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STUDIES ON THE GROUND FLORA UNDER SELECTION FORESTRY IN THE TAVISTOCK WOODLANDS ESTATE

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STUDIES ON THE GROUND FLORA UNDER SELECTION FORESTRY IN THE TAVISTOCK WOODLANDS ESTATE

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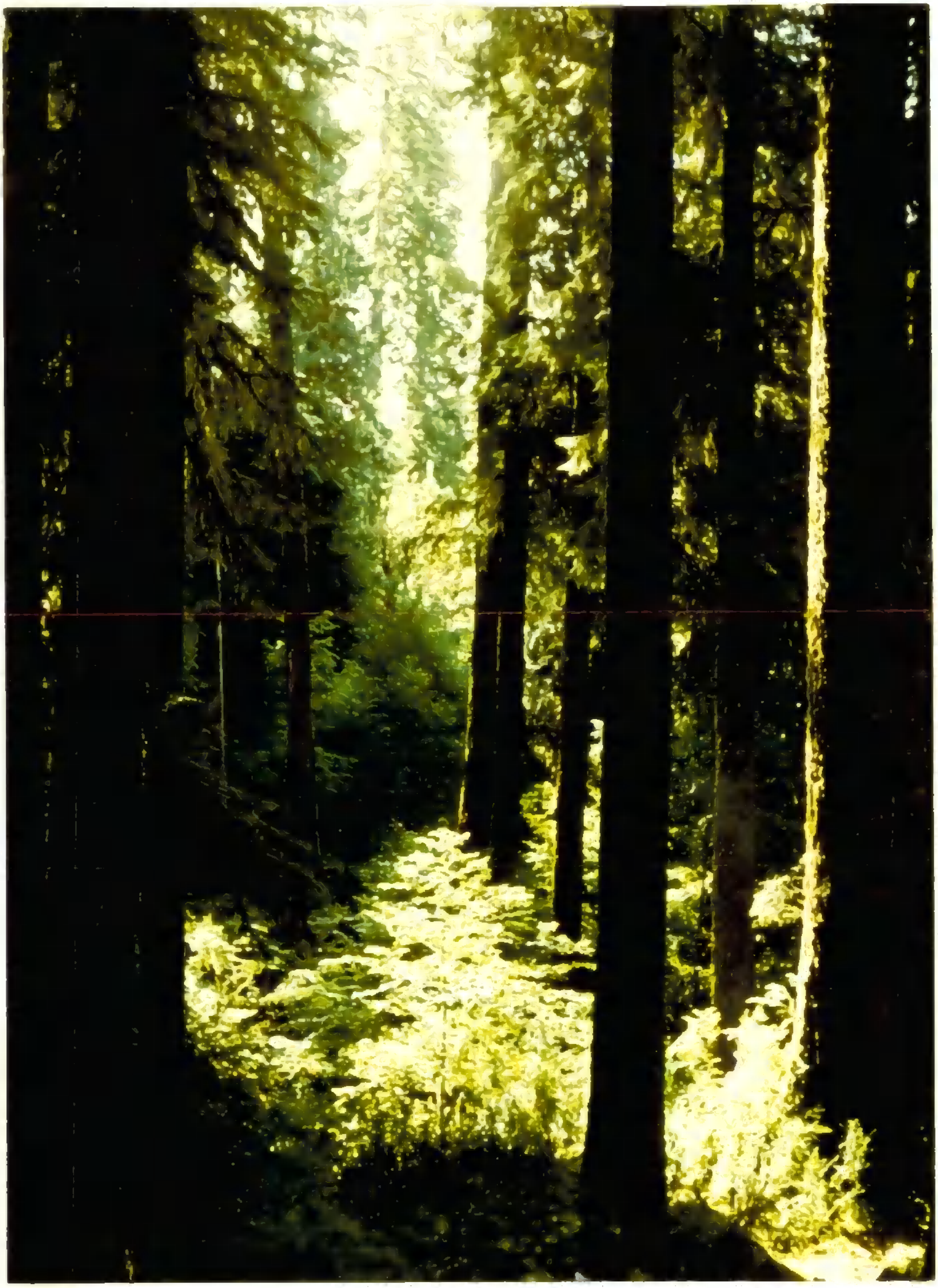
ABSTRACT

This thesis investigates the effect of the Bradford-Hutt system of selection forestry management, known as B - Plan, on the ground flora of the Tavistock Woodlands in Devon and Cornwall, England. After a review of continental selection forestry systems, the Bradford-Hutt system and its economic, production and ecological advantages are described.

The study was conducted in four phases. Firstly, the canopy types were described. Then the ground flora was examined and related to canopy type, past history and management. Secondly, a vegetational community gradient was identified and examined in relation to the environmental gradients, canopy closure and soil moisture and to effects of B - Plan management. The effects of B - Plan management on the shrub layers were then investigated. Thirdly, the effect of B - Plan management on the light climate was studied using hemispherical photographs and variations in light were related to different stages of the B - Plan system. Fourthly, the seed bank and the phenology of certain ground flora species were examined.

Successional changes in the ground flora and in the seed bank with increasing maturity of the areas under B - Plan management were identified. The system was found to create a mosaic of vegetational communities at differing successional stages within the space of the basic B - Plan management unit of 18 x 18m. Unlike the successional changes over time in natural woodlands or even-aged plantations, these changes in areas under B - Plan management occur in space as well as time.

This sustained yield system of commercial forestry management which resembles the traditional coppice with standards system, was found to have a beneficial effect on ground flora diversity and abundance. The system deserves more widespread adoption in woodland sites which require the integration of amenity value, economic return and an ecologically balanced ecosystem.



Frontispiece. The Tavistock Woodlands with Bradford Plan units set into a mature Douglas fir (Pseudotsuga menziesii) canopy. The importance of the light environment under Bradford Plan management is shown by the penetration of light into the cleared sub-unit .

ACKNOWLEDGMENTS

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I am indebted to the management staff of the Tavistock Woodlands Estate; particularly to Mr. Phillip Hutt, former chief forester, for his lively tuition in the principles of forestry management; to Mr. Roy Dyer, present chief forester, for much advice and discussion and also to Mr. Timothy Timmis and Mr. Nicholas Collins for their interest and enthusiasm in the project.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

CHAPTER 1. SELECTION FORESTRY AND THE BRADFORD-HUTT SYSTEM

CHAPTER 1. SELECTION FORESTRY AND THE BRADFORD-HUTT SYSTEM

1.1. Introduction

Since 1959, a system of selection forestry, the Bradford-Hutt continuous canopy system of forestry management, known as B - Plan, has been implemented in the Tavistock Woodlands Estate, in Devon and Cornwall. The aim of this thesis is to study the ecological effects and possible benefits of adopting the system in terms of the woodland ground flora.

The system, developed by the late Lord Bradford and his chief forester, Philip Hutt, was the result of their concern that current forestry management practices in Great Britain, which were largely organised on a clear-fell system, were not fulfilling certain important ecological criteria. As Peterken (1981) states:

> "The essential characteristic of modern forestry is its pursuit of high production by means of intensive management and this brings it into conflict with nature conservation." (p. 198)

B - Plan is a modern coniferous forestry system, which shows some resemblance to earlier sustained yield management systems, which were employed during the historical period. Until the 1800's, management involved careful husbandry and regarded woodland as a continuously renewable resource. The objective of sustained yield was written into the management plan of Hayley Wood, Oxfordshire, 600 years ago (Rackham, 1975). The traditional management of woods involved manipulating the natural vegetation of a site to yield a succession of wood products and trees were replaced by natural regeneration from coppice shoots, suckers and seed, rather than by planting (Rackham, 1980a). However, modern forestry is not a development from traditional woodmanship.

> "Modern forestry, in British practice, involves planting an arbitrarily-chosen tree crop, unrelated to the natural vegetation and re-planting it after each harvest." (Rackham, 1980b: p.9)

This is unlike modern forestry in Scandinavian and many continental countries, where an understanding and analysis of the natural vegetation plays an important role in silvicultural management. (Noirfalaise and Dethioux, 1970; Genssler, 1982; Mikola, 1982; Goldsmith et al.,1982.) Here, continuous cover with sustained yield and natural regeneration, if possible, is a primary aim of forestry management (Knuchel, 1953; Paterson, 1958; Reade, 1969; Peterken, 1981).

Since 1600, in Britain, clear-felling has coexisted with traditional woodmanship, but in the last 100 years, 'tree-farming silviculture' (Peterken, 1981) has overtaken and excluded the 'gentle husbandry' (Rackham, 1980a) of the past. In response to this, during the 1950's, Lord Bradford and Philip Hutt sought to devise a management system which would conserve the woodland ecosystem while allowing commercial exploitation of coniferous forest. They saw the ecologically undesirable features of current forestry management as:

1. planting of monocultures, lending themselves potentially open to the rapid spread of disease.
2. exposure of soil after clear-felling, creating the likelihood of soil erosion.
3. virtual elimination of the ground flora over large areas under developing and mature coniferous stands.
4. reduction of species diversity in the ground flora.
5. adverse effects on the visual landscape of even-aged coniferous planting, giving rise to negative public reaction.

The second point was seen as a particular problem on the Tavistock Woodlands Estate, where many of the slopes in the Tamar Valley are very steep, often as great as 25° and the rainfall is high (1336mm/year; Hogan, 1977). On steep slopes, clear-felling can lead to long-term changes in the structure and biogeochemistry of the woodland ecosystem (Bormann and Likens, 1979).

The third and fourth points represent the prime focus of this thesis. Lord Bradford and Philip Hutt felt that it must be possible to create a commercially viable forestry system which would conserve the ecological interest of the ground flora and its diversity.

The fifth feature was seen as:

> "... the familiar reaction against regiments of conifers marching across the hillsides." (Peterken, 1981: p. 198)

This is especially significant in the Tamar and Tavy Valleys, where the Tavistock Woodlands are sited. The woods are easily accessible to the public and adjacent to one of the major holiday routes to Cornwall (Plate 1.1).

1.2. Selection forestry and the Bradford-Hutt system

To Lord Bradford and Philip Hutt, continental selection forestry seemed to offer a management strategy which had the potential to reconcile conservation with economic exploitation (Wigston, 1976). Selection has been described as:

> "an artificially stabilised development phase of the natural forest, unaffected by man ..." (Köstler, 1956 : p.154)

1.2.1. Selection forestry in Europe and elsewhere

The selection forestry methods employed in Europe have a long pedigree, originating in the haphazard felling of individual trees which was common in the Middle Ages (Troup, 1952). This exploitative selection fell into disrepute because instead of enhancing the forest by felling poor quality trees, leaving the superior ones to grow on and produce seed, the best trees were selected leaving the poorer ones to reproduce. The Darmstadt Ordinance of 1776 and the Baden Forest Law of 1833 both prohibited selection in a reaction against the exploitative selection of the past (Troup, 1952). As a result, in

Plate 1.1. Tavistock Woodlands as seen from the A390 at Gunnislake, Cornwall

many European forests, the uniform system, involving clear-felling and shelterwood systems, replaced this kind of primitive selection. Examples of the range of types of selection forestry in Europe and elsewhere are presented in Table 1.1.

Shelterwood systems

In shelterwood systems, a compromise between clear-felling and true selection, the original stand is cleared in several 'regeneration cuttings'. This affords continuous cover of the soil, as in B - Plan, but not an uneven-aged stand. The aim is to establish the new stand by natural regeneration in the large gaps created in the original canopy. Currently, in the 'uniform' shelterwood system in Northern France (Table 1.1.), foresters may use up to six successive fellings carried out over 30 - 40 years, although 2 - 3 cuttings is more usual (Goldsmith et al., 1982). During the regenerative cuttings, the stand is uneven-aged and the new crop can have an age range of anything between seedlings and 40 years (Evans, 1982). When natural regeneration proves incomplete, it is augmented by planting, for example, oak in the Foret de Compiegne (Evans, 1982). This has the result of shortening the regeneration period to 10 - 20 years and creating a more even-aged stand with only 2 or 3 regeneration cuttings. Ultimately, the original seed trees are removed and the canopy grows together to appear more or less the same age (Peterken, 1981). Several other shelterwood systems, such as the 'group' and 'irregular shelterwood' systems are popular in Central Europe and vary from the French 'uniform shelterwood' system in the timing and number of successive fellings (Peterken, 1981) (Table 1.1.).

The Plenter and the Femelschlag systems

Although clear-felling has been accepted in lowland Switzerland, a system producing a mature 'normal' forest age structure has always been favoured in the mountains (Knuchel, 1953; Reade, 1969). Both

Table 1.1. Examples of selection and continuous cover forestry systems

Country & Place	System	Tree Species	Reference
Great Britain			
Dartington Woodlands, Dartington, Devon	Group & single tree selection, yield table controlled	Large mix including Douglas fir, red cedar, western hemlock, Sequoia Japanese larch, sweet chestnut, beech	Howell *et al.*, 1982
Rossie Priory, Dundee	Single tree selection, empirically controlled	Deciduous mix of sycamore, beech, ash, wych elm, pedunculate oak	Paterson, 1958
Tavistock Woodlands, Gulworthy, Devon	Single tree selection - Bradford Plan, check controlled	Douglas fir, red cedar, western hemlock, Sequoia, Corsican and Scots pine, oak and beech	Hutt, 1975
Weasenham New Wood, Norfolk	Single tree selection, empirically controlled	Coniferous mix of Douglas fir, Scots pine, larch, red cedar, western hemlock, Abies spp., red oak, sweet chestnut, birch	Paterson, 1958
Austria	20% of all forests selective, particularly no-yield protective ones in the mtns.	Silver fir, beech, and Norway spruce	Köstler, 1956; Troup, 1952
Switzerland			
Emmenthal, Thun district	Single tree, sustained yield, (Plenter) originated from Biolley, 1892 and later Ammon, generally 'check' controlled. 30% of all forests	Silver fir, spruce, beech, oak	Knuchel, 1953; Ammon, 1912 in Reade, 1969; Peterken, 1981; Troup, 1952
Langwiesen, Canton Zurich near Schaffhausen and in lowlands areas	Group (Femel) selection and regeneration cutting	Deciduous	Reade, 1969; Fourchy, 1953

Table 1.1. (Contd.)

Country & Place	System	Tree Species	Reference
Switzerland (Contd.)			
Couvet (Biolley)	Check control method	Silver fir, spruce, beech	Schaffer *et al.*, 1957
Belgium			
Hautfays Beech Selection Forest, Ardennes	Single tree selection, 'check' controlled	Beech and sessile oak	Paterson, 1958 (originated from Biolley, in 1892)
France			
Jura, Vosoges	Single tree selection, protection forest (Jardinage)	Silver fir, spruce	Knuchel, 1953; Troup, 1952
Aleppo pine forest, South France	Group selection to prevent fire	Pine	Troup, 1952
Jura, Auvergne	Single tree selection, controlled by 'check' method	Silver fir, spruce, beech, with other secondary species	Schaeffer *et al*, 1957 (originated with Gurnaud in 1870)
Foret de Compiegne, Foret de Belleme, & Foret D'Eawy in the north of France	'Uniform shelterwood' regeneration felling, six cuttings over 30 years, a continuous canopy system.	Oak and beech	Evans, 1982
Foret de Fontainebleau	As above	Oak	Goldsmith *et al*, 1982
Vallee de l'Ognon, Besancon in the Doubs	'Uniform shelterwood' regeneration felling, three stage cutting, a continuous canopy system	Peduculate and sessile oak with some beech and hornbeam	Goldsmith *et al.*, 1982

Table 1.1. (Contd.)

Country & Place	System	Tree Species	Reference
France (Contd.)			
AuBusson Communal Forest	Single tree selection, controlled by a 'check' method using Schaeffer-D'Averney classification curve	Silver fir, beech, Norway spruce	Paterson, 1958
Bicarrosse, Landes	Single tree selection, empirically controlled	Maritime pine for resin production	Peterken, 1981
Germany			
Wurtemberg private forests	(Plenter and Femel) 10% of all forests in 1920 single tree selection, 'check' controlled.	Silver fir, spruce, beech	Troup, 1952; Knuchel, 1953
	3% of all south German forests in 1956		Köstler, 1956
Scandinavia	Selection systems, single tree selection	Pine and mixed pine and spruce	Köstler, 1956; Smith, 1962
India and Burma	Primitive exploitation selection	Broadleaves	Troup, 1952
U.S.A.			
Southern Sierra Nevadas	Strip-selection similar to strip-shelterwood except all age classes created	Mixed conifers including sugar and ponderosa pines, incense cedar and white fir	Dunning, 1928 in Smith, 1962
Crossett Experimental Forest, Arkansas	Single tree selection	Loblolly and short-leaf pine	Reynolds, 1959 in Smith, 1962
Northern California	Single tree selection	Coast redwood	Fritz, 1951 in Smith,. 1962

Table 1.1. (Contd.)

Country and Location	System	Tree Species	Reference
U.S.A. (Contd.)			
South West	Improvement selection cutting (group selection for beetle control)	Ponderosa pine	Pearson, 1942, 1950
New England	Group selection	Old-growth northern hardwood forest with sugar maple, beech, & yellow birch	Gilbert & Jensen, 1958 in Smith, 1962

the very steep slopes and the extreme climatic conditions make a continuous canopy a necessity. The selection system provides the best protection from soil erosion, drought effects and damage by wind and snow and hence is particularly appropriate for mountain forests, especially in the high regions of the Alps (Köstler, 1956; Peterken, 1981). The 'Plenterwald' of the Thun district of Switzerland are managed by a selection system which is a refined form of shelterwood (Peterken, 1981). The woods are continuously thinned and regenerated in the individual gaps and as a consequence there is no spatial separation of age classes.

This 'Plenter' system in the Emmenthal, Thun is described by Ammon, for many years the chief state forester and a strong proponent of selection forestry, as 'optimum stepwise canopy closure' (Reade, 1969: p. 206). There should be "roots in every layer of soil" (Reade, 1969: p. 206). "One should be unable to see great distances through the wood and there should not be any free space without chlorophyll" (Fourchy, 1953: p. 60).

A 2% cut of the growing stock each year, with a 10-year thinning cycle, leaving 80% of the previously growing stock, describes the 'Plenter' system in practice. Under more extensive management, a 'Plenter' stand can have 60% of its growing stock left after thinning. In contrast, the 'Femelschlag' system (group selection) is preferred in the lowlands of Switzerland, where 20% of the growing stock is left after localized felling of small, irregularly spaced groups (Fourchy, 1953). In Germany the 'Femelschlag' has come to mean a more regular pattern of group selection for the creation of regeneration centres (Fourchy, 1953).

