# Biodiversity in Britain's Planted Forests

Results from the Forestry Commission's
Biodiversity Assessment Project

Edited by Jonathan Humphrey,
Richard Ferris and Chris Quine

Forestry Commission


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Enquiries relating to this publication should be addressed to:

Forestry Group
Forestry Commission
231 Corstorphine Road
Edinburgh
EH12 7AT

Tel: 0131 334 0303
Fax: 0131 316 4344

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## Editors

**Jonathan Humphrey**
Forest Research, Northern Research Station, Roslin,
Midlothian EH25 9SY. 0131 445 2176
jon.humphrey@forestry.gsi.gov.uk
**Richard Ferris**
Forest Research, Alice Holt Research Station,
Wrecclesham, Farnham, Surrey GU10 4LH.
Present address: JNCC, Monkstone House, City Road,
Peterborough, PE1 1JY.
**Chris Quine**
Forest Research, Northern Research Station, Roslin,
Midlothian EH25 9SY. 0131 445 2176
chris.quine@forestry.gsi.gov.uk

## Contributors

**Steven Browne**
The Game Conservancy Trust, Fordingbridge,
Hampshire SP6 2PU. 01425 652381
sbrowne@gtc.org.uk
**Simon Davey**
Stable Flat, Downsland Court, 115 East End Lane,
Ditchling, Hassocks, Sussex BN6 8UR. 01273 843375
srdavey@globalnet.co.uk
**Jim Harris**
Institute of Water and Environment, Cranfield University,
Silsoe, Bedfordshire MK45 4DT. 01525 863141
j.a.harris@cranfield.ac.uk
**Kim Harding**
Macaulay Land Use Research Institute, Craigiebuckler,
Aberdeen AB15 8QH. 01224 498200
k.harding@mluri.sari.ac.uk
**Tom Hill**
School of Biosciences, University of East London,
Romford Road, Stratford, London E15 4LZ
0208 223 4180 t.c.j.hill@uel.ac.uk
**Rob Fuller**
British Trust for Ornithology, The Nunnery, Thetford,
Norfolk IP24 2PU. 01842 750050 rob.fuller@bto.org
**Martin Jukes**
Forest Research, Alice Holt Research Station,
Wrecclesham, Farnham, Surrey GU10 4LH.
01420 22255 martin.jukes@forestry.gsi.gov.uk
**Mike Morris**
Institute of Grassland and Environmental Research, Plas
Gogerddan, Aberystwyth SY23 3EB. 01970 823137
michael.morris@bbsrc.ac.uk
**Adrian Newton**
School of Conservation Sciences, Bournemouth
University, Talbot Campus, Poole, Dorest BH12 5BB.
**Andrew Peace**
Forest Research, Northern Research Station, Roslin,
Midlothian EH25 9SY. 0131 445 2176
andrew.peace@forestry.gsi.gov.uk
**Tim Rollinson**
Forestry Commission, 231 Corstorphine Road,
Edinburgh EH12 7AT. 0131 334 0303
tim.rollinson@forestry.gsi.gov.uk

# Preface

Planted forests dominated by coniferous species such as Sitka spruce and Scots pine make up over half of the 2.8 million ha of woodland in the UK. These forests have been viewed by some as having little wildlife and even being inimical to nature conservation. However, others have suggested that such views are unduly influenced by the visual character and youthfulness of the forests.

As plantations have matured and been restructured to form diverse mosaics, so perceptions of their value for wildlife have shifted. Conservation and enhancement of biodiversity has become an important objective of much forest and rural land management, necessitating new research. In 1995 the Forestry Commission set up a project to assess biodiversity in planted forests. This publication brings together the findings of this project, demonstrates that many native species find the forest conditions to their liking, and challenges the notion that plantations are ecological deserts, or irrelevant for biodiversity. The scope for improvements in habitat quality, combined with their large area, means that planted woodland can make a significant contribution to UK biodiversity in the future as well as providing continued economic and social benefits.

The majority of papers in this publication were presented at the symposium 'Assessing Biodiversity in Britain's Forests', held in Harrogate in November 2000. The symposium brought together researchers, managers and policy-makers, with two main aims:

- To disseminate the results of the Biodiversity Assessment Project, undertaken by Forest Research; and
- To stimulate debate relating to the future management of planted forests and the identification of biodiversity indicators.

The publication is aimed at woodland managers, planners and policymakers concerned with the maintenance and enhancement of biodiversity within managed forests, particularly at the stand and habitat scales. Some of the chapters are based on more detailed papers in the scientific literature. Where this is the case, full references are given. Further valuable source material is also referenced. Participants in the symposium were encouraged to share their experiences, identify areas in which further work was required, and highlight key issues, within the framework of four separate workshops. The key points have been incorporated into the final chapter.

There are three main sections and a concluding section in these proceedings:

Section 1 **Introduction and context** reviews current international and UK forestry policies and incentives and how they relate to biodiversity conservation (Chapter 1). The origins of, and the rationale for the Forestry Commission's Biodiversity Research Programme are discussed in Chapter 2, with the Biodiversity Assessment Project itself described in more detail in Chapter 3. Chapter 4 gives an overview of the analytic methods used in the project.

Section 2 **Plant, fungal and microbial communities** comprises chapters on vascular plants (Chapter 5), the analysis of soil microbial communities (Chapter 6), deadwood volumes (Chapter 7), fungal assemblages (Chapter 8) and lichen and bryophyte communities (Chapter 9).

Section 3 **Invertebrate and bird communities** describes invertebrate assemblages recorded within and between the different forest stands in Chapter 10, while Chapter 11 gives a more general review of the effects of forest management and stand structure on forest bird communities.

Section 4 **Conclusions.** Based on the international literature, the results for the various species groups presented in Chapters 5–11 and the subsequent discussions in the four symposium workshops,

Chapter 12 presents a number of options for the future management of planted forests, and for the development of biodiversity indicators. Further research needs are also highlighted.

Following on from the Biodiversity Assessment Project, Forest Research has established a **Biodiversity Evaluation and Indicators Development Project** which aims to update and synthesise the Biodiversity Assessment Project datasets, identify potential biodiversity indicators and disseminate findings to the forest industry. Further details of this project can be obtained from the editors.

SECTION ONE

# Introduction and context

CHAPTER 1

# Introduction: the policy context for biodiversity

Tim Rollinson

## Summary

Over many thousands of years, we in the UK cleared almost all of our natural woodland cover. Our forests helped to fuel our economic development and satisfy the demands of an increasing population for timber, fuel and farm land. But we paid a price; at the beginning of the 20th century woodlands in the UK covered just 5% of the land area, and little of this resembled the natural woodland cover. In the past century a million hectares of land were reforested, increasing our forest cover to over 10%. This was a substantial achievement. Throughout this period, we have had to address the challenges of rehabilitating and restoring our woodlands and forests. Our new forests are very different from what we know of our lost natural woodlands, but they have put woodland back on the map. We are improving them and, at the beginning of the 21st century, we can hand on a *bigger* woodland legacy to the next generation. A further challenge is to make sure that it is also a *better* and truly sustainable legacy.

## The global background

In 1992 the world's leaders committed themselves to sustainable development at the United Nations Conference on Environment and Development (the Earth Summit) (UNCED, 1992). The Conference produced the world's first global agreement on how the world's forests should be managed in the *Statement of Forest Principles*. Since the Earth Summit, the UK and other European governments have built on the Rio Forest Principles and are committed to implementing:

- *The guidelines for the sustainable management of forests in Europe* – agreed at Helsinki in 1993 (Secretariat, 1993);
- *The guidelines for the conservation of the biodiversity of European forests* – also agreed at Helsinki (Secretariat, 1993);
- *The declaration and resolutions of the pan European ministerial conference on the protection of forests in Europe* – agreed at Lisbon in 1998 (Secretariat, 1998).

The Helsinki Guidelines interpreted the Rio Principles for European conditions and articulated the common concern of European countries to manage their forests sustainably. Through the Lisbon declaration, countries gave further recognition to the social and cultural importance of forestry in Europe. These international agreements are an expression of world-wide interest in sustainable forestry. Following their adoption, European countries, including the UK, have agreed a range of criteria for defining sustainable forest management and indicators for measuring progress towards it.

## Sustainable forestry in the UK

Sustainable forestry is one component of the UK Government's wider commitment to sustainable development. In 1999, the UK Government published *A better quality of life: a strategy for sustainable development in the UK* (Anon., 1999). The strategy confirmed that the Government's approach to sustainable forestry is based on better management of existing forests; the continuing expansion of the woodland area; and conservation of natural capital: biodiversity, air, soil and water. Defining sustainable forest management is complex. It results from the interaction of the three functions of forests – economic, social and environmental, as represented in Figure 1.1.

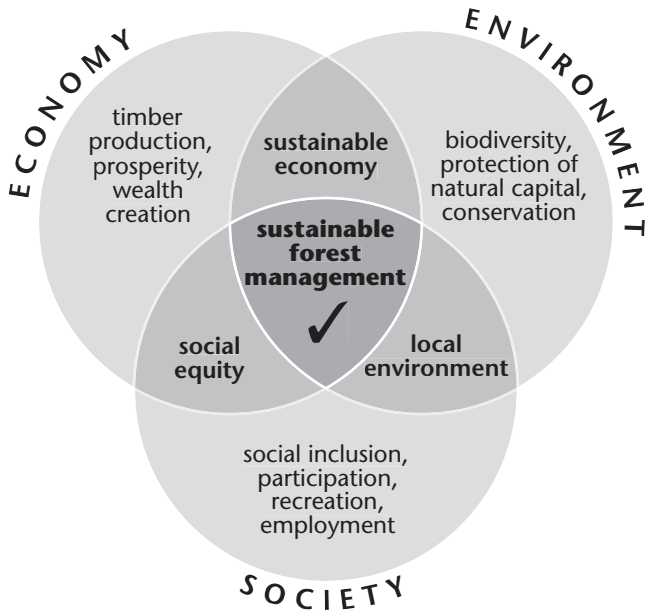


**Figure 1.1**

*A conceptual model of sustainable forest management.*

Biodiversity and the other environmental values of forests must be balanced with economic and social values in decisions about sustainable forestry. While the remnant ancient and semi-natural woodlands are the best overall for biodiversity, our maturing and restructured planted forests have an increasingly important role to play across the UK. Indeed, over the past 20 years, there has been unprecedented interest in the management of all types of woodlands and their biodiversity. Table 1.1 below gives examples of some of the policy and practice initiatives introduced in recent years which are relevant to the management of biodiversity within planted forests.

**Table 1.1**

*Some policy and practice initiatives relating to woodlands.*

| Year of publication | Initiative |
|---|---|
| 1990 | Forest nature conservation guidelines |
| 1996–8 | Habitat and species action plans |
| 1998 | UK Forestry Standard |
| 2000 | Forests and water guidelines 3rd edition |
| 2000 | Forests and Peatlands guidelines |
| 2000 | UK Woodland Assurance Standard |

## The UK Forestry Standard

A cornerstone of the Government's commitment to sustainable forest management is the *UK forestry standard* (Forestry Commission, 1998). The standard provides a single, comprehensive statement of the Government's approach to sustainable forestry in the UK. It explains how the principles of sustainability will be delivered in practice and lists the criteria and indicators for the sustainable management of all forests in the UK. The standard includes guidance on a range of forest management practices including the felling and restocking of planted woodland, management of existing woodland, and the planting and management of new woods.

## The UK Biodiversity Action Plan and forestry

The Government published *Biodiversity: the UK action plan* (UKBAP) in 1994 (Forestry Commission, 1994). The overall goal is to 'conserve and enhance biological diversity within the UK and to contribute to the conservation of global biodiversity through all appropriate mechanisms'. The emphasis is on partnership between public and private sector and NGOs at local, regional and national levels, and across sectors. The UKBAP lays emphasis on integrating biodiversity conservation

measures into all sectors of economic activity so that it becomes part of sustainable development. In addition priority species and habitats have been defined and are subject to multi-agency and cross-sectoral action plans. The focus of attention has now shifted to implementation of the Biodiversity Action Plan targets throughout the UK (Anon., 1995).

## Delivery

The development and publication of the *UK forestry standard*, *UK biodiversity action plan* and *UK woodland assurance standard*, together with the introduction of a range of schemes and incentives to encourage delivery on the ground has resulted in substantial changes in the way that plantations are designed and managed. In particular, the publicly owned forests managed by Forest Enterprise in England, Scotland and Wales, are currently undergoing a massive transformation. The large post-war forests, established as predominantly even-aged conifer plantations, are being redesigned. This involves diversifying age classes through planned, sequential felling followed by replanting and natural regeneration using a wider range of species, including a higher proportion of native broadleaves. Some stands of timber will be managed using silvicultural systems which avoid clear felling and encourage natural regeneration, for example through continuous cover systems of management. Areas of forest will be left unplanted as important open habitats to link key sites and encourage wildlife to move through the forest landscape. Forest Enterprise has recognised the importance of such landscape scale changes to forest structure, but increasingly managers are turning to the equally important 'midi' and 'micro' scale aspects of management which will enhance forest ecosystems and therefore biodiversity. Measures at these scales include diversifying stand structure, rehabilitating riparian zones and increasing the amount of deadwood.

In tandem with the diversification of the national forest estate has come a much greater awareness of the potentially damaging effects that some existing coniferous plantations can have on open-ground communities such as heathland and mires. Guidelines have been developed to help prevent further damage to valuable open habitats and to encourage restoration of areas previously planted with conifers. Native woodlands are being restored to semi-natural woodland on a large-scale across Britain. In addition, proposals for new plantations are subjected to rigorous environmental scrutiny and environmental assessments carried out when potential threats to biodiversity are identified.

## Working together

Real progress has been made in recent years in delivering a range of policies for the enhancement of biodiversity in planted forests. We have learned that the greatest progress will be made where research, policy, regulation, incentives and published guidance are made to work together effectively. This requires: a shared understanding of the issues and barriers to progress; flexibility of approach to accommodate the needs of many stakeholders; resources to deliver desirable programmes; and a more 'joined-up' approach, with stakeholders working together and not solely to their own agendas.

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CHAPTER 2

# An introduction to biodiversity research

Chris Quine

## Summary

The origins of the Biodiversity Assessment Project, which is the topic for the remainder of the publication, are described and placed in context. The Biodiversity Research Programme (BRP), of which the Assessment Project was a major component, was part of the Forestry Commission's response to the UNCED Rio Summit. The BRP sought to bridge the gap between policy developments, and management by providing sound information based on research.

The Assessment Project has provided a baseline understanding of the biodiversity of representative planted forests. Increasingly, attention is being given to the impact of forest management activities, the needs of special habitats and species and the planning of biodiversity at the landscape-scale.

## Introduction

In response to the UNCED Rio summit, the Forestry Commission introduced a Biodiversity Initiative (Ratcliffe, 1993) to develop a biodiversity policy for the management of forests supported by a multi-disciplinary biodiversity research programme. The particular objectives were to identify methods for improving biodiversity in managed forests, and to develop standards for managed forests.

The FC Biodiversity Policy has since been summarised (Forestry Commission,1998) as to:

- Conserve and where practical enhance the overall populations and natural ranges of native species, and the quality of wildlife habitats and ecosystems within woodlands.
- Contribute to the conservation and enhancement of internationally and nationally important and threatened species, habitats and ecosystems and of natural and managed habitats which are characteristic of local areas.
- Increase public awareness of and involvement with woodland biodiversity conservation.

Initial standards have also been summarised (Forestry Commission, 1998), elaborated in voluntary schemes (UKWAS, Anon., 2000), and a new suite of Biodiversity Guidelines are in preparation.

## Biodiversity research

The Biodiversity Assessment Project was the major component of the initial Biodiversity Research Programme (BRP). The purpose of the project was to provide a baseline for biodiversity in planted forests, develop methods of measuring biodiversity, and inform standards and more general policy development. Research into biodiversity necessarily involves a range of skills and techniques. The project brought together scientists with diverse interests, including Forestry Commission staff, specialist contractors, and PhD students through collaboration with institutes in Britain and abroad.

As knowledge has increased, and managers have identified new aspects of biodiversity requiring research, other projects have developed; these will assume greater prominence in the future. Brief details of these research areas – developing methods of enhancing biodiversity, and catering for the needs of special species and habitats – are given below and summarised in Table 2.1.

So far it has rarely been possible to proceed by formal experimentation. Much of the initial work has relied upon review of existing literature, primary survey or monitoring. Only after this work has refined our understanding of the problems, is it possible to consider the application of demonstration projects or full experimentation. A variety of other outputs have been developed, including technical papers and seminars for practitioners, and scientific and conference papers to inform other scientists. There is increasing demand, where knowledge is well advanced, to integrate findings into decision support tools.

## Management for special species and habitats

The conservation of special species and habitats is widely held to be desirable, and their protection is the target of domestic legislation and European Union directives (Chapter 1). Research is required to understand the specific requirements, identify the influence of forest management and identify beneficial activities.

There have been three strands to this research (Table 2.1):

- Genetic conservation, in particular the use of native tree species, and the benefits of locally-adapted trees.
- Special species, in particular species dependent upon woodland habitats, and the subject of UK Species Action Plans (Anon., 1995).
- Special habitats, in particular native woodland and important semi-natural open habitats found in close proximity (or within) forests, and the subject of UK Habitat Action Plans (Anon., 1995).

## Management to conserve and enhance biodiversity

Managed forests can provide important habitats for a range of native species. Stand management, and the resultant structure, can have an important influence on this biodiversity. Some of the beneficial features of existing stands have been obtained accidentally, but there is an opportunity for planned provision to enhance their value – for example through tree species diversity, open space, stand retention, and incorporation of deadwood (Table 2.1). The control of effects of potentially damaging species (such as the grey squirrel and deer) is important, but some grazing may also have a beneficial effect.

## An integrated approach at the landscape scale

Recently, there has been an acknowledgement that biodiversity conservation and enhancement requires planning at scales greater than the individual stand. In addition, the focus of forest planning has increased in scale, through development of strategic, long-term and forest design plans. The ability to conduct such work has benefited from the rapid developments in, and adoption of, geographic information systems (GIS). Landscape-scale solutions are required to meet the needs of special species, restore the best examples of native woodlands and gain benefits of biodiversity from the management of productive forests (Table 2.1). The Forestry Commission has developed an Ecological Site Classification to ensure that productive species and new native woodlands are placed on appropriate sites. The potential for ESC to be combined with knowledge of natural disturbance regimes to provide new processes of forest design has been explored. Most recently, the importance of the mosaic of habitat types, and the needs of special species has been combined in a landscape ecology research project.

**Table 2.1** *Main strands of Forestry Commission biodiversity research, with example publications.*

| General theme | Topics | Subjects |
|---|---|---|
| Needs of special species and habitats | Genetic conservation | *Conservation of genetic resource* (Ennos *et al.*, 2000) |
| | | *Use of local origins* (Herbert *et al.*, 1999) |
| | Special habitats | *Restoration of native pinewoods and oakwoods* (Humphrey and Nixon, 1999) |
| | | *Peatland restoration* (Patterson and Anderson, 2000; Anderson, 2001) |
| | Special species | *Red squirrel* (Pepper and Patterson, 1998) |
| | | *Raptors* (McGrady *et al.*, 1997; Petty, 1998) |
| Habitat management and enhancement | Tree species diversity | *Inclusion of broadleaves* (Humphrey *et al.*, 1998a) |
| | Impacts of herbivores | *Grazing* (Humphrey *et al.*, 1998b; Mayle, 1999; Gill, 2000) |
| | Encouragement of structural diversity | *Deadwood* (Ferris-Kaan *et al.*, 1993; Hodge and Peterken, 1998; Humphrey *et al.*, 2002); *Silvicultural systems* (Kerr, 1999) |
| Integrated research at the landscape scale | Landscape and sites | *Selection of suitable sites for woodlands – Ecological Site Classification* (Ray, 2001; Pyatt *et al.*, 2001) |
| | Mimicking natural processes | *Natural disturbance regimes* (Quine *et al.*, 1999; Quine *et al.*, 2002) |
| | Landscape ecology | *Landscape ecology* (Ferris *et al.*, 2000; Bell, 2003; Humphrey *et al.*, 2003) |

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CHAPTER 3

# The biodiversity assessment project: objectives, site selection and survey methods

Jonathan Humphrey, Richard Ferris and Andrew Peace

## Summary

The background to, and the objectives of, the Biodiversity Assessment Project are presented, together with an overview of the project methodology. The rationale for selection of sites and the types of biodiversity assessed is described together with illustrations of crop types and plot design. Fifty-two permanently marked plots were surveyed in total, covering a range of different crop and site types in three contrasting bioclimatic zones (upland, foothills and lowlands). Assessments were carried out over a 2–4 year period at each site and covered: structural aspects of biodiversity (e.g. vertical foliage cover and deadwood); taxa important in ecosystem functioning (e.g. fungi); and a range of different groups which make up the 'compositional' aspect of biodiversity (e.g. higher and lower plants, invertebrates). A chronosequence of four different stand stages was replicated twice for each crop type in each climate zone. The stages were: pre-thicket (age 8–10 years); mid-rotation (20–30 years), mature (50–80 years) and over-mature (70–250 years), selected to encompass the normal range of stand structures generated by patch clearfelling. Additional plots were established in semi-natural woodland to allow comparisons between the biodiversity of plantations and native stands. Summary data for stand structure, soil and climate are presented as a reference source for subsequent chapters.

## Introduction

The Biodiversity Assessment Project was established in 1995 in support of Forestry Commission policies relating to the conservation and enhancement of biodiversity in UK forests (Chapter 2). The primary focus of the assessment project was productive conifer forest, which at 1.54 million ha currently comprises 6.7% of the total UK land area (Anon., 1998). The majority of these forests have been established within the past 100–150 years, usually on previously unwooded ground (Hodge *et al.,* 1998), but occasionally through conversion of ancient semi-natural woodland (Spencer and Kirby, 1992). Opinions differ as to the potential value of these 'new forests' for biodiversity. Attention has often been drawn to deleterious effects on the flora and fauna of the habitats which forestry replaces or modifies (e.g. Ratcliffe and Thompson, 1989), but there have also been a number of studies which have highlighted the positive value of planted forests for wildlife (e.g. Petty *et al.*, 1995; Ratcliffe and Claridge, 1996). However, these studies have been mostly site specific, and there have been no comparative studies of plantations of different crop species in contrasting bioclimatic zones, or on a range of varied site types. Similarly, there have been few attempts to compare the biodiversity of planted forests with that of native or semi-natural woodlands. This base-line information is needed to provide a quantitative framework for understanding the levels/types of biodiversity currently found in plantations, and to offer a way of measuring future improvements, or otherwise, in biodiversity brought about by changes in management practices.

Assessing biodiversity is an extremely difficult task, as it is rarely cost-effective or practical to conduct a complete census of all taxa within a forest stand, let alone an entire catchment or forest landscape. Therefore, the identity of biodiversity 'indicators' or surrogate measures of biodiversity has become a research priority in recent years (Ferris and Humphrey, 1999). Indicators are species or features whose presence, magnitude or abundance are believed to reflect the occurrence and abundance of other species in the community (Simberloff, 1998). Ferris and Humphrey (1999) have proposed a number of easily measurable indicators which could be used by forest managers to assess biodiversity at the

forest stand scale (1–50 ha). Examples include: deadwood, vertical stand structure and the occurrence of particular tree species such as birch (*Betula* spp.). However, the link between such indicators and wider biodiversity has not be substantiated in British forests to the same degree as in other countries.

The objectives of the Biodiversity Assessment Project were therefore to:

- Obtain base-line information on the types/levels of biodiversity in planted forests.
- Evaluate the contribution of planted forests to the conservation of native flora and fauna through comparisons with semi-natural woodlands.
- Identify potential biodiversity indicators by relating the diversity of range of measured taxa to soil, climate, vegetation and stand structure variables.

## Site selection

Assessments were conducted within planted conifer forests managed by clearfelling (when stands are approximately 40–80 years old) and restocking, essentially the 'normal' silvicultural practice for commercial forests (Hibberd, 1991). Extensive 'restructuring' of these forests over the last 10–20 years in response to landscape considerations has created a patchwork of different stand ages/stages, including stands retained beyond normal economic felling age for amenity purposes or as 'natural reserves' (McIntosh, 1995; Anon., 2000). To encompass the structural variability generated by restructuring, a chronosequence approach was adopted, following Spies (1991) and Pollard (1993). This approach allows comparisons to be made between stands of different ages without the necessity for monitoring over long time periods within individual stands. However, a number of provisos must be adopted – stands should have similar soils, climate, altitude and site history and be located on comparable topographies.

In total, 52 assessment plots were sampled over a 4-year period (Figure 3.1). These were stratified initially by bioclimatic zone following the Forestry Commission's Ecological Site Classification (ESC – Pyatt *et al.*, 2001). The zones were uplands, foothills and lowlands, delineated by annual rainfall totals of: >1500 mm – uplands; 800–1500 mm – foothills; and <800 mm – lowlands. Study sites were established in the main commercial crop types found with each bioclimatic zone: Sitka spruce (*Picea sitchensis* (L.) Bong. Carr.) in the uplands; Sitka spruce and Scots pine (*Pinus sylvestris* L.) in the foothills; Scots pine, Corsican pine (*Pinus nigra* var. *maritima* L.), and Norway spruce (*Picea abies* (L.) Karst.) in the lowlands. Two replicate sites were selected for each species x bioclimatic zone combination. To minimise edge effects and the influence of non-forest habitats, sites were chosen from within large forest blocks.

At each site, a chronosequence of 1 ha (100 m x 100 m) sample plots (each with a 30 m buffer) was established in forest stands in different developmental stages (with one plot per stage):

- Pre-thicket – restock sites, crop height 2–4 m, age 8–10 years, incomplete canopy closure.
- Mid-rotation – crop height 10–20 m, age 20–30 years, canopy closure, no understorey.
- Mature – crop height 20–25 m, age 50–80 years, canopy closure, some development of understorey layers.
- Over-mature (beyond economic maturity and acquiring some of the ecological characteristics of natural old-growth forests *sensu* Oliver, 1981) – crop height >25 m, age 60–250 years, canopy break-up, well-developed understorey layers, accumulation of deadwood.

Stage 4 stands were not available in some of the lowland crop types and in the foothills Scots pine chronosequences. In the latter case, over-mature plots were set up in self-seeded 'old-growth' semi-natural pinewood areas. These represent modified remnants of the original natural boreal forest in Scotland (Worrell, 1996). In the uplands and lowlands, semi-natural oakwood plots were established for comparison with the conifer stands. Only stages 2 and 3 were available in the oakwoods owing to a lack of large areas of newly regenerating oak and lack of very old stands (as a consequence of past management). The full set of site details is recorded in Annexe 1.

