to ≥10cm g.b.h.**	**No. reduced to <5cm g.b.h.**	**No. recruited & ≥10cm g.b.h. in 1986**	**No. recruited & <5cm g.b.h. or not recorded in 1986**	**No. alive**	**No. died**	**No. grown to ≥10cm g.b.h.**	**No. recruited & ≥10cm g.b.h. in 1986**	**No. recruited & not recorded in 1986**
Holly	113	1	102	1	1	108	118	19	29	-	5	2	243	32	49	6	54
Rowan	53	4	30	0	1	19	49	4	12	1	2	-	68	15	15	4	14
Hazel	18	2	3	5	8	6	22	1	5	2	1	9	88	15	11	2	27
Birch	16	9	5	-	2	3	7	4	-	-	-	1	13	7	-	-	1
Broom	12	10	-	1	-	-	1	1	-	-	-	4	2	2	-	-	0
Rose	7	3	-	-	-	1	5	-	1	-	-	5	24	12	1	-	8
Oak	5	3	2	-	-	6	6	4	-	-	-	-	1-	6	-	-	-
Guelder rose	5	5	-	-	-	-	-	-	-	-	1	1	9	4	-	1	15
Blackthorn	4	1	2	-	1	3	5	-	2	-	1	5	71	18	7	1	32
Yew	3	-	3	-	-	-	-	-	-	-	-	2	2	-	1	-	2
Ash	2	2	-	-	-	2	2	1	1	-	-	-	4	2	2	-	-
Hawthorn	2	-	2	-	-	1	1		1	-	-	1	10	2	4	-	2
Alder	-	-	-	-	-	-	1	1	-	-	-	-	1	1	-	-	-
Beech	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	2
Bird cherry	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Total	240	40	149	7	14	149	207	35	51	3	10	51	547	116	90	15	166

Stand development from 1961 to 1998

Tables 2 and 3 show the number and basal area of large and small individuals in the core and marginal stands in 1961, 1986 and 1998. Stand development generally matched that reconstructed for the previous half century, and mostly reflected continued undisturbed growth. There was a substantial increase in basal area to 33.5m^2 ha^{-1}, an increase in large individuals, but a decline in small individuals. Some canopy disturbance did occur and canopy gaps covered 19% of transect area in 1998. Gaps were mostly limited in extent and had been caused by windthrow (from a hurricane in 1968), branch snap, and crown deterioration of canopy oaks. The marginal base-rich stand had most canopy gaps at 32% of the transect area because, in addition to windthrown and windsnapped canopy trees, some areas had failed to close over since the 1913 fellings.

Oak remained dominant throughout as its basal area steadily increased. Recruitment was very limited. Large oak individuals suffered low mortality (m = 0.6-0.8% yr^{-1} over the two periods in the two transects), but small post-1913 recruits suffered higher loss. Most mortality was linked to the exclusion of smaller-girth trees, while storms killed and damaged several of the other larger oaks. Three died after been windthrown in a hurricane in 1968, and another was windsnapped during the 1986-98 period. Records of other trees windblown in 1968 showed that the western side of the island suffered most (Figure 2 in Backmeroff and Peterken 1989), and that only a very few trees survived the fall and remained alive in 1998. Otherwise, a few dominant trees in the core woodland appeared to have deteriorated for no clear reason.

Based on observations of surviving trees made in 1998, many oaks suffered crown damage during the hurricane and in later storms. This ranged from major crown snapping to minor branch loss, and the consequent damage to understorey stems hit by falling trees and debris. In total 32 out of 126 canopy trees had some damage recorded. A few trees had or were replacing lost crown through sprout growth, the most vigorous of which came from directly below break points.

Surviving oaks grew at very different rates. Trees that ended up overtopped in the understorey and sub-canopy layers grew significantly less (average = 0.190 cm g.b.h. yr^{-1}) than canopy trees (average = 0.775 cm g.b.h. yr^{-1}) (ANOVA F = 31.4, $p<0.001$). The overtopped trees included most of the small-girth post-1913 recruits, but a few of these maintained above average growth and grew into the canopy layer; one, which was located below a large gap in the marginal base-rich stand in 1961, was the fastest-growing individual throughout.

Birches declined overall, despite a slight increase in basal area. Recruitment was minimal, although a few saplings developed in large gaps created by the 1968 hurricane. The density of both large and small individuals fell, as the post-1913 recruits thinned heavily. Mortality of large individuals was relatively high (m = 1.6-2.3% yr^{-1} over the two periods in the two transects), but the population of small suppressed individuals suffered even more (m = 3.3-7.1% yr^{-1}). Most losses were linked to exclusion by dominant trees, but storm-damage killed two out of three larger-girth trees, with the 1968 hurricane throwing a 132cm g.b.h. tree over, and a 64 cm g.b.h. tree recorded as dead in 1986 had had its top snapped off. Only a few surviving trees had suffered storm-related damage.

Growth of surviving birch was very variable, but most surviving canopy trees grew at least moderately. Most of the small-girth post-1913 recruits, which had become overtopped in the understorey and sub-canopy by 1998, grew slowly. Nevertheless, a few of these maintained above average growth and grew into the canopy. Several overtopped trees showed signs of growth release following the creation of gaps in the overstorey, although girth growth in these remained far below that of most canopy trees

Ash survived only in the marginal base-rich stand. The surviving post-1913 ash recruits remained moderately abundant and, despite the loss of the large standard that died standing and fell with its roots rotted by 1987, basal area increased. Alder was scarce in the core and marginal base-rich stands and declined to very low levels, and even in the marginal base-poor stand, where it had been most abundant, it declined greatly. Exclusion was the main cause of loss.

During 1961-98, rowan continued to develop strongly in the core stand, moderately in the marginal base-poor stands, but remained sparse in the marginal base-rich stand. Recruitment of slow-growing small seedlings far exceeded mortality which was low, especially for large individuals ($m<0.6\%$ yr^{-1} over the two periods in the two transects). Many of the 40 individuals that died were apparently excluded, but a substantial number were hit by canopy debris or falling trees, and the largest tree to die was windthrown in the 1968 hurricane.

Holly continued to develop strongly in the understorey in the core and marginal base-poor stands, but by 1998 only a single small individual had recruited into the marginal base-rich stand. The sudden increase in numbers between 1961-86 was probably partly because the 1961 population was underestimated. In addition there was low mortality of large individuals ($m<0.2\%$ yr^{-1} over the two periods in the two transects), slow growth of small individuals, and steady recruitment of new individuals.

Hazel remained a minor understorey species in the core and marginal base-poor stands. Large individuals declined greatly before 1986 mainly due to shading: mortality was high ($m = 1.9\%$ yr^{-1}) and on survivors, especially those with large girth stems, there was a reduction in the total number of live stems. After this the population stabilised as mortality and reduction dropped, and several small individuals grew on. The population remained dominated by small-sized individuals with a high turnover, but several stools appeared to be growing reasonably well in 1998 below the broken canopy and almost 50 new subsidiary stems had grown to ≥5cm g.b.h. during 1986-98. In contrast, hazels in the marginal base-rich stand developed and remained abundant. No individuals died, a few new seedlings recruited, and some exceptionally large stools developed.

In the core stand nine other minor species were recorded. Larch and beech were felled as exotic trees, but the single Scots pine *Pinus sylvestris* was retained. By 1986 two nearby beech had grown vigorously to replace a felled beech, and by 1996 two beech saplings had established elsewhere. Yews *Taxus baccata* formed a minor but persistent part of the understorey and some recruitment after 1986 increased them. A few hawthorn, crab apple *Malus sylvestris* and new brooms were present in 1998, but rose had died out. In the marginal base-poor stand, hawthorn and guelder rose died out, but a single vigorous beech sapling recruited.

In the marginal base-rich stand shrub species remained prominent. Blackthorn increased to become the most numerous species, forming a weak understorey below gaps in the main stand. Rose remained abundant as a climber or lateral sprawler growing in the stands immediately above the shoreline. Guelder rose became quite abundant, but hawthorn declined slightly. Otherwise, a few crab apple, bird cherry *Prunus padus* and new broom were present in 1998. A western red cedar that recruited and grew vigorously was felled just after the 1998 recording.

Discussion

The three detailed recordings at Clairinsh provide a basis to reconstruct past-stand change, and to extrapolate to longer-term changes in such mesotrophic oak woodland.

In general the patterns of natural stand development parallel those described by Oliver (1981) and Oliver and Larson (1996) for North American temperate forests. In the gaps left after 1913, a wave of regeneration established with shade-intolerant trees, especially birch and shrub species, common. Once the gaps filled, a period of stem-exclusion prevailed. The most vigorous trees survived and grew on to increase the stand basal area, whilst the weakest were thinned out. Losses were highest amongst the post-1913 recruits that soon became overtopped by the promoted canopy oaks. Nevertheless, a few birch, oak, ash and alder recruits managed to sustain vigorous growth and grew into the canopy. An understorey re-initiation phase began a few decades after the stand had closed: shade-tolerant holly and rowan, and a few yew developed strongly below the 10-20m high canopy layer of semi-mature oaks, although the overall distribution was distinctly patchy and most strongly developed in the core woodland. These episodes of gap-phase regeneration and understorey re-initiation increased the age-structure of the wood and produced a quasi-negative exponential size-distribution, typical of continuously regenerating woodland (Peterken 1996).

By 1998 the stands had entered the old-growth phase of forest development. Basal area levels had reached levels comparable to natural old-growth ranges of 25-35m^2 ha^{-1} (Parker 1989) and 21-42m^2 ha^{-1} (Martin 1992) for North American and 37m^2 ha^{-1} in stands in central Europe (Falinski 1986). Large trees had become more frequent (7% of oaks attained 200cm g.b.h.), and, moreover, the pattern of growth, mortality and gap creation had shifted. The surviving dominant old oaks appeared to have peaked in diameter growth at about 100cm g.b.h., and thereafter had grown at a much reduced rate in old-age. Instead of high mortality rates caused primarily by competition between individual trees, mortality had dropped and canopy trees had become increasingly affected by storm-damage and, to a lesser extent, unidentified physiological disorders, reflecting; (i) reduced competition between the crowns of dominant trees that become less vigorous in old-age (Oliver & Larson 1996); and (ii) increased susceptibility of large-sized, ageing trees to physical damage and physiological disorders (Mueller-Dombois 1986, 1987; Franklin *et al.* 1987).

Gap creation has remained relatively small-scale and moderately episodic. The loss of a few dominant canopy trees has created openings up to 0.02ha, mostly following an intense gap creation episode when a hurricane struck in 1968, but this has been followed by gradual, more-or-less annual, small-scale crown loss. Although marginal oak crowns have been generally slow to expand into gaps, several damaged trees have reformed crowns by producing vigorous epicormic shoots from below the breakage points. Light conditions below gaps have been further moderated by the presence of sub-gap growth in the form of suppressed trees, shade-tolerant understorey shrubs, and, rarely, toppled trees that have survived and developed new low-growing crowns. Although the patchy break-up of the canopy has increased the structural diversity of the main stands, it has yet to provide substantial opportunities for the regeneration of new shade-intolerant trees or shrubs. So far just one recorded group of birch and rowan saplings has grown well on the root mound of an oak toppled in the 1968 hurricane. Indeed, despite uprooting several large canopy trees, this last event has surprisingly had only a limited effect on the composition of the wood.

Despite the elimination of light-demanding shrubs from most of core and marginal base-poor stands, this layer has been conserved at the northern-end of the island in the marginal base-rich and associated shoreline shingle stands. Here, the stand has remained relatively open and well-lit. Large oaks are less abundant and the stands close to the shoreline are low-growing and composed mainly of light-crowned ash. Rather than advancing towards old-growth, these stands have tended to perpetuate themselves as young-growth and as such have remained the focus of tree and shrub diversity on the island.

The future structure and composition of Clairinsh

Predicting long-term stand change in natural woodland is problematic, not least at Clairinsh because the present stands are not even one generation removed from past-management. In addition natural woodland is subject to unpredictable disturbance events that can profoundly alter the course of stand development (e.g. Peterken & Mountford 1996).

At Clairinsh, the main form of natural disturbance has been storms. Damaging storms are a regular periodic occurrence across Scotland (Andersen 1953; Allen 1992), but they are rarely widespread catastrophic events and result mostly in localised damage (Andersen 1953; Steven & Carlisle 1959; Peterken & Stace 1989; Peterken 1996). The January 1968 storm caused far more damage to the neighbouring island of Inchcailloch (unpublished data), whereas Clairinsh appears to have escaped with little damage both from this and from severe storms in the early 1950s (Andersen 1953). Other disturbances, caused by boat visitors and reserve management, have had minor effects on the stand and promoted no unexpected regeneration.