Both these systems rely on natural regeneration for restocking and so must select tree species well adapted to a particular site.

In the main, this means native species and those exotic species from homologous life zones (Holdridge, 1966), which also regenerate freely. Silver fir (*Abies alba*), Norway spruce (*Picea abies*) and beech (*Fagus sylvatica*) are the preferred species in the Emmenthal and many other selection forests (Table 1.1.). The silver fir regenerates freely under the spruce, while the beech is shade-tolerant, improves the soil and keeps weeds in check. It is favoured for these qualities, even though it does not always produce good timber (Hiley, 1954). The natural regeneration arises in groups, but as individual thinning progresses, this structure disappears resulting in no spatial separation of age-classes (Peterken, 1981).

The 'check' method

Controlling the frequency and intensity of felling can be a great problem in these selection woods, although some small ones can be managed without keeping detailed records and measurements. (For example, Table 1.1., Weasenham New Wood, Norfolk and Rossie Priory, Dundee.) A more scientific regulation of cut by volume is widely employed in continental European woods. This is known as the 'check method'. Knuchel (1953) and Paterson (1958) describe this yield control method in detail. It is based on a full inventory of the numbers of trees in each size class, periodic 'checks' of the increment in these classes and the calculation of production with reference to volume tables. The Tavistock Woodlands Estate uses a form of the 'check method', and is in the process of preparing its own management tables, as the British Forestry Commission tables for even-aged stands are not suitable.

A few other areas in Europe have been managed on a selection basis (Table 1.1.). Smith (1962) claims that single-tree selection has failed as a means of regenerating and managing Norway spruce in Scandinavia. In North America, a system of 'selective logging' where large desirable trees were periodically removed has been employed in some locations. The results have been unsatisfactory, and the forests have deteriorated due to this negative selection pressure. This has been particularly true in virgin Douglas fir stands of the Pacific Northwest (Hiley, 1954; Smith, 1962). In the Chiltern Beechwoods, England, for hundreds of years, negative selection by timber merchants forced the abandonment of selection forestry (Troup, 1952; Hiley, 1954; Roden, 1968; Peterken, 1981).

Current selection systems in Britain

In 1943, a selection experiment was begun at Dartington Hall Woodlands as a result of a visit which Wilfred Hiley, then chief forester, made to Couvet, Switzerland.

> "It has been my good fortune to manage such woods (uneven-aged) and I have found that, if properly handled, they are not only interesting, profitable and beautiful, but that they provide a constant and continuing source of mature timber which can be reaped without devastation, and frequently without the necessity of replanting" (Hiley, 1954: p. 106).

A recent Royal Forestry Society visit to Dartington Woodlands described North Wood, where Hiley implemented his group selection system as:

> "... productive woodlands of great beauty and variety" (Leathart, 1983: p. 238).

In the 1950's, the original Douglas fir, silver fir, and beech were underplanted by groups of western hemlock and Douglas fir with sweet chestnut as both a soil improver and for timber in half-acre blocks (Harley, pers. comm.). The group selection compartment is still maintained as such and is valued for its attractiveness, the wood enclosing a nature walk, as well as for the prime timber it produces (Leathart, 1983). More recently part of North Wood has been managed under a single stem selection system. Only a small area is involved (0.6 acre), but it appears to be thriving (Harley, pers. comm.).

There are two other known single stem selection woods in Britain (Table 1.1.). A mixed deciduous stand of 15 acres is found at Rossie Priory Estate, Dundee and a mixed coniferous stand of 56 acres, at Weasenham New Wood, Norfolk. The volume of timber extraction from both woods is determined subjectively, but Paterson (1958) suggests there is a need for inventories and increment calculations in such woods as the stands, which were in the process of conversion to selection, became more irregular. Wilderness Wood, 61 acres, in the Sussex Weald, is in the early stages of the implementation of B - Plan. However, B - Plan is only being established within a small 15 acre pine plantation (Yarrow, pers. comm.).

1.2.2. The development of B - Plan in the context of the continental selection systems

Lord Bradford and Philip Hutt saw three major obstacles in applying continental selection systems to British forestry conditions:

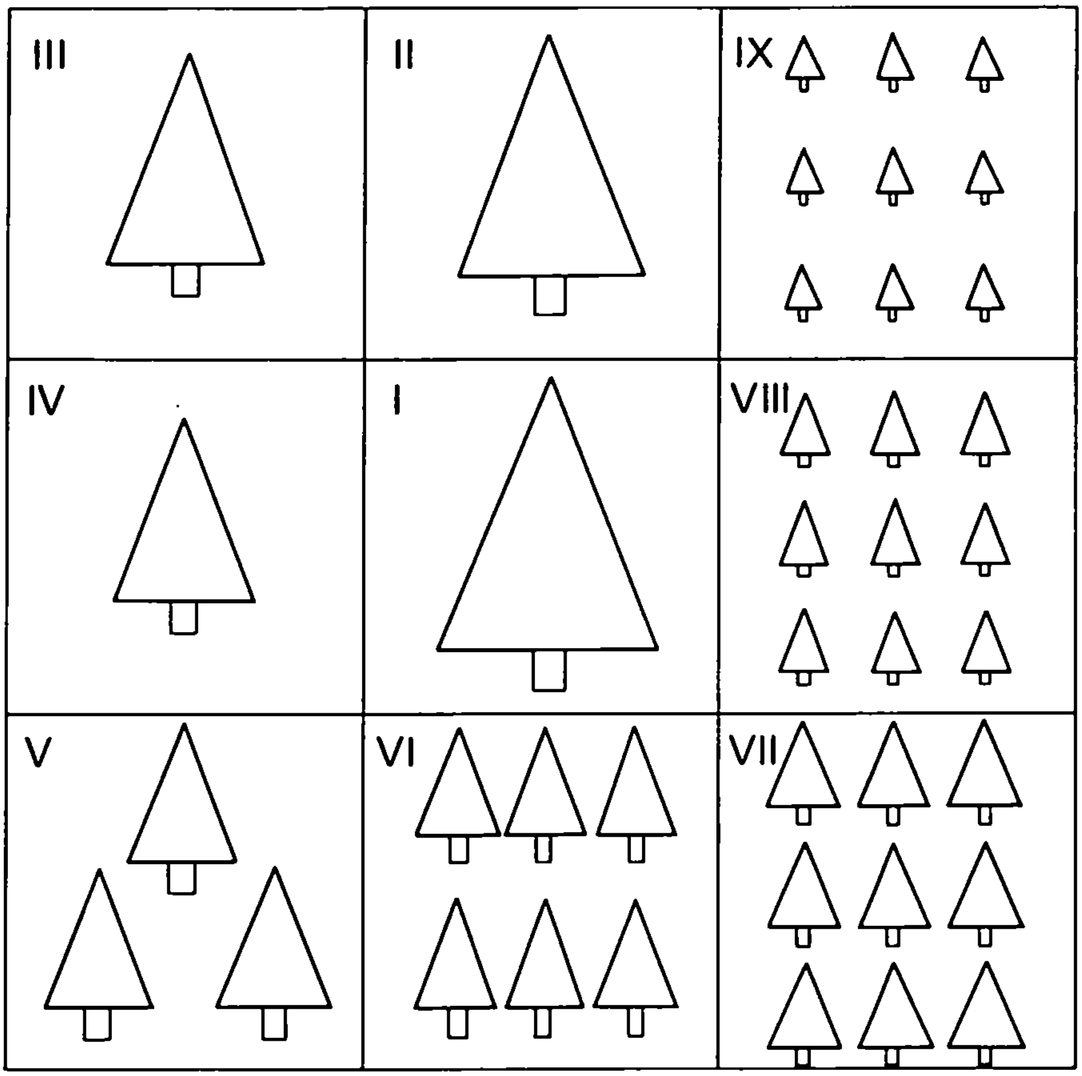
1) Such systems rely heavily on regeneration of native coniferous species. Natural regeneration in Britain is not reliable, due to climatic conditions and what can only be described as 'economic impatience'. The French are prepared to wait as long as 30 years for regeneration to occur after a regeneration felling (Goldsmith *et al*., 1982).
2) With single tree selection, extraction and management can cause problems. For example, at Dartington, some of the smaller trees had to be felled in a line to enable extraction of the mature trees. This resulted in the loss of valuable growing stock (Howell *et al*., 1982).

3) In the Alps, a rotation can extend to two hundred years (Hutt, 1976). Here, protection against severe erosion, avalanches and wind takes precedence over economically productive shorter rotations. The economics of British forestry, based on the net discounted revenue concept, compelled them to consider the time required to give a maximum financial return (Lorrain-Smith, 1969).

The current methods employed in the Bradford-Hutt system of continuous canopy forestry (B - Plan) developed from a series of experiments designed to overcome these three problems. The first experiment took place in Shropshire on Lord Bradford's estate at Nescliffe. Planting was adopted instead of relying on natural regeneration. A geometric pattern (Figure 1.1.) was adopted for planting and extraction and rackways for extraction were built into the system. Maximum financial yield was accommodated within the system by choosing a maturation period of 50 - 55 years for the main species grown, <u>Pseudotsuga menziesii</u> (Douglas fir), <u>Thuja plicata</u> (Western red cedar) and <u>Tsuga heterophylla</u> (Western hemlock). The first B - Plan plantings began in the Tavistock Woodlands estate in Blanchdown Wood in 1959-60.

1.3. A description of B - Plan

The early experiments at Nescliffe were based on a modificiation of the 'check-control' system (Knuchel, 1953) and single stem selection. Lord Bradford and Philip Hutt found that, in addition to the extraction problems, the random, silviculturally-based selection of trees including removal of poor quality trees, those with poor growth, over-mature trees and ultimately the final crop trees, created difficulties in achieving a continuous selection forest with the proper balance of age classes necessary for a sustained yield. A well-managed forest



Sub-unit	Age	Number of trees
SI	54	1
SII	48	1
SIII	42	1
SIV	36	1
SV	30	3-4
SVI	24	6-7
SVII	18	9
SVIII	12	9
SIX	6	9

Figure 1.1. Schematic representation of a B - Plan unit at the end of the 54-year rotation

should have a typical J-curve for the size/numbers relationship as shown in Figure 2.2. (Hutt, 1976).

1.3.1. The B - Plan unit

The solution which emerged was to create numerous individual units within a forest, each 18 x 18m in size (Figures 1.1. and 1.2.). Each $324m^2$ unit was to be subdivided in nine plots or sub-units, each of 6 x 6m. This latter figure approximated to the crown area of a mature tree (Plate 1.2.).

For extraction purposes, rackways, four metres in width, between rows of individual units were built into the plan (Figure 1.2.). These would allow heavy machinery to operate while minimising damage during management and extraction (Plate 1.3.). The next important aspect of the plan is the spiral planting scheme. A 54 year rotation within each $324m^2$ block is used. After initial clearance of the existing canopy, starting in the central sub-unit, nine small trees are planted. Six years later, nine more trees are planted in an adjacent sub-unit, then six years later nine more in the next sub-unit and so on up to 54 years (Figure 1.1.).

After a sub-unit has been growing for 24 years, the nine trees are thinned, so that by 36 years, there is only one mature individual left. This is the final crop tree for that sub-unit.

Once the cycle is fully established, the pattern should be as shown in Figure 1.1. and the cycle begins again once the first tree has been harvested. Thus when the system is complete, one mature tree comes out of each successive sub-unit approximately every six years.

The next important point was that because of shading effects, with adult trees so close to immature individuals, the most commonly planted coniferous species, such as Sitka spruce (*Picea sitchensis*)

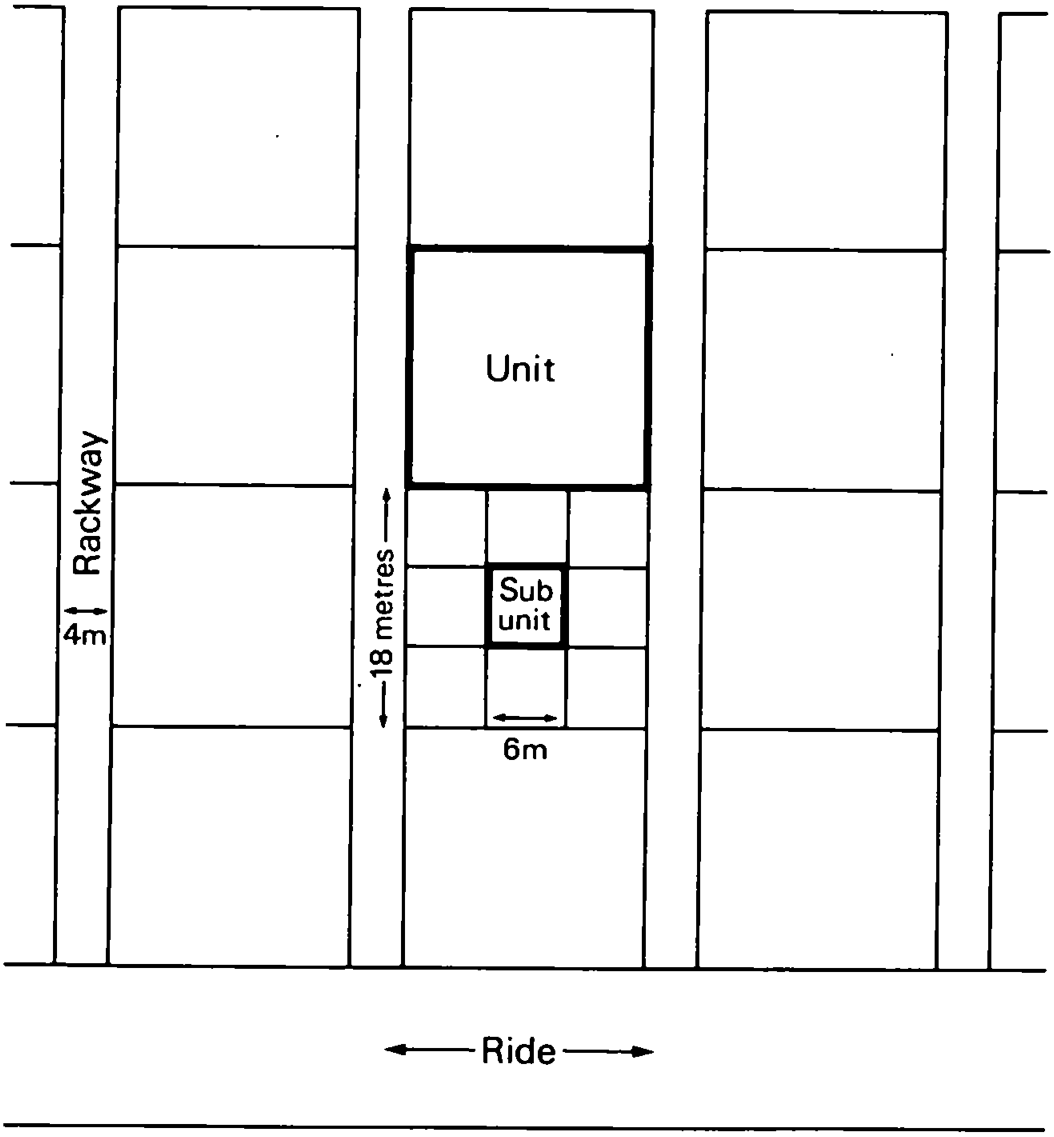


Figure 1.2. Schematic representation of B - Plan with units, sub-units, rackways and ride

Plate 1.2. B - Plan unit

Plate 1.3. B - Plan rackway

and Lodgepole or Corsican pine (*Pinus contorta/nigra*), could not be used. Instead, three shade-tolerant species were chosen:

a) Douglas fir - *Pseudotsuga menziesii*

b) Western red cedar - *Thuja plicata*

c) Western hemlock - *Tsuga heterophylla*

1.3.2. The B - Plan system in practice

The previous section has described the B - Plan model in theory. However, several additional points need to be made about its application in practice in the Tavistock Woodlands:

1) The system has been set into an existing mature canopy of either Douglas fir (*Pseudotsuga menziesii*), pine (*Pinus sylvestris* and *Pinus nigra*), larch (*Larix* spp. (hybrids)), spruce (*Picea stichensis*, *Picea abies*) or oak (*Quercus* x *rosacea*). This is the current commercial tree crop (Plate 1.4.).

2) Although the units appear to be laid out in straight lines in the theoretical model, the effects of terrain and the layout of existing rides and planting make it far more variable in practice and acceptable in landscape terms. Nevertheless, the 18 x 18m units themselves are rigorously adhered to.

3) The system was first set up in the late 1950's and early 1960's, so that the maximum stage reached by 1986 is stage V (27 years).

4) The spiral planting scheme (Figure 1.1.) has the advantage of controlling or 'sharing out' the available light, which is important as light can be a limiting factor in selection management. In addition, the fixed pattern is easily recognisable on the ground by forest workers. A stake marks

Plate 1.4. B - Plan unit in mature *Picea sitchensis* canopy - quadrat 14

the centre of each newly planted sub-unit and can be moved to the next one six years later.

5) Experience and net-discounted revenue calculations have shown that the optimum time to introduce B - Plan into an existing plantation managed according to clear-fell principles is at the first thinning, around 18 years old. In Tavistock Woodlands, the system has in the main been introduced into well-established stands. Although B - Plan and other selection systems are more wind-firm than even-aged plantations due to the storied canopy and layered root systems (Dyer, pers. comm.; Harley, pers. comm.; Troup, 1952; Hiley, 1954; Reade, 1969), opening up a mature even-aged canopy can cause wind-throw problems. However, once the first three sub-units are established, this danger is past and the stand achieves the greater wind-firmness characteristic of selection forests.

1.4. The Tavistock Woodlands Estate

The Tavistock Woodlands Estate comprises approximately 900 hectares and lies in the Tamar and Tavy valleys, 10 miles north of Plymouth (Figure 1.3.). Most of this research was completed in Blanchdown, Grenoven and Hangingcliff Woods (Figure 1.4.).