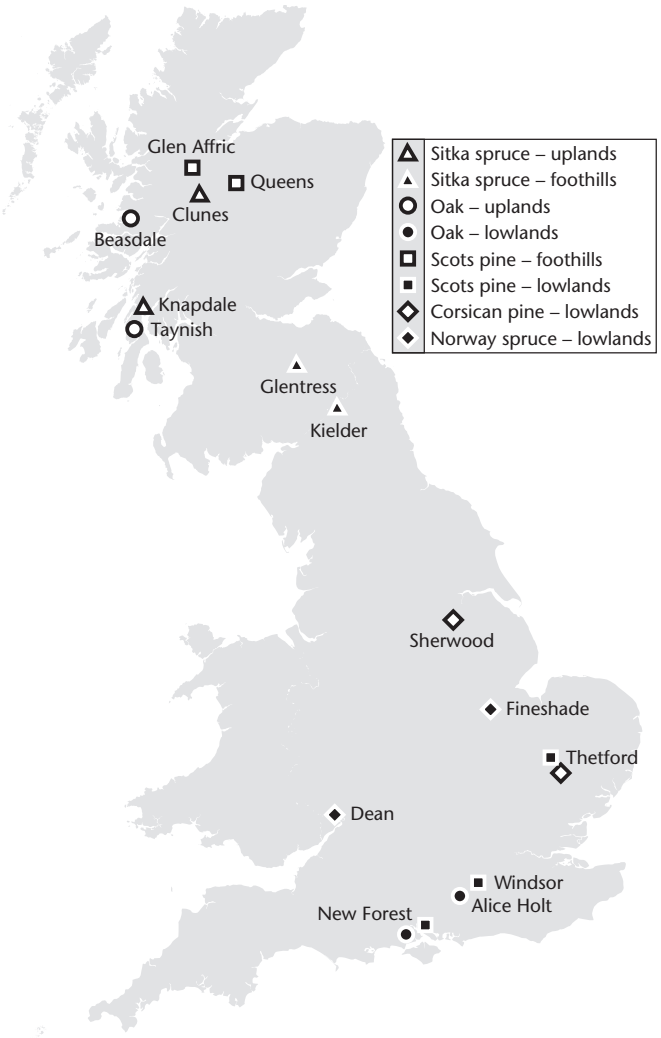


**Figure 3.1**

*Location of Biodiversity Assessment plots; 52 plots were sampled in total over a 4-year period.*

Locating suitable assessment sites according to the chronosequence rules proved to be more difficult than anticipated. Few stands were homogeneous in terms of site and crop parameters; with over-mature stands of a suitable size (2.5 ha) being very rare. The search strategy adopted was to locate over-mature stands first and then search for the three younger stages on the same site types as nearby as possible. Inevitably, suitable stands were not always found within the immediate vicinity (e.g. Knapdale – site 5.3; Windsor – site 4.4, see Annexe 1). In addition, it was impossible to select sites with the same site history and rotational age. The majority of pre-thicket plots were located in second rotation stands, but all mature and over-mature stands were first rotation. The consequence of these compromises in the site selection criteria is discussed in relation to the analyses of individual species groups (see Chapters 5–11).

## Assessment methods

Plots were selected to minimise internal heterogeneity in terms of stand structure, species composition, topography and hydrology. A standardised system of assessment stations was established to maximise potential comparisons between measured attributes and to minimise disturbance during sampling (Figure 3.2). The plots were permanently marked. Features and species groups were selected for assessment on the basis of:

- The 'structure-function-composition' model of biodiversity (Schulze and Mooney, 1994; Figure 3.3). This model rationalises biodiversity into compositional aspects (e.g. species), structure (e.g. physiognomy of forest stands and associated habitats) and function (processes such as natural regeneration, nutrient and carbon cycling).

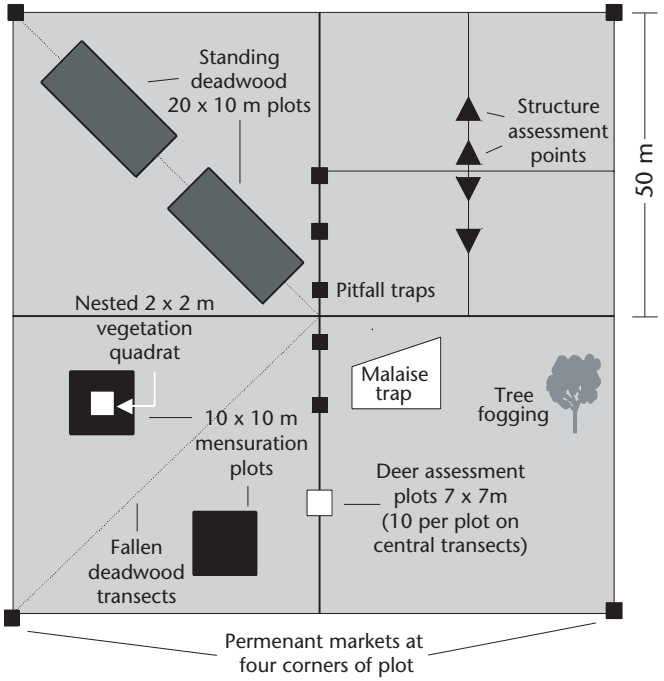


**Figure 3.2**

*Basic layout of 1 ha assessment plot. The mensuration, vegetation, stand structure and deadwood quadrats and transects were replicated within teach 50 x 50 m quadrant.*

- Practicality: the cost, and availability of taxonomic expertise were taken into consideration together with the need to identify features readily measurable by field staff.

- Ecology: species groups with wide ecological amplitude and where possible known habitat requirements were prioritised over more site-specific groups to allow comparisons between sites and stands.

A list of the main assessments stratified by the 'structure-function-composition' model is given in Figure 3.3. The full list of assessments is given in Table 3.1 with a quick overview of the assessment methodologies. Methodologies for the site and stand assessments are outlined in detail below. More details of the survey methods for individual taxonomic groups can be found in the relevant chapters. Pilot surveys of deer, songbirds and small mammals were conducted on an initial subset of plots to determine practicality of assessment methods. Deer densities were estimated from fecal pellet counts (following Mayle *et al.*, 1999). However, at the scale of 1 ha this method is not thought to provide

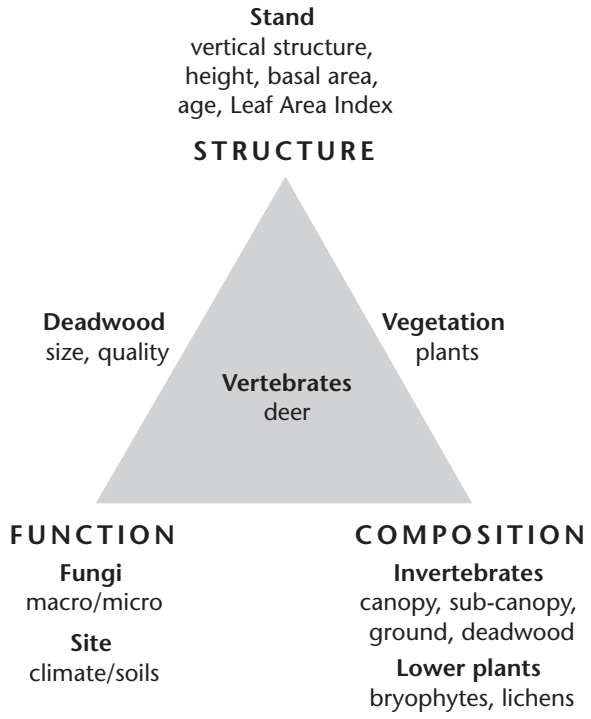


**Figure 3.3**

*Theoretical model of biodiversity attributes used to stratify selection of features and taxa to assess.*

**Table 3.1** *Assessments and summary of assessment methodologies. Locations of sampling stations are given in Figure 3.1.*

| Feature/taxonomic group | Assessment methodology |
|---|---|
| Climate variables | Output from ESC-DSS (see section below) |
| Soil chemistry and litter depth | One soil pit dug per 1 ha plot and described, chemical analysis of two strata – 32 bulked samples per strata per 1 ha sample plot (see section below). Mean litter depth/ha estimated from 32 random samples (four in each mensuration plot) |
| Vertical structure | Per cent cover of foliage estimated in four vertical strata – ground, shrub, lower and upper canopy layers – at 16 sampling points (see section below) |
| Leaf Area Index | Estimated from light measurements along transects with each 1 ha plot (see section below) |
| Mensuration | Diameter at breast height, height to live crown, height of all trees within the eight 10 m x 10 m plots (see section below) |
| Natural regeneration of seedlings (< 1.3 m in height) | Height of all seedlings recorded in 10 randomly located 40 cm x 40 cm plots within each mensuration plot (data not yet analysed) |
| Soil seed banks | One sample per plot bulked from collections in each mensuration plot (data not yet analysed) |
| Ground vegetation (bryophytes, lichens and vascular plants) | Per cent cover and frequency in 2 m x 2 m quadrats nested within the eight 10 m x 10 m mensuration plots (details in Chapter 5) |
| Soil microbial communities | Thirty-two soil samples taken from each 1 ha plot, four in each mensuration plot (details in Chapter 6) |
| Deadwood: fallen (logs), standing (snags) and stumps | Volume and length of logs recorded on two diagonal transects using the line intercept method (Warren and Olsen, 1964), volume of snags and stumps recorded in eight 20 m x 10 m plots (details in Chapter 7) |
| Macrofungi | Frequency and abundance of fruiting bodies recorded 3 times yearly over 4 years in each mensuration plot (details in Chapter 8) |
| Bryophytes and lichens growing on deadwood | Species frequency and abundance estimates on individual pieces of deadwood (details in Chapter 9) |
| Invertebrates: sampling stratified by ground, sub-canopy, canopy strata and deadwood | Five pitfall traps/ha, one malaise trap/ha, one tree fogged, deadwood emergence traps (details in Chapter 10) |
| Songbirds | Point counts within and adjacent to each 1 ha plot, plus territory mapping (details in Chapter 11) |
| Small mammals | Live capture/release using paired longworth traps (data not analysed) |
| Deer | Densities estimated from ten 7 m x 7 m fecal pellet group clearance plots per 1 ha (data not analysed) |

reliable estimates of population densities (Gill, 2000), so no interpretation of these datasets has been undertaken within this publication. Scale is also a problem with interpretation of the songbird data, bird territories range to a much greater spatial scale than 1 ha, and the problems associated with the sampling method are discussed more fully in Chapter 11. Finally, small mammal sampling was abandoned after only one year owing to excessive costs and logistical difficulties.

### Assessment of climatic variables

The climate data were obtained from datasets held within the ESC computer-based decision support system (ESC-DSS – Ray, 2001). For both accumulated temperature (AT) and soil moisture deficit (MD), 30-year means have been calculated for all 10 km squares throughout Great Britain using meteorological data collected over the 1961–1990 period (Barrow *et al.*, 1993).

AT expresses the degree of warmth or available heat energy (Bendelow and Hartnup, 1980) and is measured by the number of days-degree above 5ºC. MD is expressed as the maximum accumulated amount that monthly potential evaporation exceeds precipitation (Bendelow and Hartnup, 1980), and is essentially a measure of climatic wetness/dryness. The 'Detailed Aspect Method of Scoring' (DAMS) wind score is an index developed by Quine and White (1993), which measures the physiologically constraining effect of wind on tree growth and mortality (and hence may link with deadwood accumulations). DAMS calculations involve a windiness map, elevation, topex and aspect. Continentality expresses the seasonal variation or range of climate. Oceanic areas tend to have cool summers and mild winters, whereas continental areas exhibit more extremes of warmth and cold. This factor helps shape the length of the growing season (although it was not included as an environmental parameter within any of the subsequent analyses).

The digitised climate data did not become available until after the plots had been assessed, and with hindsight it is clear that annual precipitation totals have not been a particularly good indicator of differences in climate between sites, as AT, MD and DAMS vary on a site by site basis rather than at the zonal scale (Annexe 1). The most pronounced differences in climate were between northern (foothills and uplands) and southern sites (lowlands) with few differences in mean values between foothills and upland sites. The analyses of the various taxonomic groups described in subsequent chapters were therefore interpreted in terms of this north-south division where appropriate.

### Stand structure and mensuration assessments

Two 10 m x 10 m quadrats were arranged diagonally across the centre of each 50 m x 50 m quarter of the 1 ha plot, giving eight quadrats in total per plot. Within these quadrats, assessments of dbh, height to the base of the live crown (HTLC), and top height (TOPHT), were made by species, for all living trees ≥ 7 cm dbh. In those plots where stocking density was low (e.g. stage 4 stands), the quadrats were extended (proportionately from each corner) to 25 m x 25 m to obtain a sufficient sample of trees. Mean basal area (MBA) was calculated for each 1 ha plot following Hamilton (1975). Vertical stand structure was assessed using a visual cover method within each 50 m x 50 m quarter of the 1 ha assessment plot. Four measurements, each 10 m apart were made along a north-south transect, running through the centre point of each quarter, yielding 16 measures in total for each 1 ha plot (Figure 3.2). Four vegetation strata were defined: S1 (field) 10 cm –1.9 m in height; S2 (shrub) 2–5 m; S3 (lower canopy) 5.1–15 m; and S4 (upper canopy) 15.1–20 m. Percentage cover of vegetation within each vertical stratum was described to the nearest 5% and expressed as a mean of the 16 stand structure measures. To convert these cover values to a unified measure of stand structure, a cover index (CI) was calculated using the formula:

$$CI = 1.9s_1 + 3s_2 + 10s_3 + 5s_4$$

where $s_1 - s_4$ are the values for field, shrub, lower canopy and upper canopy strata, and numbers refer to the depth of each stratum in metres. The C.I. therefore ranges in possible values from 0–1990 (assuming a maximum cover value of 100% in each layer). Summary statistics for stand structure and mensuration data are shown in Table 3.2.

### Leaf area index

Measurements of photosynthetically active radiation (PAR) were taken under diffuse light conditions at 5 m intervals, along two diagonal transects across each assessment plot. For this purpose, a hand-held sunfleck ceptometer (Decagon Instruments, USA) with an 80 cm probe was used, held at a height of approximately 1.5 m above the ground. A second, calibrated probe was placed outside the assessment plot, in a clearing not obscured by trees. Sets of five readings were taken simultaneously at 30 second intervals with both probes, averaged and then recorded. The data were converted to Leaf area index (LAI) values using the canopy radiation model of Goudriaan (1988) for diffuse light conditions. Under these conditions of incident light ($PAR_{inc}$), only LAI and the light extinction coefficient ($K$) determine canopy light absorption ($PAR_{abs}$) i.e. ($PAR_{abs}=PAR_{inc}(1-e^{(-K*LAI))}$). Summary statistics for the LAI are shown in Table 3.2.

### Soil and litter sampling

Soil samples were taken from the four corners of the eight 10 m x 10 m plots (i.e. 32 locations per 1 ha plot) at two depths: 0–5 cm and 5–10 cm in depth. The samples were bulked to give one sample

**Table 3.2** *Summary of soil, climate, and stand data. SD: standard deviation.*

| Variable | Description | Max. | Min. | Mean | SD |
|---|---|---|---|---|---|
| pH1 | pH – layer 0–5 cm | 5.3 | 3.3 | 4.1 | 0.5 |
| P1 | Soil phosphorus (mg $l^{-1}$) – layer 0–5 cm | 45.5 | 0.6 | 12.9 | 11.5 |
| K1 | Soil potassium (mg $l^{-1}$) – layer 0–5 cm | 704.0 | 19.6 | 161.5 | 140.7 |
| Mg1 | Soil magnesium (mg $l^{-1}$) – layer 0–5 cm | 982.0 | 9.4 | 204.2 | 207.2 |
| Ca1 | Soil calcium (mg $l^{-1}$) – layer 0–5 cm | 2 499.0 | 47.5 | 514.7 | 554.6 |
| ORG1 | Soil organic matter content (%) – layer 0–5 cm | 95.1 | 2.9 | 46.8 | 31.3 |
| $NH_4$1 | Soil ammonium (mg $kg^{-1}$) – layer 0–5 cm | 373.0 | 8.0 | 111.2 | 97.8 |
| $NO_3$1 | Soil nitrate (mg $kg^{-1}$) – layer 0–5 cm | 164.0 | 0.0 | 17.3 | 36.0 |
| pH2 | As above – layer 5–10 cm | 7.9 | 3.6 | 4.3 | 0.8 |
| P2 | As above – layer 5–10 cm | 33.5 | 0.1 | 5.8 | 8.8 |
| K2 | As above – layer 5–10 cm | 415.0 | 6.7 | 84.6 | 95.4 |
| Mg2 | As above – layer 5–10 cm | 456.0 | 3.8 | 98.9 | 121.7 |
| Ca2 | As above – layer 5–10 cm | 35 270.0 | 17.2 | 1 042.4 | 6 683.7 |
| ORG2 | As above – layer 5–10 cm | 84.9 | 0.7 | 17.0 | 22.8 |
| $NH_4$2 | As above – layer 5–10 cm | 346.0 | 2.5 | 42.8 | 81.4 |
| $NO_3$2 | As above – layer 5–10 cm | 79.5 | 0.0 | 7.5 | 17.6 |
| AT | Accumulated temperature (no. day-degrees > 5°C) | 2 002.0 | 771.0 | 1 405.7 | 370.5 |
| MD | Soil moisture deficit (mm) | 225.0 | 24.0 | 128.7 | 63.5 |
| DAMS | Windiness/exposure | 18.0 | 10.0 | 13.4 | 2.1 |
| S1 | Vertical cover field layer (%) | 72.6 | 0.0 | 17.3 | 21.0 |
| S2 | Vertical cover shrub layer (%) | 40.9 | 0.0 | 4.7 | 8.2 |
| S3 | Vertical cover lower canopy layer (%) | 52.5 | 0.0 | 12.9 | 14.4 |
| S4 | Vertical cover upper canopy layer (%) | 31.6 | 0.0 | 7.2 | 9.6 |
| CI | Cover Index | 651.6 | 34.0 | 211.8 | 163.8 |
| TOPHT | Top height (m) | 32.9 | 2.1 | 15.4 | 7.5 |
| HTLC | Height to live crown (m) | 17.9 | 0.0 | 7.5 | 5.1 |
| MBA | Mean basal area ($m^2$ $ha^{-1}$) | 60.0 | 0.0 | 27.7 | 15.7 |
| LAI | Leaf area index | 10.2 | 0.5 | 2.7 | 1.9 |
| TREESP | No. of tree species per plot | 9.0 | 1.0 | 3.5 | 2.2 |
| AGE | Crop age (years) | 238 | 6.0 | 59.6 | 49.8 |
| LITTER | Litter depth (to nearest 0.5 cm) | 8.0 | 0.0 | 2.9 | 2.0 |

for each depth per plot. Available P, K, Ca and Mg were obtained by extraction, using 0.5 M ammonium acetate/acetic acid solution at pH 4.5, following a modification of Morgan's method (Morgan, 1941). Mineralised N (in $NH_4^+$ and $NO_3^-$ form) was determined before and after a 28 day incubation period at 30°C following the ADAS/MAFF method (Anon., 1986); pH was determined in aqueous solution using the MLURI/SAC method (Anon., 1985). Organic matter content was determined by loss on ignition. Litter depth was recorded in each 10 m x 10 m vegetation assessment plot by taking a mean of four random measurements. Summary values for soil chemistry, and litter depths are in Table 3.2.

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CHAPTER 4

# The use of multivariate statistics – a brief introduction

Andrew Peace

## Summary

Community ecologists can explore the ways in which abiotic environmental variables influence biotic composition by way of multivariate statistical techniques. One commonly used set of multivariate techniques is called ordination where sample plots are arranged along environmental gradients on the basis of their species composition. A brief description is given of the ordination methods used to interpret the data collected as part of the Biodiversity Assessment Project. The outputs from the various ordination analyses are described in Chapters 5–10.

## Introduction

The assessment phase of the Biodiversity Research Project has resulted in tens and often hundreds of species being recorded within individual components of the study. As a consequence, one key aim of the statistical analyses of these datasets has been to discover and summarise the main patterns of variation in the species community data, and relate these to sets of environmental variables recorded at each sample plot. Analyses of complex community datasets benefit from the use of specific multivariate statistical techniques. One such technique, that allows inferences to be made on the relationship between plant and animal communities and their environment, is known in general terms as ordination.

Ordination is simply the arrangement or 'ordering' of species and/or sample units along environmental gradients. Its purpose is to interpret patterns in species composition. Basically it summarises community data by reducing the high dimensionality of the original dataset (one dimension for each recorded species) to a lower dimensional ordination space in which ecologically similar species and samples are plotted close together, and dissimilar species and samples are placed far apart. The benefits of using ordination methods include:

- Relationships within datasets containing a large number of sites and species are virtually impossible to visualise or interpret before reduction to low-dimensional space.
- Axes of this low-dimensional space will, more often than not, represent important and interpretable environmental gradients.
- By focusing on a few important dimensions there is less risk of interpreting 'noise'.
- Environmental gradients can be ordered in terms of importance.
- Graphical outputs from ordination analyses can greatly assist the interpretation of species-environment relationships.

Ordination methods are most often applied to matrices of community data. A matrix of this type normally has rows which are species names, columns which are quadrats, sites or transects and elements (values) that contain species abundance measures such as presence/absence, counts and percentage cover.

A community data matrix tends to share several common properties whatever taxa are being recorded:

- A large part of the data matrix will contain zeros as many species are found infrequently.
- There is much redundant information as species often share similar distributions. For example the abundance of *species y* may act as a predictor for the abundance of *species z*.

- The number of factors influencing species composition is potentially very large, although typically there are not many important factors. A few factors can explain the majority of the variation in species abundance.
- There will be 'noise' in the data. Replicates are often quite variable and observer differences can create additional variability.

Several different ordination techniques can be used on a community matrix to unravel its ecological patterns. Each method differs slightly in the mathematical approach used and can be placed into one of two groups: 'direct methods' or 'indirect methods', depending on whether environmental data have also been recorded at each sampling plot. Within either group, a suitable ordination technique should be able to filter out the 'noise' component of the community data matrix and identify the few important dimensions defining the inter-relationships between samples, species and the environment. A brief description of the most commonly used methods is given below. Further details can be found in the suggested further reading (see page 21).

## Indirect ordination methods

Ordinations by indirect gradient analysis use only the species by sample community matrix. Gradients are formed from species associations and are unconstrained by any environmental data that may or may not have been collected. If there is any information about the environment it is used after the indirect gradient analysis, simply as an interpretative tool.

## Principal Component Analysis (PCA)

PCA involves the transformation of a data matrix of *p* variables into a set of *p* principal components. Each principal component is a linear combination of the original variables, computed in such a way that the first principal component accounts for the largest amount of variation in the original data. Subsequent components are computed to be uncorrelated with previous components while accounting for the maximum amount of the remaining variation in the data. All of the original variance is accounted for after all the PCA axes have been computed.

PCA can be extremely useful in interpreting environmental data matrices which contain variables that are measured in different units such as mean basal area, top height, % litter and leaf area index. In PCA these variables are standardised to zero mean and unit variance before analysis. Resulting axes can be used as input variables in subsequent ordinations (see Chapter 5 for an example).

## Correspondence Analysis (CA)

CA is based on the assumption that each species exhibits a **unimodal** response to the underlying environmental gradients. A unimodal model requires there to be a unique set of optimal conditions for a species to occur at maximal abundance and as conditions differ from this optimum, abundances in this species will decrease. Mathematically, CA maximises the correspondence between species scores and sample scores. For the first axis, species and sample scores are estimated such that the weighted correlation between the two is maximised, where weighting is the abundance of the species. Resulting axes species scores can be interpreted as estimates of the unimodal peaks for those species.

## Direct ordination methods

In direct gradient analysis, species are directly related to a set of explanatory variables. These are usually environmental variables which were thought to influence the ordering of the observed species distributions. Direct analysis tells us if species composition is related to our measured environmental variables as axes are constrained to be linear combinations of the measured environmental variables.

### Canonical Correspondence Analysis (CCA)

As with CA, CCA assumes that species responses are bell-shaped curves along environmental gradients. Sample scores are constrained to be linear combinations of the environmental variables. If a combination of environmental variables is strongly related to the species composition, CCA will use these environmental variables to create an axis in which the species response curves are separated. Further axes can be formed in a similar manner, each being orthogonal to all previous axes.

The usefulness of any CCA output is dependent on the quality of the chosen explanatory variables. One must have recorded important environmental variables. Even then, underlying gradients may be related to unmeasurable factors.

## Interpretation of ordination scatter plots

As species and samples are ordinated simultaneously they can be represented in the same ordination diagram known as a biplot. In CCA the inclusion of environmental variables into the same space creates a triplot.

- The ordination diagram graphically represents the community structure.
- The direction of the axes (e.g. left vs. right; up vs. down) is arbitrary and has no influence on any interpretation.
- The numeric scale of the axes do not generally aid interpretation.
- Samples tend to be dominated by species that are located near to them in the ordination space.
- Species that occur close together in ordination space tend to prefer the same environmental conditions.
- Sample locations indicate their similarity to each other in terms of species composition.
- Environmental variables in CCA that make small angles (i.e. point in the same direction) with one another imply high positive correlations. Arrows pointing in opposite directions will be negatively correlated.
- Projections of species onto these environmental variable arrows gives an interpretation of which species are linked with high or low values of the environmental variables.

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Web link: www.okstate.edu/artsci/botany/ordinate

SECTION TWO

# Plant, fungal and microbial communities

CHAPTER 5

# Relationships between site type, stand structure and plant communities

Jonathan Humphrey, Richard Ferris and Andrew Peace

## Summary

Ground vegetation communities within the Biodiversity Assessment Project stands were classified using the National Vegetation Classification, and community composition and diversity related to stand structure and site characteristics. Mature and over-mature pine and spruce stands in the uplands and foothills climatic zones showed the greatest similarity with semi-natural pine and oak woodland communities respectively. Vegetation communities in lowland sites were less well correlated with semi-natural woodland analogues. Variation in community composition was related principally to a soil fertility gradient (increasing pH, exchangeable Ca, and available $NO_3^-$, coupled with decreases in soil organic matter and $NH_4^+$). Vascular plant and bryophyte species diversity was inversely related to available N. Uplands and foothills Scots pine and Sitka spruce sites had plant communities typical of acid, infertile soils, whereas lowland Norway spruce sites had communities associated with high soil fertility. Plant community composition and diversity was also significantly related to measures of vertical stand structure. Pre-thicket plots, with high values for field layer vertical cover had distinctive communities and were more diverse than mid-rotation and mature plots which had high canopy cover values, and low shrub and field layer cover. This influence of stand structure suggests that plant community diversity can be enhanced in commercial conifer forests by extending rotation lengths, and introducing alternative silvicultural systems such as shelterwood.

## Introduction

Field and ground layer vegetation communities are key components of biodiversity within temperate and boreal forests (Hannerz and Hånell, 1997) as they provide habitat for dependent fauna, and influence the development of shrub layers and the natural regeneration of canopy trees. Vegetation succession through all, or part, of a managed rotation have been studied in a variety of different plantations (e.g. Hill, 1979). In general, where first rotation stands are established on non-wooded ground such as grassland or heath, there is an initial increase in the biomass of non-woodland vegetation, normally associated with a reduction in grazing pressure (Hill, 1979). After 30 or 40 years, when full canopy closure is attained, there is almost complete eradication of vascular plants under crops of densely shading spruce or fir, but greater survival under lighter shading canopies of pine or larch (Hill, 1979). After clear-felling, there is often a rapid increase in ruderal (weed) species such as rosebay willowherb *Chamerion angustifolium*[1] and tufted hair-grass *Deschampsia cespitosa* (Abdy and Mayhead, 1992) which then decrease rapidly in abundance during the second rotation.