Assuming this type of disturbance regime continues, and that the island remains free of grazing (it is naturally isolated against livestock and deer grazing, with only a few red deer seen swimming out in temporary stopovers), it is possible to broadly outline the likely future composition.

In the short-term oak looks set to remain dominant for many more decades: the canopy trees have the potential to live for several centuries (Jones 1959) and some have been able to redevelop lost crown from epicormic growth. Until the next catastrophic storm occurs, further gradual break-up of the oak canopy is likely, as the ageing oaks continue to suffer storm-damage and become less able to refill the gaps. Opportunities for regeneration appear to depend on the scale of the next catastrophic storm: oak is most likely to require large-scale openings for regeneration, with vegetative stump and trunk resprouting likely to form an important part of this (e.g. Thomas *et al.* 1994; unpublished data from Toy's Hill, Kent).

The shade-tolerant holly, rowan and yew understorey should continue to develop below the oak canopy. Further gradual canopy break-up should further release rowan and holly and encourage the growth of hazel in the understorey. Such development will reduce opportunities for gap-phase regeneration of birch, oak, and other shade-intolerant species.

Birch looks set to continue to decline as suppressed trees are excluded and larger canopy trees reach natural maturity (Harding 1981). Nevertheless, a few younger trees appear able to sustain themselves in the old-growth stands, being released into growth below small canopy openings, an attribute more often associated with shade-tolerant trees (Emborg 1998). Despite birch having regenerated best at Clairinsh in large-scale openings, a little regeneration did occur in windthrow gaps created in 1968. Birch therefore looks able to survive at low levels for many decades, and when the next catastrophic storm occurs it could form a major part of the seedling regeneration.

Long-term survival of more light-demanding trees and shrubs is most likely in the northern parts of the marginal base-rich and shoreline stands where the structure is more open and the soils are more suitable for their growth.

It appears that, without direct control, beech would infiltrate the woodland: it has, albeit in low numbers, seeded and grown into canopy trees in the core woodland and, beyond the transects, established a population of pole-sized trees at the southern-most end of the island. Similarly, sycamore appears capable of such infiltration: it presently occurs as scattered trees and suppressed saplings around the shoreline, but in the northern-most part of the marginal base-rich stand there are several vigorous saplings in open areas to the east of the permanent transect.

These findings concur with the summary given by Backmeroff and Peterken (1989) who considered that; (i) birch and oak would eventually decline to small populations; (ii) holly, rowan and yew and perhaps hazel would become more abundant in shade-tolerant understorey layer; (iii) alder would become a minor component in the marginal woodland; and (iv) beech and sycamore would spread and might become dominant unless controlled by felling.

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LONG TERM STRUCTURE AND VEGETATION CHANGES IN A NATIVE PINEWOOD RESERVE IN NORTHERN SCOTLAND

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Summary

Long term changes in stand structure and vegetation composition were studied in four large permanent plots in the Black Wood of Rannoch, a native pinewood in Northern Scotland. *Pteridium aquilinum* and *Juncus* spp. were recorded in fewer quadrats in 1993 than in 1948. *Vaccinium* spp increased in abundance in one plot, but decreased significantly in all other plots. No major changes were observed in the abundance of *Calluna vulgaris*. Tree recruitment was greater than mortality when averaged over all plots for the 45 year study period. Light levels between plots suggest some have more, or larger, canopy gaps than others. The changes in vegetation abundance and increased tree recruitment may reflect recovery of the pinewood after wartime fellings.

Introduction

The Black Wood of Rannoch is a native Scots pine reserve of 800 ha situated on the southern shores of Loch Rannoch in the Tummel Valley, Perthshire (OS Grid ref: NN 570560). It has a northerly aspect and mean elevation of 250m ASL. Mean annual precipitation is 1300mm yr^{-1} with an accumulated temperature of 1110-875 day-degrees above 5°C. Basic geology is undifferentiated gneisses and schists of Dalradian series, with deep layers of glacial drift material and granite erratics. Soils are predominately podsols on morainic knolls with poorly flushed peaty gleys between the knolls.

Plot History

Ownership of the Black Wood has changed periodically down through the centuries with fellings and disturbance occurring regularly from the seventeenth century. Whayman (1953), Steven and Carlisle (1959) and Arkle and Nixon (1996) have described how former owners systematically felled and removed many trees and allowed overgrazing by domestic and feral stock (principally sheep and deer), preventing natural regeneration. The Black Wood of Rannoch has predominately been a deer forest, although it has been fenced on occasion to keep deer out as well as in. In 1940/41 the Canadian Forestry Corps carried out an extensive felling programme, cutting over much of the wood in the area, removing only the best trees and leaving very small or rough trees (Wonders 1996).

Acquisition of the Black Wood of Rannoch in 1946 (Forest Enterprise 1995) presented the Forestry Commission with a unique opportunity to monitor long term changes in a native pinewood, under conditions of 'non-intervention' management after a period of disturbance and disruption. It was proposed to study and describe the regeneration process in seven permanent plots, located in areas of the wood where the vegetation community was typified by different vegetation species or species mix. Each plot was approximately 0.81 ha in area. Centuries of mismanagement and exploitation however, had left the Black Wood of Rannoch in a moribund and degenerate state. Some authors argued there was inadequate regeneration (Peterken & Stace

1987) and some foresters thought the wood was not capable of regenerating or returning to a natural state again (Brown 1956).

This paper presents results from monitoring changes in vegetation and stand structure over a 45-year period. Interpretation of the changes over the monitoring period is also discussed, and some of the problems encountered with long term monitoring schemes identified.

Methods

Of the seven original unfenced plots established in 1947 only four remain today (Plots 4, 5, 6 and 7). Plots 1-3 were located outwith the native reserve and were converted to plantation in 1956 (Arkle & Nixon 1996). The remaining four plots were assessed in 1948, 1956, 1983/4 and 1993/94 when broad vegetational changes and tree and seedling establishment or mortality were recorded. Several events have disrupted three of the four plots since establishment. An experiment was established over part of plot 5 in 1949, and an area of 0.25 ha fenced. A fence was also erected in part of plot 6 in 1972 as part of an ITE experiment. An electricity power line was located in plot 7 in the same year resulting in all trees under the line and 30 m either side of it being felled. Both events precluded further data recording in 0.17 ha and 0.25 ha respectively from plots 6 and 7. In all assessments and analyses, these areas have been omitted, unless stated otherwise.

Vegetation mapping

Vegetation was mapped on four occasions in each plot; in 1948, 1956 1984 and 1993. The initial mapping was completed by T. C. Mitchell in late 1948 using a Forestry Commission system that combined five main species in thirty different ways according to their dominance or frequency. The main species identified were *Calluna vulgaris* (L.) Hull., *Pteridium aquilinum* (L.) Kuhn., *Molinia caerulea* (L.) Moench., *Vaccinium vitis-idaea* L. and *V myrtillus* L., *Juncus acutiflorus* Ehrh. Ex Hoffm. and *J. conglomeratus* L. In August 1956, D.W. Henman used three levels of association (dominant, sub-dominant, subsidiary) to combine the dominant species representative of each of the five vegetation types identified in 1948. Although these three levels of association did not correspond to any accepted scale of ecological vegetation description at the time, they did allow associations of up to three species to be distinguished and recorded in map form. The 1948 maps were retraced and converted to the new scheme for continuity in 1960.

A period of 27 years passed before the plots were re-mapped in 1984 by students supervised by G.F. Peterken and H. Stace, using the same system of species dominants devised by Henman. Accurate re-location of outer plot boundaries proved difficult where marker posts had rotted and decomposed. Staff and students from Forest Research completed the most recent mapping in 1993. For the purposes of this paper, only the change between 1948 and 1993 was analysed. It has been assumed any change in vegetation frequency between these dates would reflect plot differences due to structural changes over the same period.

For each plot in 1948 and 1993 a grid system was superimposed on to each map, using tracing paper marked out in 180 quadrats. Each vegetation species was recorded as present or absent. This gave a frequency abundance value for all species. These data were then analysed using a chi-squared distribution to compare predicted change with actual change recorded.

Structural changes

The location and species of trees within each plot were marked during 1948 and 1956 using an internal grid system to estimate where the position of each tree was in relation to its neighbour. Peterken and Stace (1987) collected tree position and seedling and sapling location during a repeat exercise in 1984. In 1994, Forest Research re-surveyed all four plots. Tree height, diameter at breast height (dbh), crown depth and crown width in two directions were recorded. Trees >10 cm dbh were aged by taking increment cores. All tree positions were accurately recorded using a theodolite and standard survey techniques. Seedling (<10 cm dbh, <1.3 m in height) positions and species were also recorded.

Each plot map was scrutinised by grid square and trees identified as present, dead or missing, or as new recruits since the previous mapping exercise. The accurate re-location of every individual tree proved difficult. Many discrepancies arose, and mistakes between mapping exercises became clear when all four sets of data were analysed. Mortality and recruitment rates were calculated for each plot for both pine and birch. In cases where it was not possible to rectify discrepancies using available data, the simplest explanation for change using the least number of arguments or assumptions was used.

Light transmittance

A hand held one-metre long ceptometer, the SunScan from Delta T, was used to measure Photosynthetically-active Photon Flux Density (PPFD) (shortwave radiation in 400 -700nm range, expressed in μmol m^{-2} s^{-1}), at sample points located systematically on a 10m x 10m grid system under each permanent plot. At each sample point a mean of 64 light measurements along the one-metre length were recorded. Each value was compared with an above canopy reference value and expressed as the percentage of available above canopy light transmitted through the canopy.

Results

Vegetation

In all four plots *Juncus* spp. and *P. aquilinum* in plots 5, 6 and 7 were recorded in fewer quadrats in 1993 than in 1948. This change was significant for *Juncus* spp in all plots, and for plots 5 and 6 for *P. aquilinum* (p<0.001) (Table 1).

Table 1. Percentage abundance of plant species mapped in 1948 and 1993 in the Black Wood of Rannoch. Values indicate the percentage of quadrats in which each species was recorded. Changes in abundance are not significant unless indicated by * = P<0.05, **= P<0.01, ***= P<0.001

	Plot 4		Plot 5		Plot 6		Plot 7	
Species	**1948**	**1993**	**1948**	**1993**	**1948**	**1993**	**1948**	**1993**
P. aquilinum	10.6	11.7	97.1	74.6***	99.3	33.8***	20	17.6
C. vulgaris	100	100	96.4	93.5	99.3	98	86.4	99.2***
M. caerulea	28.3	21.7	4.3	2.2	10.6	1.3***	-	27.2***
V. *myrtillus* & *V. vitis-idaea*	78.9	88.9**	99.3	81.2***	99.3	78.8***	67.2	48.8**
J. acutiflorus & *J. conglomeratus*	28.9	3.3***	4.3	0.0*	9.9	0.0***	56	26.4***
Grasses	0.0	1.1	-	-	-	-	-	-

In both plots 5 and 6, all species were recorded with lower abundance in 1993 than 1948. This was significant in plot 6 for *P. aquilinum*, *M. caerulea*, *Vaccinium*, spp. and *Juncus* spp. (all $P<0.001$) but not for *C. vulgaris*. The abundance of *C. vulgaris* did not change significantly between recording intervals in plots 4,5, & 6 but increased significantly in plot 7 ($P<0.001$). *Vaccinium* spp increased in abundance in plot 4 ($P<0.001$) between recording intervals, but decreased significantly in all other plots.

Structure

Plot 4 had the highest basal area and mean tree age of all plots (Table 2), and was the only plot where mortality rates were higher than recruitment (Table 4). In general, recruitment of both Scots pine and birch exceeded mortality between successive assessments (Figure 1), resulting in substantial increases in tree population size since 1948. There are substantial quantities of new seedlings recorded in all plots (Table 3) which represent a large potential population of new cohorts.

Table 2. Tree species data from the four permanent assessment plots in the Black Wood of Rannoch (excluding areas disturbed by fences and power lines).

	N° Scots pine trees in 1994 (>1.3 m ht; >0.10 cm dbh)	Basal Area (m^2 ha^{-1}) all spp	Mean tree		Age range
			Ht (m)	Age	
Plot 4	130	27.3	15.7	119	23-263
Plot 5	58	21.2	14.4	80	13-204
Plot 6	81	14.9	11.0	37	9-140
Plot 7	114	25.7	14.3	57	14-153

Note:
1. Basal area calculation includes birch, rowan and pine trees.
2. Age is at 1.0 m ht above ground level.