1.4.1. History

From the dissolution of the Tavistock Abbey in 1539 until 1956, the estate was owned by the Russell family who later became the Dukes of Bedford. The main study sites at Blanchdown, Grenoven and Hangingcliff Woods (Figure 1.5.) were mainly oak coppice with standards and small

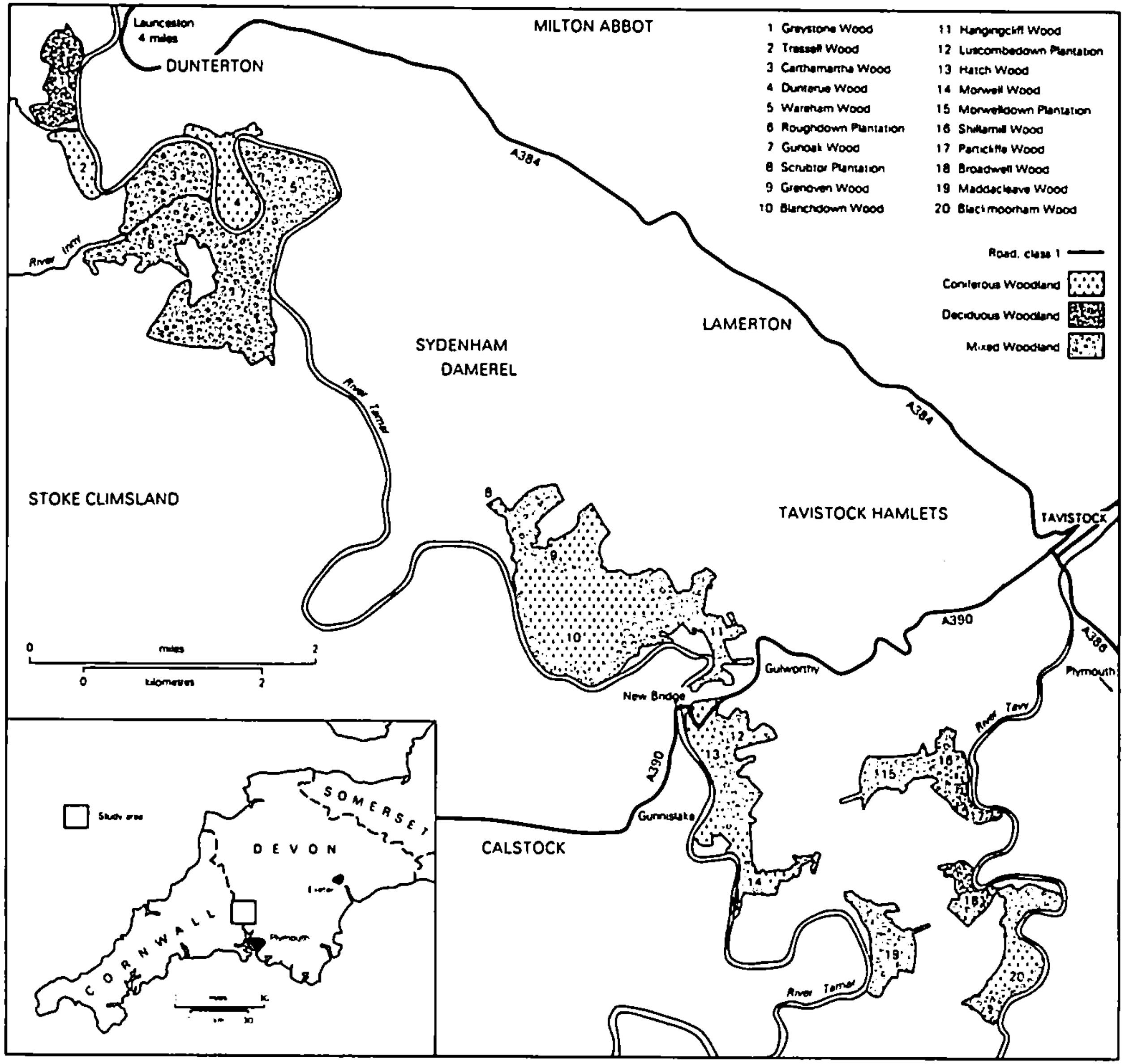


Figure 1.3. The Tavistock Woodlands

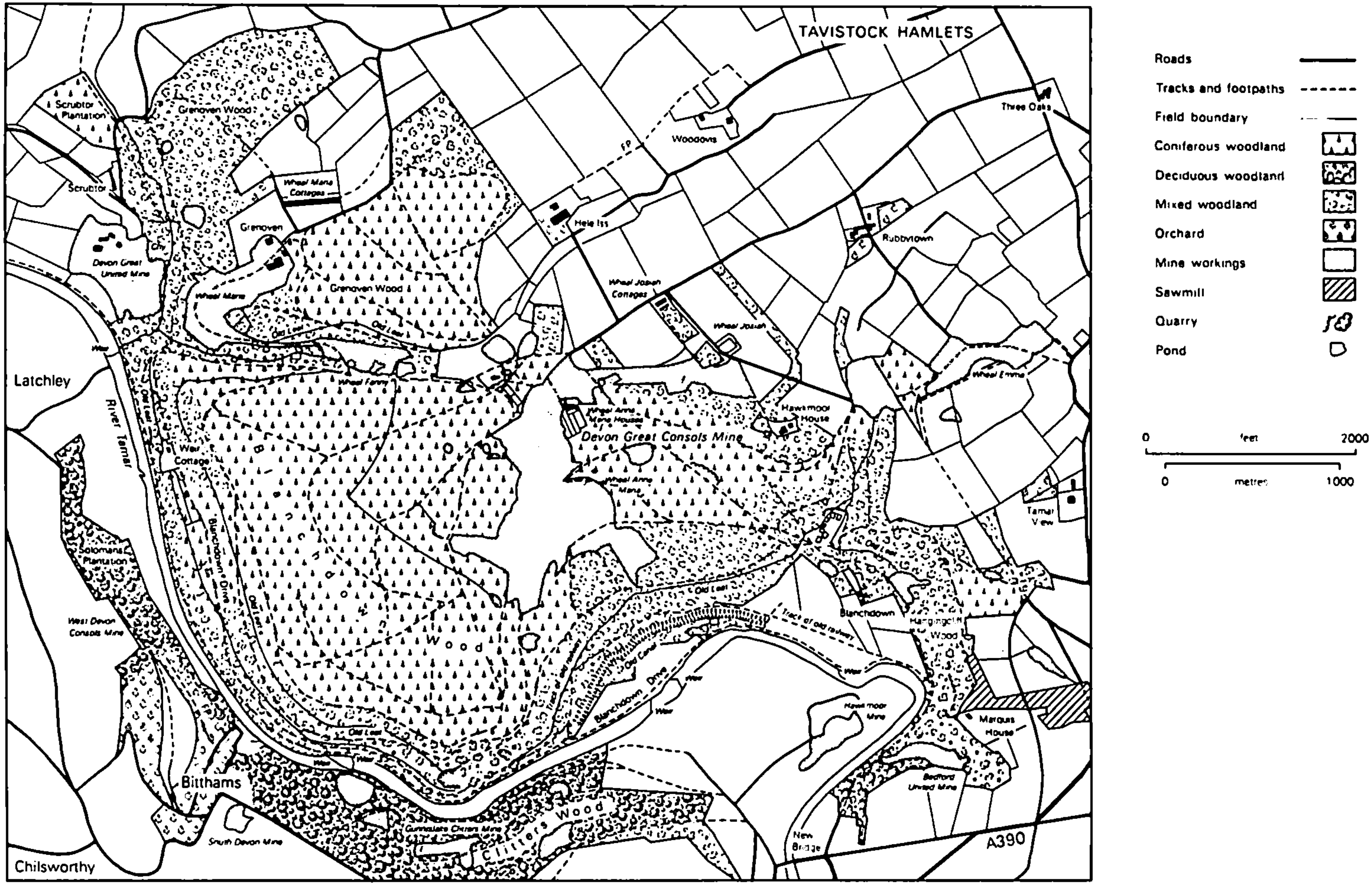


Figure 1.4. The location of Blanchdown, Grenoven and Hangingcliff Woods

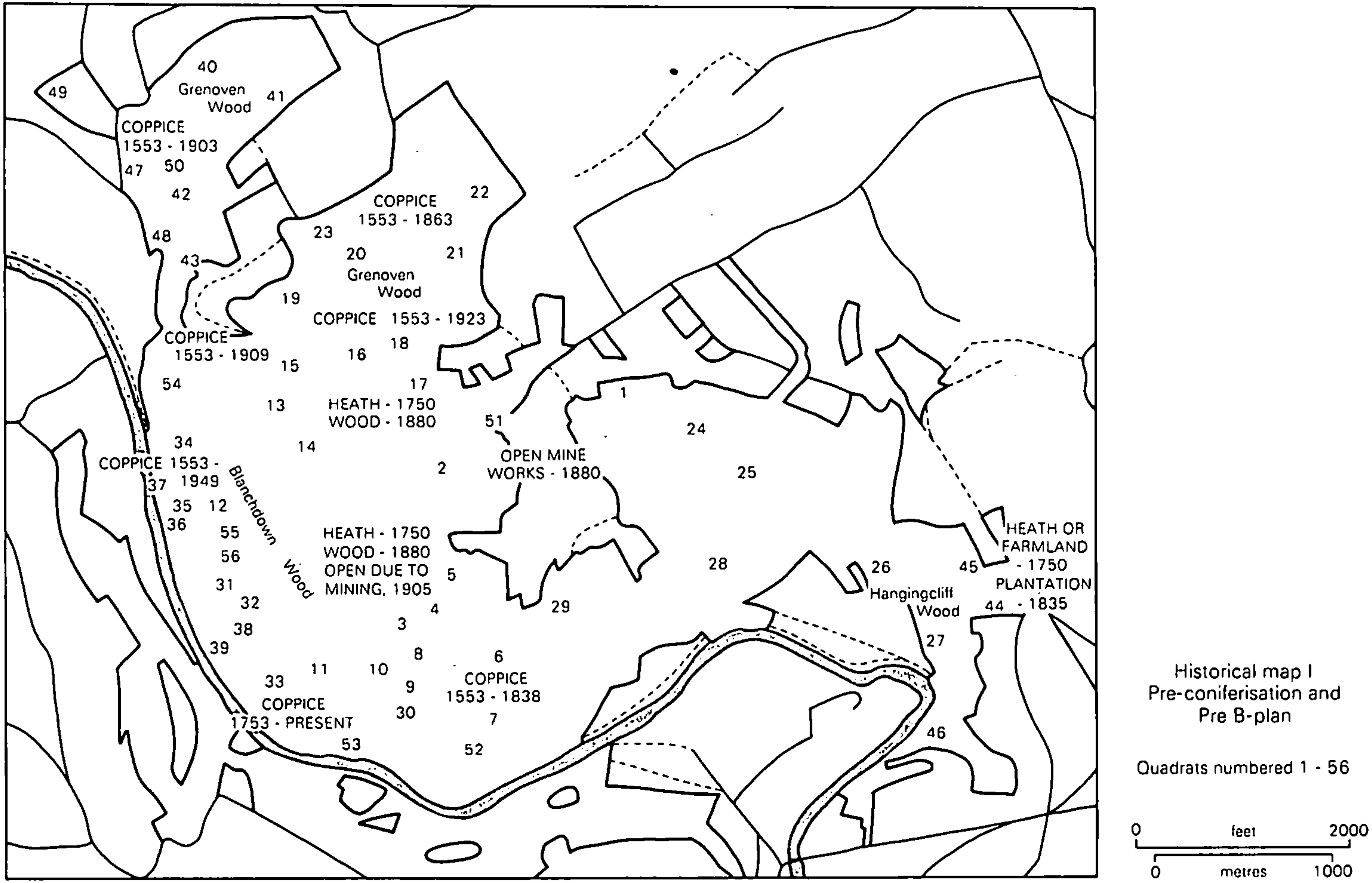


Figure 1.5. Historical map I - Tavistock Woodlands

timber groves. Relatively continuous records of woodland management were kept from the 16th century and are now lodged in the Devon Records Office, the Bedford Estate Archives and the Bedford County Records Office. Documents are available dating from 1557 until 1956. The records before 1700 are, in the main, bills of sale for the coppice wood. In addition to these bills, from 1700 onwards, there are records of labouring activities and of the sale of timber and wood products. More detailed accounts were kept from the early 1800's until the present.

Plantations of native hardwoods and exotic conifers began gradually to replace the coppice in the early 1800's. However, small parts of the study site are still relic coppice and timber groves (Figures 1.5. and 1.6.). From the 1800's until 1950, a large area of farmland and heathland in the centre of Blanchdown Wood (Figure 1.5.) had also been afforested (Hamilton, pers. comm.).

The study area of Blanchdown and Grenoven Woods was affected by mining activities from 1844 - 1903. Blanchdown Wood (Figure 1.4.) was the site of the Devon Great Consols Mine, which in the period 1861 to 1870 produced 16% of the total world production of copper and 50% of the world's supply of arsenic (Booker, 1971). The arsenic refining in Blanchdown Wood between 1860-1901 produced fumes which stunted and even killed many trees. The spoil heaps from mining activities still remain today.

With the exception of two small areas planted in 1843 and 1863, the present-day coniferous canopy in Blanchdown and Grenoven Woods has been planted at various dates throughout this century (Figure 1.6.). Pine (Pinus sylvestris/nigra), Larch (Larix spp.), Sitka spruce (Picea sitchensis), Norway spruce (Picea abies) and Douglas fir (Pseudotsuga menziesii) have all been planted, often in pure stands. The remaining areas of neglected coppice are in the south-west corner of Blanchdown

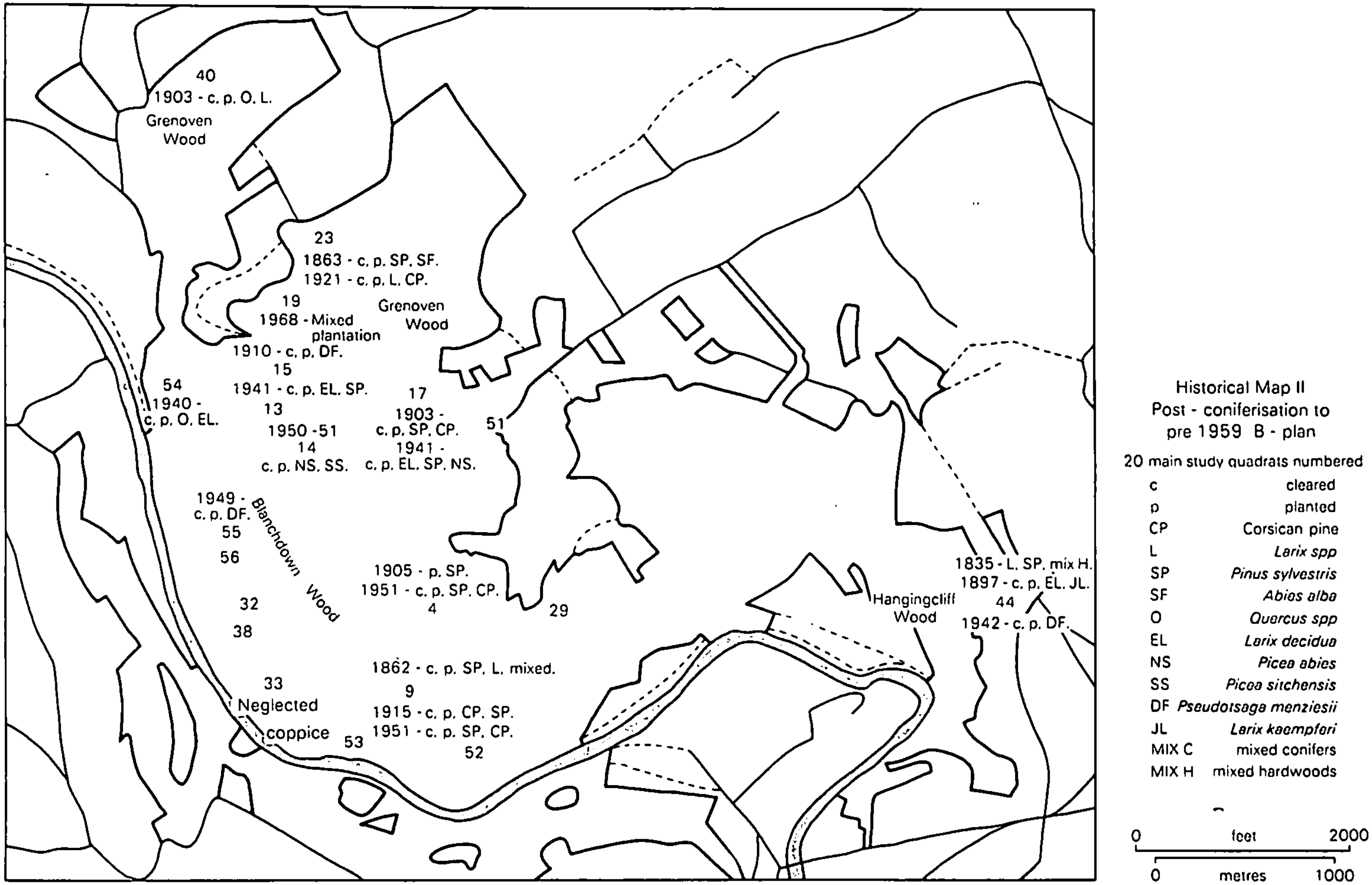


Figure 1.6. Historical map II - Tavistock Woodlands

Wood and in Grenoven Wood (Figure 1.6.). Records of woodland management practices such as clearing, planting and thinning have been kept by the estate throughout this period.

1.4.2. Soils

With the exception of some small areas of alluvial gleys (Conway series), next to the River Tamar, all soils are either acid brown podsolics (Dartington and Ivybridge series) or brown earths over coarse loamy granitic drift (Gunnislake series). A map of soil distribution is presented in Figure 1.7. Most of Blanchdown and Grenoven Woods are underlain by the Dartington Series which are stony, fine loamy and fine silty brown podsolic soils overlying head composed of slates and slaty shales. Under the woodland, there is a thin surface accumulation of mull or moder humus. The pH values are generally low due to the parent materials and leaching through acid leaf litter (Hogan, 1977). Large pyrophosphate extractable Fe and Al contents support classification as typical brown podsolic soils.