Retention of some stands beyond normal economic felling age (40–100 years depending on site factors and crop species) allows development of some of the characteristics of 'old-growth' such as fallen and standing deadwood, and veteran trees. Some species typical of native or semi-natural woodlands may begin to colonise these stands, e.g. woodland bryophytes such as *Rhytidiadelphus loreus* or herbs such as wood sorrel *Oxalis acetosella*. Such colonisation is most likely where stands have been well thinned in the past, and there are sources of propagules nearby (Williams *et al.*, 1998). The vegetation communities of these older stands (and indeed their younger counterparts) have not been properly characterised using the National Vegetation Classification system (Rodwell,

[1]Nomenclature follows Stace, C. (1997). *New flora of the British Isles*, 2nd edn. Cambridge University Press, Cambridge.

1991a, b), and it is not clear if their vegetation differs markedly from that of native woodlands on similar site types. In addition, few studies of ground vegetation in conifer plantations have attempted to relate vegetation community composition and diversity to stand characteristics and site types across a geographical range. This is important as forest managers need to know the potential benefits for plant diversity which could result from modifications to stand structure.

The objectives of the work described in this chapter were: 1) to characterise the plant communities (ground and field layer species) of planted conifer stands in terms of the National Vegetation Classification system; 2) to quantify the degree to which soil, stand structure and crop-species variables were related to variability in ground vegetation composition and diversity; and 3) to identify suitable stand management options for conserving and enhancing plant communities within plantations.

## Methods

In addition to the soil, stand structure and mensuration assessments described in Chapter 3, field and ground layer vegetation composition was assessed visually, using the DOMIN cover-abundance scale, within eight 2 m x 2 m quadrats nested in the 10 m x 10 m mensuration plots (Figure 3.2, Chapter 3). These data were compared to the National Vegetation Classification (NVC) national datasets for woodland, heathland and upland grassland communities (Rodwell, 1991a,b; 1992) using the MATCH programme (Malloch, 1995). This programme calculates similarity coefficients between the vegetation sample and the national datasets for the different NVC sub-communities. The NVC sub-community that most closely resembled the vegetation of each 1 ha plot was identified.

In addition a Woodland Vegetation Similarity Coefficient (WVSC) was calculated for each stand using the formula:

$$WVSC\ (\%) = (M_{WC}/M_{NWC}) \times M_{WC}$$

where $M_{WC}$ is the highest MATCH coefficient recorded against a woodland sub-community and $MN_{WC}$ is the highest coefficient recorded for a match against a non-woodland sub-community. The WVSC gives some indication of the relative similarity of the vegetation samples to woodland communities as opposed to non-woodland communities (Humphrey *et al.,* 2001).

Canonical Correspondence Analysis (see Chapter 4) was used to identify the relationships between soil and habitat variables and the species-composition of the floristic data. These soil and habitat variables (Table 5.1) are summative measures derived by Principal Components Analysis of the wide range of soil and habitat factors listed in Chapter 3, Table 3.2 (see Ferris *et al.,* 2000 for details of the analysis). Plant species-richness and diversity were also related to the summative soil and habitat variables using Pearson correlations.

## Results and Discussion

### Development of woodland vegetation communities

With the exception of the lowland Scots pine and Norway spruce stands, the vegetation in the over-mature stand stage was more 'woodland like' in character than the vegetation in the mid-rotation and mature stages (Table 5.2). The highest WVSC coefficients (>60%) were for the older stages of the foothills Scots pine chronosequences at Glen Affric and Strathspey, which were matched with W18 communities (*Pinus sylvestris-Hylocomium splendens* woodland; Rodwell, 1991a; Ferris *et al.*, 2000). These stands are considered to be good examples of semi-natural Scots pine woodland.

The pattern of community development in the foothills Scots pine plots was repeated in the Sitka spruce foothills and upland plots with the mature and over-mature stands more closely resembling semi-natural woodland communities than the pre-thicket and mid-rotation stands (Table 5.2). The best fits for these older stands were W17 oakwood communities (*Quercus petraea-Betula pubescens-Dicranum majus* woodland; Ferris *et al.*, 2000). This pattern of community change has been recorded

**Table 5.1** *Description of principal components of soil (SOIL 1–4) and habitat (HAB 1–4) variables related to plant community composition (CCA in Figure 5.1), species-richness and diversity (Table 5.3). Reproduced from Ferris* et al. *(2000).*

| Principal Component | Description |
|---|---|
| SOIL 1 | High P, K, Mg, organic matter and $NH_4^+$ |
| SOIL 2 | High pH, Ca and $NO_3^-$, low organic matter and $NH_4^+$ |
| SOIL 3 | High Mg, low $NH_4^+$ and $NO_3^-$ |
| SOIL 4 | Low pH, high $NO_3^-$ |
| HAB 1 | High values for field layer vertical cover (S1), low values for lower (S3) and upper (S4) canopy vertical cover, vertical cover index (CI), top height (TOPHT), height to live crown (HTLC), mean basal area (MBA) and rotten deadwood volume (DEADR) |
| HAB 2 | High values for shrub layer vertical cover (S2), S3, C.I. and DEADR, low values for HTLC |
| HAB 3 | High values for S1, DEADR and fresh deadwood volume (DEADF) |
| HAB 4 | High litter depth values |

in a number of similar studies (e.g. Hill and Jones, 1978) and could be a function of stand age where enough time has elapsed to allow slow-colonising woodland plants to become established in the stand. Site history may also be important, i.e. whether the stand was established on a site previously occupied by ancient semi-natural woodland (Humphrey *et al.,* 2001). The over-mature upland Sitka spruce stands (established on ancient woodland sites) had WVSC values approaching those of the semi-natural oakwoods (Table 5.2) and had a number of characteristic woodland herbs such as wood sorrel.

**Table 5.2** *Changes in the Woodland Vegetation Similarity Coefficient (WVSC) in relation to stand stage and crop type (– stand stage not available). The WVSC gives a measure of how closely the sampled vegetation is matched to a National Vegetation Classification (NVC – Rodwell, 1991a,b; 1992) semi-natural woodland community type relative to a non-woodland vegetation community. Each value is the mean of two stands.*

| Woodland vegetation similarity coefficient (%) | Pre-thicket | Mid-rotation | Mature | Over-mature |
|---|---|---|---|---|
| Lowland Corsican pine | 43.2 | 32.8 | 27.4 | 58.2 |
| Lowland Scots pine | 21.9 | 34.6 | 34.9 | 32.0 |
| Foothills Scots pine | 41.3 | 58.2 | 69.1 | 70.8 |
| Lowland Norway spruce | 56.6 | 41.9 | 51.0 | – |
| Foothills Sitka spruce | 33.3 | 17.5 | 25.5 | 36.8 |
| Upland Sitka spruce | 44.7 | 33.9 | 49.9 | 58.6 |
| Lowland oak | – | 88.9 | 60.7 | – |
| Upland oak | – | 75.4 | 79.2 | – |

The pre-thicket stages in the foothills and upland sites were more closely matched with heathland or upland grassland communities, and had species associated with open conditions such as heather *Calluna vulgaris* (Ferris *et al.,* 2000). Although most lowland plots were matched with woodland communities (W10 *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland and W16 *Quercus* spp.-*Betula* spp – *Deschampsia flexuosa* woodland; Ferris *et al.,* 2000), some of the lowland Scots pine plots were matched more closely with underscrub communities dominated by one or two species, often bracken *Pteridium aquilinum* (Ferris *et al.,* 2000). The lack of development of woodland

vegetation within these stands may be due to the fact that they were established on previously unwooded areas and the process of colonisation by woodland species has been restricted by the distance to sources of colonising species.

**Relationship between vegetation communities, habitat and soil variables**

Species-environment correlations were high (r>0.87) for the first two axes of the Canonical Correspondence Analysis (CCA) of the plant community data, with 29% of the variation in the species data explained by the set of environmental variables (Figure 5.1). Axis 1 separated lowland sites from those in the foothills and uplands, and was strongly correlated (r>0.51) with SOIL2 suggesting that differences in plant community composition between these site groupings were related to a gradient of increasing litter depth, pH, exchangeable Ca, and mineralised N in $NO_3^-$ form, and decreasing organic matter and N in $NH_4^+$ form. Lowland sites (such as 8.3) were dominated by species requiring high pH conditions such as slender false-brome *Brachypodium sylvaticum* and small nettle *Urtica urens* (Grime *et al.*, 1988). Northern sites (upland and foothills) had a more calcifuge flora (Grime *et al.*, 1988), with species such as blaeberry *Vaccinium myrtillus* and heather common. However, increasing pH and Ca (key factors in SOIL2) were not significantly correlated with plant species diversity (Table 5.3). In fact the only significant correlation recorded here was a positive correlation between SOIL 3 (high Mg and low N in both $NH_4^+$ and $NO_3^-$ form) and vascular plant and bryophyte species diversity. The only habitat principal component which was correlated with the first axis of the CCA was HAB4 (litter depth; Figure 5.1). Litter depth was also negatively related to total species diversity, and bryophyte cover (Table 5.3). Plots with high litter depth values were dominated by bracken (lowland Scots pine, Thetford, sites 3.2 and 3.3) which is noted for its ability to accumulate considerable quantities of litter over time if undisturbed (Marrs and Hicks, 1986).

**Figure 5.1** *Canonical correspondence biplot of assessment plots and environmental variables. Data labels for plots as in Annexe 1. The principal components of soil (SOIL 1–4) and habitat (HAB 1–4) variables are plotted as euclidean vectors (arrows); the direction and relative length of the arrows reflects the degree of correlation with the CCA axes; longer arrows are more strongly correlated.*

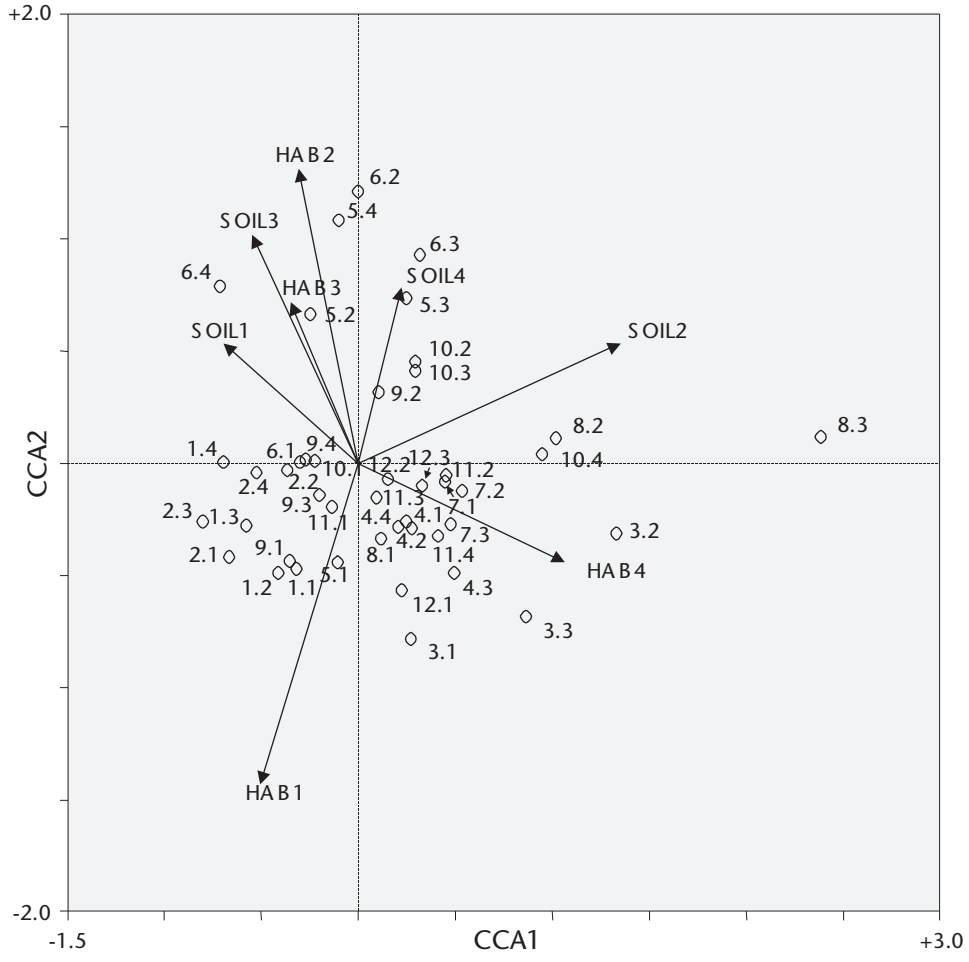

**Table 5.3** *Pearson correlations relating vegetation community variables to the first four principal components of soil and habitat data. Significant correlations (P<0.01) indicated by **.*

| | SOIL 1 | SOIL 2 | SOIL 3 | SOIL 4 | HAB 1 | HAB 2 | HAB 3 | HAB 4 |
|---|---|---|---|---|---|---|---|---|
| Total species diversity | 0.02 | -0.09 | 0.68** | 0.03 | -0.14 | 0.23 | 0.35 | -0.53** |
| Total species % cover | -0.18 | -0.33 | 0.31 | -0.07 | 0.41** | 0.01 | 0.42** | -0.27 |
| Vascular species diversity | -0.10 | -0.06 | 0.70** | -0.15 | -0.07 | 0.22 | 0.35 | -0.37 |
| Vascular species % cover | -0.36 | -0.24 | 0.24 | -0.11 | 0.54** | -0.10 | 0.37 | -0.02 |
| Bryophyte species diversity | 0.07 | -0.09 | 0.39** | 0.21 | -0.13 | 0.27 | 0.40** | -0.35 |
| Bryophyte species % cover | 0.17 | -0.32 | 0.28 | 0.03 | 0.02 | 0.18 | 0.31 | -0.52** |

Axis 2 of the CCA separated pre-thicket stands from the other stand stages, and was correlated with habitat parameters summarising differences in the vertical structure variables (HAB1 and HAB2). HAB1 describes changes in vertical stand structure through the chronosequence from older to younger plots (increasing field layer cover coupled with decreasing shrub and canopy layer cover). HAB2 describes a contrasting gradient of increasing vertical cover in the shrub and canopy layers. Pre-thicket plots had high vertical cover in the field layer, dominated by heathland and grassland species which are taller than typical woodland species growing under a canopy. Axis 2 also separated foothills spruce plots from pine plots. The pine plots tended to have a higher cover of more light demanding ericoid shrubs, grasses, rushes and sedges (Grime *et al.*, 1988) than spruce plots, reflecting the positive benefits from the lighter shading pine canopy (Hill, 1979).

HAB1 was positively correlated with the percent cover of vascular plants in the ground and field layer. Where canopy layer values were high (in mid-rotation plots) the cover of vascular plants in the field and ground layer vegetation was reduced through shading. This effect has been well documented for conifer stands on a range of different site types (e.g. Hill, 1986). Under densely shading crops such as Sitka spruce and western hemlock *Tsuga heterophylla*, vascular plants can be completely eradicated leaving only bryophytes (Hill, 1986). However, in pine forests, open old-growth stands frequently have lower plant diversity than closed canopy stands (Tonteri, 1994). The positive relationship recorded between deadwood volume (HAB 3) and bryophyte species diversity is in fact coincidental since bryophytes growing on deadwood were not recorded as part of this particular study. A separate survey of lower plants on deadwood was undertaken within the biodiversity plots and the results from this are discussed in Chapter 9.

## Management implications

Ferris *et al.* (2000) suggest that even though soil fertility is important in determining the composition and diversity of the understorey plant communities there is still scope for considering the manipulation of forest structure as a means of increasing diversity within planted conifer stands (Kerr, 1999). Peterken *et al.* (1992) have proposed that the promotion of enhanced structural diversity through retention of a greater proportion of stands beyond financial maturity would help improve the biodiversity of upland conifer forests. This is supported by the evidence from our study where the over-mature stands in the uplands had greater structural complexity than their younger counterparts, both in terms of vertical stratification and horizontal patchiness. These stands also had a more diverse flora with a greater complement of woodland herbs and bryophytes.

Lowland plantations, many of which have been established on former heathland, are typically species-poor, a feature of such stands elsewhere in NW Europe (e.g. Scots pine stands in Belgium, Lust *et al.*, 1998). They have poor and uniform structural development, with very limited cover in the shrub and lower-canopy layers. In order to transform these stands into well-structured mixtures with higher vertical and horizontal structural diversity, conversion methods should be used over a sufficiently long time period to minimise the rate of change. Rotation lengths of more than 100 years are proposed, but structural diversity comparable to that found in established selection forests could arise in less than 30 years (Lust *et al.*, 1998).

Thinning in both upland and lowland forests can promote greater understorey development as a result of improved light, moisture and temperature conditions, but a review of studies overseas (Ferris *et al.*, 2000) concluded that early thinnings without subsequent treatments were unlikely to maintain stable herb and shrub populations. A shelterwood approach may be more beneficial to the development of a woodland flora in the long-term. For example, Hannerz and Hånell (1997) found that in Norway spruce forests in Scandinavia, shelterwood regimes benefited plants preferring shaded and moist conditions, whereas these species declined after clearcutting. As a result of the development of country-based forestry strategies within the UK (e.g. Anon., 2001), much more emphasis is being placed on evaluating alternatives to clearfelling in British forests both in terms of economic benefits, as well as in respect of biodiversity and recreation values (Mason *et al.*, 1999). However, more research is needed to establish the benefits of alternative silvicultural systems such as shelterwood or group selection, for enhancing ground flora diversity.

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CHAPTER 6

# Soil microbial communities

Mike Morris, Jim Harris and Tom Hill

## Summary

Soil microbial communities in a sample of the pine and spruce stands were characterised using a biochemical analysis of lipid and fatty acid composition. Significant differences in the composition and diversity of soil microbial communities were recorded between different stand stages and tree crop types reflecting differences in ground flora composition, tree and shrub species composition, soil organic matter content and soil nitrogen content. The importance of soil microbial diversity for maintaining ecological functions within forest ecosystems is stressed and the need for more research to characterise soil microbial communities is emphasised.

## Introduction

The soil microbial community plays a vital role in the functioning of the forest ecosystems. As Jenkinson (1977) said *'The microbial biomass accounts for only 1–3% of soil organic C, but it is the eye of the needle through which all organic material that enters the soil must pass'*. As such, the microbial community lies at an interesting interface between the biotic and abiotic components of the ecosystem. Through the microbial community's activities, organic matter can be: incorporated into new microbial biomass; transformed to produce compounds which stabilise soil aggregate structures (Edgerton *et al.*, 1995); provide long-term nutrient reserves (and therefore buffers to supply); or respired to rejoin the pool of carbon dioxide in the atmosphere.

The soil microbial community may be characterised in a number of ways, but one schema involves three characteristics:

- **Size:** the total standing crop of microbial cells, expressed as numbers or, more usefully, as amount of living carbon.
- **Composition:** the relative abundance of different populations within the microbial community (e.g. bacteria vs fungi, or individual species).
- **Activity:** the rate at which the microbial community transforms or incorporates raw materials from simple sugars to complex polymers from the soil system.

This approach has been used most effectively in a number of studies not only to discriminate between different successional stages, but to gauge the effects of disturbance, such as opencast coal mining operations, on systems and the reclamation efforts made to restore them (Bentham *et al.*, 1992). In Bentham's study the microbial indices alone were demonstrated to be far better than traditional soil physico-chemical characteristics in discriminating between site history and management practices. Further to this, microbial community indices have been used specifically to address how ecosystem changes during succession from meadow to woodland affect both microbial community structure and functional characteristics related to the transition (Harris and Hill, 1995).

The study of soil microbial communities will also provide insights central to the current debate on the relationship between species diversity and ecosystem function. Because of the speed at which the whole diversity of a particular microbial system can be estimated, sometimes simultaneously with its functional measures, we can begin to construct a response model of the link between the two.

So how do we measure biodiversity in the soil? The main approaches currently employed are:

- **Traditional**
- **Genetic**
- **Biochemical**

**Traditional** methods rely on either culturing or direct observation. The extraction and culturing of soil fungi and bacteria, by means of dilution and plating onto agar media containing nutrients, leads to serious underestimates of the numbers of micro-organisms in a sample of soil. This is because of a number of factors – the most important being the need for widely different nutrients and growth conditions for different species to grow. Ideal conditions for the majority of micro-organisms known to be inhabiting the soil remain undiscovered. Underestimation is also caused by cells clumping together or by their destruction during sample homogenisation. Direct observation relies on highly skilled operators and as such is prone to operator bias. It also requires the use of universal staining procedures, i.e. stains specific for proteins, polysaccharides or nucleic acids, but staining, especially in forest soils, tends to be incomplete and success varies with the soil horizon and degree of humification.

The structure of microbial communities can also be described using **genetic** methods. Typically, the DNA sequence of the small sub-unit ribosomal RNA gene is used to define species or taxonomic groups. Numerous techniques, ranging in their resolution, are used to measure the diversity of rRNA genes. While this approach has the precision to provide a complete inventory of the microbial community in a soil sample (time and expense permitting) it also possesses several sources of error, some of which are unquantifiable. These undermine its accuracy and reliability as a tool to measure changes in relative abundances of species or broader groups in response to changes in soil conditions. Most bias occurs in the first steps of the method, the extraction of DNA from the soil sample and the many-million-fold replication of the rRNA genes using the polymerase chain reaction (PCR) needed to generate enough material to measure. Other complicating factors include the variation in copy number of rRNA genes between species and, for fungi, the frequency of occurrence of nuclei in the mycelium. The prodigious spore production by some fungi would also lead to an overestimation of their levels of vegetative growth.

**Biochemical** techniques, particularly using the analysis of lipids and fatty acids, have been the subject of rapid development in recent years as a consequence of their utility in characterising microbial community composition and diversity. Lipids are ubiquitous in their distribution and perform a vast range of structural and metabolic functions in both prokaryotes and eukaryotes (Ratledge and Wilkinson, 1988). It has long been known that various lipid classes can be powerful tools in the classification and taxonomy of microbial flora (Lechevalier, 1977). Fatty acids are long-chain carboxylic acids. Within bacterial cells they may occur free or esterified to an alcohol group. Most are component parts of large molecules such as phospholipids, glycolipids, lipoproteins, lipopolysaccharides and lipoteichoic acids. Although the fatty acids of eukaryotic organisms tend to be limited to straight chain saturated and unsaturated forms, bacteria possess a more heterogeneous selection. More than 300 different fatty acids have been found in bacteria, including soil bacteria (Sasser, 1990).

White *et al.* (1979) suggested that fatty acid composition might be useful in defining microbial community structure. Several studies have now demonstrated the usefulness of this technique in the study of terrestrial soils, especially with regard to the effects of environmental perturbations on microbial communities (Bååth *et al.*, 1995). Other workers have studied phospholipid fatty acid (PLFA) profiles in natural soils from different origins, in order to gain insight into the relative diversity of the microbial communities present (Zelles *et al.*, 1995; Bardgett *et al.*, 1997).

Although a variety of lipid classes can be used, the work presented here examines the utility of ester-linked PLFA determination to provide an indirect assessment of the diversity of microbial communities present within the Biodiversity Assessment Project sites, and to relate this diversity to factors of soil and stand structure.

## Methods

Assessments were carried out on sites 1, 2, 9, 10, 11 and 12 (see Annexe 1 for details).

### Sampling and preliminary lipid extraction

All samples were taken from the $F_H$ horizon (humus layer) since this should provide the best indicators for the microbial communities present, and particularly those responsible for the decomposition of litter and sequestration of available nutrients (Kjøller and Struwe, 1982).

Five 0.2 m x 0.2 m areas were selected at random from each of the eight 10 m x 10 m mensuration quadrats within each 1 ha plot (Chapter 3, Figure 3.2). The $F_H$ horizons of these five sub-areas were removed and bulked together. After preliminary mixing and removal of coarse debris the sample was riffled (sub-divided to obtain a representative sample), a sample placed in a plastic bag for complementary analyses, then riffled again until a representative sample of about 8 g was obtained and this placed in a 30 $cm^3$ glass vial for lipid analysis. To this sample 15 $cm^3$ of initial extraction solvent trichloromethane:methanol (1:2, v:v) was added both to fix the organisms present and begin lipid extraction. Vials were stored in the dark at ambient temperature until they were returned to the laboratory where the extraction was completed. Bagged samples were stored at 4°C until required.

### Extraction and analysis of soil microbial PLFAs

Extraction and analysis of PLFAs from soil consists of 5 distinct stages: crude lipid extraction, liquid:liquid partition (initial clean-up), fractionation, derivatisation and chromatographic separation and analysis. These stages are summarised in Annexe 2. Comprehensive methodology is given in Morris (2000). Figure 6.1 shows a typical chromatogram obtained for phospholipid derived FAMEs of the assessment site soil samples.

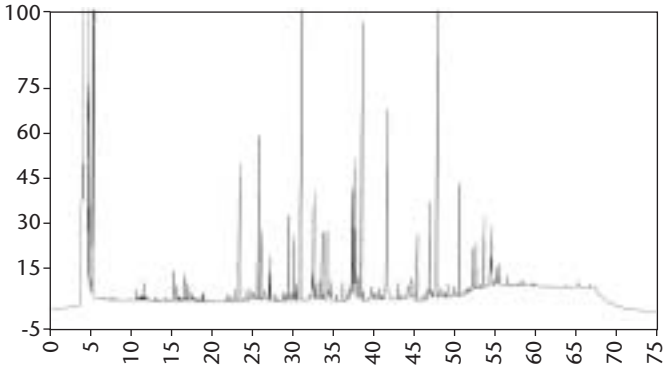



**Figure 6.1**

*Typical example of a capillary GC chromatogram of fatty acid methyl esters of the phospholipid fraction of lipids extracted from the forest soil samples.*

A total of 92 individual fatty acid peaks, selected on the basis of their occurrence in the phospholipid fractions of forest soil extracts, were chosen as a composite comparison profile for the soil PLFA extracts. The areas of identified peaks in each PLFA profile were recorded and normalised by dividing by the total profile peak area. Although eight replicate samples (one from each of the quadrats within each chronosequence) were taken, not all extracted profiles were appropriate for inclusion in the dataset due to low intensity profiles (see Morris, 2000). As a result, profile replicates from the chronosequences ranged from four to eight.