Table 3. Total number of tree seedlings (<1.3 m height) recorded in all plots, 1994. (Plot areas adjusted to exclude fenced enclosures but not disturbed area in plot 7).

Species	Number	Density (ha^{-1})
Pine	427	150
Birch	50	17.6
Rowan	11	3.9
Willow	3	1

Table 4. Recruitment and mortality rates expressed as numbers per hectare per year for the 45-year period between 1948 and 1994. A positive difference indicates that recruitment is exceeding mortality.

	Plot 4	Plot 5	Plot 6	Plot 7
Recruitment (SP and Birch)	0.87	2.00	3.52	3.28
Mortality (SP and Birch)	1.13	1.21	1.29	0.67
Difference	-0.26	0.79	2.23	2.61

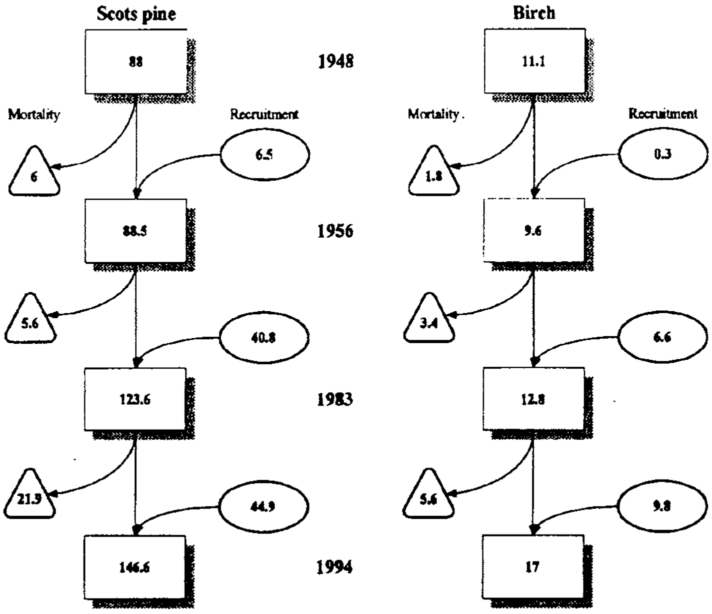

Figure 1. Mortality and recruitment rates for Scots pine and birch in all plots (1948-1994). Values indicate mean number of trees ha^{-1} present on each assessment date, and the mortality and recruitment rates between each successive assessment date.

Light transmittance

Mean values of percentage transmitted light under canopy relative to above canopy light levels, are lower in plot 4 (28.8%) than plot 5 (37.6%) or plot 6 (40.8%), although these differences are not statistically significant (Figure 2).

Discussion

Few native pinewoods in northern Scotland have the classic J-curve distribution of tree ages expected of forests with constant recruitment and mortality (Oliver & Larson 1996). Many show group recruitment after disturbance events (Goucher & Nixon 1996; Parker & Peet 1984). The four plots in this study are no exception (Figure 3); they indicate punctuated small-scale gap recruitment probably as a result of past management interventions. Typically this is identified in the age distribution by high frequency of trees in some classes and very low frequency in others.

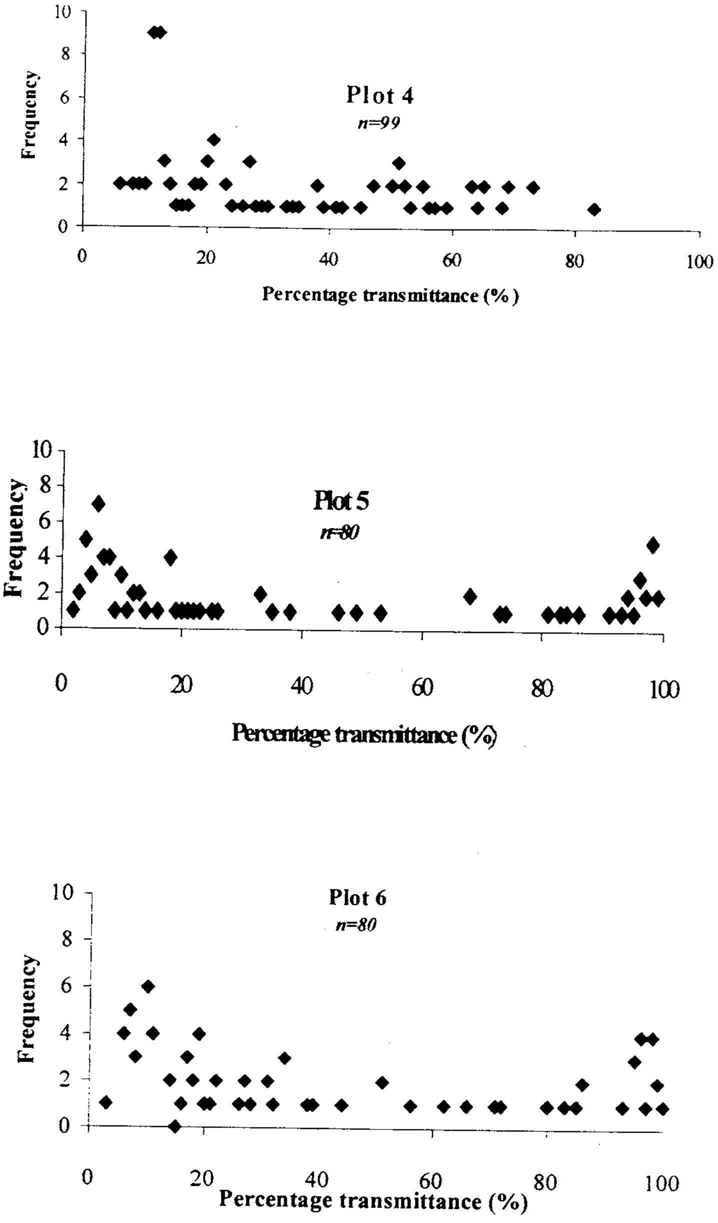

Figure 2. Light transmittance frequency scatter plot for three permanent plots in the Black Wood of Rannoch. Values indicate the percentage of light above the canopy that is transmitted to beneath the canopy. Low transmittance values are associated with increasing canopy cover.

In plots 5, 6 and 7 tree recruitment is exceeding mortality. As a consequence there is a higher frequency of individuals in the youngest age classes. Recruitment is probably occurring because stands are recovering from disturbance during felling operations in the period 1940-1942. Either advance regeneration was released by the felling operation, or new seedling germination occurred, or both. Many individuals assessed in 1994 were <20 years old and substantial numbers of seedlings, too small to accurately age, were also present, although the disturbance event occurred 50 years earlier. Either seedlings require this length of time to grow to 10 cm dbh, or there was a delay following felling before conditions under the stand became suitable for recruitment. In parts of the Black Wood reserve, seedlings have taken an average 16 years to reach 1 m height in good growing conditions (Edwards unpublished) it is conceivable they would take considerably longer under less favourable conditions.

After the 1956 assessment, Brown (1956) gave a gloomy prediction for the pine wood, which was not producing many new seedlings and still looked moribund and degenerate. Recruitment and mortality data for each interval between assessments suggests that not until after the 1956 assessment is there a substantial increase in recruitment. Seedfall patterns in the late 50s to early 60s indicate substantial seed production was occurring in the plots (McIntosh & Henman 1981). Abundant seed (i.e. 3 million seeds ha^{-1}) was recorded twice in a 5 year period, with germination percentages of 37%-100% of full seed.

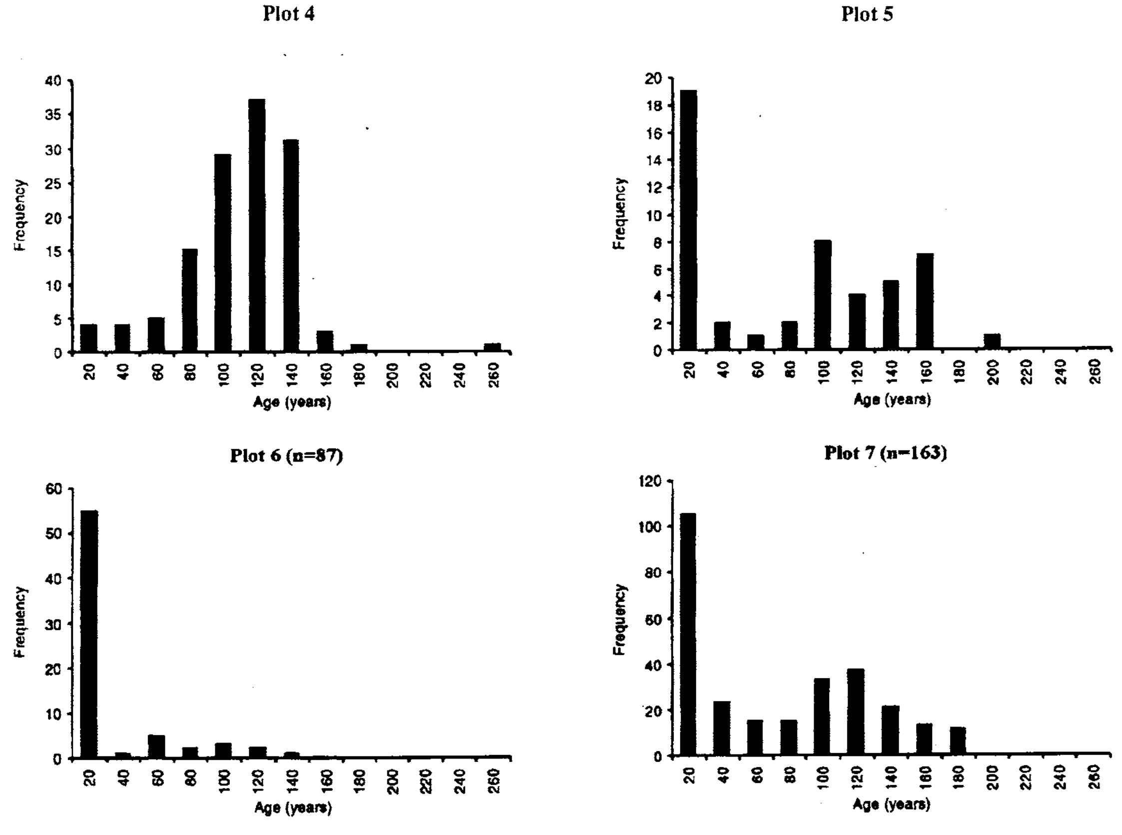

Figure 3. Age class distribution for pine and birch >10cm dbh in the four permanent assessment plots, the Black Wood of Rannoch.

The age distribution pattern for plot 4 differs significantly from the other plots in the study (Figure 3). There is a peak of individuals in the 120 years age class with lower frequency in all younger age-classes. In addition, plot 4 has a greater basal area than any of the other plots (Table 2) and is the only plot where mortality exceeds recruitment (Table 4). This suggests that the plot has passed a phase of recruitment and may now be passing into a new phase of stem exclusion.

In all plots there is a large pool of seedlings too small to be counted in the recruitment/mortality assessments. These seedlings constitute a reserve of potential cohorts ready to take advantage of any new canopy disturbance. This can be seen clearest in plot 7, under the disturbed electrical line, where conditions are now most favourable for seedling germination and establishment.

Økland and Eilertsen (1996) have shown that understorey pine vegetation abundance may vary from year-to- year, making single year studies separated by long intervals difficult to interpret. Changes may be due to long-term trends or yearly variation due to short term factors. When the permanent plots were established at the Black Wood of Rannoch, vegetation mapping proceeded without thought to the statistics to be used in analysis of results. The data collected has thus proved difficult to analysise because recording vegetation presence by mapping is subjective and has not generated interval data for analysis. Interpreting our results, based on two assessments, therefore requires caution. However, it is likely that broad overall changes and the direction in which the vegetation composition is changing are indicated, although detailed specific information about each species is limited.

Changes in stand structure may also explain long term vegetation changes. The increase in *Vaccinium* spp frequency is recorded only in plot 4, where the stand appears to be approaching maximum canopy cover. This is indicated by no transmittance values >80%. Transmittance values >80% are only possible if the canopy has large gaps allowing light to penetrate without attenuation and such gaps are by contrast apparent in plots 5 & 6. Reduced frequency of high transmittance values in plot 4 suggests a more homogeneous canopy cover, which may increase shading thus favouring the shade-tolerant *Vaccinium* spp over other species (Figure 2). In all other plots, disturbance events of the 1940s would have opened the canopy to favour light demanders, especially *Calluna*. In plots 5 and 6 the large gaps in the canopy continue to allow relatively high light levels to be maintained. Concurrent with increasing tree recruitment there will be a corresponding decrease in available soil moisture, through increased evapotranspiration and interception by the canopy (Pyatt & Craven 1979). This will act against the moisture requiring species such as *Juncus* spp. and *Molinia*.