Soils of the Ivybridge series are similar, except that they exhibit some gleying. They have a limited distribution within Grenoven Woods (Figure 1.7.). For both soils, pH values lie between 4.0 and 5.5. Values for pH of soil samples taken from quadrats located in the initial survey of the woods varied between 5.06 and 3.85, with a mean of 4.53 for the A horizon and between 5.77 and 4.01, with a mean of 4.65 for the B horizon. Percentage soil moisture was also recorded in this survey with values of between 15 - 30% over the wood.

Figure 1.7. A soil map of the Tavistock Woodlands study area (adapted from Hogan, 1977)

CHAPTER 2. THE PRODUCTION, ECONOMIC AND ECOLOGICAL ADVANTAGES OF THE BRADFORD PLAN

CHAPTER 2. THE PRODUCTION, ECONOMIC AND ECOLOGICAL ADVANTAGES OF THE BRADFORD PLAN

2.1. Introduction

Many advantages are claimed for selection forestry management systems (Hiley, 1954). In the context of British forestry, these are primarily ones of production and increased economic gain (Troup, 1952; Hiley, 1954). However, continental foresters also emphasise the ecological and conservation advantages (Goldsmith et al., 1982). Some of these advantages have already been realised at Tavistock Woodlands, particularly those concerned with production, but the ecological advantages are uncertain and in part are the aim of this thesis. The economic benefits need further time before their potential is proven because of the long term nature of forest management. The following is a brief discussion of some of the real and potential advantages of B - Plan in terms of production, economics and ecology.

2.2. Production advantages of B - Plan

2.2.1. Sustained yield

The concept of sustained yield is implicit in the design of B - Plan. Also in addition to the final crop tree, the thinnings which are produced throughout the 54 year rotation are suitable for fencing posts to satisfy a constant demand from local farmers. The final crop trees harvested in clearing sub-units are processed at a sawmill on site and are used for the manufacture of picnic tables, garden furniture and garden sheds, as well as for building timber. The estate has also established a celcuring plant on site for timber preservation. There is thus a constant and sustained yield of various wood products produced by a forest composed of B - Plan units. The resulting steady cash flow enables the estate to employ a permanent staff who are occupied at every stage in the system. Hence the problems of employing casual labour are avoided and the estate has the advantage of a highly trained and loyal work force.

2.2.2. Economic flexibility

A tree stock of varying size means that the estate is able to respond to changes in markets by harvesting those sizes in greatest demand. Profitability is thus maximised and economic flexibility is maintained. By holding back other sizes, they can wait until the market is better. Many even-aged plantations without this large variety of stock would not have this flexibility of response and the resulting steady cash inflow.

2.2.3. Natural regeneration

B - Plan is able to take advantage of any natural regeneration in the units as in continental selection systems. In Tavistock Woodlands Estate, Pseudotsuga menziesii is particularly successful in regenerating. For this species, southwest England represents an homologous life zone to that of the Pacific Northwest, its native home (Holdridge, 1966), Pseudotsuga thus regenerates prolifically. When new units are opened up in the mature stands, flowering is stimulated by this crown thinning (Dyer, pers. comm.). The resulting sub-units need only thinning and no planting, thus reducing the initial establishment costs of new sub-units.

2.2.4. Harvesting flexibility and variety of species

In addition to the major B - Plan species (Pseudotsuga menziesii; Thuja plicata; Tsuga heterophylla), Sequoia sempervirens (Coast redwood) and Nothofagus procera (Southern beech) have been introduced into some of the units under both mature Pseudotsuga and Larix. The Nothofagus grows very rapidly and will probably reach its final crop size at 30 years, having already reached 70 feet at 24 years. The flexibility of B - Plan means that this species can be harvested at 30 years and another tree in the sub-unit can be selected for the final crop at 54 years. Nothofagus is also beneficial in that it creates a mixed broadleaf/ evergreen wood with the resulting favourable light mosaic and mixed leaf-litter, while still being economically as viable as most conifers. Currently it appears that Nothofagus timber will find a use in the wood turning industries, such as in the making of broom heads (Dyer, pers. comm.). Sequoia sempervirens is particularly useful in the manufacture of garden sheds because of its rot-resistant properties.

Of the other species, Pseudotsuga menziesii has been a familiar tree in British forestry, first being planted as a commercial conifer in the 1800's. It also has well established markets in the building trade.

Tsuga heterophylla and Thuja plicata are more recent introductions from the 1930's (Aldhous and Low, 1974). Tsuga can be used as sawwood, chipboard, fibreboard, and for pulping. Thuja does not pulp well but the thinnings can be used for the local fence post market, as it is durable in the open and the final crop can be used as sawn timber. Thuja may also fill the demand for exterior cladding in the future (Aldhous and Low, 1974).

2.2.5. Maximum production

Another production advantage results from the mixture of species. Because of differences in geometry and physiology between tree species, early crown competition between individuals is reduced and the vigorous crown development produces maximum radial stem increment (Troup, 1952) similar to the free-growth technique employed with oak which stimulates vigorous crown development by heavy thinning (Jobling and Pearce, 1977). With heavy thinning of oak, there is a loss of biomass. This does not occur in the many layered B - Plan wood.

> "Layering of the root systems in a mixed species and age stand serves to reduce competition between trees too, and results in increased vigour and growth"
> (Packham and Harding, 1982: p. 5)

Advocates of selection, such as Bourne (Hiley, 1954) and Knuchel (1953) even claim the total increment to be greater by as much as 50%. Malcolm (1979) feels valid comparison of 'utilisable productivity' between an irregular and an even-aged stand is difficult, but that an even-aged stand would have the advantage because poor illumination means the lower parts of an irregular canopy are inefficient. In the Dartington Woodland Selection Experiment, this claim of 50% greater total increment appears to be invalid, but the timber quality is extremely high and hence the price paid for the final crop is good (Harley, pers. comm.).

Where it is not economically feasible to fertilize, selection forestry has been recommended as an alternative (Jorgensen et al., 1975). Phosphates for food production are in short supply, so it is probably not ethical to use them in forests in any case (Packham and Harding, 1982). Fertilizer is unnecessary in the Tavistock Woodlands. Also, leaving the lop and top after harvesting as well as the weed trimmings after mechanical weeding will return some nutrients to the soil.

2.2.6. High quality timber

High quality timber is another production advantage of selection forestry and this has become the aim in producing the final crop tree in the Tavistock Woodlands. The trees grow at a steadier rate and ring-width is more constant throughout the thickness of a stem than in an even-aged stand, where the ring-width either declines as the canopy closes, or suddenly becomes very large after a thinning, making the timber of poorer quality for building (Hiley, 1954). This consistent quality makes the final crop wood attractive to buyers (Leathart, 1983).

2.2.7. Frost and wind protection

Selection forests afford young trees a larger degree of protection from wind dessication and frost damage (Ovington, 1965). This is true for B - Plan and as a result, few newly planted trees have to be replaced or beaten up. Survival rate is thus near 100%, unlike young even-aged plantations, where many trees die of exposure (Dyer, pers. comm.). There are sometimes problems of windthrow in opening up the mature even-aged canopies to introduce B - Plan, but these disappear after the third stage and Tavistock Woodlands expect that like other selection forests, B - Plan will be very wind-firm in future rotations, because the roots are able to take advantage of all layers in the soil and the force of the wind will be broken by a storied canopy (Dyer pers. comm.).

Late spring frosts are a particular danger in some areas of Tavistock Woodlands due to the topography of the river valleys. Again these dangers are reduced by the structure of B - Plan.

2.2.8. Lower establishment and management costs

The cost of establishing B - Plan per unit area can be lower than that of replanting large areas after clear-felling, particularly if the natural regeneration of Pseudotsuga is utilised, (Dyer, pers. comm.). The lop and top, left after clear-felling, is usually collected up and burned to clear the area for planting, thus increasing the labour costs. The quantities left after clearing a B - Plan sub-unit are small and the lop and top can be left in-situ.

Weed control is a serious and expensive problem in new plantations where the area needs to be cleared every year for the first five years, and sometimes twice during the first year. Weed growth under B - Plan is less than in even-aged plantations due to lower light intensities, less soil disturbance and possibly a lower temporary surge of nutrients following planting, promoting excessive growth (Bormann and Likens, 1979). The B - Plan sub-units only need weeding in the 2nd and 3rd years after establishment.

2.2.9. Fire protection

A group selection system has been employed in the Aleppo pine forsts of southern France as a fire preventative measure.

> "It is a common experience when fighting a forest fire to find that its progress goes unhindered through a crop of one species and age of tree, but is checked as soon as it greets woods of another species or age class, thus giving fire fighters a chance to defeat it" (Blatchford, 1978: p. 55).

Although fire is not a problem in southwest England, this added advantage of selection forests in general might be significant if B - Plan was established elsewhere.

2.2.10. Advantages for small woodland owners

Crowther (1978) recommends current Forestry Commission practices for the management of small woodlands, with a heavy emphasis on replanting, weeding and fertilizing. Adoption of B - Plan could obviate such practices:

> "... the system (continental selective forestry) makes use of all mast years and provides a constant income from even small woods, hence it is appropriate for small private woodlands" (Peterken, 1981: p. 72).

Other non-production economic advantages of selection systems and B - Plan in particular, have not escaped notice. As an example, Wilderness Wood in Sussex, is used for teaching purposes by many local schools and a small fee is charged. There B - Plan has the advantage of a pleasant atmosphere as well as providing a starting point for a discussion of forestry versus conservation.

> "They (selection forestry experiments) can become an absorbing interest and a wood of 50 or 100 acres is sufficient to engage the inventiveness and sagacity of an enterprising owner who will experiment in this way" (Hiley, 1954).

Evidence thus indicates that in the future, B - Plan could become more than just an experiment and a more widely accepted management practice.

2.3. <u>Economic advantages of B - Plan</u>

2.3.1. Measurement of growth

The economic aim of B - Plan management is to produce large, high quality saw logs as the final crop at the end of a 54 year cycle. The high quality is judged both by size and the number of rings per inch. Four rings per inch is the optimum (Dyer, pers. comm. and Harley, pers. comm.).

This fast, even growth rate of 4 rings per inch is achieved by careful monitoring of the stands and thinning to reduce competition for resources, so that no tree is checked in its growth rate. Every six years, three 324m^2 sample plots in a stand are measured using diameter breast high and increment boring. A graph is then compiled of the number of individuals in each five centimetre size class (Figure 2.1.), which is then compared to the ideal B - Plan distribution (Figure 2.2.). This ideal distribution follows a curve similar to the Biolley Plan, the check control method used in continental selection forestry

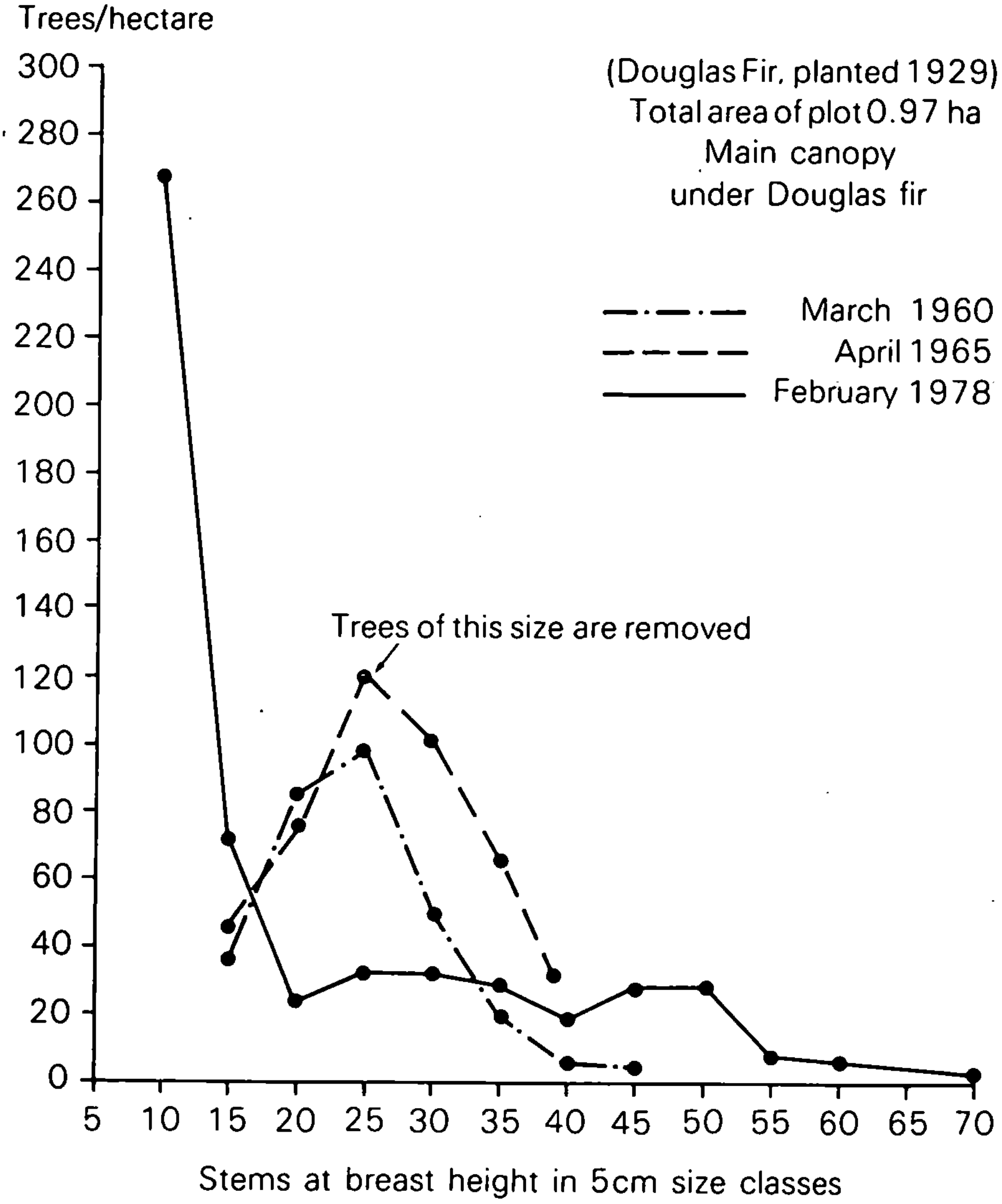


Figure 2.1. Graph of stem numbers per size class under Bradford Plan management within a *Pseudotsuga menziesii* stand - 1960-1978

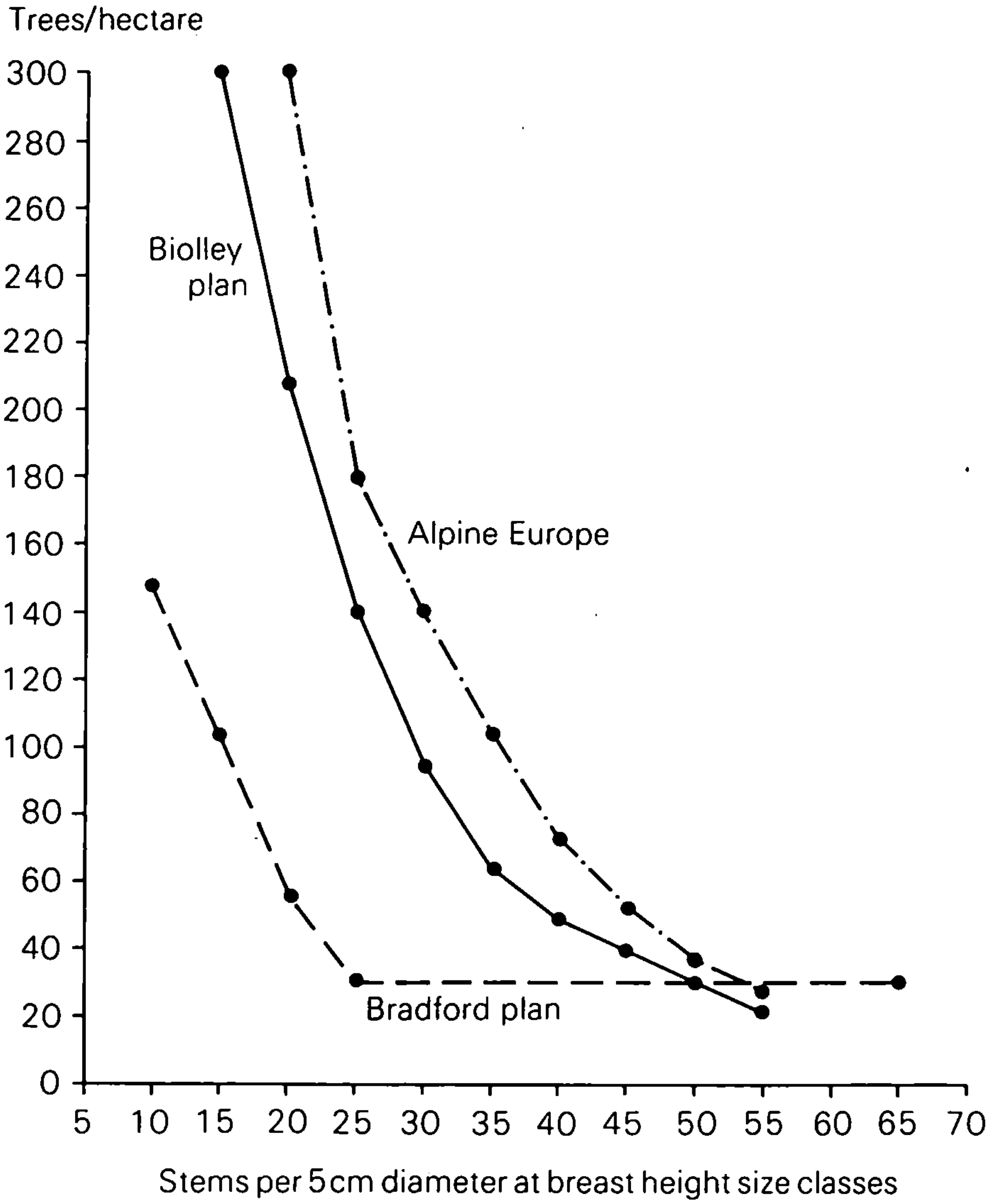


Figure 2.2. The ideal B - Plan size distribution compared with distributions for systems in Alpine Europe and under the Biolley Plan

(Table 1.1.). It is also similar to the age distributions in natural uneven-aged forests such as those in Alpine Europe (Figure 2.2.) or in North America (Figure 2.3.). The main difference is the more evenly distributed number of trees in the older age classes of B - Plan. Where the sample plot graph deviates from the ideal curve at the point on Figure 2.1. labelled 'Trees of this size are removed', trees in these classes are harvested and these thinnings are sold primarily as fence posts. Figure 2.1. shows the progression from 1960 to 1978 toward the ideal B - Plan selection curve.