### Data analysis

Statistical analyses were carried out using the Statistica version 5.1 (Statsoft, Inc., Tulsa, OK) and Statgraphics Plus version 7.0 (Manugistics Inc., Rockville, MD). The normalised PLFA profiles were transformed to their $\log_{10}$ values prior to principal components analysis (PCA; ter Braak, 1995) as performed by Bååth *et al.* (1995). The Shannon indices were determined using the EstimateS version 5 *Statistical estimation of species-richness and shared species from samples* programme (copyright Robert K. Colwell, 1994–97). Pearson product-moment correlations were calculated to investigate the statistical relationships between soil microbial community PLFA diversity and vegetation composition and diversity, soil chemistry variables, deadwood and stand structure (see Chapters 3, 5 and 7 for descriptions of these latter datasets). The ground vegetation data were divided into separate groups:

ericoid shrubs, ferns and herbs, forbs (grasses, sedges and rushes), bryophytes, lichens, trees and shrubs and bracken. The variation in PLFA composition of the assessment sites was also assessed using PCA (see Chapter 4 for a description of this technique).

## Results

### Diversity of PLFA profile data

The simplest indication of richness in traditional community studies is the total number of species present. Analogous to this in the present dataset is the total number of PLFAs (*S*) identified in each soil extract chromatogram. The maximum possible value of *S* is 92, but no individual site profile presented with this many. Although *S* is relatively limited in its information content, Table 6.1 shows that the pre-thicket stands consistently exhibit the fewest peaks in each chronosequence. Similarly, with the exception of Site 2, the over-mature stands present fewer peaks than those of the intermediate chronosequences.

The Shannon index ($H'$) is a measure of the amount of information in the system and is positively correlated with both PLFA richness and evenness. This universally applied index of diversity is surprisingly well adapted to these data since it assumes that each data set comprises a random sample from an effectively infinite population in which the total number of peaks is known (i.e. 92 with these data; Krebs, 1985). While $H'$ is weighted by the evenness of peak abundance, a more specific measure of evenness (*E*), based on $H'$, can be determined by calculating the ratio of the observed $H'$ to its maximum possible value. Maximum $H'$ occurs when there is complete equitability (an equal abundance of all PLFAs). *E* is limited to a value between 0 and 1.0 with 1.0 representing maximum evenness. The calculated values for $H'$ and *E* for the plots are given in Table 6.1. In contrast to *S*, the pre-thicket or post-mature stands tended to have the highest values for both $H'$ and *E*, although the trends were generally less clear.

**Table 6.1**

*Diversity indices calculated for normalised mean PLFA profile data from the BRP assessment sites. Key to site labels in Annexe 1; SP = Scots Pine; SS = Sitka spruce; CP = Corsican pine.*

| Site label | PLFA diversity index | | |
|---|---|---|---|
| | Richness (max. value 92) (S) | Shannon index ($H'$) | Shannon evenness (range 0–1) (E) |
| SP1.1 (*n* = 4) | 68 | 3.12 | 0.83 |
| SP1.2 (*n* = 7) | 78 | 3.28 | 0.80 |
| SP1.3 (*n* = 6) | 77 | 3.23 | 0.79 |
| SP1.4 (*n* = 4) | 76 | 3.19 | 0.78 |
| SP2.1 (*n* = 8) | 79 | 3.32 | 0.80 |
| SP2.2 (*n* = 8) | 81 | 3.18 | 0.78 |
| SP2.3 (*n* = 7) | 79 | 3.22 | 0.79 |
| SP2.4 (*n* = 8) | 82 | 3.19 | 0.78 |
| SS9.1 (*n* = 4) | 67 | 3.33 | 0.83 |
| SS9.2 (*n* = 7) | 80 | 3.19 | 0.81 |
| SS9.3 (*n* = 5) | 86 | 3.23 | 0.80 |
| SS9.4 (*n* = 5) | 74 | 3.30 | 0.85 |
| SS10.1 (*n* = 5) | 79 | 3.41 | 0.81 |
| SS10.2 (*n* = 5) | 83 | 3.41 | 0.82 |
| SS10.3 (*n* = 5) | 85 | 3.50 | 0.82 |
| SS10.4 (*n* = 5) | 81 | 3.70 | 0.87 |
| CP11.1 (*n* = 5) | 82 | 3.54 | 0.84 |
| CP11.2 (*n* = 5) | 85 | 3.53 | 0.82 |
| CP11.3 (*n* = 5) | 87 | 3.53 | 0.81 |
| CP11.4 (*n* = 8) | 85 | 3.40 | 0.80 |
| CP12.1 (*n* = 6) | 79 | 3.32 | 0.79 |
| CP12.2 (*n* = 6) | 82 | 3.34 | 0.81 |
| CP12.3 (*n* = 5) | 78 | 3.36 | 0.81 |

### Correlation of PLFA diversity with stand structure, soil and vegetation data

Significant correlations between PLFA diversity and stand, vegetation and soil variables are given in Tables 6.2 and 6.3. The percent cover of both the ericoid and the trees and shrubs groups showed significant negative correlations ($p < 0.01$) with PLFA richness. Percent cover of the ericoids also showed a significant negative correlation ($p < 0.05$) with $H'$. Further, ericoid richness was significantly negatively correlated with both $H'$ and $E$ ($p < 0.01$). By contrast, species-richness and percent cover of the ferns and herbs group was positively correlated ($p < 0.05$) with PLFA diversity and evenness ($H'$ and $E$).

**Table 6.2** *Pearson product-moment correlations relating the PLFA derived diversity measures to vegetation and stand structure variables. Analyses methods for stand structure and vegetation variables are described in Chapters 3 and 5 respectively. Marked correlations: * p < 0.05 ; ** p < 0.01; ns: not significant (n = 23, with casewise deletion of missing data).*

| | | PLFA diversity index | | |
|---|---|---|---|---|
| **Vegetation category/ vertical stand structure** | **Measure** | **Richness (S)** | **Shannon index ($H'$)** | **Shannon evenness (E)** |
| Ericoid | No. species | -0.26$^{ns}$ | -0.60** | -0.63** |
| | % cover | -0.59** | -0.47* | -0.34$^{ns}$ |
| Trees & shrubs | No. species | -0.32$^{ns}$ | -0.34$^{ns}$ | -0.32$^{ns}$ |
| | % cover | -0.62** | -0.03$^{ns}$ | 0.19$^{ns}$ |
| Ferns & herbs | No. species | 0.09$^{ns}$ | 0.50* | 0.50* |
| | % cover | 0.16$^{ns}$ | 0.49* | 0.48* |
| **Field layer vertical cover** | **cover** | **-0.46*** | **0.22$^{ns}$** | **0.39$^{ns}$** |

| Chemical variable | PLFA diversity index | | |
|---|---|---|---|
| | **Richness (S)** | **Shannon index ($H'$)** | **Shannon evenness (E)** |
| Organic content | -0.48* | -0.80** | -0.74** |
| Moisture content | -0.47* | -0.69** | -0.60** |
| C | -0.15$^{ns}$ | -0.71** | -0.75** |
| C:N ratio | -0.58** | -0.57** | -0.44* |
| P | -0.25$^{ns}$ | -0.53** | -0.52* |

**Table 6.3**

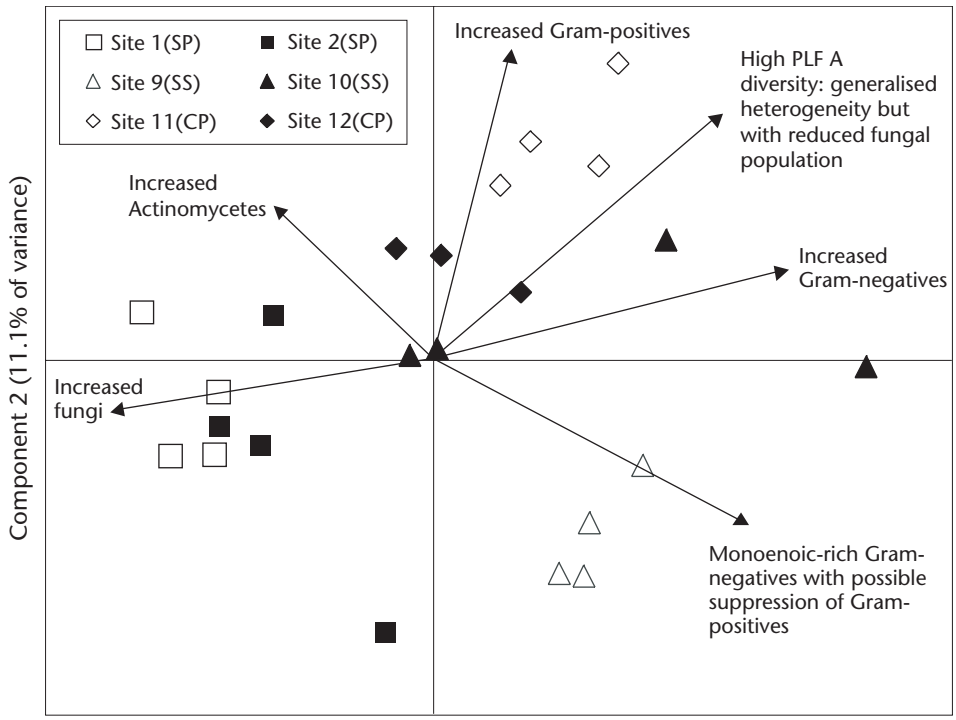
*Pearson product-moment correlations relating the PLFA derived diversity measures to vegetation and stand structure variables. Analyses methods for stand structure and vegetation variables are described in Chapters 3 and 5 respectively. Marked correlations: * p < 0.05; ** p < 0.01; ns: not significant (n = 23, with casewise deletion of missing data).*

Significant correlations between the PLFA diversity indices and soil chemical variables of the $F_H$ horizon were always negative (Table 6.3). $H'$ and $E$ tended to be more strongly correlated than $S$, especially with the interrelated measures of amount of organic material present, percent moisture content and carbon content. Of the extractable metals, only phosphorus showed significant correlations. Although pH of the $F_H$ horizon was not correlated with PLFA diversity, the pH of the lower soil horizon was positively correlated with both $H'$ (r = 0.51, $p < 0.05$) and $E$ (r = 0.54, $p < 0.01$; Morris, 2000).

### Ordination

The PCA site ordination diagram is presented in Figure 6.2. Using all the individual PLFA profiles the first three axes of the PCA ordination accounted for 35% of the total variability in the dataset.

**Figure 6.2** *PCA ordination of the Biodiversity Assessment Project sites with summary vectors indicating some of the general conclusions suggested in the text.*




However, when the analysis was carried out using the mean site profiles the first three axes explained 49% of the variance. Component 1 of the PCA separated the Scots pine sites from both the Corsican pine and Sitka spruce sites. It also had a major influence on separating the older two Glentress (Site 10) stands from the 'pre-thicket' and 'mid-rotation' stages. Component 2 separated the Corsican pine sites from the Sitka spruce stands at both Kielder (Site 9) and, to a lesser extent, at Glentress (Site 10). Component 2 also showed a negative gradient with age separating the Strathspey (Site 2) stands from the rest.

## Discussion

### Correlation of PLFA diversity with vegetation diversity

A possible explanation for the strong negative correlations between PLFA richness and percent cover of trees and shrubs and of ericoids is that both these vegetation classes are known to have strong mycorrhizal associations. Ericoid ectendomycorrhizas are a ubiquitous feature of the tribes Ericoideae (*Erica*, *Calluna*) and Vaccinoideae (*Vaccinium* spp). The vegetation assessment data showed that, while the Scots pine sites tend to be dominated by *Calluna vulgaris* and possess larger populations of *Vaccinium myrtillus* (bilberry) and *V. vitis-idaea* (crowberry) with age, *Calluna* is absent from all but the 'pre-thicket' stages of Sitka spruce stands and is an even rarer inhabitant of the Corsican pine stands. Similarly, while *V. myrtillus* is found occasionally on the Sitka stands, neither this species nor *V. vitis-idaea* were present in the Corsican pine stands.

It is not particularly surprising, given the known preference of these types of plants for heathland type areas and acidic or peaty soils (Richards, 1987) and considering the extent of canopy closure seen in the mid-rotation Sitka sites, to find such a divergence in distribution of PFLA-richness between stand types. However, the suppression of PLFA richness associated with dominant ericoid cover may well be attributable, to some extent, to their ectendomycorrhizal associations. These plants are typically woody shrubs with an extensive system of fine roots, the greater part of which is mycorrhizal. The dense nature of their root systems, together with the fact that soil within the mycorrhizosphere generally has lower microbial population densities than the rhizosphere adjacent to non-mycorrhizal roots (Killham, 1994), is a plausible explanation for the decrease in PLFA richness.

It would therefore be expected that, along with a generalised decrease in PLFA richness caused by a reduced population density of the microbial (bacterial) community, we should see a concomitant increase in the recovery of fatty acids associated with polar lipids of the mycorrhizal fungi (see the following section on PCA for the examination of individual fatty acid/site associations).

**Correlation of PLFA diversity with soil variables and stand structure**

Of the correlations displayed in Table 6.3, the fact that the organic matter content, elemental carbon and percent moisture all showed similar patterns of significant negative correlations is not surprising. Soil moisture content is partially dependent on organic matter content, and the proportion of organic material has been used in allied studies as a surrogate for the available water capacity when determining habitat preferences of indigenous species (Jukes *et al.,* 2001). Similarly, the bulk of the organic material tends to be composed of cellulose, lignin and other recalcitrant large molecule classes that, while containing relatively large amounts of other elements in functional groups, are primarily polymeric carbon chains. Thus organic material content will generally be proportional to elemental carbon content. A high C:N ratio is generally an indication of low quality, woody humus (usually dominated by fungi) and is characteristic of forest soils (Harris and Hill, 1995). The Scots pine stands show closest correlation to this generalisation demonstrating high organic matter and moisture contents along with high levels of fungal specific fatty acids and concomitant low fatty acid diversity.

A significant negative correlation ($r = -0.46$, $p < 0.05$) was also observed between the field layer vertical cover assessment (S1 = 10 cm to 2 m in height – see Chapter 3) and PLFA richness (not shown). This is probably due, primarily, to the association recorded between high field layer vertical cover values and the occurrence of heathy vegetation (as reported in Chapter 5). As the ericoids tend to be low growing, high-density shrubs it would be expected that sites with a high cover of ericoids would score highly in the S1 vegetation strata cover assessment.

**Ordination**

The fatty acids having the greatest influence in separating the Scots pine sites from the other sites (i.e. those fatty acids that correlate well with component 1) were proportionally high levels of C16:1w5, C16:1w7, C18:1w9*tr*+C18:1w7*cis*, C18:2w6 and C18:1w9*cis*. Following on from the tentative conclusions made with regard to the correlations between ericoid richness and low PLFA diversity, it would be expected that those fatty acids positively aiding the separation of the Scots pine sites from the other sites (i.e. those negatively correlated with component 1 of the PCA) would be associated with fungi and particularly ectendomycorrhizal species. Of those peaks which satisfy that criteria, C16:1w5, C18:2w6 and C18:1w9*cis* have been used in previous studies as markers for eukaryotic (fungal) presence. Stahl and Klug (1996) demonstrated that the latter two fatty acids comprise two of the four most abundant fatty acids (up to 95% of the total fatty acid content) found in whole cell extracts of 100 cultured filamentous fungi (72 of which were isolated from experimental soil samples). Though one should be circumspect about transposing whole cell, culture derived, profile data to *in situ* derived consortia data, Stahl and Klug (1996) showed that, in the species of Ascomycetes studied, C18:2w6 and C18:1w9*cis* comprised around 70% of the total fatty acid content. Ascomycetes are commonly implicated in ericoid type mycorrhizal infections.

The separation of the chronosequences within the Glentress site is also explained essentially by component 1 of the PCA and hence is also affected by the relative proportions of those fatty acids discussed above. The fatty acids demonstrating greatest effect on separating the Kielder stands from the other sites (vectors in the lower right quadrant of the ordination diagram) consist mainly of monoenoic forms, usually associated with Gram-negative bacteria. This area of the ordination showed virtually no methyl branched fatty acids, suggesting a possible suppression of Gram-positive bacteria. While not exclusive to Gram-positive bacteria (Lechevalier, 1977) branched chain fatty acids are invariably found as major lipid components of most Gram-positive bacteria (Zelles, 1997). A large number of fatty acids (42% of the total) showed positive correlations with both component 1 and component 2 of the PCA (upper right quadrant). It is an increase in the proportion of these fatty acids that helps to separate the Corsican pine sites from the other sites. The fatty acids comprising this group are a heterogeneous mix of methyl branched, unsaturated, cyclopropyl and hydroxy fatty acids. As no particular class of fatty acid is dominant it is not possible to claim that any specific group or groups of microorganism are particularly dominant at these sites. Such a heterogeneous mix of

fatty acid classes necessarily suggests the presence of a similarly heterogeneous mix of microorganism classes. As far as one can make sweeping judgements with regard to the Corsican pine sites, it is possible only to state that (on the evidence of their PLFA profiles) their microbial communities contain a much lower fungal proportion than the Scots pine sites and a much higher proportion of Gram-positive bacteria than the Kielder Sitka spruce sites.

Because some aspect of equitability is included in the calculation of Shannon $H'$ it would be reasonable to assume that those sites scoring highly for diversity ($H'$) would be placed near to where the majority of peaks lie on the ordination. Thus it is no surprise that the three sites scoring highest for diversity (10, 11 and 12) are all represented in the upper right quadrant of the PCA.

## Conclusions

The results of this investigation demonstrate that: there are clear links between vegetation type, rotational stage and microbial community composition and diversity; the diversity of the microbial community tends to be greatest at the mid-rotational stage; and the microbial community is a clear indicator of successional status. Management of conifer forests to maximise diversity while maintaining their function needs to address all parts of the ecosystem – the producer, the consumer and the decomposer subsystems – since all are interconnected and co-dependent. The plants impose top-down control over the soil community via the quantity and quality of their organic inputs, while, simultaneously and reciprocally, the decomposers exert bottom-up control. The soil microbial community is extremely diverse – every handful of forest soil may contain more than 10 000 bacterial 'species' alone – but is essentially unknown. There is also evidence of endemism among microbes, which, due to their small size and their rapid rate of evolution, may occur over distances of tens of metres. Until methods advance and we are able to make even partial inventories of microbial diversity in natural environments, and we start to understand their functional role in the ecosystem, it would be wise to be conservative and manage forests to encourage diversity of all groups, not just the things we can see. After all, size isn't everything.

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CHAPTER 7

# Deadwood

Jonathan Humphrey and Andrew Peace

## Summary

The frequency and volume of fallen deadwood (logs), standing deadwood (snags) and stumps were recorded in each of the biodiversity assessment plots. Volumes ranged from zero in newly planted stands to over 300 $m^3 ha^{-1}$ in the over-mature upland Sitka spruce stands. Upland stands had significantly higher deadwood volumes, particularly of snags, than the lowland and foothills plots. This relates to the increased occurrence of windthrow in upland stands and to a past policy of no thinning. Deadwood volumes were significantly higher in the mature and over-mature stands than in the younger stand stages. Mean decay score for logs was the same through the chronosequence for all forest types, whereas mean decay score for snags tended to increase in the older stand stages, especially in pine stands. The foothills Scots pine plots and upland Sitka spruce plots had significantly higher volumes of large diameter (> 15 cm) and well-decayed (decay classes 4 and 5) deadwood compared to the other forest types. Deadwood volumes are considered to meet or exceed current guidelines over most of the sites surveyed, but volumes were very low in some of the lowland plots. Large diameter, well-decayed deadwood is generally considered to have the most value for wildlife, but occurs at a very low frequency and volume in most of the forest and stand types.

## Introduction

The importance of deadwood in forest ecosystems is widely recognised (Samuelsson *et al.,* 1994). Standing (snags) and lying (logs or coarse woody debris) dead trees play a key role in the functioning and productivity of forest ecosystems through effects on carbon storage, soil nutrient cycling, energy flows and hydrological processes, natural regeneration of trees and biodiversity (Ratcliffe, 1993). In temperate and boreal forests, decaying wood provides important habitat for small vertebrates, cavity-nesting birds, and a host of lichens and bryophytes, polypores and other saproxylic fungi and invertebrates (Esseen *et al.*, 1997). Different species require different types and quality of deadwood. Important factors include: tree species, stage of decay, size and whether standing or fallen (Ferris-Kaan *et al.,* 1993). A number of systems for estimating decay state have been developed and currently variants of the five point scale of Hunter (1990) are the most widely used.

The amount of deadwood in British forests has decreased markedly over the last few hundred years due to timber harvesting and sanitation measures to reduce disease risk. Substantial accumulations of deadwood are now restricted to old-growth forest reserves, or to remnant habitat with old trees such as ancient parkland in the English lowlands (Harding and Rose, 1986). A large percentage of rare and endangered saproxylic species are often restricted to these relict habitats and the inputs of deadwood are governed largely by natural disturbance processes such as wind and fire (Kirby and Drake, 1993). Recognition of the value of deadwood for biodiversity has led to a plethora of guidance in different countries (see Hodge and Peterken, 1998 for a review) accompanied by surveys of the resource.

There have been few surveys of deadwood in British forests (Hodge and Peterken, 1998) with most studies covering individual woods or woodland types (e.g. Reid *et al.*, 1996; Green and Peterken, 1997). Kirby *et al.* (1998) provide an overview and analysis of available datasets, but stress the necessity for more information from planted stands. Plantations have been overlooked in general with respect to deadwood and there is a need to relate deadwood accumulations and quality to successional stage and crop species type.

Here we present data on deadwood accumulations recorded within the assessment plots and relate the quality and quantity of snags, logs and stumps to stand stage and crop type. The results are discussed and compared with deadwood data from temperate and boreal forests in Britain and elsewhere. The role of management and natural disturbance in maintaining and enhancing the deadwood resource in planted forests is explored.

## Methods

Accumulations of fallen deadwood (logs) were recorded along two transects bisecting the 1 ha plot diagonally from the plot corners (see Figure 3.2, Chapter 3) giving a total transect length of 180 m. Total length and volume of logs with a mean diameter ≥ 5 cm were estimated using the line intercept method (Warren and Olsen, 1964). The formula used to calculate length was taken from Kirby *et al.* (1998). Diameter classes were measured in 5 cm intervals and deadwood quality was described using a visual five-point decay class scale following Hunter (1990): 1 – bark intact, small branches present; 2 – bark loose or sloughing off, no sapwood degradation; 3 – no bark, some sapwood degradation; 4 – no bark, considerable sapwood degradation; 5 – sapwood and heartwood degradation. These categories were also used in the analysis of the lichen and bryophyte data (Chapter 9). However, for the analysis of the fungal data (Chapter 8), the 5 categories were simplified into two: 'fresh' (categories 1–3) and 'rotten' (categories 4 and 5). Volumes were calculated by assuming that the logs were cylindrical. In addition to carrying out estimates of total log volumes in all plots, specific measures of sizes and volumes of individual logs and stumps were made in all sites excluding the oak stands (sites 13, 14, 15 and 16).

The height and diameter at breast height (dbh ~1.3 m) of all individual snags ≥ 7 cm dbh were recorded within the eight 10 m x 20 m plots (Figure 3.2, Chapter 3). There were two of these plots placed diagonally and equidistant between the corners of each 50 m x 50 m quarter of the 1 ha plot. The total plot area was 1600 $m^2$. As with logs, volumes of snags were calculated by assuming that they were cylindrical.

## Analysis

General linear models with log link functions were used to determine the effect of stand stage, location (uplands, foothills and lowlands) and crop species type on log, snag and total deadwood volumes including the frequency and volume of logs and snags in different diameter classes. The Kruskal-Wallis test was used to compare decay class distributions between crop species and locations, and to test the hypothesis that deadwood occurred in similar proportions across diameter classes. The classes used were 5–15 cm, 16–25 cm, 26–35 cm and > 35 cm. These classes were selected to encapsulate the spread of the diameter data, and ensure that there was enough replication within each class. This Kruskal-Wallis test on frequency distributions is used in preference to a standard chi-square test as it makes use of the fact that the decay classes have a natural ordering (1–5). There was insufficient stump volume data to carry out any statistical analyses.

## Results

Total deadwood volumes ranged from zero to over 300 $m^3 ha^{-1}$ with a mean value per plot of 36 $m^3 ha^{-1}$ (Table 7.1). Log volumes were generally higher than snag volumes, with stump volumes extremely low (Table 7.1). Log and snag frequencies were higher in the upland and foothills spruce plots and the upland oak plots than in the foothills Scots pine plots and lowland plots (Figure 7.4a). Total deadwood volumes were significantly greater ($P < 0.001$) in the mature (stage 3) and over-mature stands (stage 4) than in the other stand stages (Figure 7.1). Upland stands had significantly ($P < 0.001$) more deadwood than stands in the foothills and lowlands. For snags, there was a strong positive correlation between stand stage and the amount of deadwood ($P < 0.01$), with mature and over-mature plots having the higher volumes. Upland and foothills plots had significantly higher snag volumes than the lowland plots ($P < 0.001$). Log volumes were highest in the over-mature stands and in the uplands ($P < 0.001$ in both cases; Figure 7.1).