Bracken may well have benefited initially from disturbance, but has reduced in frequency in all plots with increasing recovery of the stand. The dense bracken stand in the first few years following felling may also have acted as a barrier to seedling recruitment and may partially explain the 20 year delay in seedling recruitment. It is likely *Calluna* would have also increased following disturbance, and has remained abundant while conditions have been favourable.

Conclusions

The Black Wood of Rannoch is recovering from the most recent intervention event with population and stand structural development following an apparent 30 year time lag. Information on structural changes during this period has been collected at appropriate intervals. Vegetational changes were more difficult to interpret due to the long time period between assessments. However, we need to make assessments at intervals at an appropriate time-scale to pick-up changes in structural development and vegetational fluctuations. Long term monitoring need not necessarily mean long time intervals between measurements, but more the sustained commitment to recording at intervals suited to answer the basic questions underlining the monitoring objectives.

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A CENTURY OF VEGETATION CHANGE AT BROADBALK WILDERNESS

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Summary

Broadbalk Wilderness contains a small area of secondary woodland which developed following the abandonment of a wheat field in 1882. Archived and published data from the area has provided the best available information on the long-term dynamics of natural colonisation at a single site in Britain. However, despite continuity of ownership and a good system of data recording and retrieval, the area has lacked a clear objective and a common assessment protocol. Hence the area has fragmented and it has been difficult to piece together exactly what has happened. Future projects which involve long-term monitoring of woodlands must ensure they meet basic criteria, otherwise resources could be wasted.

Introduction

The Continuous Wheat Experiment (CWE) is one of the classic long-term studies at IACR Rothamsted (Johnston 1994) and was established by Sir John Lawes in 1843. Broadbalk Wilderness is an area which was formed following a decision by Lawes to make the area of each of the plots in the CWE equal by cutting off a portion of the experimental field. This presented Lawes with an opportunity to study how the wheat crop would perform if it was not harvested and meticulously hand weeded as the rest of the CWE. In 1882 he told the 39th wheat crop just before the harvest of 1882 "I am going to withdraw all protection from you, and you must for the future make your own seedbed and defend yourself in the best way you can against the natives, who will do everything in their power to exterminate you" (Lawes 1884 quoted in Garner 1965). As predicted the area quickly became dominated by couch grass *Agropyron repens* and smaller and smaller amounts of self-sown wheat were noted in 1883, 1884, 1885 until there was none in 1886. The area has survived but is now divided into three areas: (a) an undisturbed area which has colonised to mixed woodland, (b) an area where invading woody plants have been removed ('grubbed') for over 90 years, and (c) an area created in 1957, when half the grubbed area was changed to a regime of regular grazing by sheep (Figure 1). The objective of this paper is to summarise the methods used to monitor the area during the past 117 years and to learn lessons which may be useful in designing future long-term monitoring studies in woodlands.

Description of study site

The Wilderness (Figure 1) is a small area (0.26 ha) situated 700 m northwest of the main building at IACR - Rothamsted near Harpenden, Hertfordshire (National grid reference TL121137). It is on a gently undulating plateau at an elevation of about 130 m. The underlying geology is chalk. The soil is classified as a leached brown soil with a loamy surface layer overlying clay-with-flints; it is moderately well drained with a pH of 7.8 (Jenkinson 1971). The soil contains between 3 and 5% free $CaCO_3$ which is a residue of heavy liming of the site before 1843; this has probably buffered any significant change in pH over time (Blake 1994).

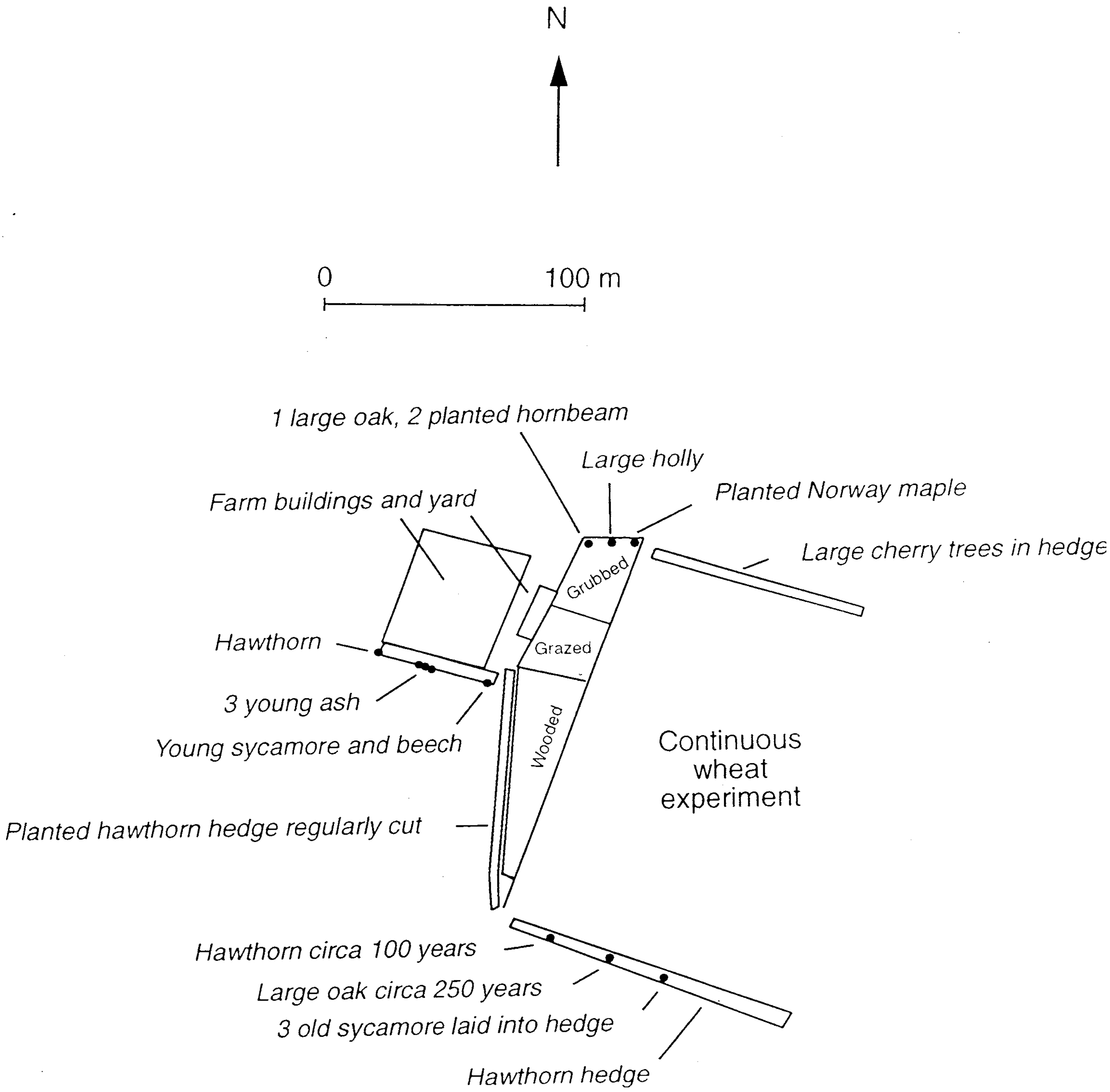

Figure 1. Layout of the Broadbalk Wilderness

Monitoring of Broadbalk Wilderness

Table 1 describes how Broadbalk Wilderness has been monitored in the period 1886 to 1999.

Table 1. Chronology of monitoring at Broadbalk Wilderness

Date and surveyor	Method	Results and comments	Woody species recorded in wooded area
1886 27 July J.J. Willis	List of species on a 9 point DAFORS scale (which spanned exceedingly abundant to rare).	40 herbaceous species were recorded. No formal experiment plan and neither methods nor surrounding vegetation were described. Published in Lawes (1895)	none
1894 Autumn J.J. Willis	List of species on a 9 point DAFORS scale (exceedingly abundant to rare).	51 herbaceous and 5 woody species recorded. Methods were not described and the presence of the woody species was only noted in the text. Published in Lawes (1895)	*Corylus avellana, Crataegus monogyna, Fraxinus excelsior, Quercus robur, Rosa* sp.
1903 3 April and 3 July J.J. Willis	List of species on a 9 point DAFORS scale (exceedingly abundant to rare).	56 herbaceous and 10 woody species recorded. Methods again not described. Published in Brenchley and Adam (1915) who omitted records of woody species.	*Corylus avellana, Crataegus monogyna, F. excelsior, Hedera helix, Ligustrum vulgare, Lonicera periclymenum, Prunus avium, Q. robur, Rosa* sp, *Rubus fruticosus.*
190?	Half of the area was grubbed.	No record of the date the work was carried out. Reasons for the change were not documented.	n/a
1913 Several dates in summer Brenchley and Adam	**Wooded area**: species list	10 herbaceous and 5 woody species recorded. No estimate of cover except recording the area as an oak-hazel wood in Brenchley and Adam (1915).	*Corylus avellana, H. helix, Q. robur, Rosa* spp., *R. fruticosus.*
	Grubbed area: list of species on 9 point DAFORS scale.	75 herbaceous species Published by Brenchley and Adam (1915) which compared results with earlier information.	n/a
1938 May Clapham and Baker	**Wooded area**: list of species with a DAFORS scale for woody plants only.	13 herbaceous and 15 woody species recorded. Published in Tansley (1939)	*Acer campestre, A. pseudoplatanus, Cornus sanguinea, Corylus avellana, Crataegus monogyna, F. excelsior, H. helix, Ilex aquifolium, Ligustrum vulgare, P. spinosa, Q. robur, Rosa* spp., *Rubus fruticosus, Salix caprea, Sambucus nigra.*

Date and surveyor	Method	Results and comments	Woody species recorded in wooded area
1944 November Thurston	**Grubbed area**: listed woody species to be grubbed.	Written description with some indication of abundance.	n/a
1945 March Thurston	**Wooded area**: list of species and diameter of some trees and shrubs at 0.91 m above ground level.	5 herbaceous and 16 woody species. Records well documented. Written description of vegetation with indication of distribution and abundance but not all trees and shrubs were measured. Briefly mentioned in Witts (1965) and data referred to in Kerr, Harmer and Moss (1996).	*A. campestre*, *A. pseudoplatanus*, *Cornus sanguinea*, *Corylus avellana*, *Crataegus monogyna*, *F. excelsior*, *H. helix*, *I. aquifolium*, *L. vulgare*, *Lonicera periclymenum*, *P. avium*, *P. spinosa*, *Q. robur*, *Rosa* spp., *Rubus fruticosus*, *S. nigra*.
1951 29 August Curtis	**Grubbed area**: list of species	35 herbaceous and 11 woody species. Unpublished but briefly described by Witts (1965).	n/a
1957	The Field Plots Committee decided to convert half of the grubbed area to a grazing regime.	This was to investigate the changes in herbage induced by stocking. Initially mown but grazing began in March 1960 (Garner 1965).	n/a
1957-65 10 dates in 1956/57 and in subsequent years 1 day in March/April. Thurston	**Wooded area** Not surveyed	In December 1959 six trees were felled as they were shading the continuous wheat experiment (Witts 1965).	n/a
	Grubbed/grazed area 17 permanent quadrats, species lists and % cover.	49 herbaceous and 10 woody species initially present. Five quadrats were abandoned as being atypical. Vegetation of ungrazed part remained unchanged whereas grazed area showed changes in species composition. Briefly described in Witts (1965).	n/a
1960 4 April Witts	**Wooded area**: girth of all 'large' trees measured at 0.91 m above ground level.	10 woody species noted, no definition of 'large'. Some description of vegetation on site. Referred to briefly by Witts (1965) and in Kerr, Harmer and Moss (1996).	*A. campestre*, *A. pseudoplatanus*, *Corylus avellana*, *Crataegus monogyna*, *F. excelsior*, *H. helix*, *I. aquifolium*, *P. spinosa*, *Q. robur*, *S. nigra*.