2.3.2. Growth rates under B - Plan

The constant monitoring of the growth rates coupled with constant thinning is producing steady growth of four rings per inch by virtually all of the B - Plan trees on the estate (Dyer, pers. comm.). With some species, adjustments had to be made to the conventional thinning ages precribed by the Forestry Commission for trees in an even-aged plantation. For example, Tsuga heterophylla is usually thinned at 15 years. Under the protection provided in a B - Plan unit, this species achieves a size which requires thinning at ten years of age. If left unthinned for longer, Tsuga's growth rate is checked by competition with its neighbours.

The conventional Forestry Commission yield tables (Hamilton and Christie, 1971) developed for even-aged plantations proved inappropriate for prediction in Tavistock Woodlands, mainly because they assume an uneven growth rate over time. Figure 2.4. shows a comparison in the volume increment in a B - Plan stand versus that in an even-aged plantation. The figures are extracted from the Forestry Commission yield tables (Hamilton and Christie, 1971). For Pseudotsuga menziesii in the yield class 22 which is the class of much of the Pseudotsuga

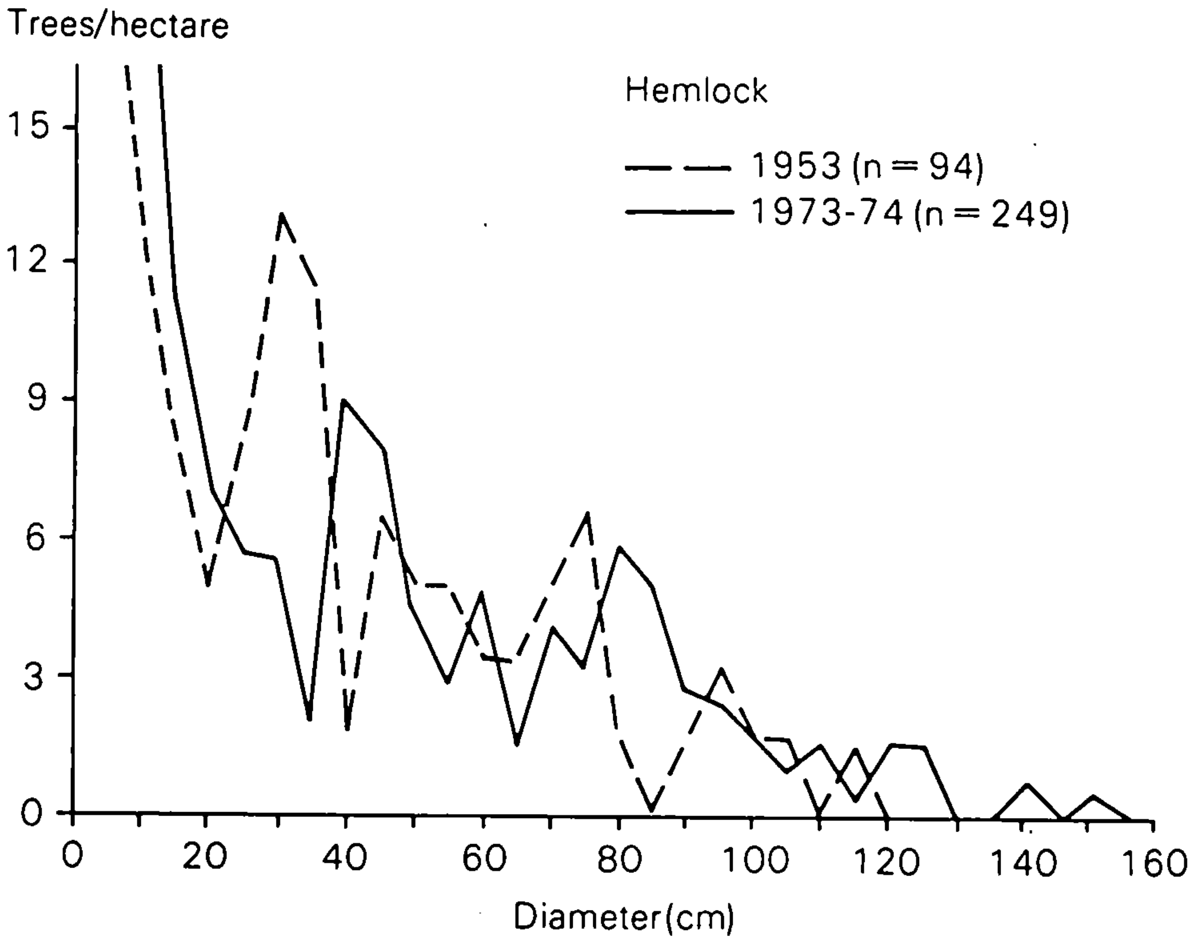


Figure 2.3. Size distribution in a natural *Tsuga* forest in North America (from Lorimer, 1980)

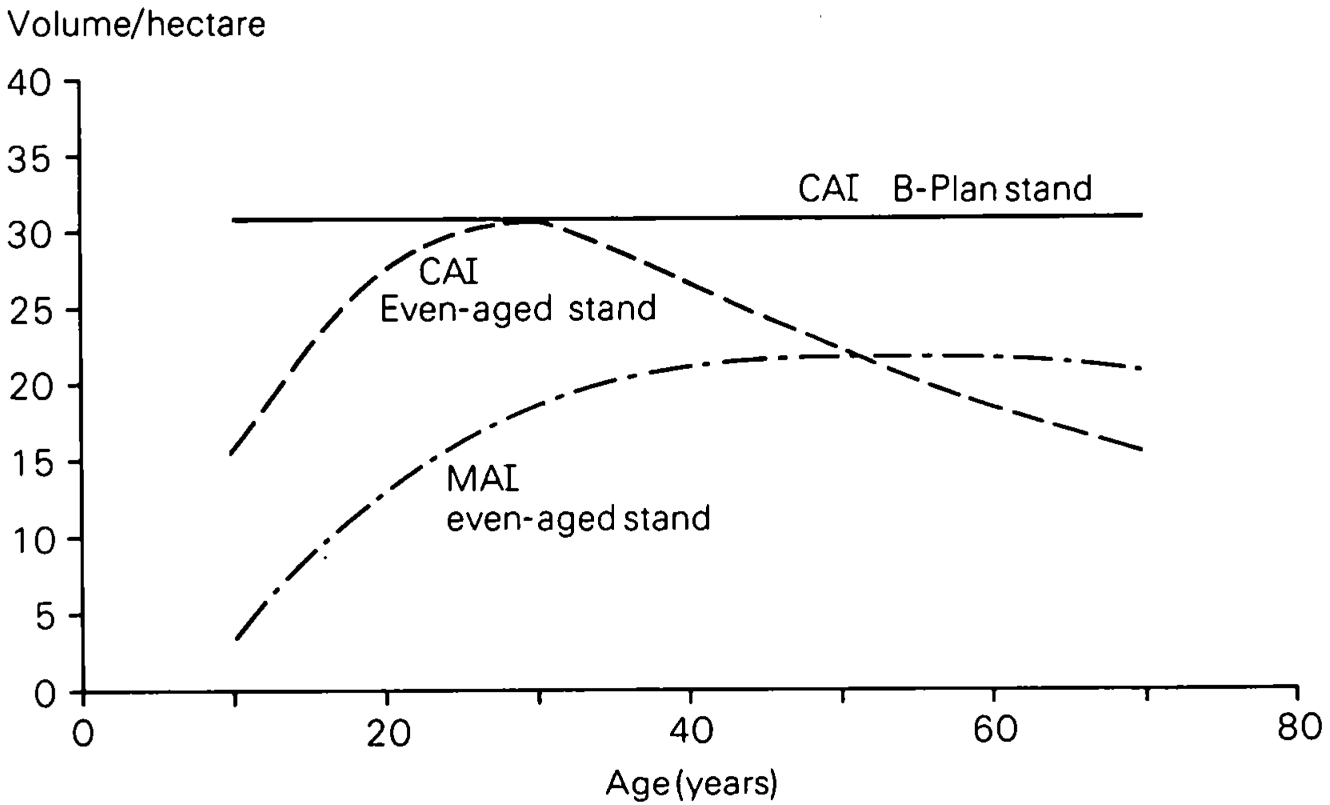


Figure 2.4. Comparison of volume increment in an even-aged plantation with a B - Plan stand of *Pseudotsuga menziesii* - yield class 22
CAI - current annual increment
MAI - mean annual increment

on the estate. The height of this curve varies with the species and the site. A particular species producing greater volume (cubic metres per hectare) than another on the same site is said to have a higher yield class.

Figure 2.5. shows the uneven growth in an even-aged plantation over time. In the establishment phase, the trees have to conquer the harsh environment of a clear-felled site and hence the rings are much smaller than those of the B - Plan trees. As the trees grow together in the even-aged stand, competition increases and at the pole stage (15 years), the rings per inch have increased showing a great need for thinning to reduce competition. Under B - Plan management each mature tree is able to develop a full crown and hence the steady growth rate does not slow down. This is in effect like the permanent crown thinning in oak woodlands (Jobling and Pearce, 1977) (Section 2.2.5.), which is used in conventional management to increase the growth rate of a mature tree.

B - Plan yield tables (Table 2.1.), developed by Philip Hutt, can be compared to those of the Forestry Commission (Hamilton and Christie, 1971) to produce a bar graph of the cumulative production for Pseudotsuga in the yield classes 22 and 24 (Figure 2.6.). The volume includes both the thinnings and the final crop trees over a period of 54 years. In theory, at the end of 54 years, the total Pseudotsuga production under B - Plan, assuming the crop continues to grow at its current rate of four rings per inch, should exceed that of the tree under conventional management by about 30%. Hiley (1954) suggests that selection forestry may even exceed even-aged forestry production by as much as 50% (Section 2.2.5.). Even comparing B - Plan Pseudotsuga yield class 22 with a more productive yield class 24 in an even-aged stand (Figure 2.6.), the B - Plan tree still shows

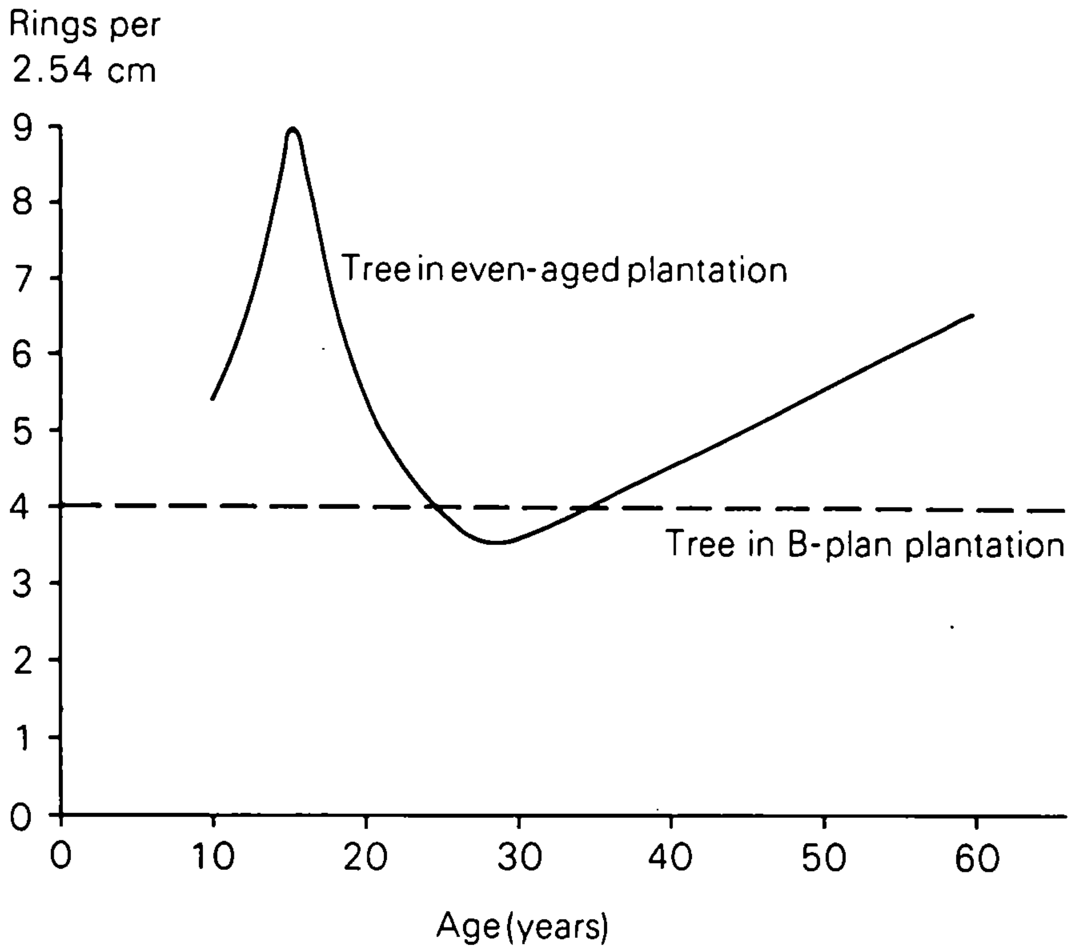


Figure 2.5. Growth increment for *Pseudotsuga menziesii* - yield class 22 - B - Plan versus even-aged management (Rings per inch for even-aged stand from Hamilton and Christie, 1971)

Table 2.1 Bradford plan yield tables 1983 - (for one hectare)

	VOL PER TREE (m^3)		BEFORE CUT				COUPE (harvested)				6yr CUT		TOTALS	
AGE	FINAL CROP	OTHERS	FINAL CROP		OTHERS		FINAL CROP		OTHERS		TOTALS		BEFORE CUT	
			TREES	VOL	TREES	VOL	TREES	VOL	TREES	VOL	TREES	VOL	TREES	VOL
	4 R P 2.5 cm (YC 22 Equiv)													
12	.027	.02	30	.81	210	4.2							240	5.01
18	.145	.07	30	4.35	210	14.7			90	6.3	90	6.3	240	19.05
24	.39	.21	30	11.70	120	25.2			60	12.6	60	12.6	150	36.90
30	.85	.495	30	22.50	60	29.70			30	14.85	30	14.85	90	52.20
36	1.38	.99	30	41.40	30	29.70			30	29.70	30	29.70	60	71.10
42	2.12		30	63.60									30	63.60
48	3.01		30	90.30									30	90.30
54	4.03		30	120.90			30	120.90			30	120.90	30	120.90
											per 6yr Cut	184.35	870	459.06
											CAI 30.725m^3		6.66% of stock	
	4.5 R P 2.5 cm (YC 20 Equiv)													
12	.018	.01	30	.54	210	2.1							240	2.64
18	.106	.055	30	3.18	210	11.55			90	4.95	90	4.95	240	14.73
24	.28	.165	30	8.40	120	19.80			60	9.90	60	9.90	150	28.20
30	.60	.38	30	18.00	60	22.80			30	11.40	30	11.40	90	40.80
36	1.09	.75	30	32.70	30	22.50			30	22.50	30	22.50	60	55.20
42	1.59	1.35	30	47.70									30	47.70
48	2.32		30	69.60									30	69.60
54	3.14		30	94.20			30	94.20			30	94.20	30	94.20
											Per 6yr Cut	142.95	870	353.07
											CAI 23.825m^3		= 6.75% of stock	

Key: CAI = current annual increment; Coupe = trees harvested at one point in time; Volume = m^3

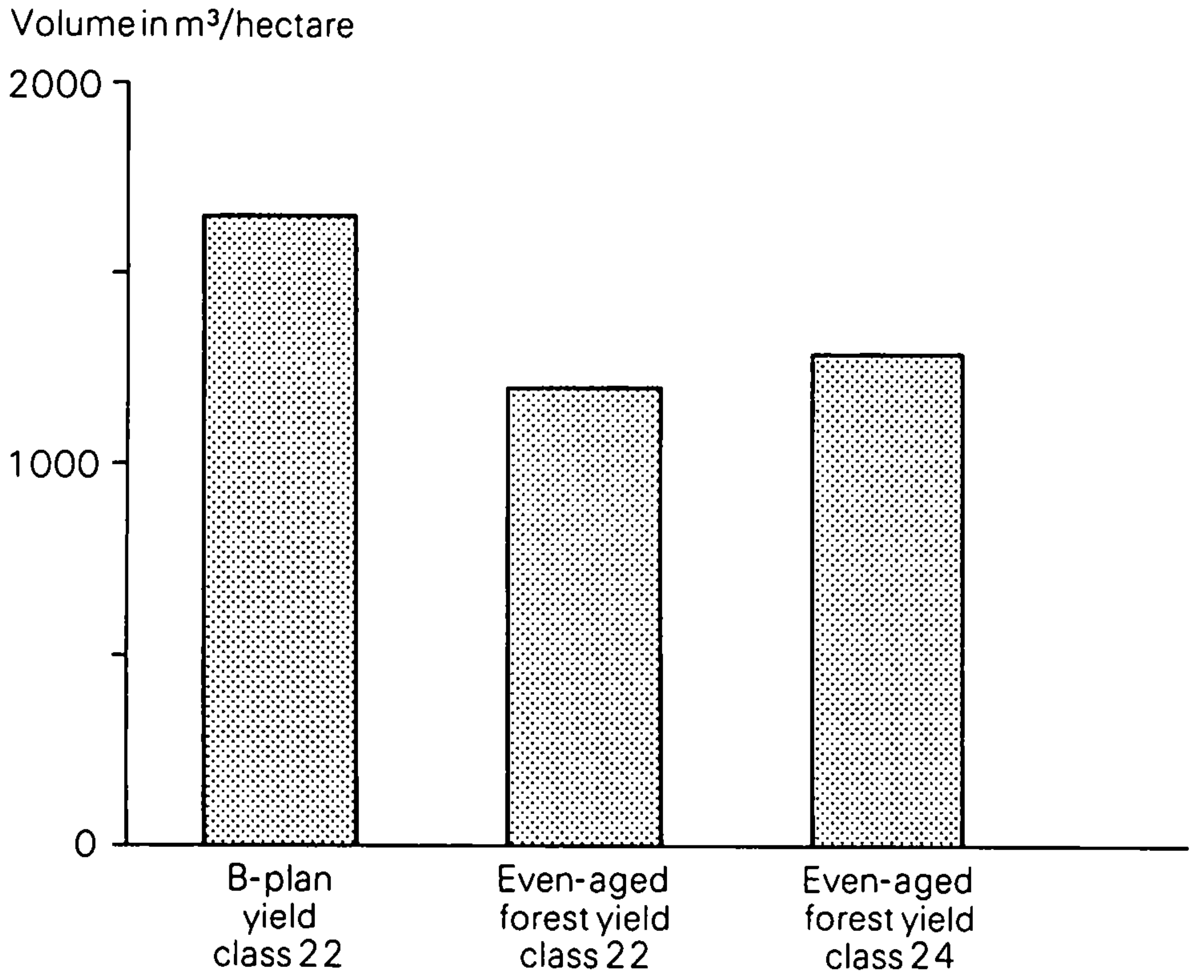


Figure 2.6. Cumulative volume production (m^3ha^{-1}) at the end of a 54-year rotation. B - Plan stand versus even-aged stand of *Pseudotsuga menziesii* yield class 22 and 24

a higher total production. This as yet theoretical higher production could thus mean higher profits for the estate in the future.