**Table 7.1** *Summary of deadwood data. Values are per 1 ha plot. SD = Standard Deviation. Volumes are in $m^3$ $ha^{-1}$. No stumps < 15 cm in diameter were recorded. Fresh deadwood category includes decay classes 1–3; rotten category includes decay classes 4–5. Deadwood variables are assigned codes referred to in Table 8.2. Minimum values were 0 in all cases.*

| Variable | Description | Max. | Mean | SD |
|---|---|---|---|---|
| LOGL | Length of fallen deadwood (m) | 6381.4 | 1132.8 | 1485.8 |
| FLOG | Volume of fresh fallen deadwood | 161.8 | 12.6 | 31.7 |
| RLOG | Volume of rotten fallen deadwood | 77.8 | 10.4 | 17.0 |
| LOG < 15 | Volume of fallen deadwood with mean diameter < 15 cm | 38.9 | 5.9 | 9.6 |
| LOG ≥ 15 | Volume of fallen deadwood with mean diameter ≥ 15 cm | 189.2 | 17.1 | 38.2 |
| TLOG | Total fallen deadwood volume | 194.0 | 22.9 | 39.9 |
| FSNAG | Volume of fresh standing deadwood | 123.7 | 8.8 | 27.5 |
| RSNAG | Volume of rotten standing deadwood | 66.1 | 3.3 | 13.2 |
| SNAG < 15 | Volume of standing deadwood with mean diameter < 15 cm | 102.6 | 4.2 | 20.6 |
| SNAG ≥ 15 | Volume of standing deadwood with mean diameter ≥ 15 cm | 136.7 | 8.3 | 29.3 |
| TSNAG | Total standing deadwood volume | 139.7 | 12.2 | 32.5 |
| FSTUMP | Volume of fresh stumps | 1.2 | 0.1 | 0.3 |
| RSTUMP | Volume of rotten stumps | 11.3 | 0.8 | 2.3 |
| STUMP≥15 | Volume of stumps with mean diameter ≥15 cm | 11.3 | 0.9 | 2.3 |
| TSTUMP | Total stump volume | 11.3 | 0.9 | 2.3 |
| TFRESH | Total fresh deadwood volume | 285.5 | 21.5 | 55.0 |
| TROTTEN | Total rotten deadwood volume | 87.0 | 14.5 | 20.2 |
| T < 15 | Total volume of deadwood with mean diameter < 15 cm | 106.5 | 9.7 | 21.7 |
| T ≥ 15 | Total volume of deadwood with mean diameter ≥ 15 cm | 325.9 | 25.8 | 62.8 |
| TVOL | Total volume of deadwood | 333.7 | 36.0 | 65.2 |

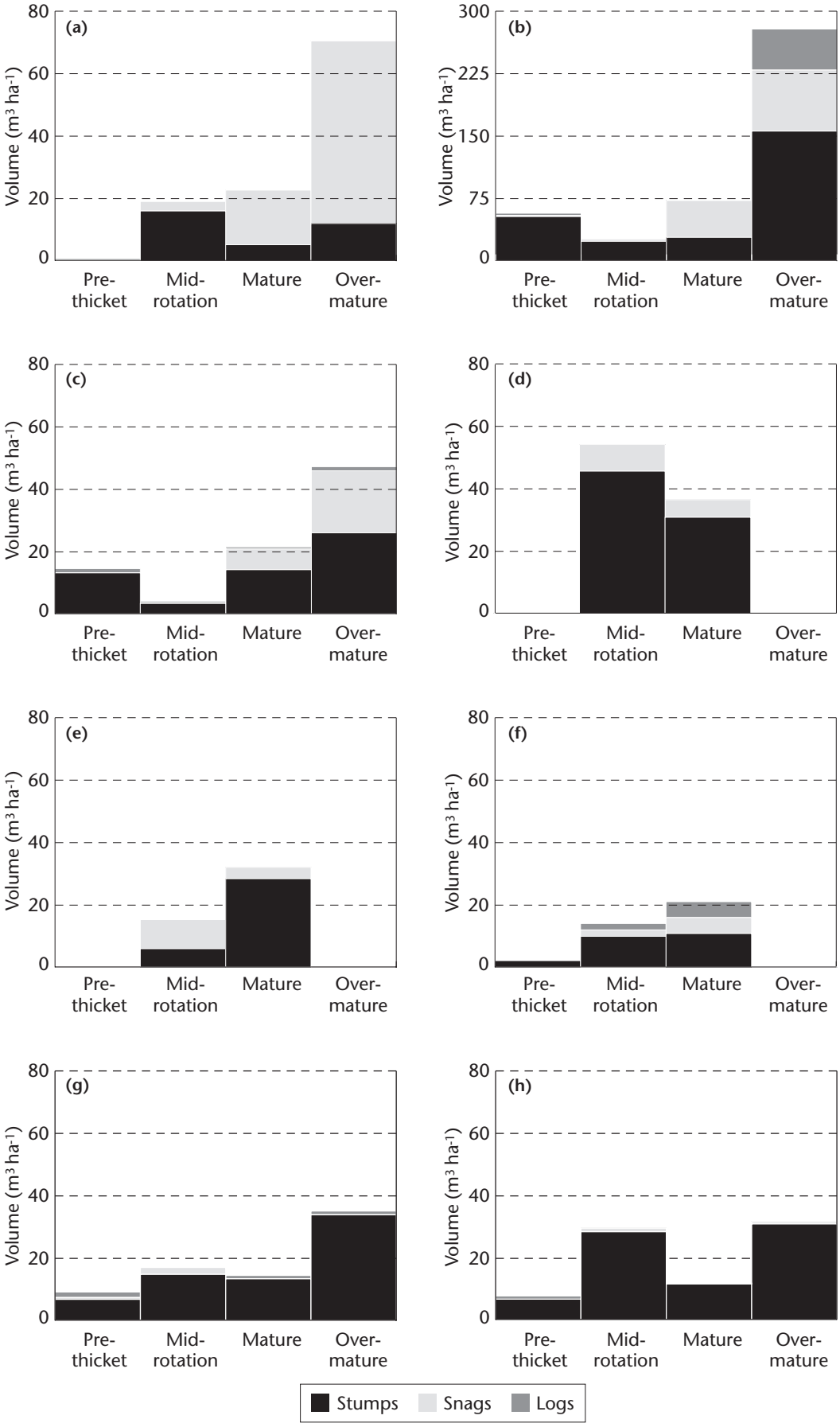
Mean decay scores for logs were constant throughout the chronosequence for pines, spruces and the upland oak sites (Figure 7.2), but mean snag decay score increased through the chronosequence ($P < 0.01$; Figure 7.2). There were no differences in log decay class distributions amongst the pines (foothills Scots pine, lowland Corsican pine, lowland Scots pine), the spruces (upland Sitka spruce; foothills Sitka spruce; lowland Norway spruce), between crop species within foothills and lowlands, or generally between pines and spruces (Figure 7.3a). There were significant differences between the lowland and upland oak sites ($P < 0.001$) with the upland oak sites having large numbers of decay class 5 deadwood items (Figure 7.3a).

Snag decay class distributions did not differ significantly amongst the pines (Figure 7.3a), but there were significant differences ($P < 0.01$) between the spruces, with upland Sitka spruce having a greater proportion of decay classes 4 and 5 snags in comparison to the other spruce stands. There were no differences between crop species within climate zones. The decay class distributions between logs and snags differed significantly for pines, spruces and upland oak (all $P < 0.001$). Across all sites there were proportionately more logs in the higher decay classes (3, 4 and 5) in comparison to snags (Figure 7.3a).

The relationship between the volume and number of pieces of deadwood was tested with respect to decay class. This tests the null hypothesis that there should be no differences in the relationship between volume and frequency between different decay classes. Similar results were obtained for both logs and snags. In the foothills Spruce plots, volumes by decay class were as expected, but for pines there were greater volumes of deadwood in decay classes 4 and 5 than expected relative to the number of pieces of deadwood within those classes (Figure 7.3b).

In the uplands and lowlands, greater volumes of spruce deadwood were recorded in decay classes 1, 2 and 3 relative to what could have been expected from the observed distribution of deadwood pieces of spruce amongst decay classes (Figure 7.3b). Pieces of deadwood in the oak stands were much smaller in volume terms than in the pines and spruces.

**Figure 7.1** *Volume of stumps, logs and snags recorded in (a) Foothills Scots pine; (b) Upland Sitka spruce; (c) Foothills Sitka spruce; (d) Upland oak; (e); Lowland oak (f) Lowland Norway spruce; (g) Lowland Scots pine; (h) Lowland Corsican pine. Means of two crop type/stand stage replicates. Note change in abscissa scale on graph (B). For plot details see (Annex 1). All pre-thicket plots in pine and spruce stands are second rotation except Glen Affric plot 1.1.*



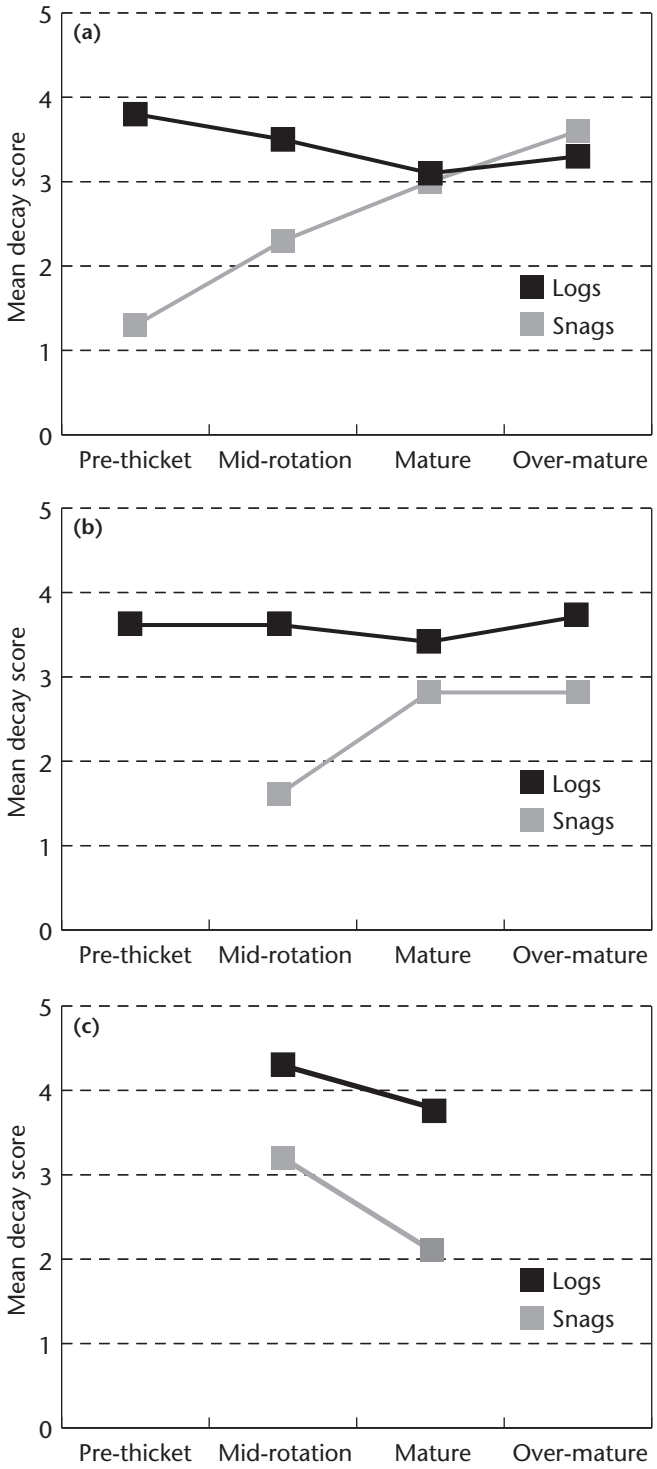


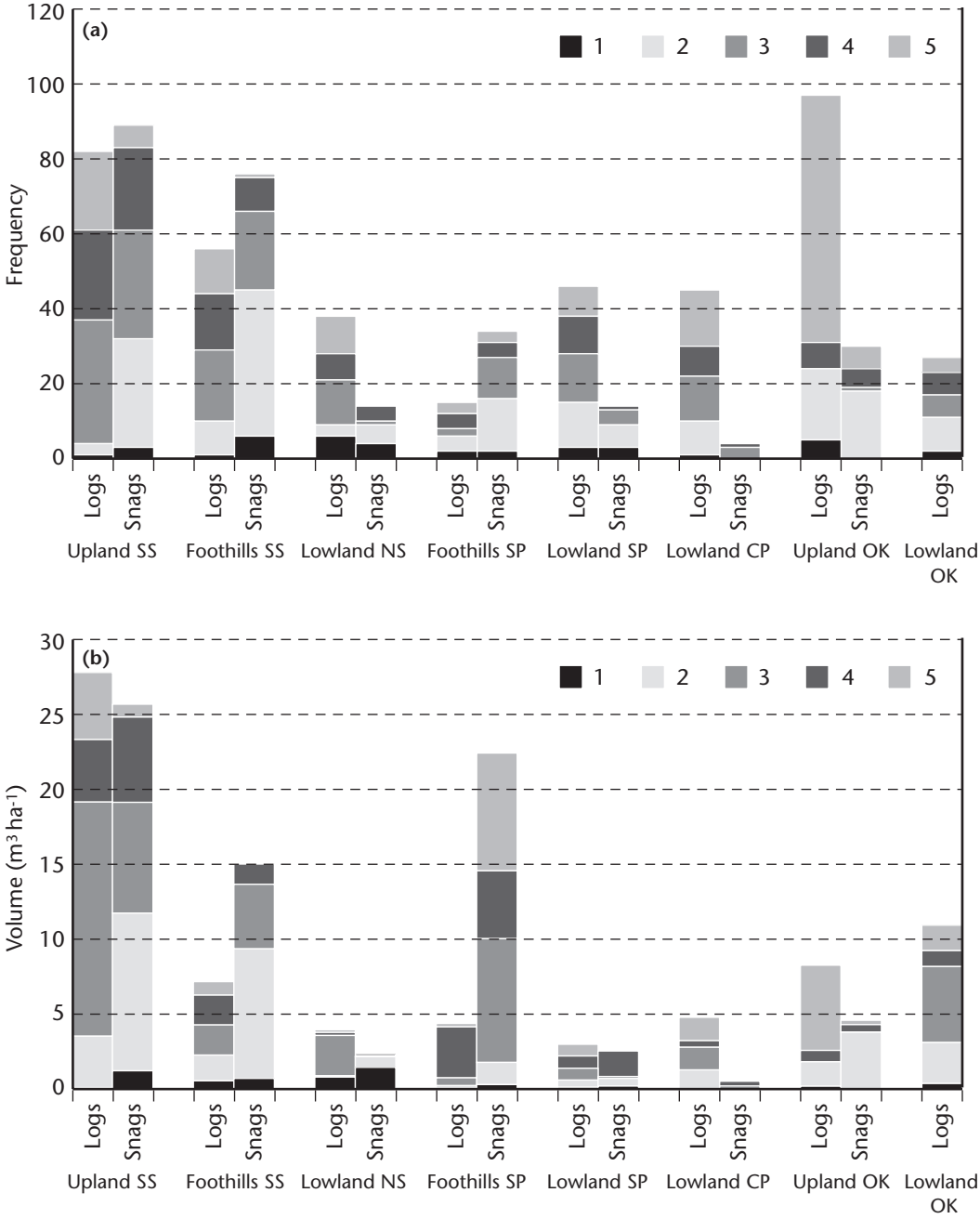

**Figure 7.2**

*Mean decay score of logs and snags in relation to stand stage; (a) pine stands; (b) spruce stands; (c) upland oak stands.*

There were no significant differences in the proportions of logs amongst diameter classes between foothills and lowland Scots pine plots, between Scots and Corsican pine or between upland and lowland oak plots (Figure 7.4a). Upland Sitka spruce plots contained proportionately more logs and snags in the larger diameter classes compared to the foothills Sitka spruce and lowland Norway spruce plots ($P < 0.001$ for both logs and snags). Upland oak plots had fewer large diameter logs than the upland spruce plots ($P < 0.01$), but similar snag distributions (Figure 7.4a). Foothills Scots pine plots had proportionately more snags in the larger diameter classes than the lowland Scots and Corsican pine plots ($P < 0.05$), but there was no difference between Scots and Corsican pine (Figure 7.4a).

Although there was much greater frequency of deadwood in the smaller compared to the larger diameter classes, the cumulative volume of the former was generally much lower than that of the latter (Figure 7.4b). Upland Sitka spruce and Foothills Scots pine had significantly higher volumes of large diameter logs and snags than the other crop types ($P < 0.01$).

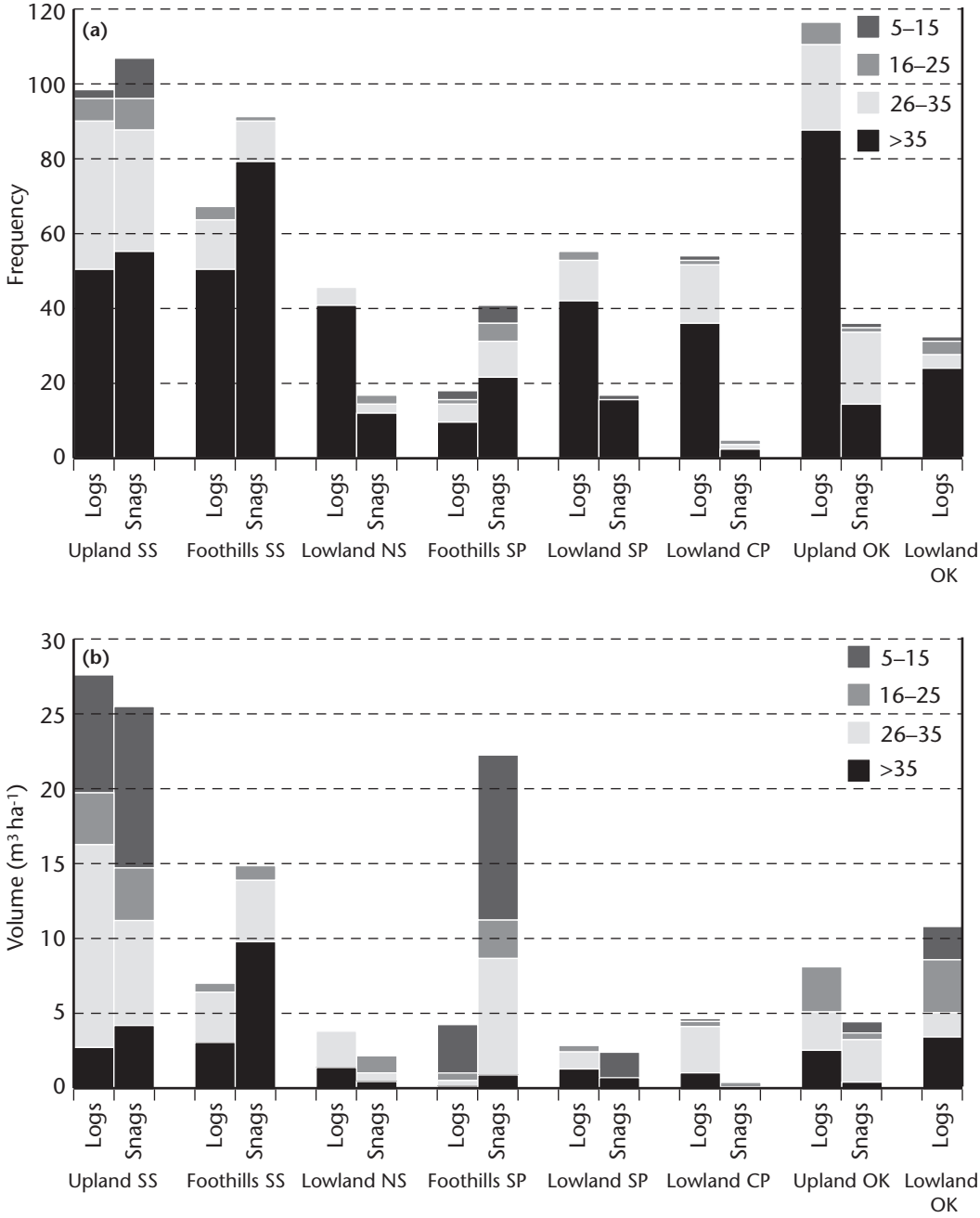
**Figure 7.3** *Logs and snags in different decay classes (1–5 in key) and crop types; (a) frequency; (b) volume. Snag decay state was not recorded in the lowland oak stands. Number of plots given in Annexe 1.*




## Discussion

Since deadwood is recognised as having an extensive range of ecological values in forest ecosystems, it is perhaps surprising that there have been few large-scale assessments of the resource in British forests before this current survey. The volume range (4–20 $m^3 ha^{-1}$) estimated by Hodge and Peterken (1998) for conifer plantations appears conservative as our survey found the average deadwood volume per hectare was more than 30 $m^3$, with a considerable number of stands having more than 40 $m^3$. This latter estimate falls within the 'high' deadwood benchmark proposed by Kirby *et al.* (1998) for British forests, and approaches the values normally associated with neglected coppice woodland, or unmanaged semi-natural broadleaved woodland (Green and Peterken, 1997; Kirby *et al.*, 1998). These values for planted forests are also considerably in excess of average volumes of deadwood recorded in Swedish managed and old growth forests (6.1 $m^3 ha^{-1}$ and 12.8 $m^3 ha^{-1}$ respectively – Fridman and Walheim, 2000), but are between the values recorded for over-mature managed and old growth forests in southern Finland (Siitonen *et al.*, 2000). Deadwood volumes in near-natural forests in the Pacific Northwest region range from 40 $m^3 ha^{-1}$ in middle-aged stands through to over

**Figure 7.4** *Logs and snags in different diameter classes and crop types; (a) frequency; (b) volume. Snag diameter was not recorded in the lowland oak plots. Number of plots given in Annexe 1.*




500 $m^3 ha^{-1}$ in old-growth stands (Spies *et al.*, 1988). Only deadwood volumes in the over-mature upland Sitka spruce stands at approximately 250–330 $m^3 ha^{-1}$ approached these kinds of values.

Despite the variability in deadwood volumes between crop types and stand stages, plots in the north and west of Britain (uplands and foothills) had significantly higher volumes of both logs and snags than stands in the south and east (lowlands). The particularly high volumes recorded in the Sitka spruce stands are probably directly related to two factors: increased occurrence of windthrow and self-thinning in mature and over-mature stands. Wind speeds are generally higher in the north and west of Britain than in the south and east and damaging storms are more common (Quine *et al.*, 1995). Tree density and thus rates of self-thinning are much higher in Sitka spruce stands than in other crop types, owing to a policy of no commercial or pre-commercial thinning to reduce the risk of windthrow (Quine *et al.*, 1995). A typical characteristic of mature Sitka stands is a high frequency and volume of snags, mostly of small dimensions. Many of these snags remain undisturbed within the stand for a considerable length of time before felling, and this may explain why average decay class for snags tended to increase through the chronosequence.

In contrast, most of the mature and over-mature stands in the lowlands had been conventionally thinned and this, coupled with the lack of windthrow, are probably the main reasons why deadwood volumes were lower in these stands. However, catastrophic wind and other events such as drought are not unknown in the lowlands, and both Green and Peterken (1997) and Kirby *et al.* (1998) stress the general importance of individual events in determining the nature of the deadwood resource in British forests. The low deadwood values recorded in some of the stands may simply be due to the fact that no significant disturbance event has affected these particular stands.

Considerable volumes of deadwood are also left as harvesting residue, and some of the pre-thicket plots had quite significant log volumes (only one pre-thicket plot – Affric 1.1 – was a newly planted stand and this had no deadwood). This may in part explain the why decay scores for logs remained constant throughout the chronosequence for pines, spruces and the upland oak sites, whereas log volumes changed considerably. Some logs may have been present in a stand before felling and been left to decay further on site after harvesting, thus being more decayed than might be expected if felled when living.

Pine plots had a greater volume of deadwood in decay classes 4 and 5 than might be expected relative to the number of pieces of deadwood (when compared to spruce). It is possible that larger pieces of pine decay faster than large pieces of spruce (John Gibbs, personal communication). Decay rates in Norway spruce have been modelled by Kruys *et al*. (in press) for mid-northern Swedish conditions, but no comparisons have yet been made between different tree species, so it is not possible to confirm or refute this theory at the present time.

Deadwood volumes in the over-mature or semi-natural stands within the foothills Scots pine chronosequences were similar in magnitude to those within semi-natural pinewood stands recorded by Reid *et al.* (1996) at about 40–60 $m^3 ha^{-1}$. Large logs were much less common than large snags within the pinewoods and this observation tends to support the theory of Reid *et al.* (1996) that most old pine trees die *in situ*, rot gradually, and then shatter into smaller fragments when they are eventually blown over and become logs. A similar phenomenon may occur in the upland oak stands where large quantities of decay class 5 logs were recorded but with a small cumulative volume. These logs were mostly branches in the 5–15 cm diameter class. Large oak trees tend to lose branches during storms and snow rather than blow over entirely. In contrast, most of the high log and snag volumes in upland and foothill Sitka spruce plots were made up of a small number of large diameter pieces, in most circumstances whole trees which had been up rooted.

## Conclusions

This preliminary analysis of the deadwood data has shown that both management and natural disturbance agents appear to have a considerable impact on both the quantity and quality of the deadwood resource. The fact that such high deadwood volumes were recorded across a considerable number of sites is encouraging, and many sites appear to meet or exceed current guideline volumes for plantations (Hodge and Peterken, 1998; Kirby *et al*., 1998). The log and snag frequencies recorded were also well in excess of current standards (frequencies of 3 logs and 3 snags per hectare) recommended in the UK Woodland Assurance Scheme (UKWAS – Anon., 2000).

None of the planted stands had been managed in any special way to encourage the accumulation of deadwood, so 'normal' plantation management seems to deliver acceptable volumes supplemented by windthrow. However, compared to near natural boreal and temperate forests there is a lack of large diameter, well-decayed snags and logs, particularly in the lowland stands. Chapters 8 and 9 will illustrate the value of large, well decayed material as a habitat for lower plants. The best option for encouraging the accumulation of this type of material is to retain stands beyond normal felling age, and this option is discussed further in subsequent chapters.

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CHAPTER 8

# The value of conifer plantations as a habitat for macrofungi

Jonathan Humphrey, Richard Ferris, Adrian Newton and Andrew Peace

## Summary

Macrofungal communities were surveyed over a 4-year period in all the biodiversity plots, and species-richness and community composition were related to climate, soil, vegetation and stand variables. Six hundred and eighty species were recorded in total (223 mycorrhizal species, 262 litter saprotrophs, 180 wood saprotrophs, 15 parasites). Each crop species type had a distinctive mycota related to differences in climate, soil, stand structure, deadwood and site history. There were no significant differences in fungal species-richness between plantations and semi-natural woodlands. Mycorrhizal species-richness was highest in upland Sitka spruce stands and was positively correlated with shrub and lower canopy cover, soil magnesium and potassium. Host tree species diversity was positively correlated with mycorrhizal species-richness in lowland pine, spruce and oak plots. Wood saprotroph-richness was most closely correlated with fresh (bark intact) log volume in the southern plots, and log length per hectare in the northern plots, with older lowland Scots pine and oak stands having the highest species counts. Litter saprotoph richness was positively correlated with soil fertility. Twenty-nine Red Data list species of fungi were recorded; planted stands nearer to semi-natural pinewood areas in the Scottish Highlands, or on ancient woodland sites, had a higher number of records of threatened species. These results highlight the importance of planted forests as a habitat for native fungi. Habitat value could be further enhanced through increasing fallen log volumes (up to 20–40 $m^3 ha^{-1}$), enhancing tree species diversity, and establishing more non-intervention 'natural' reserves preferably near to existing semi-natural woodland fragments.

## Introduction

Fungi are a diverse taxonomic group with more than 16 000 species recorded in the UK (Usher, 1997). Macrofungi may be defined as those species of fungi which produce a relatively conspicuous sporocarp; this is an artificial and somewhat arbitrarily defined group which includes many Basidiomycetes (excluding rusts, smuts and yeasts) and some Ascomycetes (Pezizales; Watling, 1995). Woodland fungi play a key role in a number of ecosystem processes, such as the decomposition of cellulose and lignin, mediation of soil processes and the enhancement of tree growth through the development of mycorrhizal associations (Killham, 1994). Fungi also enhance habitat quality for other species. For example wood boring insects require wood infected by fungi before they can digest the lignin, and many other insect groups depend on fungi as a food source (Hodgetts, 1996).

Concern about the conservation of native woodland fungi has increased in recent years (Arnolds, 1991). Given the decline over the last 3000 years in the extent of native woodland habitat in the UK, it is likely that many native fungi must have declined substantially in abundance over the long-term (Newton and Humphrey, 1997). Whilst the recently published Habitat Action Plans for native woodlands (Anon., 1995) should (indirectly) go some way to redressing this decline in native fungi, there is a possibility that planted forests may offer potential habitat. Few mycological surveys have been undertaken in plantations to date (Newton and Haigh, 1998), although recent data suggests that they could have the potential to support a significant fungal diversity. For example, some 151 species of ectomycorrhizal fungi have been found associated with *Picea* spp. in the UK (Newton and Haigh, 1998). However, very little is known about the factors which influence the composition or diversity of fungal communities (Crites and Dale, 1998), as there has been little research concerned

with clarifying the relative influences of factors such as site type, stand structure or climate (Humphrey *et al.*, 2000). In this chapter, four questions are addressed.