Date and surveyor	Method	Results and comments	Woody species recorded in wooded area
1969 Jenkinson	**Wooded area**: girth of trees and shrubs >2.5 cm diameter at 1.3 m above ground level.	Only seven woody species measured. Only trees ≥5 m from woodland edge measured. Carried out as part of detailed study of soils, results published in Jenkinson (1971).	*A. campestre, A. pseudoplatanus, Corylus avellana, Crataegus monogyna, F. excelsior, Q. robur, S. nigra.*
1995-9 Harmer, Kerr and Peterken 16/17 August 1995 6+18 May 1998	**Wooded area** Species list, cover estimated by Braun-Blanquet scale. Height, dbh and position of all over- and understorey trees > 2.5 cm at 1.3 m. Species list by extensive walking survey.	20 herbaceous and 17 woody species recorded. Flora of nearby Knott Wood and local hedgerow recorded (the hedgerow was laid in winter 1998/9). Some tree information published in Kerr, Harmer and Moss (1996).	*A. campestre, A. pseudoplatanus, Cornus sanguinea, Corylus avellana, Crataegus monogyna, F. excelsior, H. helix, I. aquifolium, Ligustrum vulgare, P. spinosa, P. avium, Q. robur, Ribes uva-crispa, Rosa* sp., *Rubus fruticosus, S. nigra, Taxus baccata.*
6 May 1998 and 7 April 1999	**Grubbed/grazed area** Casual observations of species present	16 dicotyledons observed , many were woodland species or weeds that can tolerate shade.	

Conclusions

The information collected and archived about Broadbalk Wilderness is the best available data for studying natural colonisation over a long period of time at a single site. In terms of contemporary interest in natural colonisation as a method of woodland creation, the site is a useful demonstration of its advantages and disadvantages (Kerr, Harmer & Moss 1996).

The survival of the site has been assured by being under a single ownership and there have not been any development pressures which have led to loss of area. However, the erection of the farm buildings in 1913 and its subsequent development into a major operational focus may have disturbed the hydrology and/or the nutrient balance of the site.

The site owner has been primarily focused on agricultural research and has a culture of record keeping, information storage and, importantly, the ability to retrieve it.

The motivation for the establishment of the area was the desire of Lawes to rationalise the CWE and observe the performance of untended wheat against invading weeds. As stated objectives for the area they were quickly achieved. However, we have been unable to find any amended statement of objectives for the area since and the lack of an objective has had the following effects:

i. Fragmentation of the area: the grubbed and grazed areas were formed for reasons of contemporary research interest at the time the changes were made. The reasons for these changes, and others, have not been well documented.

ii. Lack of a long-term systematic plan for assessing the area: periodic assessments have used different methods and reflect the interests of the surveyors. Subsequently it has been difficult to piece together exactly what has happened and when it occurred.

Some difficulties have arisen, which are not unique to Broadbalk, due to the use of common names for plants and changes in botanical nomenclature.

Using the experience of Broadbalk Wilderness it is possible to identify important factors for successful long-term monitoring of woodlands.

i. The existence of the woodland must be assured and there must be an ability to control changes to the surrounding area.

ii. There must be a clearly defined objective for the study.

iii. The assessment protocol must be clearly thought out in terms of the objective and the practicalities of carrying it out over a long period of time. Subsequent assessments must use the same protocol, or if change is deemed necessary, in a way that does not prevent direct comparison with previous assessments.

iv. Information must be clearly recorded and safely stored so that it can be easily retrieved.

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THE COLONISATION OF GROUND FLORA SPECIES WITHIN A 38 YEAR OLD SELF-SOWN WOODLAND

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Introduction

The Monks Wood Wilderness (Figure 1) is a self-sown woodland which developed on a former barley field adjacent to Monks Wood National Nature Reserve in Cambridgeshire. This 4 hectare field, which was probably cleared in Roman times, is known to have been cultivated continuously from at least 1820 to 1960 when it was abandoned and allowed to revert naturally to woodland (Mellanby 1967). Since then a self-sown woodland of mainly *Quercus robur* and *Fraxinus excelsior* has developed with an understorey of *Prunus spinosa*, *Cornus sanguinea* and *Crataegus monogyna/laevigata*. Given the proximity of ancient woodland, which surrounds the wood on three sides, the Wilderness offers an ideal opportunity to examine the colonisation and establishment of woodland species, under near optimal conditions. This short paper summarises the results of a survey of the ground flora 38 years after reversion.

Method

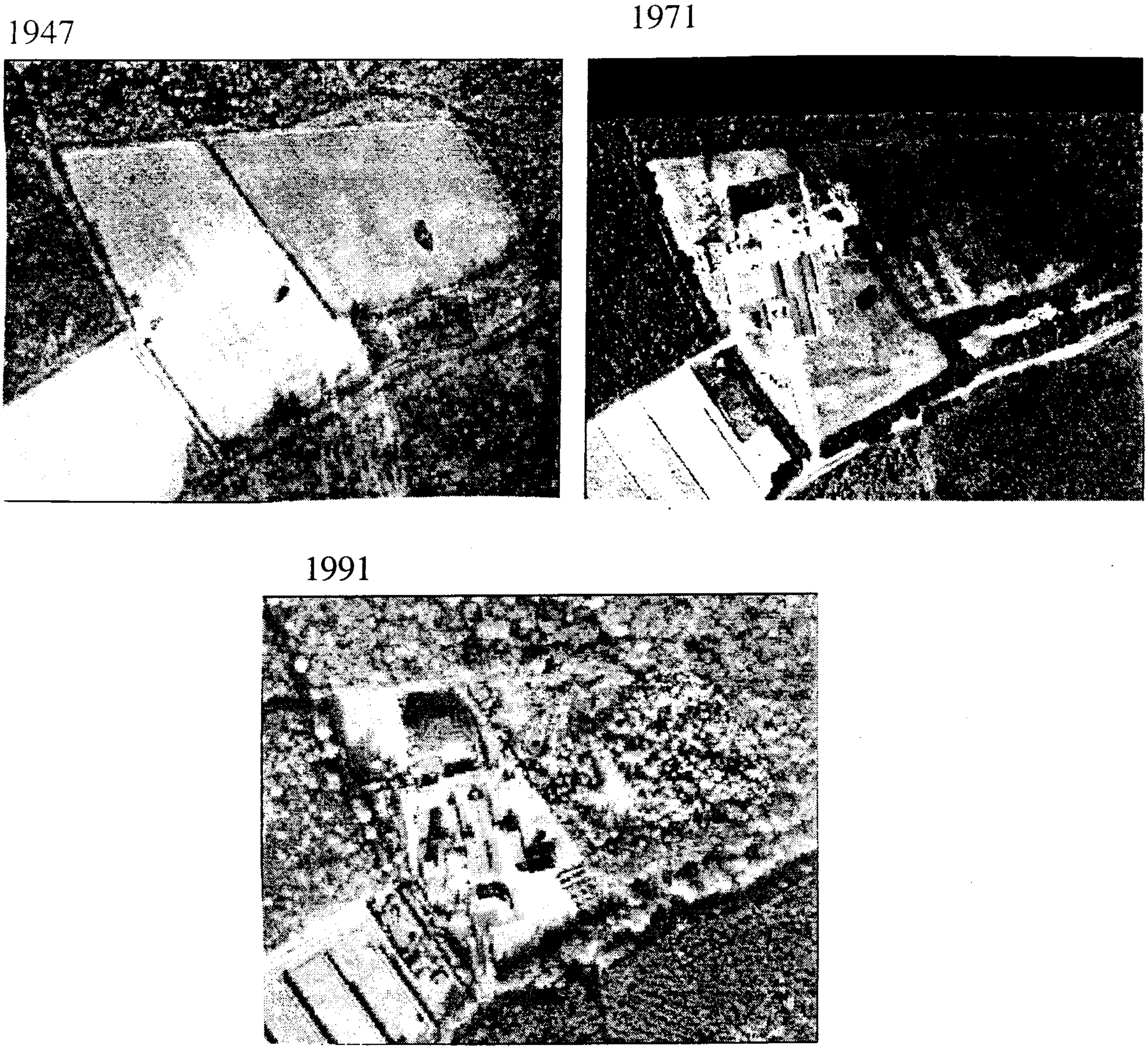
In 1998 the Wilderness was divided into 20 by 20 metre permanently marked plots. These were then further divided into 10 by 10 m grid cells (n = 408), within which the position of tree and shrub species were mapped and ground flora species recorded.

Results

89 ground flora species were recorded during the survey, as well as saplings of 10 species of tree and shrub. 16 typical woodland herbs were recorded of which *Arum maculatum* (Figure 2), *Carex sylvatica* and *Rumex sanguineus* were the most abundant. *Ajuga reptans*, *Geum urbanum*, *Mercurialis perennis* and *Moehringia trinerva*, all of which are uncommon in the surrounding wood, occurred in small numbers and were largely confined to the edges of the Wilderness (Figure 2). The majority of the remaining species are more typical of woodland glade/edge and hedgerows in the vicinity. These include *Glechoma hederacea* and a number of coarse grasses, most notably *Brachypodium sylvaticum*, *Calamagrostis epigejos* and *Carex pendula* (Figure 2) which have increased markedly within the surrounding woodland in recent years (Pollard *et al.* 1998) apparently due to selective grazing by Muntjac deer (*Muntiacus reevesi*) (Cooke 1994).

Discussion

The results of this study show that the establishment of self-sown woodland on ex-arable land can be effective where local seed sources are plentiful (i.e adjacent to ancient woodland). Not surprisingly, colonisation was most rapid for species with large animal or wind dispersed seeds, particularly shrubs and trees with large fruits such as *Quercus robur*, *Fraxinus excelsior, Cornus sanguinea*, *Crataegus* spp., *Rosa* spp. and coarse grasses and sedges. In contrast, a number of herbs present in the surrounding woodland are only now beginning to colonise, 38 years after



1947

1971

1991

Figure 1. The development of woodland cover in the Wilderness prior to and after the construction of Monks Wood Experimental Station in the early 1960s.

abandonment, and are confined to the edges of the Wilderness. This may be due in part to poor dispersal ability (e.g. *Lamiastrum galeobdonum*, *Hyacinthoides non-scripta*) and/or declining abundance within the surrounding woodland due to grazing by Muntjac (e.g. *Mercurialis perennis*) (Wells 1994). This deer species was first recorded in the wood in 1972 and has presumably affected the fate of the ground flora and regeneration of tree species (Cooke *et al.* 1995). As a result, less palatable species which are common in the surrounding wood and hedges, such as *Arum maculatum*, *Calamagrostis epigejos* and *Glechoma hederacea*, are now particularly abundant. These results illustrate the efficacy of self-sowing (and non-intervention management) as a means of restoring woodland where seed-sources are plentiful.

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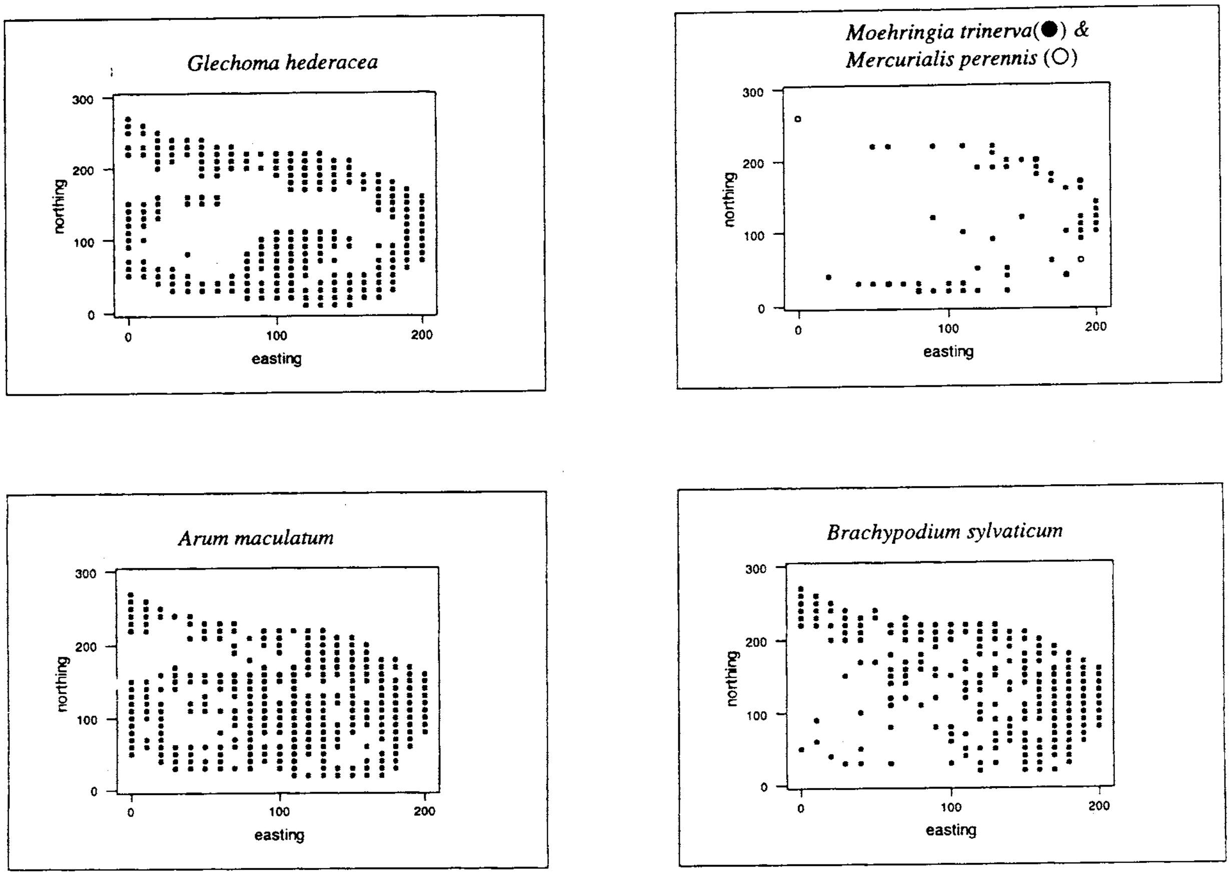

Figure 2. Distribution of typical woodland species within the Wilderness (each circle represents one 10 x 10 m plot).