2.3.3. Economic predictions

Although no final crop B - Plan trees have as yet been produced, predictions can be made about the economic advantages of the system. Assuming the growth rate of four rings per inch, at the end of 54 years, a B - Plan final crop tree will have a diameter at breast height in the region of 35 cms. Using the Forestry Commission yield tables (Hamilton and Christie, 1971) for Pseudotsuga yield class 22, the diameter at breast height at the end of 55 years would be in the region of 28 cms. Prices paid for saw logs increase linearly with increasing diameter at breast height, a greater premium being paid for larger size in southwest England (Aldhous, 1983) (Figure 2.7.). This is because the conversion rate is more efficient for larger timber, as well as there being a great demand for large dimension timber in southwest England (Aldhous, 1983). Extrapolating from Figure 2.7., the price paid for a final crop B - Plan Pseudotsuga tree with a diameter at breast height of 35 cms, would be £16-£20 per cubic metre. The sum paid for the same species from an even-aged plantation with a diameter at breast height of 28 cms would be £11-£15 per cubic metre. The B - Plan returns would thus be around 40% more than that of conventional management.

Furthermore, in a conventional forest, the ratio of saw logs to thinnings is usually 50 - 50. Assuming the steady four rings per inch achieved under B - Plan, this ratio would be about 75 - 25. Consequently, if 75% of B - Plan trees are of the more profitable saw log size, compared with 50% for an even-aged stand, then the profit could be even higher for the products of B - Plan management. Some

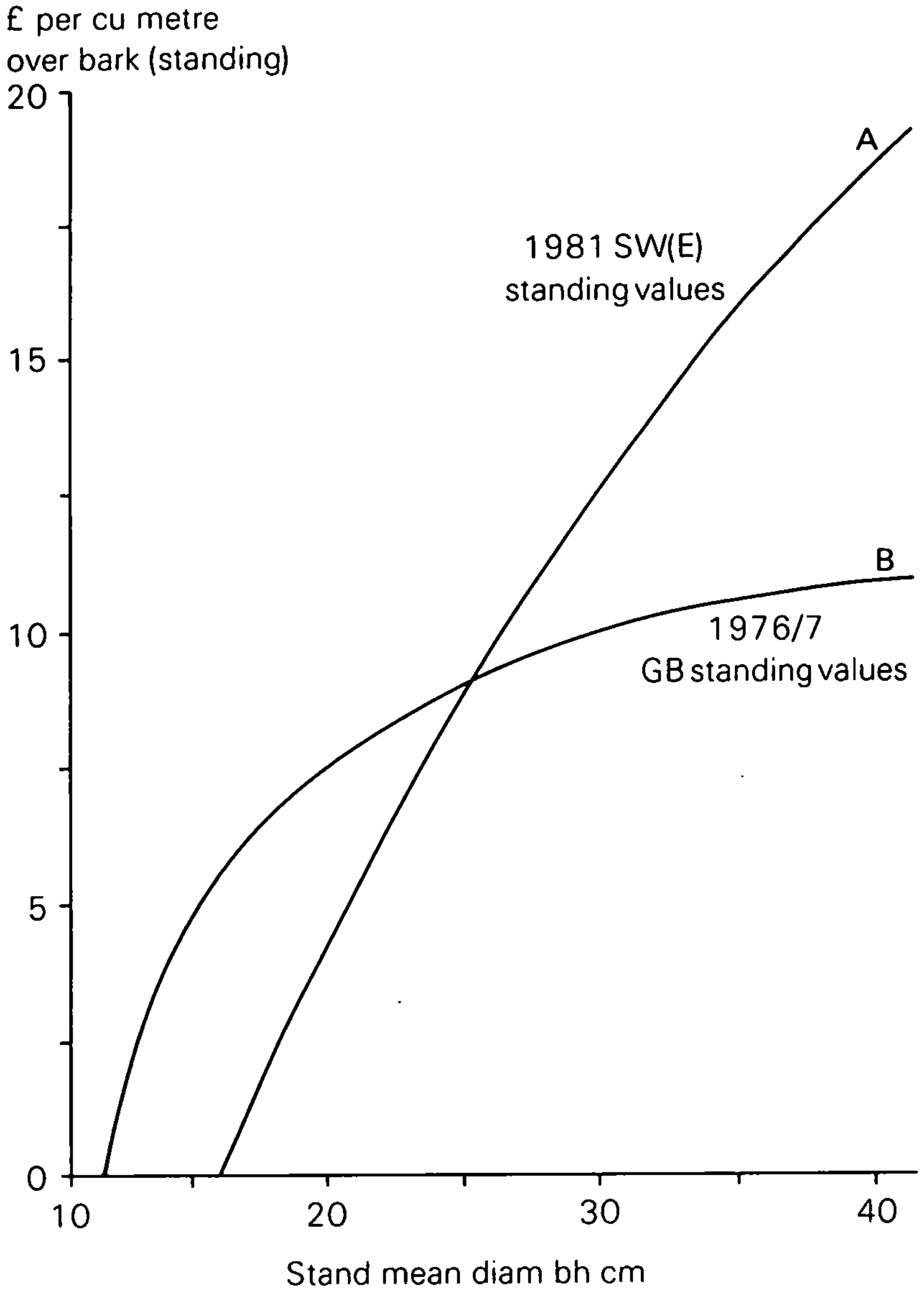


Figure 2.7. Timber price-size curves.
Curve A - standing timber values for conifers - generalized average curves for southwest England
Curve B- standing timber values for conifers - generalized average curves for Great Britain 1976/77
(from Aldhous, 1983)

B - Plan costs are higher, particularly during extraction. Here the costs can be 10% more than extraction in a conventional plantation. However, these are recouped to some extent by the need for less weeding and by higher young tree survival rates than in a conventional plantation. Hence B - Plan, by the production of larger and higher quality final crop trees, may well prove to be far more profitable than conventional even-aged management systems.

2.4. Ecological advantages of B - Plan

2.4.1. Introduction

In addition to the production and economic advantages of the adoption of the Bradford Plan, the Earl of Bradford and Philip Hutt foresaw a number of ecologically desirable aspects of the system. Over-riding all of these was the need to encourage and increase both habitat and species diversity in plant and animal communities under coniferous forestry. While it was clear that plantations managed under the system would not have outstanding ecological and conservation value, substantial improvements could be made over existing areas under clear-fell forestry.

This fits well within the ideas of O'Connor (1974), who described one important part of biological conservation as 'conservation as an attitude to land use management'. The goal of maintaining ecological interest and diversity within commercially viable forestry operations is an excellent example of this concept. However, the Earl of Bradford and Philip Hutt also saw beyond this into another category of conservation described by O'Connor (1974) as 'creative conservation'. Here, conservation can be taken further within economic land use by creating new features of ecological interest as part of new land uses. Creative conservation thus accepts land use change and new land uses and seeks to create new opportunities for ecology in the process. Examples exist throughout the historical period, the most relevant here being the coppice with standards woodland management system in deciduous woodlands which actually increased the ecological interest of many British woodlands, while being primarily established as an economic system of land use.

Within this overall framework, individual ecological and conservation advantages of B - Plan may be described.

2.4.2. Increased habitat diversity

The nine different stages of B - Plan (Figure 1.1.) provide the complete range of habitat from open ground up to mature tree within each $324m^2$ unit. This habitat diversity is then replicated numerous times throughout the forest. An important result of this is that, in theory, the ground flora is maintained at all stages within each individual unit and once the cycle is fully operational, there are always several sub-units within each $324m^2$ unit at early stages of succession, when the light environment is optimal.

In this respect, B - Plan mimics the traditional coppice with standards particularly in its continuously changing light pattern.

> "Timber trees come and go; the continuity of the wood is maintained by the long-lived underwood stools and by the herbaceous plants which constitute the ground vegetation" (Rackham, 1980a: p. 5).

The standards produced the timber and the coppice stools produced wood or underwood especially for fuel. The coppice system had a cutting rotation of between 7 to 20 years (Rackham, 1976). This had a conservative effect on the fauna and ground flora allowing the various species to follow the coppice cutting around the wood according to their particular requirements for light, shade and moisture. Individual species could not become extinct as easily or as rapidly from a wood as they do under the closed canopy of a modern coniferous forest. (Hill and Hays, 1978; Hill, 1979a; Brown, 1981).

Clearly, differences exist between B - Plan and the former coppice with standards system, but the similarities are also there in terms of the potential for increased habitat diversity.

2.4.3. Maintenance and possible increase of species diversity

Largely because of the increase in habitat diversity, the species diversity of flora and fauna is maintained and after the system has been in operation for a reasonable length of time may actually be increased. A total of 16 planted tree species, 11 native or naturally regenerating tree species and 5 native shrub species has been recorded in the study site. Diversity thus exists in the canopy as well as in the ground flora.

The numerous rides and rackways also provide many edges where light-demanding species can grow. The light environment within the B - Plan units is very critical in the maintenance of species diversity. Less intensive weeding is a further aspect of the system when compared with clear-felled plantations.

The main focus of this thesis is the ground flora. However, there is evidence of increased faunal interest and diversity under B - Plan. Casual observation of bird species and their populations indicates that there has been an increase in diversity and numbers. Insect populations have also benefitted. One example of this is that a species of woodland butterfly has been recorded for the first time since 1952 (Warren, pers. comm.) in the wood, the Heath Fritillary (Mellicta athalia), which now has the status of probably the most endangered resident butterfly in Britain (Warren et al, 1984). A colony of this species was noted feeding on Rubus agg. flowers in a clearing between Bradford-Hutt units in July, 1985. The previous year's larvae probably fed on the abundant *Melampyrum pratense* growing along the ride and in the relic oak coppice adjoining the units (Warren, pers. comm.).

2.4.4. Increased tree and shrub diversity with related beneficial effects on leaf litter

Birch (*Betula* spp.) and holly (*Ilex aquifolia*) are known soil improvers (Dimbleby, 1952; Dimbleby and Gill, 1955; Miles, 1981). By the nature of the open structure of B - Plan, species such as *Quercus* x *rosacea*, *Sorbus aucuparia*, *Castanea sativa*, *Betula spp.* and *Ilex aquifolia* can grow successfully in and around the B - Plan units. The light-demanding species *Quercus*, *Sorbus* and *Castanea* also thrive. Timber oak stands have been successfully underplanted with B - Plan units. These native species along with *Nothofagus procera* in some of the units, provide a good deciduous addition to the leaf litter and beneficial effects on soil nutrient cycling. This is similar to a coppice wood where many species can be grown together, such as hazel with ash standards (Rackham, 1980a).

2.4.5. Soil protection and improvement

A further aim of B - Plan is to build up and protect the forest soil complex by encouraging a variety of soil improver species in mixture and with constant cover to protect the soil physically, particularly in areas of high rainfall and on steep slopes (Hutt, 1976).

Selection systems are especially favoured on the continent because they prevent erosion (Troup, 1952; Knuchel, 1953; Hiley, 1954; Köstler, 1956; Packham and Harding, 1982). Rapid leaching of soil nutrients after clear-felling has been observed by Bormann and Likens (1979) in eastern North American hardwood stands. In their experimentally clear-felled plots, leaching of soil nutrients, as measured in the solute content of water in the catchment area, was eight times greater than that in an intact forest with a maximum at 2 years after clear-felling. Over the first 2 years, when the site was kept artificially bare, particulate matter content in runoff water was three times greater than the adjacent wooded control site. In the third year, this factor increased to 16 times, suggesting that the mechanism limiting erosion broke down after 2 years. In a clear-felled site, however, the area is usually revegetated in the second year with the consequent water yield in the watershed returning back to normal and minimisation of erosion (Swindel _et_ _al_,1982). Nevertheless, significant loss of nutrients in solute form occurs.

Ternan (pers. comm.) working on erosion and solute loss in market gardens in the Tamar Valley downstream from Tavistock Woodlands, suggests that the soils are not particularly prone to severe erosion. However, soluble nutrient loss is a serious problem and this could be overcome by the adoption of B - Plan rather than clear-cutting on the steep valley sides.

2.4.6. Conservation of nitrogen

Clear-cutting results in increased nitrogen availability (as NO_3-N), which is thought to induce germination of buried seed (Cole and Gessel, 1965; Harper, 1977; Bormann and Likens, 1979). This and the reduction of competition from tree roots results in the sudden burst of vegetation after clear-felling. Bormann and Likens (1979) describe it as a homeostatic mechanism for re-establishing stability after ecosystem disturbance. However, it costs the ecosystem in loss of the 'capital' necessary for future wood production. This is analogous to fertilizing a new plantation, as Tamm (1974) demonstrated with the enhancement of raspberry growth, a species frequently colonizing a clear-cut stand.

> "Even with revegetation, nutrient leakage occurs which suggests that the rapid increase in productivity is inefficient and is costly in terms of nutrient and biomass storage within the ecosystem, but this sacrifice of efficiency might be an effective strategy of ecosystem stability, because it stops greater sacrifice in biotic regulation of erosion" (Bormann and Likens, 1979: p. 161).

Under B - Plan, this sacrifice is reduced and the forest ecosystem can put the nutrient energy into tree growth.

2.4.7. Improved fungal associations

In describing the beneficial effects new regeneration has on an old and deteriorating even-aged stand, Ammon in his "Das Plenterprinzip in der Waldwirtschaft" (1937) (translated by Reade, 1969) observes:

> "It is obvious, in fact, that old trees and young growth have a biological need for one another, in a manner that the exponents of even-aged working and clear-felling are unwilling to accept or recognise" (p. 210).

Recent mycorrhizal research has shown that ectomycorrhizal mycelial strands connecting plants together through their root systems may act as pathways for the transfer of nutrients and water (Reid and Woods, 1969; Whittingham and Read, 1982; Brownlee _et al._, 1983). Seedlings growing under low light intensities could then rely on the mature trees, with their leaves in full sunlight, for sustenance. Working on _Pinus sylvestris_ seedlings, Brownlee _et al._ (1983) suggest that:

> "... since mycelial strands provide for inter-plant distribution of nutrient and water it is necessary to re-assess the pattern of nutrient acquisition and cycling in forest ecosystems. Clearly plants in such systems do not occur as individuals but as part of an inter-connected system through which nutrients flow along concentration gradients both at the intra and interspecific levels. The significance of these inter-connections for seedling survival and plant productivity is currently being examined" (p. 442).

Such inter-connections under selection systems such as B - Plan may play an important role in productivity and ecological stability.

2.4.8. Pest and disease control

Another claim for B - Plan is:

> "... to encourage a stable ecological balance with a varied flora and fauna ... achieving a considerable pest and disease control" (Hutt, 1975: p. 20).

Vasecho (1983) suggests that increasing the stability of the forest ecosystem is an alternative to chemical and biological pest control in forests. He proposes creating a multistorey forest formation of mixed species, leaving small reserves of old trees. Since 1935, spruce forests in the Belgian Ardennes have been in the process of being transformed into mixed species woodland with irregular canopies to increase resistance to insect attack, as well as to improve site ecology (Roisin, 1959). B - Plan creates this many-layered, mixed forest.

2.5. General conservation advantages of B - Plan

Peterken (1981) suggested 15 principles for nature conservation in woodlands, several of which are fulfilled by B - Plan. The principles particularly relevant to the Tavistock Woodlands and B - Plan are as follows:

2.5.1. Minimise rates of change within woods

Peterken proposed that plants which are slow colonizers and hence more extinction-prone should be favoured by creating distinct age classes spatially, so that the habitats are constantly available for 'point to point' colonization. B - Plan mimics the traditional coppice light pattern and thus allows the ground flora species to follow the cycle of disturbance and open ground in the B - Plan units. Species have time to adapt or to re-establish themselves in more suitable niches within the wood. Many of the species still present in the wood are those of the upland pedunculate oak assemblage (Peterken, 1981) which were present before the wood was coniferised (Figure 1.5.). There are many former coppicing species there as well. The greater part of the woods at Blanchdown and Grenoven were probably ancient woodland which was converted to coppice and then subsequently to even-aged plantation (Hamilton, pers. comm.) (Figures 1.5. and 1.6.). In the sense that these sites have always been wooded, albeit now with conifers, they could be considered as a form of primary woodlands (Rackham, 1980a; Peterken, 1981).

Using recent Nature Conservancy Council definitions (Kirby _et al._, 1984), they would be classified as 'plantations on ancient sites' second only in conservation value to the 'ancient semi-natural woodland' of the remaining oak coppice in Blanchdown and Grenoven (Figure 1.5.). Irregular working, selective felling or, if possible, traditional coppicing has been recommended for the latter by the Forestry Commission in their consultative paper on broadleaves (Forestry Commission, 1984).

An interesting aspect of the present implementation of B - Plan in these woods is that the new woodland structure may enable some species of the former oak coppice to survive, despite coniferization.

Rides also act as reserves of species (Crowe, 1978; Peterken, 1981). In Tavistock Woodlands, most of the rides have remained unchanged for many hundreds of years (Hamilton, pers. comm.). B - Plan has the additional advantage of providing permanent rackways where many light-demanding species can survive.