- What types of fungal communities are there in planted forests?
- Which environmental/habitat parameters influence fungal diversity and community structure?
- Can plantations contribute to the conservation of rare and threatened taxa?
- What management, if any, is appropriate for enhancing fungal diversity?

The results presented update those published by Humphrey *et al*. (2000) for northern Britain and Ferris *et al*. (2000) for a subset of sites in southern Britain.

## Methods

### Fungal survey

Fungi were assessed in all plots except 8.1 (Fineshade – lowland Norway spruce). The presence/absence of macrofungal sporocarps (macroscopic ascomycetes and basidiomycetes) was recorded in the eight 10 m x 10 m mensuration quadrats (see Figure 3.2 – Chapter 3), giving an abundance score of between 1 and 8 for each species. Assessments were made over the August–October period to coincide with the main time of sporocarp production. Three visits were made to each plot at roughly monthly intervals over this period, and repeated over 3–4 years. This sampling period was designed to allow an estimated 80% of total species to be recorded for each plot (based on asymptotes for yearly species-accumulation curves). A total census would need a much longer time period and was beyond the scope of this study. Collections were identified by reference to standard texts, involving microscopic examination where necessary. Material of particularly critical taxa was dried for reference and deposited in national herbaria (Royal Botanic Gardens, Edinburgh and Kew). Species were placed into functional groups following Newton and Haigh (1998) and Ferris *et al*. (2000): M – mycorrhizal; P – parastic; L – saprotrophic species on litter and other fungi; W – deadwood saprotrophs.

### Analysis

The effects of crop species type and stand stage on fungal species-richness were analysed using a generalised linear mixed model (see Humphrey *et al*., 2000). Fungal community composition was examined using correspondence analysis (CA; see Chapter 4 for details) to provide vectors (axes) summarising the main gradients of variability amongst the sample plots. The CA vectors (F1, F2 – all plots; FN1, FN2 – northern sites only; FS1, FS2 – southern sites only) together with values for species-richness (number of fungal species per hectare by functional group) were related to climate, soil, stand, and vegetation variables using correlation analysis. Separate analyses were carried out for the northern (1, 2, 5, 6, 9, 10, 15, 16) and southern (3, 4, 7, 8, 11, 12, 13, 14) groups of sites, and for all sites combined. Survey and analysis methods for stand structure, climate, soils, ground vegetation and deadwood, are described in Chapters 3, 5 and 7 respectively.

## Results

The total number of fungal species recorded was 677. Of these, 29 were classed as threatened according to the provisional Red List for fungi in the UK (Ing, 1992). This total includes 22 species associated preferentially with native pinewood. There were two apparently new records for Britain: *Panellus violaceofulvus* (Glen Affric, Scots pine, pre-thicket stage plot 1.1 ) and *Cortinarius callisteus* (Clunes Sitka spruce plots 6.2 and 6.3). Over 50% of species were recorded only once and only 16 species were found in 50% or more of the plots (Table 8.1). The breakdown into functional groups was 223 mycorrhizals, 262 litter saprotrophs, 180 wood saprotrophs and 15 parasites. There were significant differences ($P < 0.01$) in species counts between different crop types for the four main functional groups (parasites are not considered further here) but no effect of stand stage.

**Table 8.1** *Most common fungi recorded in the survey. Functional groups are: M – mycorrhizals, L – litter saprotrophs; W – wood saprotrophs. Habitat information was obtained from Philips (1981), Lange and Bayard-Hora (1985), Bon (1987), Jordan (1995), Buczacki (1992), Watling and Gregory (1993), Courtecuisse and Duhem (1994). Nomenclature follows these publications.*

| Species | Functional group | Frequency (No. of plots) | Status and habitat in Britain |
|---|---|---|---|
| *Mycena galopus* | W | 44 | Very common, widespread in all kinds of woods |
| *Mycena sanguinolenta* | L | 42 | Very common, widespread in grass and litter in woods and heaths |
| *Marasmius androsaceus* | L | 37 | Very common, widespread on dead heather, pine needles and conifer litter |
| *Mycena leptocephala* | L | 37 | Very common, widespread in short grass, or woods |
| *Calocera viscosa* | W | 36 | Very common, widespread on conifer wood |
| *Hypholoma fasciculare* | W | 35 | Very common on wood of deciduous and coniferous trees |
| *Mycena filopes* | L | 35 | Uncommon, widespread on buried twigs in mixed wood |
| *Mycena epipterygia* | L | 31 | Common, widespread among moss and leaf litter in woods |
| *Entoloma cetratum* | L | 30 | Common, widespread in coniferous woodland |
| *Mycena cinerella* | L | 28 | Common, in birch and pinewood on broadleaf litter under mosses |
| *Mycena galericulata* | W | 28 | Very common, widespread on stumps and fallen branches of broadleaves |
| *Hygrophoropsis aurantiaca* | L | 27 | Very common, widespread in conifer woodland and heaths |
| *Cystoderma amianthinum* | L | 26 | Common, widespread on soil in woods and pastures |
| *Hypholoma marginatum* | W | 26 | Common, widespread on rotting conifer wood |
| *Laccaria laccata* | M | 26 | Very common, widespread on soil in woods, moorland and short grass |
| *Russula ochroleuca* | M | 26 | Very common, widespread on soil in conifer and broadleaved woods |
| *Mycena rorida* | L | 25 | Uncommon, widespread on plant debris in woods |

### Mycorrhizal species-richness

Upland Sitka spruce plots had the highest mycorrhizal species counts ($P < 0.01$) followed by the Scots pine and oak plots (Figure 8.1). Foothills Sitka spruce and lowland Corsican pine had the lowest counts. Species-richness was positively correlated with increasing lower canopy cover (S3), shrub layer cover (S2), cover index (CI) and soil phosphorus, potassium, magnesium and organic matter (Table 8.2) For the northern set of sites, there were positive correlations between species-richness and increasing magnesium, calcium and potassium, and a negative correlation with nitrate (Table 8.2). Similar relationships with soil factors were recorded for the southern sites, but here there were also positive correlations between species-richness, S2 cover, the number of tree species, increasing litter depth and accumulated temperature (AT). Negative correlations were recorded between species-richness, height to live crown and non-vascular plant species count (Table 8.2).

### Litter saprotrophs species-richness

As with the mycorrhizals, litter saprotroph species counts were significantly lower ($P < 0.01$) in the foothills Sitka spruce and lowland Corsican pine stands than in the other crop types (Figure 8.1). Species counts were significantly correlated with increasing pH (Table 8.2). In the north, there was a positive correlation between litter saprotroph richness and species-richness of the ground flora; litter saprotroph richness was negatively correlated with increasing litter depth (Table 8.2). Nitrate and pH were the only variables that were significantly correlated with species-richness in the southern plots, with more nutrient-rich, high pH sites having more species.

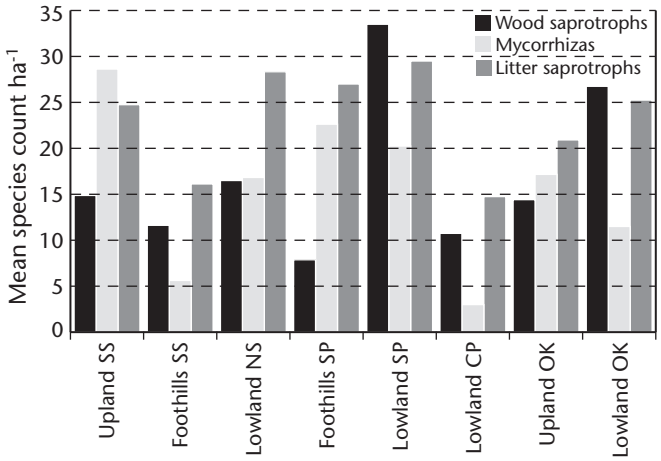


**Figure 8.1**

*Number of fungal species recorded in the different stand growth stages of Scots pine (SP), Corsican pine (CP), oak (OK), Sitka spruce (SS) and Norway spruce (NS). Values are means for each stand/crop type within each climate zone.*

**Table 8.2** *Summary of significant correlations between fungal species counts and soil, climate, structure, vegetation and deadwood variables, based on Pearson correlation coefficients. Northern plots (sites 1, 2, 5, 6, 9, 10, and 15); southern plots (sites 3, 4, 7, 8, 11, 12, 13, and 14); (-) negative correlation; * P < 0.05; ** P < 0.01. For the key to soil, climate and stand structure variables see Table 3.3 (Chapter 3). For deadwood variables see Table 7.1 (Chapter 7). Vegetation variables: NVASC = number of vascular plant species; VASC = vascular plant diversity.*

| | | Species counts (number ha$^{-1}$) | | |
|---|---|---|---|---|
| | | All plots | Northern plots | Southern plots |
| Mycorrhizals | Soil | P1* Mg1** ORG1** K** | Mg1** Ca1* K* (-)NO32* | pH1* P1* K* |
| | Climate | | | AT* |
| | Structure | S2** S3* CI* | | S2** (-)HTCL* |
| | Vegetation | | | (-) NVASC* TREESP* LITTER** |
| Litter saprotrophs | Soil | pH1* pH2* | | pH1* pH2* NH41* NO31* |
| | Vegetation | | (-) LITTER* VASC* | |
| Wood saprotrophs | Soil | Ca1* | | P1* Mg1** |
| | Climate | AT** MD** | | |
| | Vegetation | VASC** LITTER** | | |
| | Deadwood | FSTUMP* | LOGL** | RLOG** |

### Wood saprotrophs species-richness

There was a significant positive correlation between the quantity of deadwood and wood saprotroph species-richness (Table 8.2). Lowland Scots pine and oak plots had significantly higher ($P < 0.01$) species counts than the other plots (Figure 8.1 and Table 8.2), relating primarily to higher fresh stump volumes. There were also positive correlations between wood saprotroph richness and increasing litter depth, accumulated temperature (AT), moisture deficit (MD) and soil calcium (Table 8.2). Within the northern set of plots, there was a significant correlation between species-richness and log length per hectare; the relationship is illustrated in Figure 8.2a. No other significant correlations were recorded. In the south, rotten log volume was positively correlated with higher species counts as shown in Figure 8.2b. Positive corrrelations were also recorded between species-richness, increasing litter depth, phosphorus and magnesium. The only negative correlation was with non-vascular plant species count (Table 8.2).

### Fungal community composition

The first two axes of the correspondence analysis (CA) of all plots combined (Figure 8.3a) accounted for 20.7% of the variability in the data; eigen values were 0.26 for axis 1 and 0.22 for axis 2. The

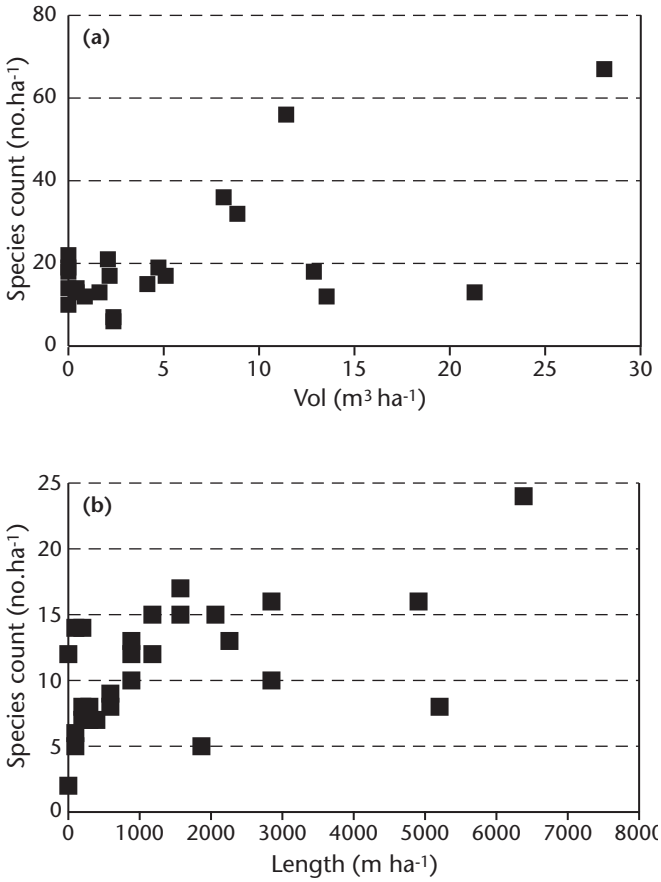


**Figure 8.2**

*Relationships between wood saprotroph species counts (log transformed) and: (a) total fresh log volume per hectare in southern plots only; y = 2.62 + 0.04x; R2 = 0.26; df = 21; F = 7.43; P < 0.05; (b) total log length per hectare in northern plots only; y = 2.09 + 0.0001x; R2 = 0.21; df = 26; F = 6.96; P < 0.05.*

Sitka spruce and foothills Scots pine plots were grouped separately from the other plots along axis 1 (F1). This axis was positively correlated with magnesium, organic matter and the number of non-vascular plant species. Axis 1 was negatively correlated with pH, nitrate, accumulated temperature (AT) and soil moisture deficit (MD), height to base of live crown (HTLC), and the number of tree and litter saprotroph species. Axis 2 (F2) which separated the oak and lowland Norway spruce plots from the other plots was positively correlated with ground vegetation (all species and vascular plants), tree and mycorrhizal species counts, stand age, pH and major soil nutrients. Negative correlations were recorded between axis 2 and ammonium, field layer cover (S1) and height to live crown (HTLC).

For the CA of northern plots only (Figure 8.3b), eigen values were 0.26 and 0.21 for axes 1 and 2 respectively, with these two axes accounting for 26.9% of the variability in the data. Axis 1 (FN1) separated the foothills Scots pine plots from the other plots and was positively correlated with litter depth, ammonium, accumulated temperature (AT) moisture deficit (MD), upper canopy cover (S4), and wood saprotroph richness (Table 8.3). Negative correlations were recorded between this axis mycorrhizal and litter saprotroph species-richness, and soil organic matter (Table 8.3). The oak, upland and foothills Sitka spruce plots were grouped separately from the pine plots along axis 2 (FN2) relating to a gradient of increasing pH, calcium, potassium, magnesium, vascular plant, tree and mycorrhizal species-richness. Organic matter and ammonium were negatively correlated with axis 2 (Table 8.3).

Axes 1 and 2 (FS1 and 2) of the CA of southern plots accounted for 28.9% of the variability in the data (eigen values of 0.32 and 0.19 respectively). Axis 1 separating lowland oak and Norway spruce from lowland Corsican and Scots pine (Figure 8.3c) was positively correlated with pH and major soil nutrients, leaf area index (LAI), stand age and species-richness of vascular plants, trees, and mycorrhizals (Table 8.3). Moisture deficit (MD) and field layer vertical cover (S1) were negatively correlated with Axis 1. Axis 2 separated Corsican pine plots from the other crop types and was negatively correlated with accumulated temperature (AT), litter depth, litter saprotroph and mycorrhizal species-richness (Table 8.3).

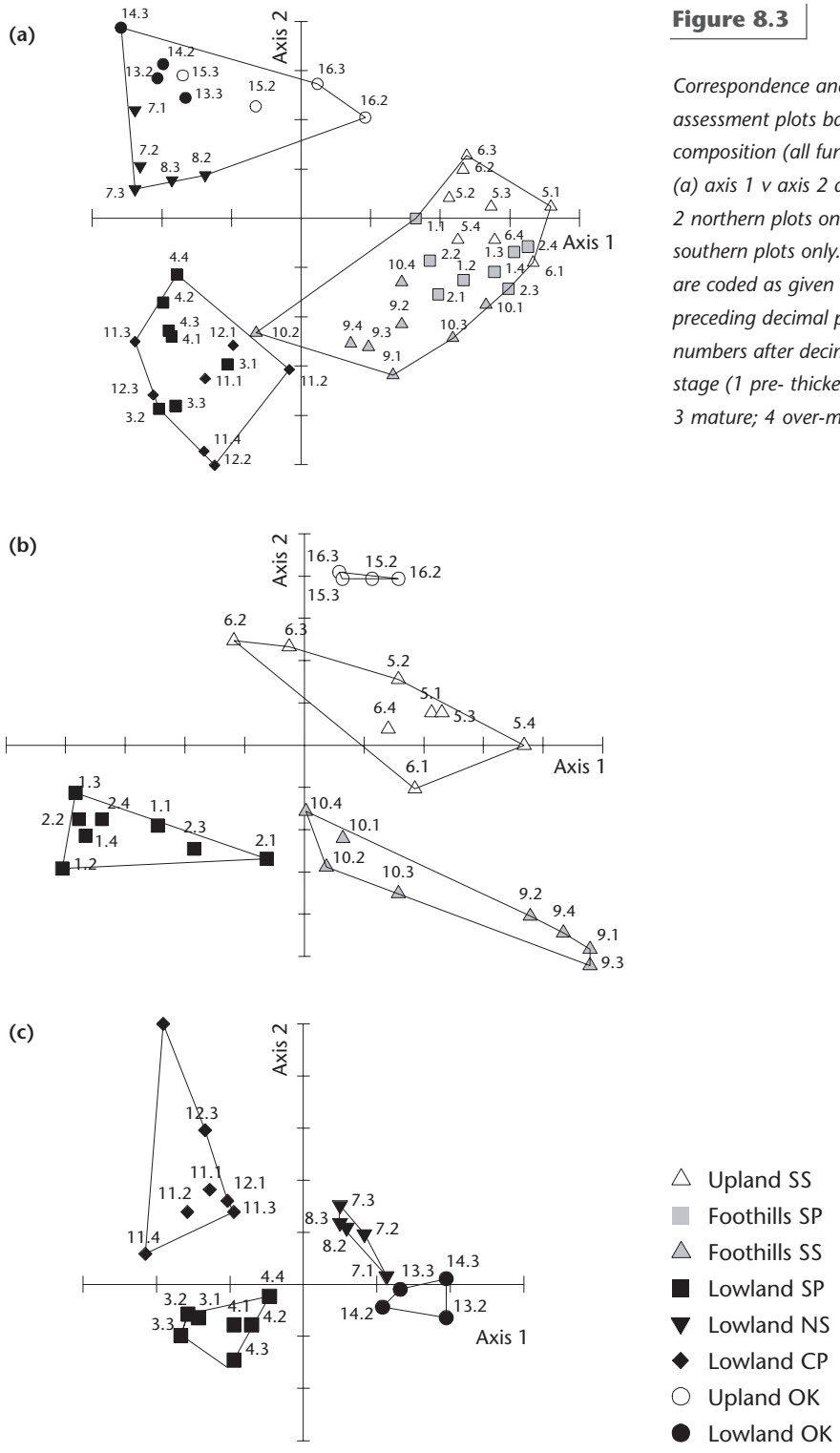


**Figure 8.3**

*Correspondence analysis ordination of assessment plots based on fungal species composition (all functional groups); (a) axis 1 v axis 2 all plots (b) axis 1 v axis 2 northern plots only. (c) axis 1 v axis 2 southern plots only. Data labels for plots are coded as given in Annexe 1. Numbers preceding decimal point refer to sites, numbers after decimal point refer to stand stage (1 pre- thicket; 2 mid-rotation; 3 mature; 4 over-mature).*

### Species of conservation importance

Of the 29 threatened species recorded, 11 were specific to foothills Scots pine, five to Sitka spruce, four to lowland Scots pine, one to lowland oak, one to upland oak and one to lowland Norway spruce (Table 8.3). Norway spruce and lowland oak shared one species; foothills Scots pine and Sitka spruce had 5 species in common. Most species were recorded as being associated with conifer woodland, acid soil and mosses or conifer deadwood. Three species were associates of broadleaved or coppice woodland (Table 8.3). A negative correlation (Figure 8.4) was recorded between the distance to an extant native pinewood and the number of records of threatened pinewood species (all species in Table 8.3 excluding those found in the lowland plots and the oak plots). No other significant correlations were recorded between the number of threatened species records and any other habitat measure or site variable.

**Table 8.3** *Threatened fungal species recorded during the survey. 'Status' refers to the IUCN categories of threat, as employed in Red Data Lists (see Mace and Lande, 1991 for Scotland). Abbreviations (following Ing, 1992): E – endangered; V – vulnerable; R – rare. W – wood saprotrophs; M – mycorrhizal species; L – litter saprotrophs; P – parasites. n/a – no habitat information available.*

| Species | Functional group | Status | Plots where recorded | Habitat |
|---|---|---|---|---|
| *Collybia acervata* | L | V | 2.4 | Conifer stumps |
| *Collybia racemosa* | L | R | 4.2 | Decayed mushrooms or conifer litter |
| *Cortinarius camphoratus* | M | V | 6.2, 6.3 | Conifer woods, notably pine |
| *Cortinarius laniger* | M | V | 6.2 | n/a |
| *Cortinarius limonius* | M | V | 1.2, 2.4, 6.2, 6.3, 6.4, | Soil – conifer woods |
| *Cortinarius purpurascens* | M | - | 1.3 | Acid soils in conifer/deciduous woods |
| *Cortinarius scaurus* | M | V | 6.2 | Conifer woods, especially spruce |
| *Cortinarius violaceus* | M | E | 5.2 | Deciduous woods, birch/beech |
| *Craterellus cinereus* | M | V | 13.3 | n/a |
| *Fayodia gracilipes* | L | R | 5.2, 6.2, 6.3 | Mosses especially under conifers |
| *Galerina stylifera* | L | V | 3.1, 3.2, 3.3 | Wet rotten wood/conifer debris |
| *Hydnellum peckii* | M | E[1] | 2.2 | Plant debris – conifer woods |
| *Lactarius musteus* | M | V | 1.2, 2.1, 2.2 | *Sphagnum*/moss – conifer woods |
| *Leucoagaricus georginae* | L | V | 3.3 | Mixed coppice especially disturbed |
| *Lycoperdon lambinonii* | L | V | 7.2 | n/a |
| *Mycena purpureofusca* | W | V | 2.1, 6.3, 10.2 | Pine cones and woody debris |
| *Mycena rosella* | L | V | 1.1, 1.3, 1.4, 2.4, 6.2 | Fallen conifer needles |
| *Mycena rubromarginata* | L | V | 1.4, 2.1, 2.2, 2.3, 3.1, 5.1, 5.2, 5.3, 5.4, 6.1, 6.3, 6.4, 8.3, 10.1, 10.4, 11.3 | Twigs/ litter – conifer woods |
| *Mycena urania* | L | E | 2.3 | n/a |
| *Pholiota astragalina* | W | R | 4.1 | Rotten conifer wood |
| *Pseudocraterellus sinuosus* | M | V | 16.3 | Leaf litter – deciduous woods |
| *Ripartitis metrodii* | L | R | 8.2, 8.3, 13.3 | Conifer woods, especially spruce |
| *Rozites caperata* | M | V | 1.3, 1.4, 2.4 | Acid soil – conifer woods/heather |
| *Russula declorans* | M | V | 1.3, 1.4 | Soil – conifer woods |
| *Russula obscura* | M | V | 1.3 | Soil – conifer woods |
| *Sarcodon imbricatus* | M | V[1] | 2.2 | Soil – conifer woods |
| *Suillus flavidus* | M | V | 1.4 | Wet soil/*Sphagnum*-Scots pine |
| *Tricholoma sejunctum* | M | V | 1.4, 6.2 | Soil – mixed/conifers especially birch |
| *Xeromphalina campanella* | W | V | 2.1 | Rotting conifer wood |

[1]Species with Action Plans (SAPs – Anon., 1995)

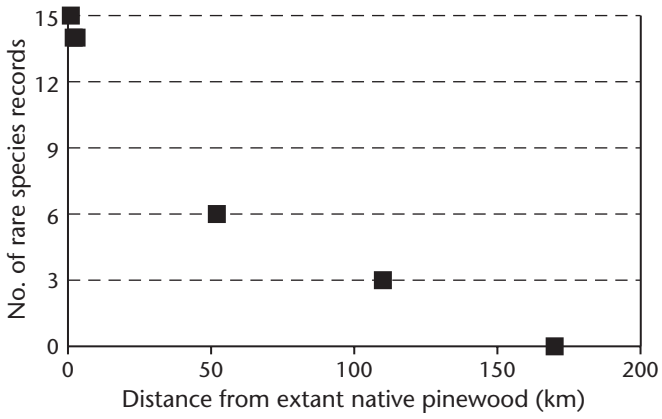


**Figure 8.4**

*Records of threatened native pinewood fungi in relation to distance of recording site from extant native pinewood area; y = -0.0154x + 2.785; R2 = 0.9799; df = 4; F = 194.8; P < 0.001 (log transformation of count data).*

# Discussion

### Limitations of the data

Fungal communities are notoriously difficult to assess comprehensively in the field. Surveys depend upon the presence of sporocarps to denote species occurrence, rather than the vegetative mycelia that generally form the greater part of fungal biomass. Sporocarp production is strongly influenced by weather conditions with sporadic and sometimes shortlived fruiting varying between different months and years (Watling, 1995). Orton (1987) considered that at least 10 years of survey data were required to define the species of macromycete present in an area with any precision, and there have been numerous studies where new species were still being recorded after 20 years (Watling, 1995). In this current survey, plots were only surveyed on three occasions and given this limitation the current data must therefore be viewed with caution. However, the fact that the plots were surveyed over the same period should increase the validity of comparisons drawn between them.

### Relationships between environmental variables, fungal species-richness and community composition

Altogether, 679 fungal species were recorded during this survey. This figure compares favourably with those obtained from mycological surveys of temperate and boreal forests in Scandinavia and North America (e.g. Lindblad, 1998). Of the 16 most common species, over half were litter saprotrophs comprising widespread and abundant species found in both wooded and non-wooded habitats (e.g *Mycena sanguinolenta* and *Marasmius androsaceus*). As with the lichen and bryophyte data (see Chapter 9), a large proportion of the species were recorded only once. Consequently, fungal community composition differed markedly between sites, and even between plots within a site. Despite this variability three clear groupings were evident in the CA of all plots: a northern spruce/pine group, an oak/Norway spruce group and a lowland Corsican/Scots pine group. Part of the variability between these groups was related to large differences in the species-richness of wood saprotrophs and mycorrhizals. Mycorrhizal species-richness was significantly higher in the upland Sitka spruce plots (towards the right-hand end of axis 1 – Figure 8.4a) than in the other plots including oak. This finding contrasts with those of other studies that have suggested that the fungal flora of conifer stands is often less diverse than that of broadleaved stands. For example, Villeneuve *et al.* (1989) found that the diversity of both ectomycorrhizal and saprotroph species in Quebec forests was significantly lower in conifer stands than in deciduous stands, owing mainly to the scarcity of saprotrophs in conifer mor humus. In addition, Newton and Haigh (1998) in their study of ectomycorrhizal fungi in the UK, found that exotic conifer species displayed a lower mycorrhizal diversity than would be expected from their distributional areas (151 mycorrhizal associates of *Picea*, 201 for *Pinus* and 233 for *Quercus*).