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THE EFFECT OF SHADE AND WEATHER ON WILD DAFFODILS IN WEST DEAN WOODS, WEST SUSSEX

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Summary

This paper describes the results of monitoring of a population of wild daffodils *Narcissus pseudonarcissus* in a woodland nature reserve from 1979. Shade was the major factor controlling daffodil density. After 12-years, the optimum shade treatment for their conservation had been determined and was put into practice. Shade, unless it was very dense, had little effect on the fraction of bulbs in flower. Flowering was largely controlled by the weather of the previous spring, when warm dry conditions were most favourable.

Introduction

West Dean Woods was created a nature reserve of what is now the Sussex Wildlife Trust in 1975 and was notified as a Site of Special Scientific Interest in 1980. Since its reservation, research and monitoring have been encouraged and there is ongoing, long-term, annual monitoring of several groups: the BTO woodland common bird census since 1975; the ITE butterfly recording survey from 1979; and vascular plants, bryophytes and lichens since 1985. This paper describes the results of monitoring the daffodils *Narcissus pseudonarcissus* since 1979. Nomenclature follows Stace (1991).

One of the four main reasons for making the site a reserve was a colony of wild daffodils, but what is the optimum shade treatment for the conservation of the daffodil colony?

This paper describes an experiment to determine the effects of shade - of both woody plants and of undergrowth - on daffodil density. The effects of weather were also investigated. After twelve years the optimum treatment was clear and was put into practice. The experimental treatments were discontinued, but monitoring continued. The flowering of the daffodils was studied in the same experiment. This is relevant to their conservation both biologically and because their flowering attracts many human visitors.

A fuller account of this work is given in Hopkins (1999).

The site

West Dean Woods Nature Reserve is on the South Downs in West Sussex, where the Upper Chalk rock is covered by up to 1 m of non-calcareous deposits. Woodland, coppice or shrub cover have been continuous since at least 1604 AD (Stewart 1976) and the reserve is species-rich. Much of the area had been managed as coppice-with- standards, although this had been neglected. On reservation, both coppicing and the felling and replanting of oak standards were re-established over most of the reserve. Most standards were oak *Quercus robur*, planted *c*1870, and most coppice was hazel *Corylus avellana* with some sweet chestnut *Castanea sativa*.

The wild daffodil colony covers 1.65 ha at an altitude of 140-160 m above sea level on an ESE aspect in the north-western corner of the reserve in Compartment 123 (National Grid reference

SU 847159). Coppicing was not re-established here, but the dead fronds of bracken *Pteridium aquilinum* and the tangles of bramble *Rubus fruticosus* agg. have been swiped using a tractor and a 'Bushhog' swipe (an approximately 1.4 m diameter rotary blade at a height of 40-50 cm) during a dry period (when there was little danger of compressing the soil or the bulbs) each winter to allow more light to reach the daffodils.

The mean annual rainfall in West Dean village (4 km SSE and 110 m lower) is 971 mm; in the reserve it is about 1000 mm (Potts & Browne 1983). The nearest, comparable climatic data are for Rustington (24 km SE, 3 m altitude). Allowing for lapse-rate cooling, these give a mean maximum temperature for the hottest month (normally July or August) of about 19 °C and a mean minimum temperature for the coldest month (normally January or February) of about 0 °C.

Methods

Plots and treatments

Five 30 x 20 m plots were selected (Table 1) to give three degrees of woody-plant shade: dense, light and open (virtually none). Two plots under both light shade and open conditions were chosen. One of each was swiped (as already described); the other was left unswiped. Swiping was not possible under dense shade because the closeness of the trees and shrubs prevented the use of a tractor. Care was taken to ensure sufficient differences in cover between the three shade categories and to make the paired plots as similar as possible. Unfortunately the daffodil colony occupied too small an area for the treatments to be replicated.

Table 1: Initial tree and shrub densities and covers of bramble and bracken; densities of mature and flowering daffodil bulbs and increases in these at West Dean Woods

Plot	1	2	3	4	5
Shade treatment	dense	light	light	open	open
Swiped	no	yes	no	yes	no
Woody plants >2cm dbh (1977) (density per sq m)	0.49	0.10	0.10	0.02	0.04
Bramble cover (1979)	light	very sparse	sparse	sparse	light
Bracken cover (1979)	sparse	very sparse	sparse	light	dense
Daffodil density (per sq m) (1979)	98.9	77.2	76.5	10.4	6.1
Density mean increase * (1977-91)	1.5	6.2	2.9	1.9	0.7
Proportional increase‡ (1977-91)	1.5	5.9	3.0	8.1	6.3
Flower density (1979-91) (mean per sq m)	4.7	9.5	8.4	2.5	0.7
Flowers (1979-91 (mean % of mature bulbs)	4.8	9.0	8.8	9.1	7.9

* regression slope; increase per sq m per year
‡ annual increase as a percentage of density

The area covering the experimental plots was about 0.5 ha and contained 18 standards. All were oak and all were large. The dense-shade plot had five times the density of woody plants (>2 cm dbh) on each of the light-shade plots and seventeen times that on the open plots.

The density of undergrowth of both bramble and bracken varied between the plots and bramble appears to have declined during the experiment. The great storm of October 1987 (Kirby & Buckley 1994) blew over some trees on or near the plots and caused an increase in illumination to the edges of Plots 1-3 due to the devastation of a plantation immediately north of the reserve.

Numbers of daffodils

The density of sterile-mature and of flowering daffodil bulbs was determined between late March and late April each year from 1979 to 1987. (The numbers of seedlings and young plants were also recorded, but are not considered in this paper.) Most of the recording was done by trained amateur volunteers under supervision. To confirm the trends, the experiment was continued until 1991 but with the density determinations in alternate years. Following the completion of the experiment, the management was changed but the density of daffodils in the plots continued to be monitored but, from 1995, at five-year intervals. For each assessment, quadrats (25 x 25 cm) were placed at 200 randomly-selected points on each plot. This process was repeated on each plot and in each year with a fresh randomization each time.

Weather

The annual changes in density were compared with weather data for each of the fourteen calendar months from March of the year before recording to April when the records were made. Seven variables were examined for each calendar month: mean maximum temperature; mean minimum temperature; mean temperature (average of the two previous variables); mean soil temperature at 10 cm depth (most bulbs were near the surface); number of days (nights) of ground frost (recorded by a grass-minimum thermometer); total rainfall; and total hours of sunshine. Correlation coefficients were calculated for the mean results on all five plots. When a factor showed significant correlations for two or more consecutive months, additional correlation coefficients were determined for the combined periods.

Density

The initial densities of mature bulbs were very similar on the three shaded plots (77-99 m^{-2}); they were much less on the two open plots (6-10 m^{-2}). Table 1 and Figure 1 show the changes during the experiment and subsequently. (Note the absence of a mean line after yearly counts ceased and the interrupted line for the extrapolation of the regression). During the 12-years, statistically-significant increases in density occurred on all plots ($P < 0.05$ to < 0.001). The only significant differences between the rates on these plots were between Plot 2 (light shade, swiped), which had the highest rate, and Plots 1, 4 and 5 ($P < 0.02$ or < 0.01).

Increases can also be considered in proportion to density, and the annual (compound- interest) percentage increases are also shown in Table 1. These show the open plots (4 and 5) had the highest values, whilst Plot 1 (dense shade) had the lowest increase. These values showed significant differences between all pairs of plots at $P < 0.01$ or < 0.001.

The significant correlations (at $P < 0.05$) for the mean annual change in density on all five plots with the monthly weather variables are presented in Table 2. As yearly monitoring ceased in 1987, annual changes in density are only available for the eight years 1979-80 to 1986-87. There were 17 in two seasonal groups: positive with temperature in the previous spring; and negative with both temperature and rainfall, but positive with sunshine, in the autumn.

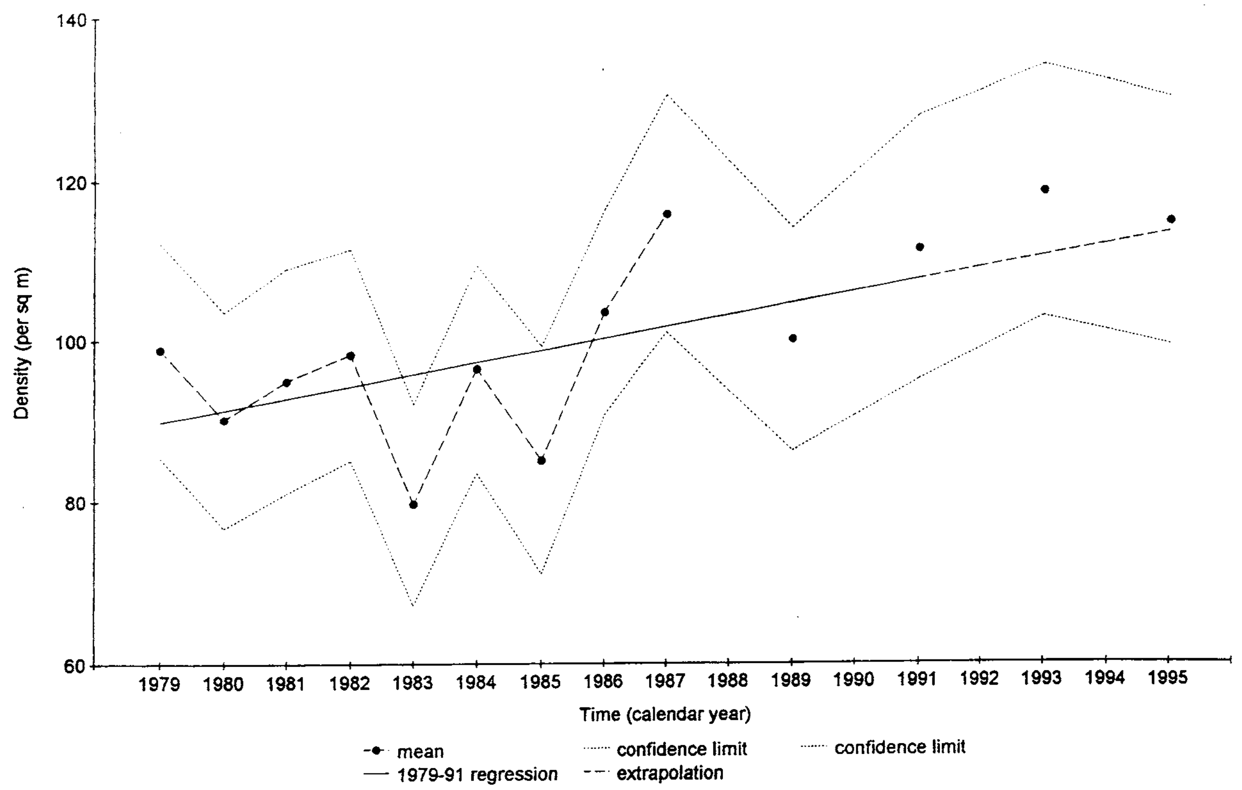

Figure 1(a). Mature bulb density (Plot 1: dense woody plants, unswiped). The confidence limit is for 95%