2.5.2. Encourage maturity by maintaining long rotations

Where it is not possible to grow trees on a long rotation, Peterken (1981) suggests retaining a scatter of old trees to encourage hole-nesting birds and wood-eating invertebrates. Many invertebrates are threatened with extinction and 972 different species are associated with dead and dying wood especially under the bark (Stubbs, 1972).

The economics of modern forestry mean that the trees in the Tavistock Woodlands must be harvested when they reach what a forester considers to be maturity (financial maturity), but well before what a conservationist would consider to be maturity (several hundred years). The estate policy of leaving old oak stands, especially on steep river banks, where it tends to be uneconomic to grow conifers, and of allowing the lop, top and brashings to remain in the woods ameliorates this problem to some extent. This wood not only provides niches for fungi and invertebrates, but also provides a substrate for nitrogen fixing bacteria (Bormann and Likens, 1979). Leaving dead timber in the wood is not enough, it needs the moisture and shade provided by a continuous canopy such as that under B - Plan to begin the decay process because timber exposed to the sun becomes heat-sterilised (Stubbs, 1972).

2.5.3. Encourage diversity of structure of tree and shrub species and of habitat

As described in Sections 2.4.2 and 2.4.3., B - Plan provides structural and habitat diversity. A diversity of both native and exotic tree and shrub species have been planted, resulting in significant ecological benefits.

2.5.4. Maintain or restore traditional management where this is possible and appropriate

Systems based on coppicing and natural regeneration are normally advantageous (Peterken, 1981). B - Plan shows similarities to traditional coppice management with the resulting benefits of a varied light environment in relation to the 54 year cycle. Also the system enables the forester to take advantage of any natural regeneration where it is appropriate.

2.5.5. When traditional management is not possible use conservation-conscious management systems and maintain species native to the site

Selective forestry management is conservation-conscious. After 22 years of B - Plan coniferous forestry, many species native to the site appear to be thriving (Wigston, 1976), particularly on the edges of units and rackways where they remain relatively undisturbed by management.

2.6. Aims and objectives

At the start of this project, the Bradford Plan had been in operation in the Tavistock Woodlands for 20 years, with the oldest sub-units entering the fourth and subsequently the fifth stages. The overall aim of the thesis was to examine various aspects of the ground flora under these early stages of implementation of B - Plan. Within this, four distinct objectives emerged:

a) Determination of the floristic composition of the ground flora under B - Plan stages I - V and comparison of this with adjacent areas of clear-fell forestry.

b) Examination of the environmental controls affecting floristic composition under early B - Plan and in particular to study light as an ecological factor.

c) Since most of the sites in the Tavistock Woodlands had always been under woodland, although this was not coniferous, study of the seed banks, to find out if species of the former deciduous oak coppice were still present and to look for similarities and differences between the composition of the seed bank and the present-day ground flora.

d) Analysis of certain aspects of the phenology of ground flora species under B - Plan, with the aim of determining the timing and relative abundance of certain critical species and seeing how they responded to Bradford Plan management.

2.6.1. Determination of the floristic composition of the ground flora under B - Plan stages I - V and comparison with adjacent areas of clear-fell forestry

The primary aim of the project was to complete a phytosociological survey of the early stages of B - Plan in the Tavistock Woodlands. It was necessary to define the plant communities present at each stage and also to examine similarities and differences with adjacent areas of clear-fell forestry. A further important aspect was to see if the various stages of succession which occur after clear-felling were replicated within the small sub-units of each $324m^2$ Bradford plan unit.

Another reason for defining and recognising the ground flora communities at this stage was to provide a baseline study which will provide information for future research when B - Plan reaches maturity.

Finally, from the conservation standpoint, a detailed survey of the ground flora will provide information on key ecological variables, such as the relative diversity of plant species under B - Plan and also any possibly rare or uncommon species.

2.6.2. Examination of environmental controls and in particular the light environment

Early reconnaissance indicated that the primary gradient affecting the species composition of the ground flora was probably the quality and quantity of light reaching the forest floor under B - Plan. Also, one of the major claims of B - Plan is that the replicated spiral structure allows light to penetrate through to ground level at regular intervals throughout the woodland. Accurate quantification of relative light intensities was thus seen as a very important objective.

2.6.3. Seed Bank studies

Most of the Tavistock Woodlands were formerly composed of oak coppice with a typical associated ground flora. Conversion to conifers has occurred largely in the present century, and areas of the former oak coppice still remain on the steepest slopes (Figure 1.6.). Several interesting questions and ideas arose in relation to the seed banks under the B - Plan system. Firstly, were the species now in the seed bank the same as those in the ground flora? Secondly, were any of the former oak coppice species not present in the ground flora still present in the seed bank? Thirdly, the past management history of Tavistock Woodlands will be reflected in the seed bank, including the past 20 years of B - Plan. Therefore, the results may have predictive value for future diversity under this management system. Fourthly, a study of plant response through the seed bank under B - Plan could be the basis for certain value judgments about the potential of this management system for conservation. Finally, few forest or woodland seed banks have been studied and thus examination of the content of the seed bank would be of wider interest in terms of woodlands in southwest England.

2.6.4. Analysis of certain aspects of the phenology of the ground flora

B - Plan provides a very different environment for ground flora species when compared to deciduous oak coppice or clear-fell coniferous forestry, particularly in terms of light. Under a deciduous canopy, many of the herbs are vernal or autumn light phase species (Curtis, 1959; Auclair and Goff, 1971; Mahall and Bormann, 1978). Under B - Plan, a variety of phenological strategies would be expected in response to the environmental heterogeneity inherent in the system and to the Bradford Plan management practices. For this reason selected phenological attributes of a number of critical species were studied in some depth.

Through a synthesis of these four objectives, the prime aim of the thesis, an evaluation of the ecological and conservation interest of the ground flora under B - Plan was achieved.

CHAPTER 3. PROJECT DESIGN AND FIELDWORK

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3.1. Project design

The study was completed in several stages allowing 'successive refinement' of the methods (Cain and Castro, 1959; Gauch, 1982):

1) Reconnaissance
2) Pilot study - phase I - 50 random quadrats for canopy, ground flora and soil variables.
3) Main survey - phase II - 20 quadrats to examine the effects of B - Plan on the ground flora and the effects of canopy closure - moosehorn measurements.
4) Main survey - phase III - shrub survey in 17 of the 20 quadrats at phase II - second soil survey to check soil variation - re-check of ground flora in 19 quadrats of phase II.
5) Detailed studies - phase IV - the light, seed bank and phenological surveys in eight selected quadrats from phases II and III.

Adopting this five-stage approach provided time in which to develop hypotheses and to experiment with and develop research techniques. The approach also supplied information on which to base the later more detailed surveys (Gauch, 1982).

3.2. Reconnaissance

The original reconnaissance was completed in 1977 and 1978. After interviewing the chief forester, Philip Hutt, examining the estate records, and touring the estate, the study sites were chosen. The adjoining woods of Blanchdown, Grenoven and Hangingcliff were selected as they provided a representative variety of canopy types, site conditions and past histories (Figures 1.4. and 3.1.). They

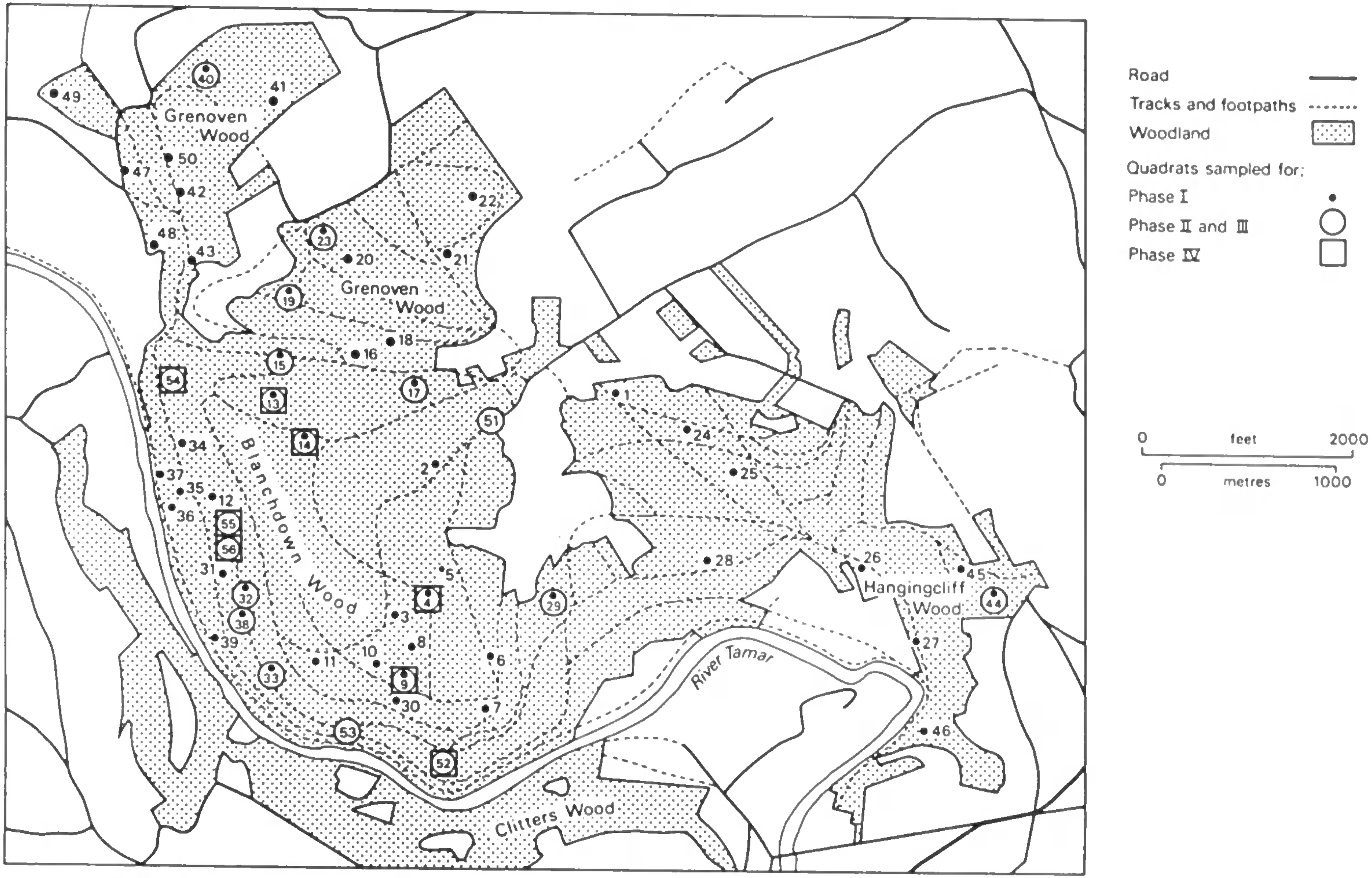


Figure 3.1. Location of quadrats in Blanchdown, Grenoven and Hangingcliff Woods

also contained the earliest B - Plan sub-units. These woods were easily accessible and conveniently close to the estate office and sawmill.

After viewing the woods, it was decided that to adequately sample the differing canopies and the diversity of the site, an initial survey based on randomly placed quadrats would be necessary.

3.3. Pilot study - phase I

3.3.1. Phase I - location of 50 random quadrats

The aim of this first phase was to characterize the overall variation in the canopy types and the ground flora and to gain information about the effect of B - Plan on the ground flora.

Fifty quadrats were located using random co-ordinates to eliminate any bias in their selection (Mueller-Dombois and Ellenberg, 1974; Gauch, 1982). The entire area was sampled which included a variety of site conditions such as areas of mining disturbance. (Figure 3.1.) A grid of numbers was superimposed on the 1953 Ordnance Survey 1 : 2500 maps and random numbers were selected to provide co-ordinates for 50 points. These were located on the ground by pacing from ride intersections. Quadrats were then permanently marked because they were to be visited many times especially during the later phenological survey (Greig-Smith, 1983). Stakes 1.45 m in height were hammered into the ground at the intersection of the random co-ordinates. This served as the lower left hand corner of the quadrat, with the remaining three corners of the 20 x 20m quadrat being located upslope and to the right of that point. These three corners were staked with one metre high stakes, which were painted red for ease of visibility in the dense vegetation. The quadrat was sited exactly parallel to the maximum site slope using a clinometer, ranging poles and a 20 m measuring tape. The second and third corner stakes were sited at right angles to the first stake using a right angle prism, ranging poles and measuring tapes.

Quadrat shape and size

Plotless sampling, which assumes a random distribution (Greig-Smith, 1983) is not suitable for plantations. Square plots are historically preferred in European plant ecology (Mueller-Dombois and Ellenberg, 1974), although a rectangular plot with the main axis running against any gradient such as a contour has been recommended as more accurate for sampling (Bormann, 1953; Ohmann, 1973). In Bormann's (1953) study of plot size and shape in forests, the variance for a 400m^2 quadrat was found to be equal to that for rectangular plots of the same area (4 x 100m or 10 x 40m).

> " ... but in some situations the modest gain in accuracy compared to a square may not be justified if a square is more convenient or leads to data more comparable with those of existent studies of interest." (Gauch, 1982: p. 57)

A square had the advantage of relating to the shape of B - Plan units - 324m^2 (18 x 18m). The 400m^2 (20 x 20m) area chosen was thus large enough to contain a complete B - Plan unit, if necessary. Mueller-Dombois and Ellenberg, (1974) give 200m^2 as a typical quadrat size for North American mixed deciduous forests, although other woodland studies have used quadrats within the range of 200 to 800m^2. (Westhoff and van der Maarel, 1978.) A square was also more convenient to use because some areas of the study site were dissected by rides, leats and other mining features. A long narrow rectangle would have been more difficult to locate within these areas, in addition to creating edge effect problems with a longer perimeter.

3.3.2. Phase I - tree survey - 1977-78

During the winter of 1977-78 the trees within each of the 50 randomly located quadrats were surveyed by recording species, height and diameter at breast height - 1.5 metres (Mueller-Dombois and Ellenberg, 1974). Height is an indicator of dominance in forestry management, while basal area is an ecological measure of dominance used particularly in North American studies (Curtis, 1959; Mueller-Dombois and Ellenberg, 1974). A Haga tree altimeter was used to record height. Diameter at breast height was measured using a diameter tape graduated in centimetre intervals. Sketch maps were also made of each quadrat with the precise measured location of any special feature and in particular B - Plan units. Finally, slope angle and aspect were measured in each quadrat.

Definition of trees and shrubs

The nature and definition of trees and shrubs in a woodland community depends on many factors. Thus definitive height limits cannot always be chosen in advance (Mueller-Dombois and Ellenberg, 1974). This first tree survey was based on two commonly used criteria for separating trees from the sapling and shrub layers:

a) those individuals capable of reaching the canopy;

b) trees having a diameter at breast height greater than or equal to five centimetres (Bunce, 1982).

The broad age classes of trees, seedling, sapling, mature and over-mature (Chapman, 1976; Kershaw and Looney, 1985) are applicable in 'natural' woodlands but are of limited value in commercially managed woods. In the Tavistock Woodlands Estate, practices such as six-yearly clearing for new sub-units, weeding during the first two years after the establishment of a sub-unit, and extraction through the rackways meant that vegetation levels below the canopy are not continuous in height from seedlings to high canopy (Plate 3.1.). Instead the trees in the B - Plan units follow a size continuum, but the naturally

Plate 3.1. Clearing and weeding beneath a *Pseudotsuga menziesii* canopy

regenerated trees usually do not. When these naturally regenerated trees reach a size over about five metres in height, they tend to interfere with the management operations and are cut back. There are exceptions to this, particularly along the rides, at the edges of rackways and in odd corners between units, but generally the shrub layer is less than two metres in height and the naturally regenerated trees are in the two to five metre height range. The result of this cutting is that much of the secondary natural regrowth is in the form of resprouts from stools.

The lower growing trees and saplings could not be reliably aged, because the stool of a Betula or a Quercus may be many years old. The relatively short and numerous stems may be recent regrowth (Harper, 1977). These stools, although short, could be classified as trees. They have a similar ecological effect on the ground flora because of a well-developed mature root system and a dry matter weight of leaves and stems comparable to a much taller single-stemmed sapling.

There is disagreement in the literature on the criteria for separating the various layers of the under and over-storey. Mueller-Dombois and Ellenberg (1974) suggest that the common height divisions in forest communities are:

Trees - individuals greater than five metres

Shrubs - individuals between 50 centimetres and five metres.

However they cite other studies, for example, Daubenmire (1968), which include saplings with trees as those individuals greater than one metre in height. Other authors adapt size criteria to suit the aims of their study. For example:

Trees - individuals greater than or equal to four inches diameter at breast height.
Saplings - individuals less than four inches and greater than or equal to one inch diameter at breast height.
(Monk, 1967)

Shrubs - all woody plants less than 3.6 metres in height. (Bormann and Buell, 1964)

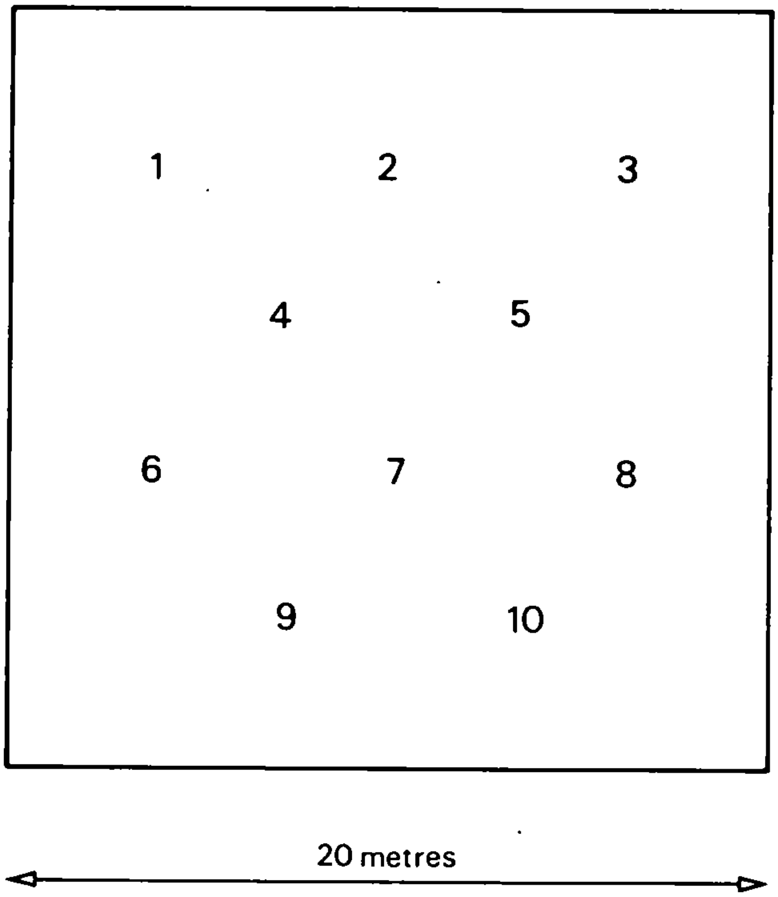
Trees - individuals greater than 2.54 centimetres in diameter at breast height. (Ohmann, 1973)

One aim of this study is to determine the effect of all the components of the B - Plan management system on the ground flora. Naturally regenerated vegetation is a significant component of B - Plan structure. Hence in phase III of this study, when only 17 quadrats were examined in great detail, all those individuals greater than five metres in height were considered as trees. This change, which then included the shorter, naturally regenerating trees in a tree survey, resulted in a clearer representation of the vertical structure of the woodland under B - Plan management. Occasionally this meant the inclusion of a species with the trees such as Corylus avellana or Sambucus niger, which Bunce (1982) considers to be a shrub. However, it was felt that these contribute significantly to the influence of the canopy over the herb layer and particularly to the light environment.