The trend in mycorrhizal species-richness is driven mainly by plots 6.2 and 6.3 (Clunes, mid-rotation and mature stands). These plots, characterised by large numbers of *Cortinarius* and *Inocybe* spp., form a distinct grouping along axis 2 of the CA of northern plots, associated with increases in soil magnesium and potassium, shrub and lower canopy cover, and the number of tree species. It is possible that the denser stand conditions associated with the mid-rotation and mature spruce stands are conducive to the development of mycorrhizal communities by affording freedom from competing ground vegetation and providing a higher tree root density for mycorrhizal associations. The significant correlation recorded between mycorrhizal species-richness and the number of host tree species present confirms recent analyses indicating that many tree species in Britain are associated with distinctive assemblages of ectomycorrhizal fungi (Newton and Haigh, 1998).

These results therefore suggest that the diversity of host tree species could be used potentially as a simple indicator to infer patterns of diversity in this group of fungi. This finding also lends support to the inclusion of hardwood species in conifer plantations as a means of increasing biodiversity. For example, the addition of birch in spruce stands was found to increase numbers of vascular plant, bryophyte and lichen species (Humphrey *et al.,* 1998), and the same may be expected for mycorrhizals on the basis of the current study.

Paradoxically the foothills Sitka spruce stands, although comparable in terms of stand age and structure to the upland Sitka spruce plots were not nearly as rich in fungal species. Annexe 1 indicates

that the upland and foothills Sitka stands differ markedly in their site histories; the upland plantations in Clunes and Knapdale having been established on ground previously occupied by ancient semi-natural woodland (Hamilton, 1995), whereas the foothills Kielder and Glentress stands were established on grass and heathland. Site history also appears to be a significant factor in the south. Low species counts were recorded in Corsican pine stands (sites 11 and 12) established on heath and grassland land, whereas the Norway spruce stands (sites 7 and 8), established on old oakwood sites, shared a number of species with the oak stands which were either absent, or much less common in the other plots (e.g. species such as the litter saprotrophs *Clitocybe fragrans*, *Collybia butyracea*, *Lycoperdon perlatum*, *Megacollybia platyphylla*, *Mycena polygramma* and *Ripartitis metrodii*, and the wood saprotroph *Xylaria hypoxylon)*.

The abundance and decay state of deadwood is a key factor influencing the diversity of wood saprotrophs in semi-natural temperate and boreal forests (Crites and Dale, 1998; Kruys *et al*., 1999; Hodgetts, 1996). In this current study, a number of positive relationships were recorded between log and stump volumes and the number of wood saprotroph species. Wood saprotroph richness was negatively correlated with axis 1 of the CA of all plots (Figure 7.3a), with plots 4.4 (Windsor, over-mature Scots pine) and 13.3 (Alice Holt mid-rotation oak) having significantly higher numbers of species than the other plot types and lying well to the left on this axis. Plot 4.4 was characterised by a high abundance of *Hypochnicium*, *Phlebia* and *Phlebiella* spp.; plot 13.3 had species which were not recorded in any other plots such as *Bulbillomyes farinosus, Peniophora quercina* and *Tomentella bryophila*.

Whilst this trend in species-richness was also correlated with factors such as accumulated temperature and soil moisture deficit, the strongest correlation was with fresh stump volume, plots 4.4 and 13.2 having very high values for this variable compared to the other plots. The importance of these two plots tends to mask other trends in the deadwood data that become apparent when the northern and southern plots are considered separately. In the north, log length (all decay categories) was the best predictor of species-richness, whereas rotten log volume was more important in the south. Unfortunately, the value of stumps as a predictor of wood saprotroph-richness appears to be limited as a high proportion of plots had no stumps.

In a number of studies in boreal forests, correlations have been recorded between wood saprotroph diversity and deadwood with both initial and advanced bark loss (e.g. Crites and Dale, 1998; Lindblad, 1998; Kruys *et al*., 1999). In Swedish Norway spruce forests, a number of Red Listed fungi showed strong preference for fallen deadwood with well-rotted bark (Kruys *et al*., 1999). Deadwood in more advanced states of decay, where the wood itself starts to rot, does not appear to support such diverse saprotroph communities (Kruys *et al*., 1999; Crites and Dale, 1998), although some specific fungi show a preference for this stage (Lindblad, 1998). This stage-specific factor may explain to some extent why higher species numbers were strongly correlated with rotten log volume in the south. However, no direct measurements of fungal species growing on different types of deadwood were undertaken in this study, so this assumption is difficult to verify.

Lowland Scots Pine and Norway spruce plots had the highest numbers of litter saprotroph species, but the differences between the crop types was less marked than for the other functional groups. Soil fertility appears to be the underlying factor influencing species-richness. The negative correlation recorded between litter depth and saprotroph richness is possibly a consequence of increased rates of decomposition.

### Fungi of conservation importance

A striking feature of the survey results was the extensive new records for rare and threatened fungi, including one species not previously recorded the UK (*Panellus violaceofulvus*) and one not previously confirmed as being native (*Cortinarius callisteus*: Orton, 1987). In addition, a further 29 species are considered to be threatened with extinction, in that they have been listed on the provisional Red Data List for British fungi. The recording of 10 Red Data List species in spruce-dominated plots in Clunes and Knapdale was unexpected and suggests a possible ability of these fungi to 'host-shift' (Watling, 1995), as all are generally associated with native pine forests. Information on the distribution of native pinewoods taken from the Forestry Commission's Pinewood Inventory (Tuley, 1995) indicates that the spruce plots in Clunes forests are, on average, 5 km from existing pinewoods

in the Loch Arkaig area. However, as noted earlier, the Clunes stands were planted on sites previously occupied by ancient semi-natural woodland. Thus temporal continuity as well as spatial proximity of pinewood habitat within the locality could help explain the relatively large number of rare species records from Clunes forest. In contrast, the Knapdale spruce plots are over 50 km from native pinewoods, the nearest group being in Glen Orchy and Glen Strae. It is possible that these plots could have acquired pinewood fungi in the short time since planting (in the 1920s and 1930s) and suggests that long-distance dispersal is possible in such species. There were few pinewood fungi recorded in Glentress and none in Kielder, reflecting perhaps the increasing distance of these sites from the nearest native pinewood fragment in Glen Falloch (Argyll). However, the ecological characteristics of these threatened pinewood fungi are poorly understood, particularly with respect to their ability to disperse and colonise new habitats. It is conceivable that some species may have been translocated during forestry operations, for example mycorrhizal species could have been transported via the root systems of planting stock (see Humphrey *et al.*, 2000).

## Conclusions and management recommendations

Although the observed relationships between environmental parameters and fungal community composition and diversity are obviously very complex and little understood, some general conclusions can be drawn which have important implications for management. Firstly, it is clear that planted forests provide a range of environmental conditions suitable for the development of diverse native fungal communities that include a number of rare and threatened species. Different crop types support different species assemblages and it is therefore important to maintain a diversity of crop types at the landscape or whole forest scale. Mycorrhizal community development is influenced by stand structure, host tree species diversity and site history. The best sites for mycorrhizals, in terms of species-richness, appear to be relatively dense upland spruce plantations on ancient woodland sites, although pine and spruce plantations on ancient woodland sites in the lowlands are also valuable (for litter saprotrophs as well as mycorrhizals).

Wood saprotroph richness is strongly correlated with increases in fallen deadwood and stump volumes. A mix of fresh and well-decayed large diameter logs and stumps should provide a range of habitat types (Kruys *et al.*, 1999) with volumes in the range of 20–40 $m^3$ $ha^{-1}$ providing for maximal diversity (based on the asymptotes of the regression curves of species-richness on deadwood volumes). This range falls close to the high (> 40 $m^3$ $ha^{-1}$) benchmark for deadwood in British broadleaved forests, as proposed by Kirby *et al.* (1998) and exceeds the 4–20 $m^3$ $ha^{-1}$ range for fallen deadwood volume in conifer plantation forests reported by Hodge and Peterken (1998). Litter saprotroph community composition and diversity appears to be more closely related to soil variables than to any other environmental factors and is therefore less amenable to enhancement by management.

The high incidence of rare and threatened fungi in plantation stands of pine and spruce, was an unexpected finding of the survey. Temporal and spatial linkage with native woodland appears to be important for determining the occurrence and distribution of these species, particularly those associated with native pinewood. The Forest Habitat Network model of Peterken *et al.* (1995) provides an appropriate mechanism for the successful integration of plantations and native woodlands, and plans are in place to develop these principles further in a native pinewood area (Ratcliffe *et al.*, 1998). Such approaches could encourage the rapid colonisation of newly established pinewoods by native fungi.

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CHAPTER 9

# Lichen and bryophyte communities: the influence of site type, stand structure and deadwood

Jonathan Humphrey, Simon Davey, Andrew Peace, Richard Ferris and Kim Harding

## Summary

A survey of deadwood lichen and bryophyte communities was carried out over a 2-year period within all 52 biodiversity assessment plots. Community composition and diversity were related to measures of climate, site, stand structure and deadwood (snags, logs and stumps). Altogether, 106 lichen species and 77 bryophytes were recorded. The planted stands had a less species-rich lichen flora than the semi-natural stands. Bryophyte species counts were similar in plantations and semi-natural stands, and were positively correlated with large diameter (≥20 cm), well-decayed logs and stumps. Lichens species-richness was higher on well-decayed snags (especially in semi-natural Scots pine stands in the Scottish Highlands). Early successional stands were often the richest for lichens, stumps being important for Caliciales and Cladonia species. There is greater scope for enhancing the diversity of epixylic lichen and bryophyte communities within plantations in the north and west of Britain than in the south and east, as lower plant communities in the north and west have been less damaged by high pollution levels in the past and the cooler and wetter climate is more conducive to community development. Two management strategies are suggested: 1) introducing alternative silvicultural systems to clearfelling (e.g. single-tree selection) to foster continuity of woodland conditions and increase deadwood volumes; 2) modifying restocking practices on clearfells to avoid excessive shading of deadwood. The first strategy is most suited to spruce stands in areas of low wind risk, whilst the second is more appropriate for Scots pine forest in the Scottish Highlands.

## Introduction

Lichens and bryophytes are now an increasingly valued component of woodland biodiversity, and this is reflected in the recent production of Species Action Plans targeted at maintaining and improving habitat for the most threatened and rarest species (Anon., 1995). However, lichens and bryophytes also fulfil a number of important ecological functions within woodland ecosystems such as: regulation of hydrological processes through interception and retention of precipitation (i.e. reducing peak flows in streams during floods), stabilising steep ground in western woodlands, contributing to nutrient cycling, and providing food and shelter for a range of dependent organisms (Hodgetts, 1996). Lichens and bryophytes are often described as being 'epiphytic' (using living trees or shrubs for anchorage, but not as a source of nutrients) and/or 'epixylic' (using dead woody material for anchorage).

Semi-natural woodlands in Britain are of international importance for lichens and bryophytes (Hodgetts, 1996). Key biotopes include lowland pasture woodland (e.g. the New Forest, Suffolk), Atlantic oak-birchwoods (*Quercus-Betula* spp.) in northern and western regions, and native Caledonian pinewoods (*Pinus sylvestris* L.) in the Scottish Highlands (Rose, 1993). The particular value of these woodland types as a habitat for lower plants is related to low pollution levels, continuity of woodland conditions over many hundreds of years, the survival of very old trees, and relatively open canopies ensuring adequate light levels for growth and development (Rose, 1993; Fletcher, 1999).

Deadwood is a key habitat for lower plants in boreal and temperate forests (Esseen *et al.*, 1997; Crites and Dale, 1998). A number of studies in Fenno scandian boreal forests have highlighted the value of large diameter, well-decayed fallen and standing deadwood for rare and threatened taxa (e.g.

Gustafsson and Hallingbäck, 1988; Kruys *et al.*, 1999). Old, unmanaged stands usually have the highest diversity of deadwood habitats (including a high proportion of large, well-decayed material) and hence have a more diverse lower plant flora (Gustafsson and Hallingbäck, 1988; Kuusinen and Siitonen, 1998).

Currently, there is very little information on the potential value of conifer plantations for lower plants, or how they might be managed to improve habitat quality. Despite numerous calls for managers to increase deadwood volumes in managed forests, the value of deadwood as a substrate for lower plants remains to be investigated (e.g. Hodge and Peterken, 1998). In this chapter, we present the results of a survey carried out in all 52 biodiversity plots of lichen and bryophyte communities associated with deadwood. Community composition and diversity were related to climate, stand structure (successional stage and vertical foliage cover) and deadwood parameters. The potential of conifer plantations as a habitat for native lichens and bryophytes is discussed, and management strategies are proposed for enhancing habitat quality. For a more detailed analysis of the lower plant data, including species recorded on substrates other than deadwood, see Humphrey *et al*. (2002).

## Methods

### Lichen, bryophyte and deadwood assessments

Lichen and bryophyte species were recorded in four 10 cm x 20 cm quadrats on individual pieces of deadwood. The quadrats were spaced more or less evenly along the length of each piece, on the upper surface of logs and stumps (i.e. omitting the sides and lower portions), and up to 2 m in height on snags (aspect was selected randomly for snag sampling). The abundance of individual species was estimated using the DOMIN scale (see Chapter 4 for details of this approach). Volume and size measurements for individual items of deadwood were only carried out in sites 1–12 (the oak stands, sites 13, 14, 15 and 16 were excluded). Methods for calculating deadwood volumes are described in Chapter 6.

### Analysis

Generalised linear models (see Humphrey *et al.*, 2002 for details) were used to assess the relative importance of crop type (combining species and bioclimatic zone), stand stage, deadwood type, decay stage, size and volume in determining species-richness of lichens and bryophytes growing directly on deadwood. As no quantitative measures of deadwood were undertaken in the oak stands these were not included in the model. The species count data were then related to climate, soils and stand variables using correlation analysis. The assessment methods for these variables are described in Chapter 3. Variability in the species-composition of deadwood communities (all crop types, including oak) was examined using correspondence analysis (CA). This analysis provides vectors or axes summarising the main gradients of variability amongst the sample plots (see Chapter 4). The principal CA vectors (BRYO1 and 2; LICH1 and 2) were correlated with climate, soil and stand variables.

## Results

### Overview

Altogether, 106 lichen species and 77 bryophytes were recorded on deadwood. Over 40% of lichen and 27% of bryophyte species were recorded only once (Table 9.1) and no single species of either group was recorded in all plots. The most commonly recorded lichen genera were: *Cladonia* (25 species); *Parmelia* (14 species); *Pertusaria* (9 species) and *Lecanora* (8 species). The most common species were: *Cladonia coniocraea*, *Hypogymnia physodes*, *Cladonia chlorophaea*, *Cladonia squamosa* and *Lepraria incana*. Lichen species counts were generally higher in the semi-natural stands (oak and over-mature foothills Scots pine plots) than in the planted stands (Figure 9.1). The main bryophyte genera were: *Dicranum, Calypogeia, Plagiothecium* and *Polytrichum*, and the most common species were: *Hypnum cupressiforme*, *Dicranum scoparium*, *Eurhynchium praelongum*, *Polytrichum formosum* and *Plagiothecium undulatum*. Bryophyte species-richness was similar in planted and semi-natural stands (Figure 9.2).

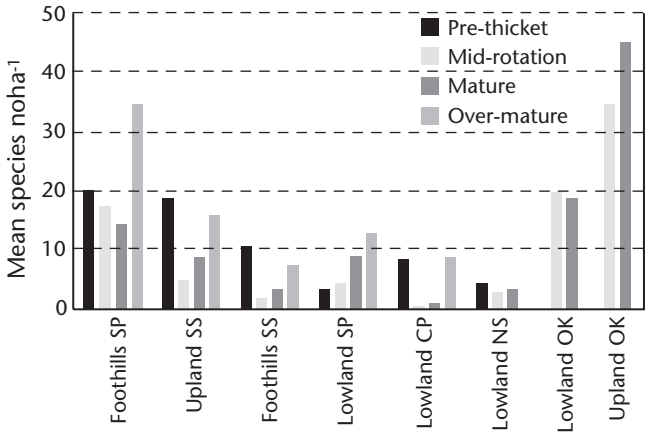



**Figure 9.1**

*Number of lichen species recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak. Values are means for each crop/stand type within each climate zone. Details of site history are given in Annexe 1.*

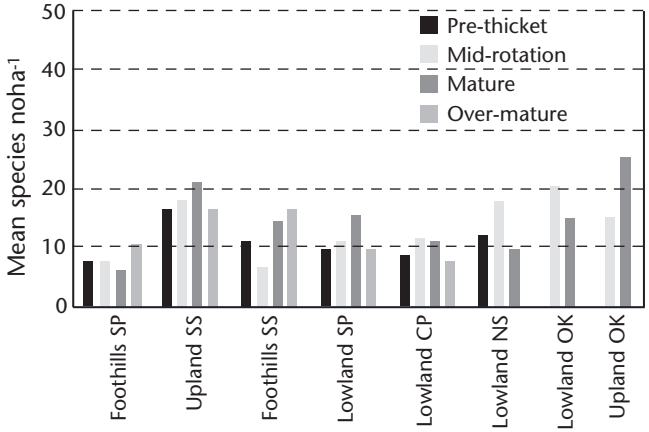



**Figure 9.2**

*Number of bryophyte species (mosses and liverworts) recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak. Values are means for each crop/stand type within each climate zone. Details of site history are given in Annexe 1.*

One Red Data Book lichen species was recorded on deadwood: *Bryoria furcellata* (Glen Affric, over-mature Scots pine – plot 1.4). *B. furcellata* is classed as 'Vulnerable' in accordance with the revised IUCN categories of risk (World Conservation Union, 1994), and is a Wildlife and Countryside Act 1981, Schedule 8 species (Church *et al.*, 1996). The number of NIEC (New Index of Ecological Continuity – Rose, 1993) lichen species recorded was 18, and the number of RIEC (Revised Index of Ecological Continuity – Rose, 1976) species was 9 (Table 9.1). These indices give a measure of long-term continuity of woodland conditions at the stand level and of habitat quality for uncommon species (Rose, 1993). However, their relevance is restricted to lowland England and Wales (Rose, 1993). The only sites with NIEC or RIEC species falling into this zone were: Alice Holt oak (2 species); New Forest oak (10 species) and New Forest Scots pine (2 species).

**Table 9.1** *Lichen and bryophyte summary data. RDB – Red Data Book species (Church* et al., *1996). NIEC – New Index of Ecological Continuity (Rose, 1993); RIEC – Revised Index of Ecological Continuity (Rose, 1976). Mosses and hepatics were combined for subsequent analyses. n/a – not applicable.*

| | Lichens | Mosses | Hepatics | Total |
|---|---|---|---|---|
| Species count | 106 | 49 | 28 | 183 |
| RDB species | 1 | 0 | 0 | 1 |
| NIEC species | 18 | n/a | n/a | 18 |
| RIEC species | 9 | n/a | n/a | 9 |
| Mean species count/plot | 9 | 8 | 3 | 18 |
| Max. species count/plot | 51 | 15 | 10 | 56 |
| Min. species count/plot | 0 | 0 | 0 | 0 |
| Species recorded only once | 43 | 12 | 8 | 63 |
| Species recorded in >50% of plots | 2 | 4 | 0 | 6 |

**Conifer stands only: effects of crop type, stand structure and deadwood on lichen and bryophyte species-richness**

Crop type (combining species and bioclimatic zone) was the most significant factor ($P$ <0.01) influencing both lichen and bryophyte species counts on deadwood. For lichens the ranking was (Figure 9.1): foothills Scots pine > upland Sitka spruce > (foothills Sitka spruce and lowland Scots pine) > (lowland Corsican pine and lowland Norway spruce) ($P$ < 0.01). This south to north gradient in increasing species-richness was positively correlated with decreasing accumulated temperature (AT) and soil moisture deficit (MD) (Table 9.2). A contrasting pattern was recorded for bryophytes, with the ranking being (Figure 9.2): (upland Sitka spruce, lowland Norway spruce and foothills Sitka spruce) > (lowland Corsican pine and lowland Scots pine) > foothills Scots pine ($P$ <0.01).

**Table 9.2** *Pearson correlations between climate and stand structure variables, lichen and bryophyte species-richness, and the first two ordination axes of the CA plots (Figure 9.5). Species counts exclude oak stands; ordinations include oak stands. Significance levels are *P < 0.05; **P < 0.01. The key to the soil, climate and stand structure variables is in Chapter 3, Table 3.2.*

| | Species counts ha$^{-1}$ | | Ordination axes | | | |
|---|---|---|---|---|---|---|
| | Bryophytes | Lichens | BRYO1 | BRYO2 | LICH1 | LICH2 |
| AT | -0.01 | -0.59** | 0.48** | 0.21 | 0.49** | 0.33* |
| MD | -0.08 | -0.59** | 0.54** | 0.22 | 0.61** | 0.21 |
| S1 | 0.16 | 0.24 | 0.03 | -0.02 | 0.09 | -0.43** |
| S4 | 0.51** | -0.25 | 0.06 | -0.46** | 0.36* | 0.37* |
| CI | 0.39** | -0.24 | 0.01 | -0.32* | 0.00 | -0.04 |
| HTLC | -0.05 | -0.39** | 0.35* | -0.27 | 0.47** | 0.28 |
| MBA | 0.12 | -0.34* | -0.06 | -0.38** | 0.13 | 0.22 |
| LAI | 0.05 | -0.47** | 0.16 | -0.09 | 0.18 | 0.17 |
| TREESP | -0.04 | -0.34* | 0.29 | 0.09 | 0.10 | 0.52** |
| AGE | -0.26 | 0.55** | -0.13 | 0.17 | -0.33* | 0.42** |
| Bryophytes (total species count.ha$^{-1}$) | – | -0.18 | – | – | – | – |
| Lichens (total species count.ha$^{-1}$) | -0.18 | – | – | – | – | – |

Stand stage also had a significant effect on lichen species-richness, with pre-thicket plots having higher lichen counts than over-mature plots followed by mature then mid-rotation plots ($P$<0.01). Lichen species-richness was positively correlated with stand age (Table 9.2) and negatively correlated with height to live crown (HTLC), mean basal area (MBA) and leaf area index (LAI). High values for these latter three parameters indicate stands with dense, well-developed, tall canopy layers. The difference in bryophyte species-richness between stand stages was less marked, but there were positive correlations between richness, upper canopy cover (S4) and cover index (CI) (Table 9.2).

Stumps and logs had significantly lower lichen species counts than snags ($P$ < 0.01, Figure 9.3), but higher bryophyte counts ($P$ < 0.01). Bryophyte species-richness was positively related to increasing diameter of logs and to decay class (Figure 9.4a), with classes 4 and 5 having significantly higher species numbers than classes 1, 2 and 3 across all deadwood types. There was no significant effect of increasing snag diameter on lichen species-richness, but the relationship with decay class was highly significant (Figure 9.4b). Classes 3, 4 and 5 were more species-rich than classes 1 or 2 ($P$ < 0.01).

**All stand types: differences in the species-composition of lichen and bryophyte communities**

Axis 1 (LICH1) of the lichen ordination separating foothills Scots pine, upland oak and upland Sitka spruce from lowland Scots pine, oak, Corsican pine, Norway spruce and foothills Sitka spruce (Figure 9.5a), was positively correlated ($P$ < 0.01) with accumulated temperature (AT), moisture deficit (MD)

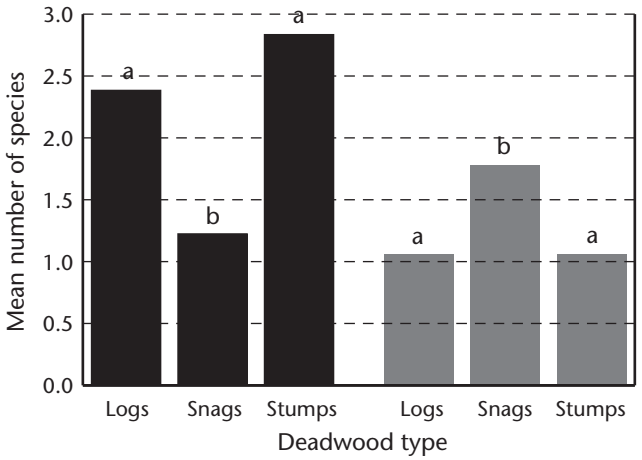



**Figure 9.3**

*Mean number of bryophyte (black) and lichen (grey) species recorded on different types of deadwood. Bars annotated with different letters are significantly different at the P < 0.05 level (within each taxonomic group).*

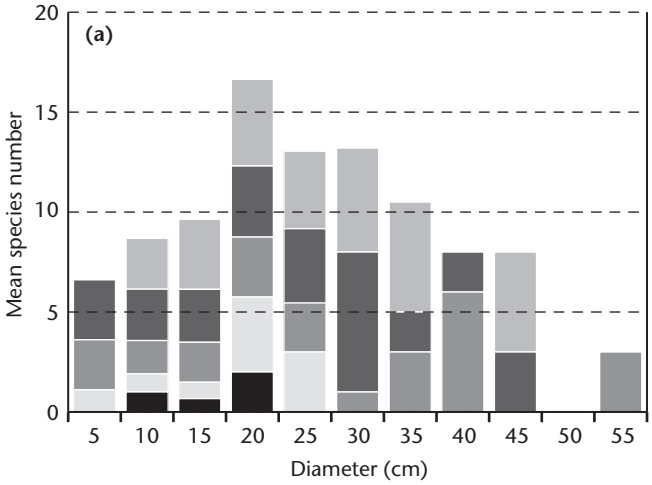
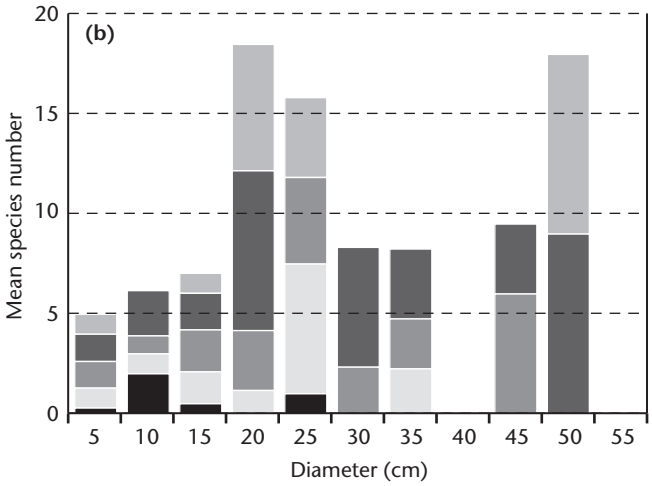



**Figure 9.4**

*(a) Mean number of bryophyte species recorded on different sizes and decay stages of logs; (b) mean number of lichen species recorded on snags.*




and height to live crown (HTLC) (Table 9.3). The oak plots (both lowland and upland) were grouped at the upper end of axis 2 (LICH2), with the pre-thicket spruce and pine plots grouped towards the lower end. LICH2 was positively correlated ($P < 0.01$) with tree age, the number of tree species in the canopy (TREESP), and upper canopy cover (S4). A negative correlation was recorded with field layer vertical cover (S1) (Table 9.2). In the bryophyte ordination (Figure 8.5b), most of the upland and foothills plots were grouped towards the lower end of axis 1 (BRYO1), with axis 2 (BRYO2) separating over-mature pine plots (1.4, 2.4, 4.4) at the upper end of the axis from some of the over-mature Sitka spruce plots (5.4, 9.4, 10.4) at the lower end. The Clunes Sitka spruce plots formed a distinctive grouping with the upland oak plots. BRYO1 was positively correlated with AT and MD; BRYO2 was negatively correlated with upper canopy cover (S4) and mean basal area (MBA), (Table 9.2).