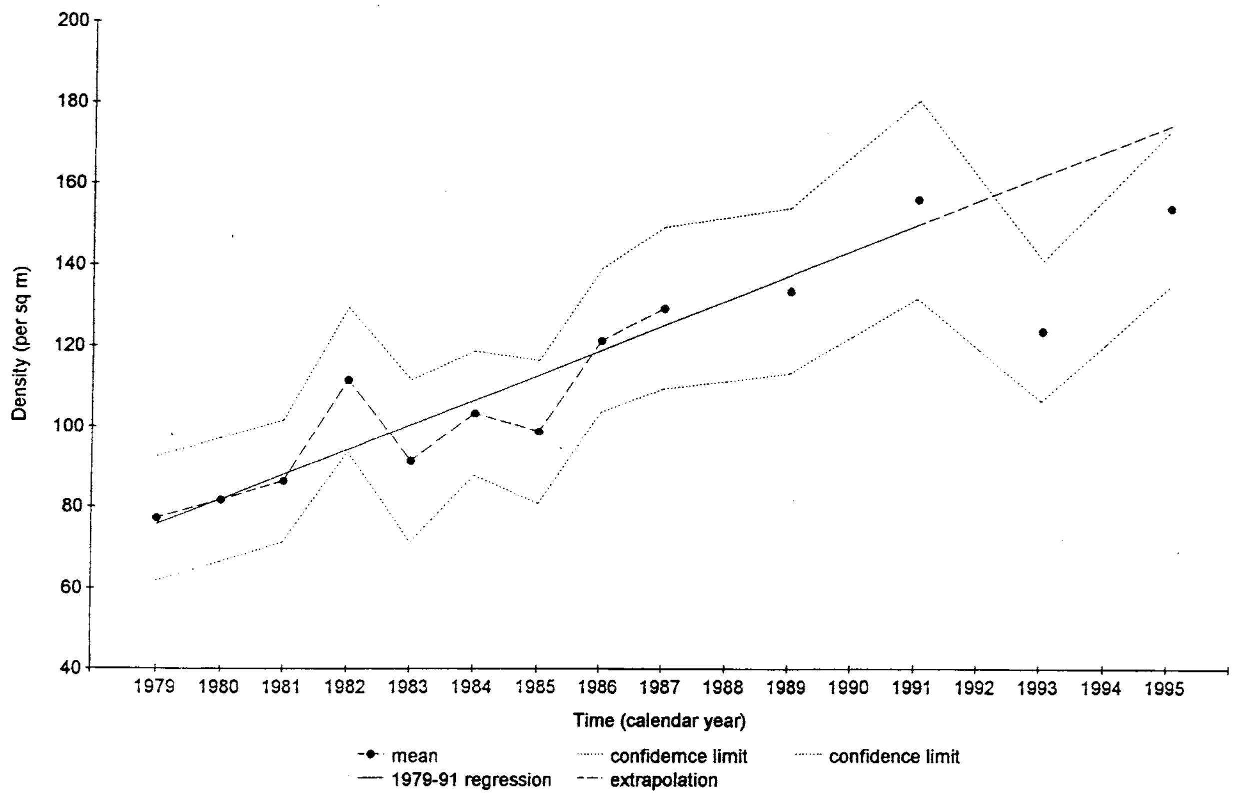

Figure 1(b). Mature bulb density (Plot 2: light woody plants, swiped). The confidence limit is for 95%

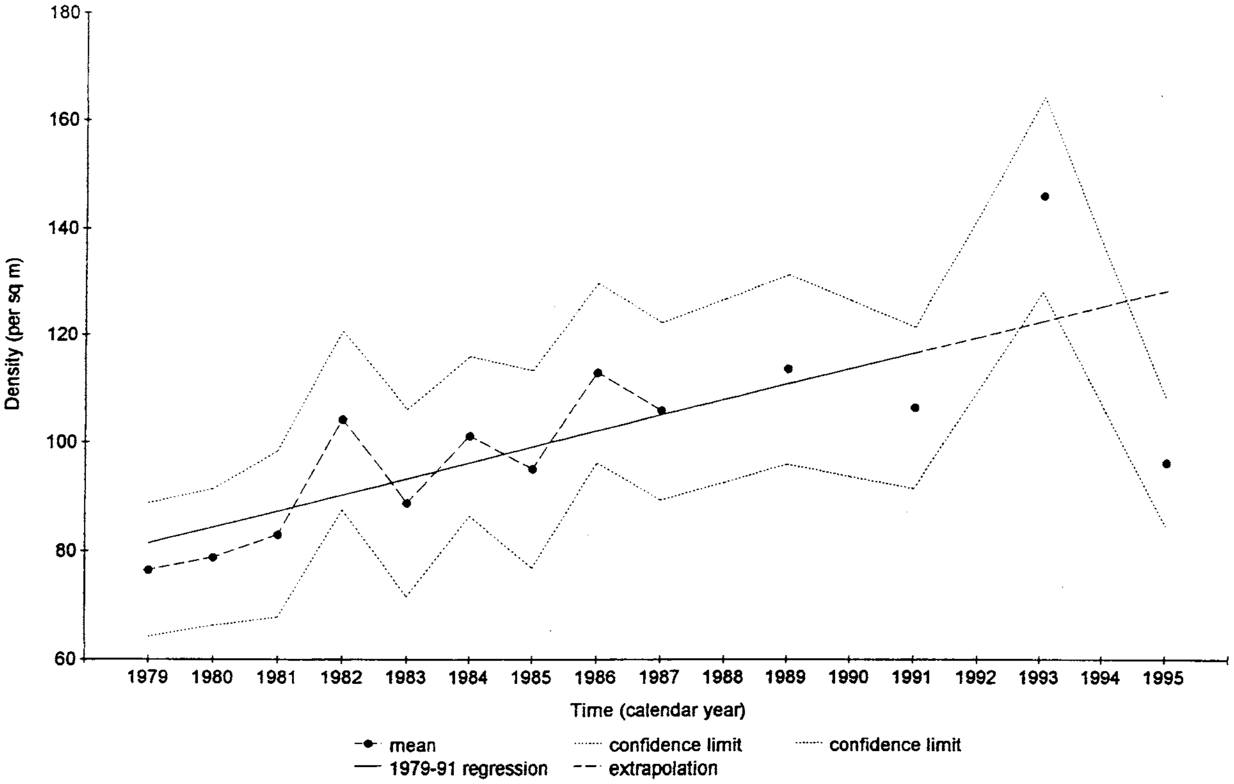

Figure 1(c). Mature bulb density (Plot 3: light woody plants, unswiped). The confidence limit is for 95%

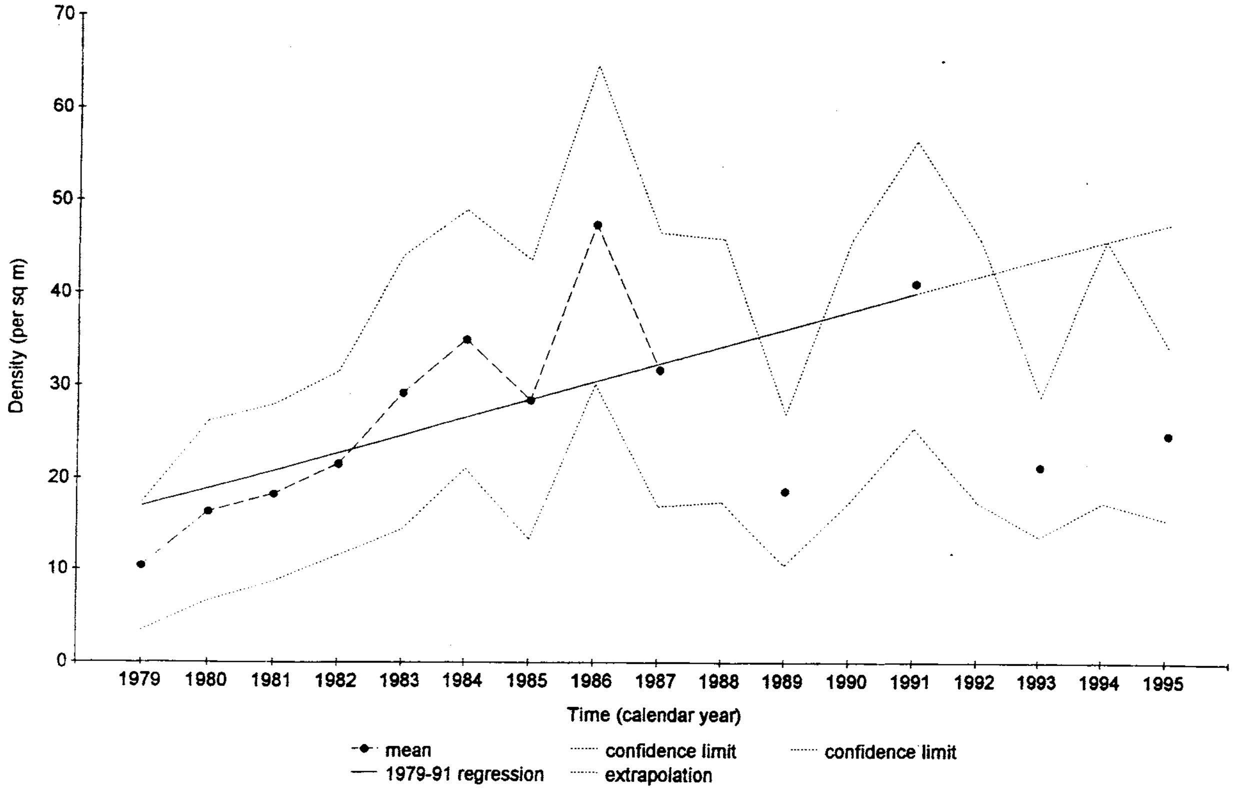

Figure 1(d). Mature bulb density (Plot 4: open, swiped). The confidence limit is for 95%.

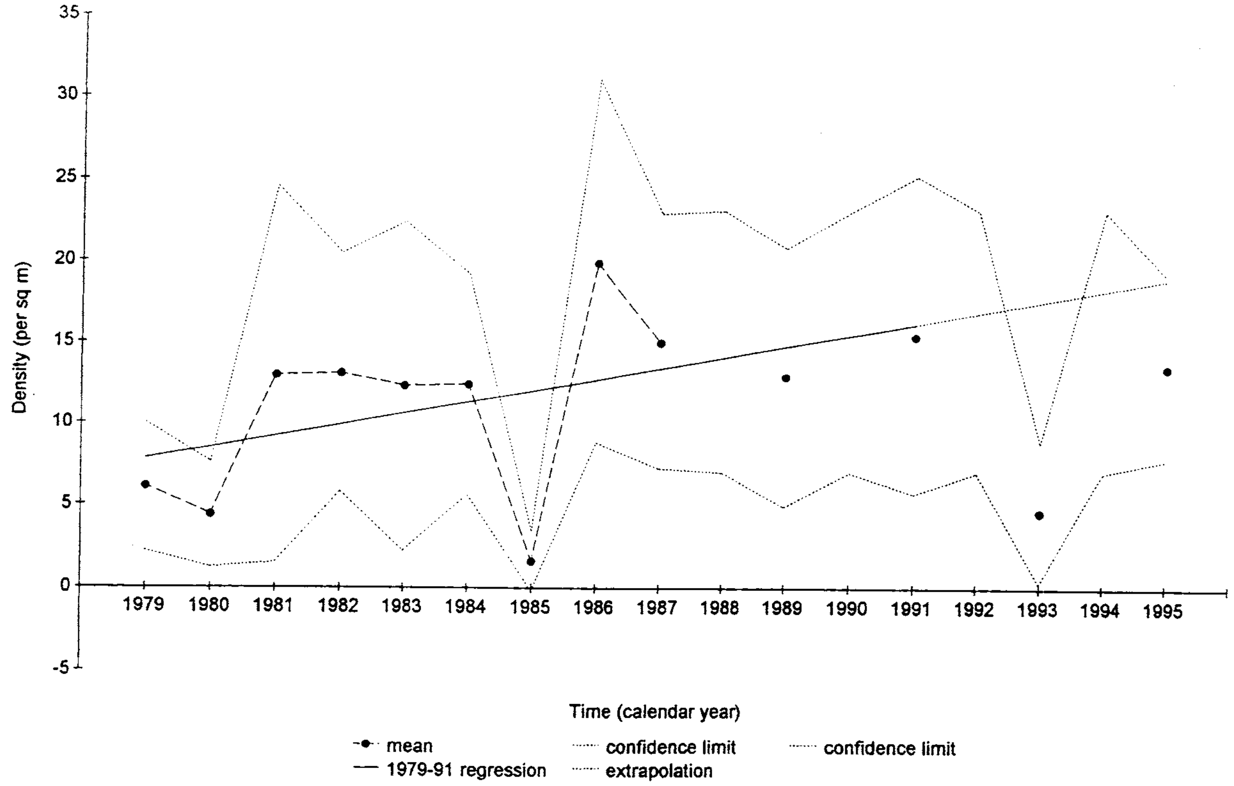

Figure 1(e). Mature bulb density (Plot 5: open, unswiped). The confidence limit for 95%.