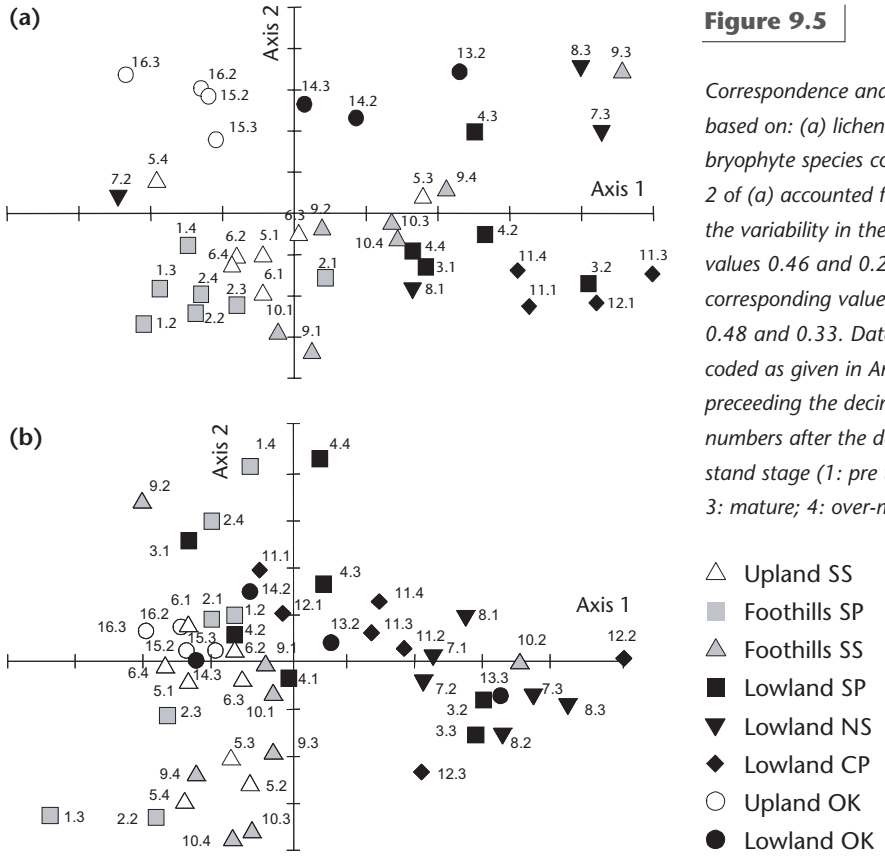



**Figure 9.5**

*Correspondence analysis of assessment plots based on: (a) lichen species composition, (b) bryophyte species composition. Axes 1 and 2 of (a) accounted for 19.2% and 13.4% of the variability in the data respectively (eigen values 0.46 and 0.28). For (b) the corresponding values were 16.5% and 10%; 0.48 and 0.33. Data labels for plots are coded as given in Annexe 1. Numbers preceeding the decimal point refer to sites, numbers after the decimal point refer to stand stage (1: pre thicket; 2: mid-rotation; 3: mature; 4: over-mature).*

## Discussion

### Effects of conifer crop type, stand structure and deadwood on the species-richness of lichen and bryophyte communities

Very few species were recorded in more than half the plots. The fungal data showed a similar pattern (Chapter 8) as have other studies (Vitt *et al.*, 1995). It is possible that the 1 ha sampling plot used is too small to capture a representative sample of lower plant diversity in forest stands, as a minimum sampling area of 1 km$^2$ is recommended (Rose, 1993). However, this may not always be practical in fine-grained heterogeneous landscapes where the aim is to relate diversity to different stand types, many of which will be less than 1 km$^2$ in size. The low frequency of rare species records (one species only) for lichens and bryophytes contrasts greatly with the results for the fungi (Chapter 8) where 29 rare and threatened species were recorded. The contrasting results are probably due, in part, to under-recording of fungi in the past, coupled with a long history of intensive recording of lower plants (e.g. Ratcliffe, 1968). However, the key semi-natural woodlands for lichens and bryophytes were under-sampled in this survey, so it is perhaps not surprising that the count of rare species was quite low.

The north-south effect on species richness was much more pronounced for lichens than bryophytes, substantiating existing views that oceanic conditions in the north and west of Britain provide much better conditions for lichen growth (Rose, 1993). The positive correlation between lichen species-richness and decreasing moisture deficit confirms this view. Bryophyte species-richness was more closely related to crop type than climate, with spruce stands being richer than pine stands regardless of climate zone. This observation has not previously been recorded in Britain, but is consistent with findings in Scandinavia, where spruce is generally considered a more notable habitat for bryophytes than pine (Esseen *et al.*, 1997).

Low light levels are considered to be highly detrimental to lichen growth (Rose, 1993; Fletcher, 1999) which explains why stand structure had such a significant effect on lichen species-richness; mid-rotation and mature stages having lower species counts than the pre-thicket and over-mature stands. Under denser stand conditions, only the most shade-tolerant of lichen species such as *Hypogymnia physodes* and *Cladonia coniocraea* were recorded. However, bryophytes were less affected by shading,

and most spruce stands had a reasonable complement of deadwood species in all stand stages. The best stands appear to be those with high values for upper canopy cover (i.e. mature and over-mature stand stages). It is possible that these stands offer a more optimal combination of high humidity, adequate light levels and constancy of microclimate.

The finding that bryophyte species-richness was higher on logs and stumps, whilst snags were more important for lichens, supports observations from overseas (Andersson and Hytteborn, 1991; Esseen *et al.*, 1997; Kruys *et al.*, 1999). In Scandinavian old growth swamp forests dominated by Norway spruce, logs are not considered to be especially important as lichen habitat (Ohlsson *et al.*, 1997). Bryophytes (particularly hepatics) appear to dominate successional processes on spruce logs in these moist stands, whereas lichens are more common on standing dead trees (Kuusinen and Siitonen, 1998). In drier Scots pine-dominated boreal forest, both logs and snags are key habitats for crustose lichens (Esseen *et al.*, 1997). It is possible, therefore, that humidity and soil moisture status (together with size and decay state) are the most important determinants of the relative value of logs for bryophytes and lichens, rather than tree species in itself.

Well-decayed (decay class 3 and above) logs of 20 cm in diameter or more provide a more valuable habitat for mosses and liverworts than small and fresher material. Reasons for this include: greater potential surface available for colonisation; improved moisture retention and greater range of microhabitats; provision of niches from competing vascular plant species or dense leaf litter (Samuelsson *et al.*, 1994; Crites and Dale, 1998). Intermediate to late decay classes provide additional heterogeneity and hence more niches for different species (Kruys *et al.*, 1999). The results from our study support the view (Esseen *et al.*, 1997; Kruys *et al.*, 1999) that lichen species-richness tends to be highest in decay classes 3–5 , whereas bryophyte richness peaks in stages 4 and 5.

**Differences in the species-composition of epixylic lichen and bryophyte communities**

The main gradients of variability in the lichen community relate to differences between northern and southern crops and between mid-rotation and mature oak stands and pre-thicket spruce and pine stands. The negative correlation between axis 2 (LICH2) and field layer cover is relevant here, because it is known that the pre-thicket pine and spruce stands have a well-developed field layer vegetation characterised by tall ericoid vegetation (see Chapter 5) which supports a range of heathland lichens (e.g. *Cladonia glauca*, *C. gracilis* and *C. uncialis).*

The foothills pinewood plots (sites 1 and 2 – Glen Affric and Strathspey) formed a distinctive grouping in the ordination. Lichen growth on living Scots pine is rarely as luxurious as it is on oak, mainly because the bark has a low water capacity, and a high rate of evapotranspiration (Barkman, 1958). Scots pine bark is also unstable and flakes off readily (Fletcher, 1999) so the lichen communities are often rather fragmentary and temporary assemblages, and comprise species able to tolerate drier conditions such as *Bryoria*, *Usnea* and *Cladonia* spp. The most important substrate for lichens in native pinewoods is deadwood (Fletcher, 1999). Stumps and snags provide a key habitat for crustose species, and a number of these (e.g. *Chaenotheca brunneola* and *C. trichialis*) were recorded on deadwood in the over-mature pine stands.

Both pine and spruce deadwood is recognised as a key habitat for crustose lichens in Scandinavian boreal forest (Esseen *et al.*,1997), and it is interesting to note that the upland Sitka spruce stands (particularly Clunes – site 6) share some of the species found within the native pinewoods (e.g. *Calicium viride, Cladonia glauca* and *Cetraria chlorophylla*) and are located in a similar position on the ordination. Historical map evidence supports the suggestion derived from the data that the Clunes stands were planted on sites previously occupied by ancient semi-natural woodland (see Chapter 8). Interestingly, in the bryophyte ordination, the Clunes Sitka spruce plots formed a distinctive grouping with the upland oak plots on axis 2, and shared many characteristic oakwood bryophytes such as the liverworts *Frullania dilatata*, *F. tamarsci* and *Lejeunea cavifolia*. It appears, therefore, that site history may also be an important determinant of both lichen and bryophyte diversity, as well as fungal diversity in planted stands.

The negative correlation between axis 2 of the bryophyte ordination, upper canopy cover (S4) and mean basal area (MBA), explains to some extent why over-mature pine plots (1.4, 2.4, 4.4) were

grouped at the upper end of the axis with over-mature Sitka spruce plots (5.4, 9.4, 10.4) grouped at the lower end. The pine plots have an open parkland structure, with low canopy cover and basal area, whereas the spruce stands have a higher stem density (Chapter 5). Because of their open structure and dry microclimate, old-growth pine stands are not noted for their bryophyte flora (Fletcher, 1999) but even so, the Affric, Strathspey and Windsor plots were surprisingly species-poor.

## Conclusions and suggested management strategies

Clearly, there is more scope for increasing the lower plant diversity of planted forests in the north and west of Britain than the south and east, and this relates to the historical effects of air pollution as well as climatic influences. Although not discussed in detail in this chapter (for a more detailed review see Humphrey *et al*., 2002), it is clear that the planted stands have poorer lichen communities than the semi-natural stands. The differences were less pronounced for bryophyte communities, but the general principle of retaining semi-natural features within planted stands such as gaps, streams, rides, rocks and mature broadleaves will apply equally to both groups and will be of significant benefit to the conservation of lower plant diversity.

The positive correlation between the species-richness of lower plant communities and the size and quality of deadwood fills an important gap in knowledge of the value of deadwood for biodiversity in British forests (Hodge and Peterken, 1998). It is important that continuity of deadwood supply is maintained so that there is no truncation in the delivery of the more valuable later stages of decay (Kruys *et al.,* 1999). In north and west Britain, silvicultural systems such as irregular shelterwood or single-tree selection could have the potential to deliver supplies of large diameter (≥ 20 cm) deadwood within stands, thus enhancing bryophyte diversity. However, this approach would not be so appropriate in areas of high windthrow risk (Mason *et al*., 1999).

Much could be done in both pine and spruce plantations to increase their value for lichens of early successional forest stages. Snags, stumps and logs left after clearfelling or windthrow can provide a key habitat for the Caliciales and Cladonias. Where the forest area is large enough to allow planning at the landscape scale, then a temporally continuous supply of this habitat type will be maintained through normal patch clearfelling, provided that some larger items (≥20 cm diameter) are left permanently unshaded during restocking to form a reservoir of species for potential colonisation of future stands. This type of management approach is most appropriate within the 'native pinewood zone' in the Scottish Highlands (Rodwell and Patterson, 1994) where plantations could play a major role in providing additional habitat for native pinewood species.

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# Annexe 1

## Details of assessment sites

*Details of assessment sites. Pyear is planting year, n/a indicates that stands were unlikely to have been established by planting but site history is not known. NR = stand established by natural regeneration. DAMS = detailed aspect Method of Scoring (Quine and White, 1993 – see Chapter 3); AT = accumulated temperature; MD = moisture deficit (Pyatt* et al., 2001 *– see Chapter 3).*

| Site No. | Site | Crop species | Pyear | Age | Rotation | Previous land-use | Grid ref. | Long/lat | Elevation (m.asl) | Wind exposure DAMS | AT (>5˚C) | MD (mm) | Continentality (Conrad Index) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **1** | **Glen Affric** | | | | | | | | | | | | |
| 1.1 | Lochan Dubh, Cannich | Scots pine | P84 | 12 | 1 | Heath/grassland | NH363317 | 57°23´N 4°48´W | 220 | 12 | 1045 | 70 | 5 |
| 1.2 | Knockfin | Scots pine | P61 | 35 | 1 | Heath/grassland | NH279261 | 57°18´N 4°51´W | 300 | 15 | 954 | 48 | 5 |
| 1.3 | Plodda Falls | Scots pine | P1900 | 96 | 1 | Native pinewood | NH273237 | 57°17´N 4°55´W | 190 | 13 | 1089 | 77 | 5 |
| 1.4 | Loch Beinn a' Mheadhoinn | Scots pine | n/a | 238[a] | n/a | Native pinewood | NH238258 | 57°16´N 4°52´W | 300 | 13 | 955 | 48 | 5 |
| **2** | **Strathspey** | | | | | | | | | | | | |
| 2.1 | Moor of Alvie | Scots pine | P88 | 8 | 2 | Native pinewood | NH853084 | 57°9´N 3°54´W | 235 | 12 | 1039 | 78 | 6 |
| 2.2 | An Slugan | Scots pine | P64 | 32 | 1 | Native pinewood | NH943129 | 57°12´N 3°45´W | 350 | 10 | 893 | 49 | 6 |
| 2.3 | Glenmore Lodge | Scots pine | P32 | 64 | 1 | Native pinewood | NH988101 | 57°10´N 3°40´W | 450 | 14 | 772 | 25 | 6 |
| 2.4 | Airgiod-meall | Scots pine | n/a | 165[a] | n/a | Native pinewood | NH966074 | 57°9´N 3°43´W | 450 | 14 | 773 | 24 | 6 |
| **3** | **Thetford** | | | | | | | | | | | | |
| 3.1 | Lynford | Scots pine | NR 78 | 18 | 1 | Heath/grassland | TL833901 | 52°29´N 0°42´E | 30 | 12 | 1781 | 220 | 11 |
| 3.2 | Horsford Woods | Scots pine | P59 | 37 | 1 | Heath/grassland | TG197180 | 52°43´N 1°15´E | 30 | 13 | 1748 | 225 | 10 |
| 3.3 | High Lodge | Scots pine | P28 | 68 | 1 | Heath/grassland | TL825846 | 52°26´N 0°41´E | 40 | 12 | 1768 | 217 | 11 |
| **4** | **New Forest/Windsor** | | | | | | | | | | | | |
| 4.1 | Knightwood Inclosure | Scots pine | P70 | 26 | 1 | Native oakwood | SU254064 | 50°51´N 1°38´W | 40 | 11 | 1969 | 197 | 9 |
| 4.2 | Denny Lodge | Scots pine | P47 | 49 | 1 | Native oakwood | SU333052 | 50°51´N 1°32´W | 20 | 10 | 2011 | 203 | 9 |
| 4.3 | Denny Lodge | Scots pine | P30 | 66 | 1 | Native oakwood | SU341038 | 50°50´N 1°31´W | 20 | 10 | 2012 | 204 | 9 |
| 4.4 | The Look Out, Windsor | Scots pine | P30 | 66 | 1 | Native b/l woodland | SU883656 | 51°23´N 0°44´W | 110 | 12 | 1760 | 188 | 11 |
| **5** | **Knapdale** | | | | | | | | | | | | |
| 5.1 | Dunardy | Sitka spruce | P87 | 9 | 2 | Heath/scrub | NR814907 | 56°4´N 5°31´W | 160 | 18 | 1246 | 83 | 4 |
| 5.2 | Dunardy | Sitka spruce | P72 | 24 | 2 | Heath/scrub | NR814910 | 56°4´N 5°31´W | 130 | 15 | 1287 | 91 | 4 |
| 5.3 | Gortonronach, Kilmichael | Sitka spruce | P52 | 44 | 1 | Heath/scrub | NR937925 | 56°5´N 5°19´W | 150 | 18 | 1257 | 88 | 4 |
| 5.4 | Dunardy | Sitka spruce | P34 | 62 | 1 | Heath/scrub | NR817912 | 56°4´N 5°30´W | 130 | 11 | 1287 | 91 | 4 |
| **6** | **Clunes** | | | | | | | | | | | | |
| 6.1 | South Laggan | Sitka spruce | P88 | 8 | 2 | Heath | NN257938 | 57°0´N 4°52´W | 90 | 14 | 1238 | 104 | 5 |
| 6.2 | Clunes | Sitka spruce | P68 | 28 | 1 | Heath/native woodland | NN185908 | 56°58´N 4°59´W | 350 | 16 | 917 | 36 | 5 |
| 6.3 | Clunes | Sitka spruce | P34 | 62 | 1 | Heath/native woodland | NN189892 | 56°58´N 4°59´W | 150 | 16 | 1169 | 87 | 5 |
| 6.4 | South Laggan | Sitka spruce | P29 | 67 | 1 | Heath | NN248936 | 57°0´N 4°53´W | 130 | 11 | 1189 | 93 | 5 |
| **7** | **Forest of Dean** | | | | | | | | | | | | |
| 7.1 | Ruddle Marsh | Norway spruce | P81 | 15 | 1 | Native woodland | SO608130 | 51°49´N 2°34´W | 120 | 11 | 1713 | 157 | 8 |
| 7.2 | Cannop | Norway spruce | P65 | 31 | 1 | Native woodland | SO612106 | 51°48´N 2°34´W | 80 | 9 | 1794 | 167 | 8 |
| 7.3 | Ruardean | Norway spruce | P43 | 56 | 1 | Native woodland | SO637164 | 51°51´N 2°32´W | 260 | 16 | 1437 | 121 | 8 |
| **8** | **Fineshade** | | | | | | | | | | | | |
| 8.1 | Fineshade | Norway spruce | P79 | 17 | 1 | Native woodland | SP982978 | 52°34´N 0°33´W | 80 | 13 | 1692 | 190 | 10 |
| 8.2 | Fineshade | Norway spruce | P57 | 39 | 1 | Native woodland | SP977976 | 52°34´N 0°34´W | 80 | 13 | 1692 | 189 | 10 |
| 8.3 | Fermyn Woods | Norway spruce | P31 | 65 | 1 | Grassland | SP985837 | 52°27´N 0°33´W | 80 | 13 | 1706 | 190 | 11 |

| Site No. | Site | Crop species | Pyear | Age | Rotation | Previous land-use | Grid ref. | Longitude/ latitude | Elevation (m asl) | Wind exposure DAMS | AT (>5°C) | MD (mm) | Continentality (Conrad Index) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **9** | **Kielder** | | | | | | | | | | | | |
| 9.1 | Falstone | Sitka spruce | P90 | 6 | 2 | Grassland | NY715860 | 55°10´N 2°27´W | 260 | 15 | 1162 | 101 | 8 |
| 9.2 | Falstone | Sitka spruce | P73 | 23 | 2 | Grassland | NY708838 | 55°9´N 2°27´W | 280 | 15 | 1133 | 96 | 8 |
| 9.3 | Falstone | Sitka spruce | P39 | 57 | 1 | Grassland | NY671849 | 55°9´N 2°31´W | 300 | 14 | 1103 | 90 | 7 |
| 9.4 | Archie's Rigg | Sitka spruce | P27 | 69 | 1 | Grassland/mire | NY704830 | 55°8´N 2°28´W | 305 | 15 | 1096 | 90 | 8 |
| **10** | **Glentress** | | | | | | | | | | | | |
| 10.1 | Glentress | Sitka spruce | P86 | 10 | 2 | Heathland | NT277421 | 55°40´N 3°9´W | 380 | 13 | 954 | 58 | 7 |
| 10.2 | Glentress | Sitka spruce | P68 | 28 | 1 | Heath/grassland | NT288408 | 55°39´N 3°8´W | 310 | 13 | 1055 | 77 | 7 |
| 10.3 | Glentress | Sitka spruce | P41 | 55 | 1 | Heath/grassland | NT279428 | 55°40´N 3°9´W | 400 | 14 | 925 | 54 | 7 |
| 10.4 | Cardrona | Sitka spruce | P35 | 61 | 1 | Grassland | NT305368 | 55°37´N 3°6´W | 300 | 10 | 1072 | 80 | 7 |
| **11** | **Thetford** | | | | | | | | | | | | |
| 11.1 | Kings Forest | Corsican pine | P88 | 8 | 2 | Heath/grassland | TL815761 | 52°21´N 0°40´E | 50 | 12 | 1758 | 215 | 11 |
| 11.2 | Kings Forest | Corsican pine | P63 | 33 | 1 | Heath/grassland | TL809763 | 52°21´N 0°40´E | 50 | 12 | 1758 | 215 | 11 |
| 11.3 | Kings Forest | Corsican pine | P37 | 59 | 1 | Heath/grassland | TL810747 | 52°20´N 0°39´E | 40 | 12 | 1778 | 218 | 11 |
| 11.4 | High Lodge | Corsican pine | P27 | 69 | 1 | Heath/grassland | TL815845 | 52°26´N 0°40´E | 40 | 12 | 1769 | 217 | 11 |
| **12** | **Clipstone** | | | | | | | | | | | | |
| 12.1 | Clipstone | Corsican pine | P87 | 9 | 2 | Heath/grassland | SK606621 | 53°9´N 1°6´W | 105 | 14 | 1591 | 172 | 10 |
| 12.2 | Clipstone | Corsican pine | P53 | 43 | 1 | Heath/grassland | SK632627 | 53°9´N 1°3´W | 75 | 13 | 1643 | 180 | 10 |
| 12.3 | Clipstone | Corsican pine | P47 | 49 | 1 | Heath/grassland | SK613644 | 53°10´N 1°5´W | 90 | 13 | 1615 | 176 | 10 |
| **13** | **Alice Holt** | | | | | | | | | | | | |
| 13.2 | The Straits | Oak | P35 | 62 | n/a | Native b/l woodland | SU794401 | 51°9´N 0°51´W | 70 | 10 | 1866 | 198 | 10 |
| 13.3 | Goose Green | Oak | P1820 | 177 | n/a | Native b/l woodland | SU807403 | 51°9´N 0°50´W | 95 | 10 | 1814 | 191 | 10 |
| **14** | **New Forest** | | | | | | | | | | | | |
| 14.2 | Salisbury Trench | Oak | P36 | 61 | n/a | Native b/l woodland | SU255147 | 50°55´N 1°38´W | 110 | 13 | 1815 | 178 | 9 |
| 14.3 | Fletcher's | Oak | P1829 | 168 | n/a | Native b/l woodland | SU272043 | 50°50´N 1°36´W | 25 | 11 | 2002 | 201 | 9 |
| **15** | **Taynish** | | | | | | | | | | | | |
| 15.2 | Taynish | Oak | n/a | 104[a] | n/a | Native oakwood | NR732849 | 56°0´N 5°38´W | 50 | 14 | 1404 | 110 | 4 |
| 15.3 | Taynish | Oak | n/a | 112[a] | n/a | Native oakwood | NR762853 | 56°0´N 5°35´W | 40 | 12 | 1417 | 113 | 4 |
| **16** | **Beasdale/Moidart** | | | | | | | | | | | | |
| 16.2 | Beasdale | Oak | n/a | 111[a] | n/a | Native oakwood | NM707847 | 56°53´N 5°45´W | 90 | 15 | 1254 | 94 | 4 |
| 16.3 | Moidart | Oak | n/a | 131[a] | n/a | Native oakwood | NM705729 | 56°47´N 5°45´W | 40 | 15 | 1329 | 107 | 4 |

[a]Semi-natural stand, mean age. Ages range were: plot 1.4: 183–270; plot 2.4: 100–242; plot 15.2: 39–150; plot 15.3: 60–140; plot 16.2: 19–154; plot 16.3: 55–201.

# Annexe 2

## Methods for extraction and analysis of soil microbial PFLAs (see Chapter 6)

The current extraction process is a relatively passive technique and is an adaptation of a well-established method for lipid extraction (Bligh and Dyer, 1959). It uses the principle of initial extraction into a single phase mixture of trichloromethane, methanol and buffer (taking into account the residual moisture in the sample) which is then split into organic and aqueous phases by the addition of more trichloromethane and buffer. The extracted lipids (neutral, glyco- and polar lipids) partition into the organic (lower) layer. The extracted lipids were then separated into classes according to their polarity by adsorption to activated silica and selective elution with progressively more polar solvents. Polar lipids, including phospholipids, are eluted last with the most polar eluant, methanol.

The fatty acid components of the isolated phospholipids must then be cleaved from the glycerol backbone and their carboxylic acid groups derivatised by the addition of a methyl group to reduce their polarity and enable them to be analysed by gas chromatography. Extracts were transmethylated using potassium hydroxide in dry methanol (mild alkaline methanolysis) (Christie, 1989). The resulting extracts were reconstituted in HPLC-grade hexane, and 0.5–1.0 μl of this injected onto a capillary gas chromatograph where they were separated (essentially on the basis of their boiling point) and detected using a flame ionization detector. Two Gas Chromatographs, a Shimadzu 9A and a Pye-Unicam PU4550, fitted with 60 m x 250 mm i.d SE54 (0.25 μm δf) capillary columns, were used for the analyses (see Morris, 2000 for further details).

A bacterial fatty acid methyl ester (FAME) mix (Supelco Inc., Bellefonte, PA and Matreya Inc., Pleasant Gap, PA) was used as a qualitative reference standard and comprised 26 FAMEs of bacterial origin. Initial identification of soil extract FAME peaks was made by retention time correlation with peaks in this bacterial standard mix. Peak identities were confirmed using a Varian Saturn GC with ion trap mass selective detection. Further validation of the extraction and analytical procedures was also carried out. This included injection reproducibility, limit of detection and quantification, linearity of derivatization, solid phase extraction, and linearity of PLFA recovery from high and low humus content forest soils (from which PLFAs had been pre-extracted) at two moisture levels. Although this showed the extraction to be linear it also indicated that the efficiency of the extraction process decreased with increasing lipid content (inverse log relationship, $R^2 = 0.943$). Chromatograms were acquired and manipulated using a Kontron 450 MT2/DAD data handling system.

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