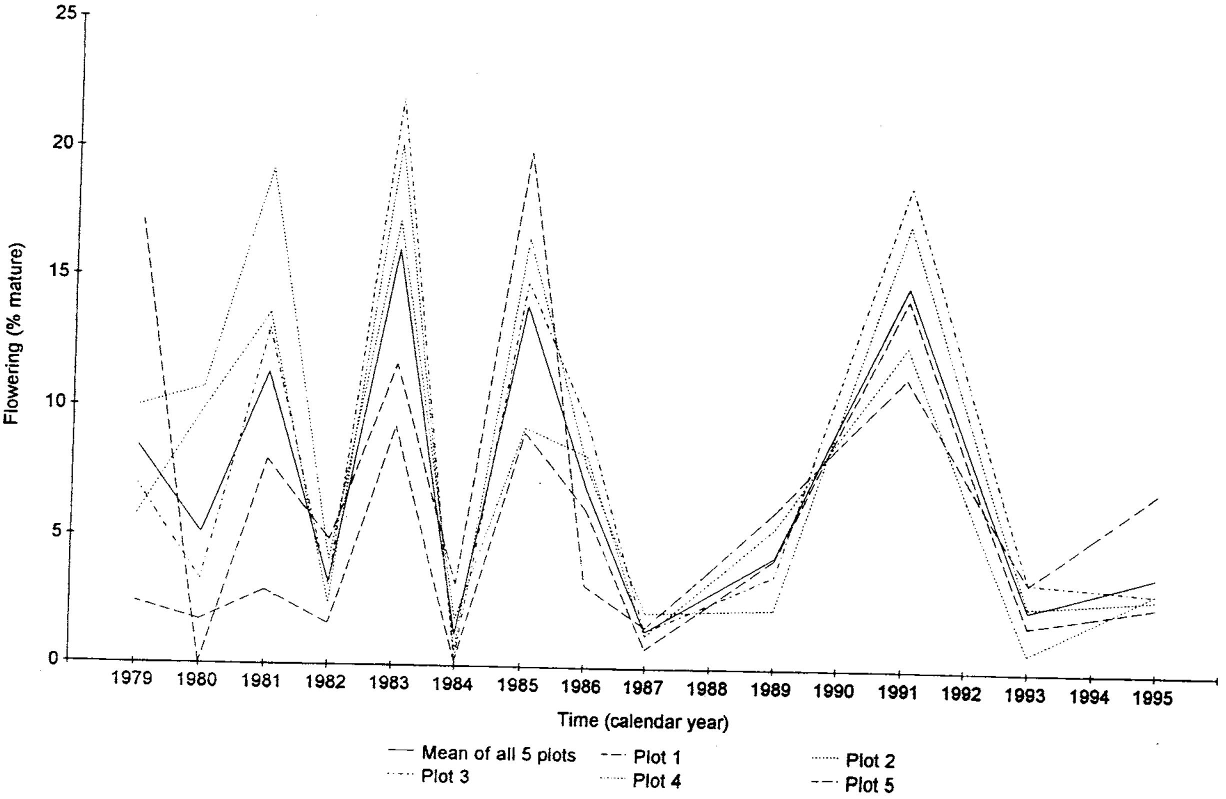

Figure 2. Flowering bulbs (% mature). (Note alternate year records from 1987).

Table 2: Statistically-significant ($P < 0.05$) correlation coefficients (r) of weather factors and changes in the density of mature daffodils (1979-87) and in the fraction of these daffodils in flower (1979-93) at West Dean Woods

(Values for which $P < 0.01$ are shown in bold print)

	Weather factor						
Months	**Temperature**					**Rain**	**Sun**
	max	**min**	**mean**	**frost**	**soil**		
		Mature daffodils (mean annual increase in density)					
April		0.743		-0.758			
April-May		**0.904**		**-0.909**			
May		0.799		-0.782			
October				0.813	-0.783	0.710	
Oct-Nov		-0.833	-0.757	**0.887**	-0.778	**-0.869**	
November		-0.759	-0.762		-0.756		
		Flowering daffodils (mean (%) fraction of mature)					
March							0.577
Mar-Apr						**-0.859**	0.702
April	**0.767**					**-0.745**	0.650
Mar-May				0.578		**-0.736**	
April-May						**-0.722**	
May				0.590			
July		-0.607					
February*				0.625			

* in year of flowering

Discussion on density changes

Shade

Population increase may be measured either as number per unit area (density) or in proportion to the population size. Both measures showed a considerable range. The highest increase in density was on Plot 2 (light shade, swiped), followed by Plot 3 (light shade, unswiped), with Plot 5 (open, unswiped) the lowest. Plot 5 had a dense undergrowth of partly-collapsed dead bracken fronds which over-topped many of the daffodil leaves. New bracken fronds emerge and expand as the daffodil foliage is senescing and the dead fronds acted in a similar way to the dense trees and shrubs on Plot 1. However, the two open plots are not really comparable with the others because of their very much lower densities. The highest proportional increases were in the open (Plots 4 and 5), with the least under dense shade (Plot 1).

As expected, woody-plant shade was very important for daffodils, but shade from the undergrowth also had a very strong influence. This is clear from a comparison of the pairs of swiped and unswiped plots where, in all cases, the swiped plots had higher values. Thus, the plots with dense *total* shade showed the least increases, whilst the greatest increases were on the swiped plots.

Later changes

Resulting from this conclusion, the management of the daffodil area was changed to annual swiping in mid-July (or as soon as possible afterwards) in order to have maximum effect on the bracken. Monitoring continued and the general trends of density continued but were more erratic. In 1993, three plots had densities (and 95% confidence limits) well below the extrapolated regression line - and increases in 1995. Plot 3 did the opposite, whilst Plot 1 (which could not be swiped) continued its general trend. In 1993 and 1995, most mean densities were well below the extrapolated regression lines. It seems likely that these changes were caused by the great storm of 1987 rather than from the change in management or other factors. There were some wind-blown trees on the plots with the resulting increase in microhabitats of exposed root plates and hollows. This would account for both the death of bulbs and for the increase in variation both between and within plots. By 1999 the bracken had decreased enormously and was largely replaced by grass, so that the open-plot area appeared like parkland. Monitoring is being continued and the next count, scheduled for 2000, will be interesting.

Weather

The variation within Figure 1 suggests that other factors are also operating. The most likely is the weather. With seven variables for 14 months there are 98 correlations. So, of the ten *monthly* correlations in Table 2 (which were all at $P < 0.05$) five are likely to be due to chance. The only higher-probability correlations (at $P < 0.01$) were for two-month periods. These (and most of the monthly ones) strongly suggest that spring temperature is the key weather factor controlling daffodil density. Spring is the growing season for daffodils and, clearly, it is the low temperatures (minimum temperatures and nights of frost) which are restricting their increase. In cultivation, daughter-bulb dry weight is correlated with soil temperature (Rees 1972).

Flowering

The means of flowering individuals expressed as density and as 'fraction of mature' bulbs are given in the last two lines of Table 1. On average, 8-9% of the mature bulbs flowered, except on Plot 1 (dense shade) where only 5% did so. All the plots showed large between-year fluctuations in the proportion of bulbs in flower. In most years all five plots behaved in a very similar manner (Figure 2), and the mean ranged from 1.2% (1984) to 16% (1983).

The significant correlations between flower density and weather factors for the combined plots are shown in (Table 2). Those at $P < 0.01$ were for maximum temperature and lack-of-rain in the spring and, particularly, for April of the year prior to flowering.

Discussion

The fraction flowering was least under dense shade (Plot 1) and second lowest on the open, unswiped plot with dense bracken (Plot 5). This agrees with earlier work (Salisbury 1924; Barkham 1980; Peterken 1981).

The very large between-year variation in the fraction of flowers suggests that weather, or some other random factor, is playing a more important role in controlling flowering than in governing vegetative increase.

Most of the five *monthly* correlations at $P < 0.05$ between the mean fraction-flowering and weather could be due to chance. However, all those at $P < 0.01$ strongly suggest that the weather of the spring of the year prior to flowering is very important, especially the maximum temperature in April and a lack of rain during March-May. Warm sunny weather is favourable to plant growth and, no doubt, enhances the formation of floral initials. Why spring rainfall should depress flowering the following year is less clear; possibly it is connected with the genus *Narcissus* being of Mediterranean origin. In cultivation, high temperatures followed by low temperatures are required for flower initiation and, in the field, these are satisfied by high summer and low winter soil temperatures (Rees 1972).

Density and flowering are inter-related: populations that are expanding rapidly vegetatively produce overcrowded bulbs and few flowers. Nevertheless, the new swiping management gives the best available shade treatment for both bulb density and flowering and it should be possible to inform potential visitors of the likely flowering display a year in advance.

Conclusion

After 12 years, the experimental shade treatments provided a firm basis for the sound conservation management of the wild daffodil colony in terms of both bulb density and flower production.

It was not originally intended to study the effects of weather on the daffodils but, as is often the case in monitoring, other uses of data become apparent. The literature contains many examples of how the effects of unexpected events have been able to be investigated because monitoring (which had been set up for a different purpose) was able to provide base-line data.

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A COMPARISON OF THE STRUCTURE AND COMPOSITION OF THE WARBURG RESERVE BETWEEN 1973 AND 1992.

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Introduction

In this paper we give preliminary results from a comparison of the structure and composition of the Warburg Nature Reserve in south Oxfordshire in 1973 with that in 1992. This study complements work done on a similar set of plots at Wytham Woods (Kirby *et al.* 1996; Kirby & Thomas 1999). Fuller results will be published later this year as an English Nature Research Report. The Warburg Reserve, near Henley in South Oxfordshire (National Grid Reference SU715880) covers about 100 ha and was acquired by the Berkshire, Buckinghamshire and Oxfordshire Naturalists' Trust (BBONT) in 1967 (BBONT 1988).

Methods

In 1973 a 100 m grid was set up across the reserve and 10 x 10 m plots were recorded at the intersections (Dawkins & Field 1978). Each grid point formed the north-west corner of the plot. The corners of each plot were marked with underground metal markers so that they could be relocated precisely. In 1992 the plots were re-recorded. The recording on both occasions took place between April to August.

Vegetation cover was assessed by laying out a tape across the north-west to south-east diagonal of the plot. Percentage vegetation cover immediately above the tape was estimated by eye in three height bands: top or canopy cover > 2.5 m high; mid or shrub cover 0.5-2.5 m high; and ground cover < 0.5 m high. All vascular plants in the ground flora in the plot were listed but in the analysis seedlings and saplings of woody species were excluded.

Table 1. Changes in the vegetation cover across the south-east/north-west diagonal of the plot.

Layer	**Mean value 1974**	**S.E**	**Mean change to 1992**	**S.E.**
Canopy layer (>2.5 m)	72.9	3.5	-3.1	3.9
Mid-cover (0.5 - 2.5 m)	32.5	2.9	-9.6	2.8
Field and ground layer (<0.5 m)	62.4	3.6	11.1	3.2
No of plots showing cover change	>40% increase		>40% decrease	
In canopy layer	11		13	
In mid-cover	2		8	
In field and ground layer	15		3	

Results

The wood as a whole is characterised by a relatively dense canopy cover, moderate shrub cover and abundant ground layer at both dates, based on the estimates across the diagonal of the plots. The vegetation cover showed no significant change overall in the canopy cover; although there were small, but significant changes in the shrub layer and the field layer (Table 1). The mean values however hide some large changes in individual plots, with for example 25% of plots showing declines or increases of more than 40% in the canopy.

For the site as a whole the pattern of ground flora species diversity has been maintained - there is little change in the total number of species, the balance between common and scarce species, or between ancient woodland indicators and non-woodland species (Table 2). There have however been major fluctuations in the richness of individual plots.

Table 2. Comparison of species richness at plot and wood level.

	1974		1992	
Total no of species (all plots)	161		145	
No. of species recorded on only one date	37		21	
No. of species present in >10% of plots	51		53	
No. of ancient woodland indicators (no. of occurrences)	25	(228)	28	(240)
No. of other woodland species	71	(1285)	67	(1152)
No. of non-woodland species	65	(286)	50	(207)

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