3.3.3. Phase I - ground flora study - 1979

The aim of the phase I ground flora study in 1979, in which each of the 50 random quadrats was examined, was to provide base-line information about overall variation under the different canopies on the estate. Subsequent, more detailed work and the sampling design in phases II and III were also based on these 1979 results.

During the 1979 growing season, the $400m^2$ quadrats were sub-sampled using ten $1m^2$ sub-quadrats. The location of these were marked permanently with small red stakes in equally spaced rows of three-two - three-two across the slope (Figure 3.2.). This systematic sub-sampling was adopted because it is less time consuming (Greig-Smith,



number = sub-quadrat location

Figure 3.2. Location of sub-quadrats within 400m^2 quadrat for phase I ground flora survey - 1979

1983). To facilitate replicate sampling, the $1m^2$ sub-quadrat was aligned parallel to the side of the large $400m^2$ quadrat using a compass. The lower left hand corner of the metal quadrat was placed at each red peg (Plate 3.2.).

Initially a collapsible aluminium dexion quadrat with legs and with a grid of one hundred $100cm^2$ divisions was used. These divisions tended to crush the vegetation, so sliding rods were employed, although this added to the sampling time. The extra accuracy gained in the cover estimates was not justified by the considerable time lost, and the decision was made that more less accurate quadrats are of greater value than fewer more accurate ones (Gauch, 1982).

Data for terrestrial vegetation are collected at an "intermediate level of accuracy of one digit estimates" (Gauch, 1982: p. 51). Presence and absence data were judged sufficient for this phase I pilot study, with cover estimates being used later in the main more detailed phase II and III studies.

The quadrats were visited twice in 1979, once during the late spring and again during the early autumn when any additional species were recorded. Bryophytes as well as vascular plants were recorded. Observations were also made on soil disturbance, current forestry operations, brash, rotting logs and litter.

3.3.4. Phase I - first soil survey - 1979

During April 1979, a preliminary soil survey was conducted on the first 50 quadrats. A pit was excavated at each sampling point and the litter depth (L) and the humus depth (F and H) were recorded. Four points per quadrat were located halfway between each corner post. A soil auger was used to obtain a relative measure of the total soil depth to the bottom of the C horizon. Any soil depth greater than the depth of the auger was noted (63 centimetres).

Plate 3.2. Red pegs marking sub-quadrat locations

A sample from the A horizon and one from the B horizon for each of the four sampling points was analysed for pH (400 samples). Samples were stored overnight in a cold room at 4°C to lessen the likelihood of any chemical changes due to heightened bacteriological or fungal activity. The pH was measured with an EIL 7050 meter (Electronic Instruments Ltd.). The pH meter was buffered at both 4 and 7 although the expected pH was to be around 4 (Smith and Atkinson, 1975). A solution of soil to distilled water - 1 to 2.5 - was mixed and stirred regularly for 15 minutes (Smith and Atkinson, 1975). The sample was then gently agitated with the electrode until the reading had stabilised (Kent et al, 1981).

Soil moisture samples of the B horizon were taken and analysed using the gravimetric method (Smith and Atkinson, 1975). Soil moisture was expressed as an average of the percent loss for the four samples per quadrat.

3.4. Phase II - survey of the effects of B - Plan on the ground flora - 1981 - Main survey

3.4.1. The ground flora survey

This survey involved 20 quadrats whose choice was based on the results of the phase I survey of both the trees and the ground flora, as well as on historical information. Of the 20 quadrats, 14 were chosen from the original 50 in phase I because they contained B - Plan units of varying ages (Table 3.1.). The remaining six were new ones included for comparative purposes to enable the effects of B - Plan to be separated from those of the previous major canopy types. These six were chosen subjectively. The locations of the quadrats are shown in Figure 3.1.

Table 3.1. Final 20 quadrats selected for phases II and III

Quadrat No.*	Major Canopy Type (based on dominant planted species)	B - Plan Stage (completed)	Special Considerations
29	*Pinus* spp.	I	Later omitted - trees and ground flora affected by mine waste runoff
4		II	
9		III	
15	*Larix* spp. and *Pinus* spp. or *Larix* spp.	IV	Stages IV and V are the same age - a double sub-unit was cleared for more light
23		V	
13		V	
17	*Picea sitchensis* or *Picea abies*	V	*Picea abies*
14		III	*Picea sitchensis* After 1979 Stage IV planted
40	*Quercus* x *rosacea*	I	Planted oak
54		IV	Planted oak
53		No B - Plan	Timber stand
33	*Quercus* x *rosacea* with some planted *Fagus sylvatica*	No B - Plan	Oak coppice with standards
52		No B - Plan	Oak coppice with standards
51	*Fagus sylvatica*	I	Failed B - Plan with *Larix* spp.
19	Mixed Conifers	New Plantation No B - Plan	New Plantation clear-felled area
44	*Pseudotsuga menziesii*	III	Rabbit damage to plantings
55		IV	
56		IV	
32	No canopy	No B - Plan	*Quercus* and *Fagus* cleared 1979
38		No B - Plan	*Nothofagus* plantation

* Quadrat numbers underlined are the six new quadrats

> "A workable approach, if the terrain allows, is to record stands initially by a scheme stratifying ... if appropriate and then add any stands that appear to be different from those already recorded." (Greig-Smith, 1983: p. 306)

Preferential sampling is used most frequently by plant ecologists (Poore, 1962; Goldsmith and Harrison, 1976) and as suggested by Gauch (1982) this can cause bias. However, when the data are analysed using multivariate analysis for descriptive purposes, preferential sampling is acceptable (Crovello, 1970).

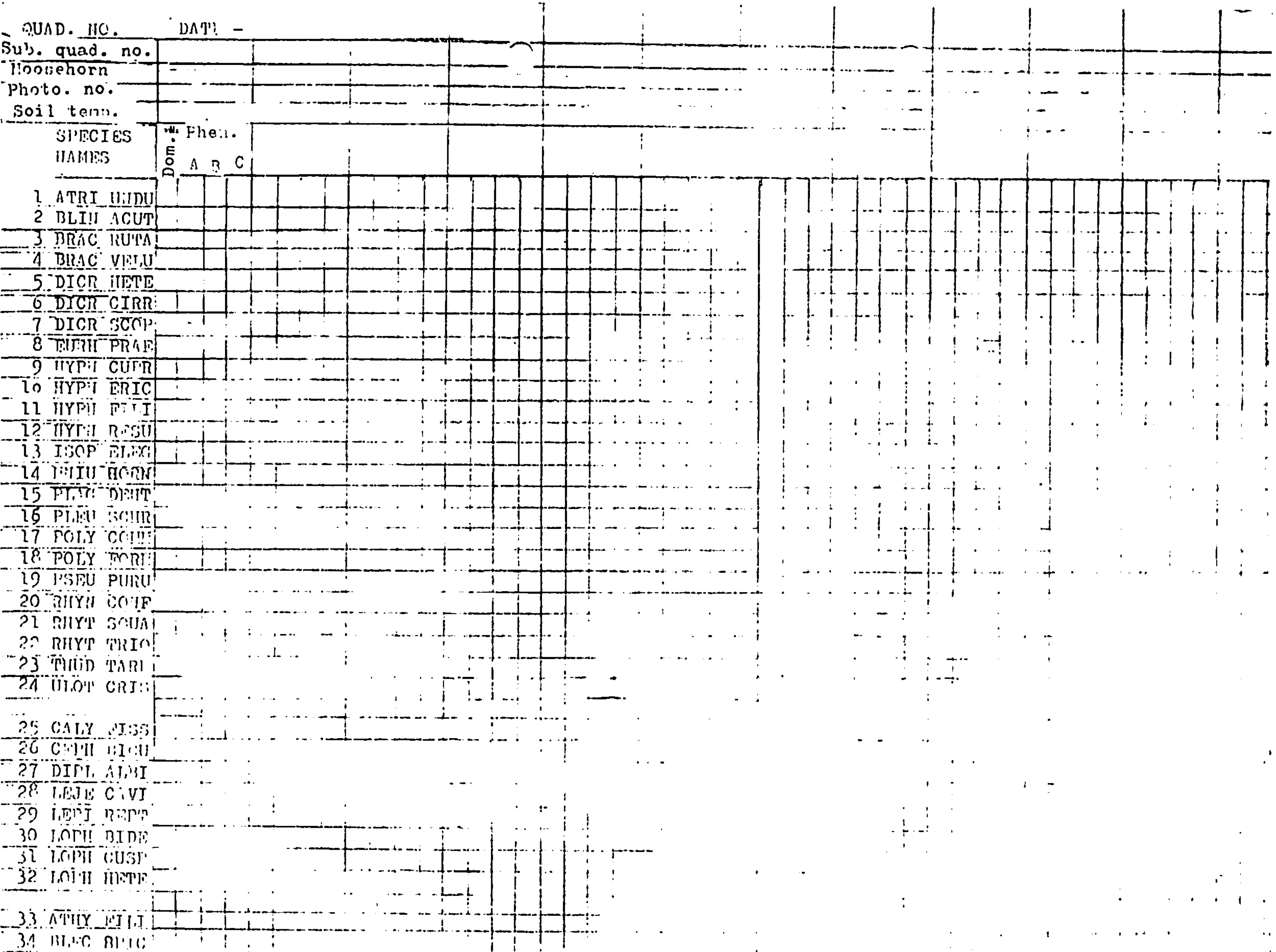
To reduce sampling time and simplify recording, duplicated recording sheets were produced with all the species expected to occur in these 20 quadrats (Figure 3.3a-d).

In the phase I ground flora survey, some areas were over-sampled, particularly those quadrats without B - Plan and with a uniform canopy and a resultant uniform ground flora. The B - Plan quadrats needed more selective samples.

> "If elucidation of correlations between vegetation and environment is the primary objective, stands should, as far as possible, include all variants of vegetation and an equal representation of all variants."
> (Greig-Smith, 1983: p. 305)

Hence in the new sampling scheme for phase II, the number of sub-quadrats was allowed to vary. In those quadrats without B - Plan, eight sub-quadrats were sited (Figure 3.4a), one at each corner and one at the midpoint of each side, each being marked with a small red peg. In the quadrats containing B - Plan, the first eight sub-quadrats were sited as in Figure 3.4a. However, in addition, two further sub-quadrats were placed within each B - Plan sub-unit, including those recently cleared but not yet planted (Figure 3.4b). The number of sub-quadrats then varied between 8 and 18. A total of 244 sub-quadrats were thus sited within the 20 main quadrats.

During phase I, handling a $1m^2$ quadrat proved difficult because the area in the centre proved impossible to examine without crushing



QUAD. NO. DATE -

Sub. quad. no.

Moosehorn

Photo. no.

Soil temp.

SPECIES NAMES	Dom.	Phen. A	B	C
1 ATRI UNDU				
2 BLIN ACUT				
3 BRAC RUTA				
4 BRAC VELU				
5 DICR HETE				
6 DICR CIRR				
7 DICR SCOP				
8 EURH PRAE				
9 HYPN CUPR				
10 HYPN ERIC				
11 HYPN FILI				
12 HYPN RESU				
13 ISOP ELEG				
14 MNIU HORN				
15 PLAG DENT				
16 PLEU SCHR				
17 POLY COMM				
18 POLY FORM				
19 PSEU PURU				
20 RHYN CONF				
21 RHYT SQUA				
22 RHYT TRIQ				
23 THUD TAMA				
24 ULOT CRIS				
25 CALY FISS				
26 CEPH BICU				
27 DIPL ALBI				
28 LEJE CAVI				
29 LEPI REPT				
30 LOPH BIDE				
31 LOPH CUSP				
32 LOPH HETE				
33 ATHY FILI				
34 BLEC SPIC				

Figure 3.3.a-d Recording sheets

QUAD. NO. DATE –

subquad. no.

[illegible]

photo no.

[illegible]

SPECIES NAMES	Dom.	Phen. A	B	C
36DRYO FILI				
37PTER AQUI				
[illegible]				
38[illegible]				
39CALL VULG				
40CARE PILU				
41CHAM ANGU				
42DIGI PURP				
43EPIL ROSE				
44GALI SAXA				
45HEDE HELI				
46HYPE PULC				
47JUNC EFFU				
48LONI PERI				
49LUZU PILO				
50LUZU SYLV				
51MELA PRAT				
52OXAL ACET				
53POTE EREC				
54RUBU FRUT				
55RUME CRIS				
56SARO SCOP				
57SOLI VIRG				
58TEUC SCOR				
59ULEX GALL				
60VACC MYRT				
61VERO OFFI				
62VIOL RIVI				
63AGRO GIGA				
64AGRO CAPI				
65DACT GLOM				
66DESC CAES				
67DESC FLEX				
68FEST RUBR				
69FEST TENU				

QUAD. NO. DATE -

Sub. quad. no.

Moonehorn

Photo. no.

Soil temp.

SPECIES NAMES

Dom. Phen. A B C

71 HOLC MOLL
72 MOLI CAER
73 POA ANNUA
74 POA NEMOR
75 ACER PSEU
76 BETU SPP.
77 CARP BETU
78 CAST SATI
79 CORY AVEL
80 CRAT MONO
81 FRAN ALNU
82 FRAX EXCE
83 ILEX AQUI
84 PRUN AVIU
85 PRUN SPIN
86 QUER CERR
87 RHOD PONT
88 SALI CINE
89 SORB ACUP
90 VIBU OPUL
91
91 FAGU SYLV
92 LARI DECI
93 LARI EURO
94 LARI KAEM
95 NOTH PROC
96 QUER X RO
97 ABIE ALBA
98 PICE ABIE
99 PICE SITC
100 PINU NIGR
101 PINU RADI
102 PINU SYLV
103 PSEU MENS
104 SEQU SEMP

QUAD. NO. DAT -

b quad. no.

ehorn

o. no.

oil temp

SPECIES NAMES	Dom.	Phen. A	B	C
06 TSUG HETE				
07 BARE SOIL				
08 BRAS LOOS				
09 ROTT STUM				
10 ROCK STON				
11 DEAD CONI				
12 POLY AURA				
13 CALY MUEL				

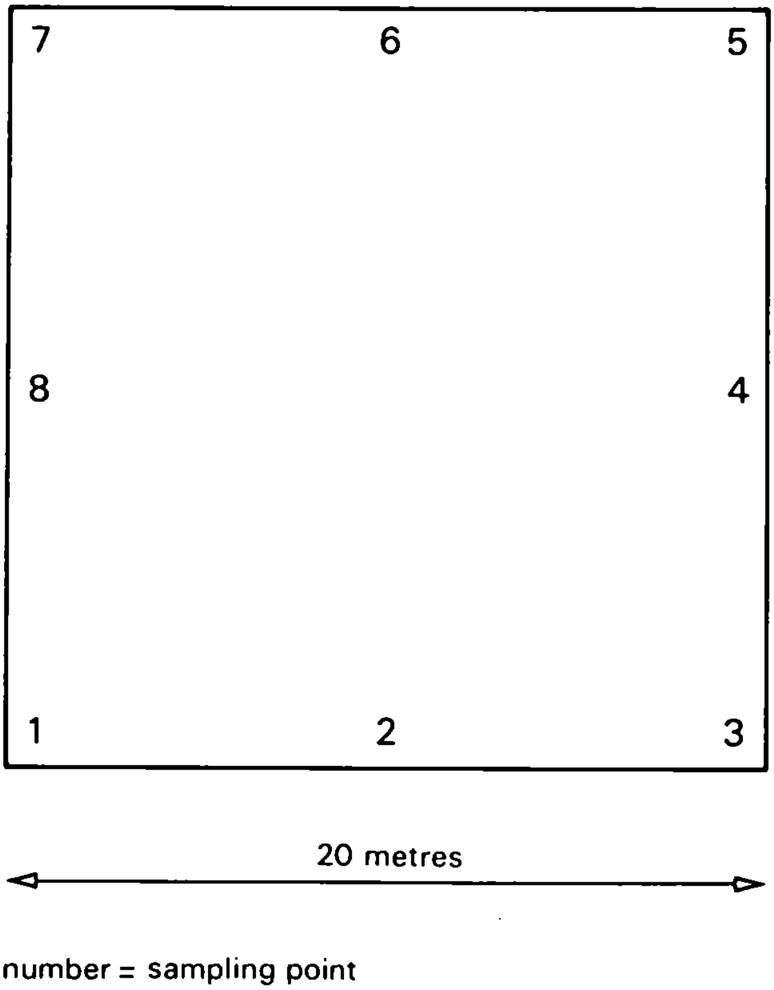


Figure 3.4a. Location of sub-quadrats within a 400m^2 quadrat without B - Plan sub-units for phases II, III and IV

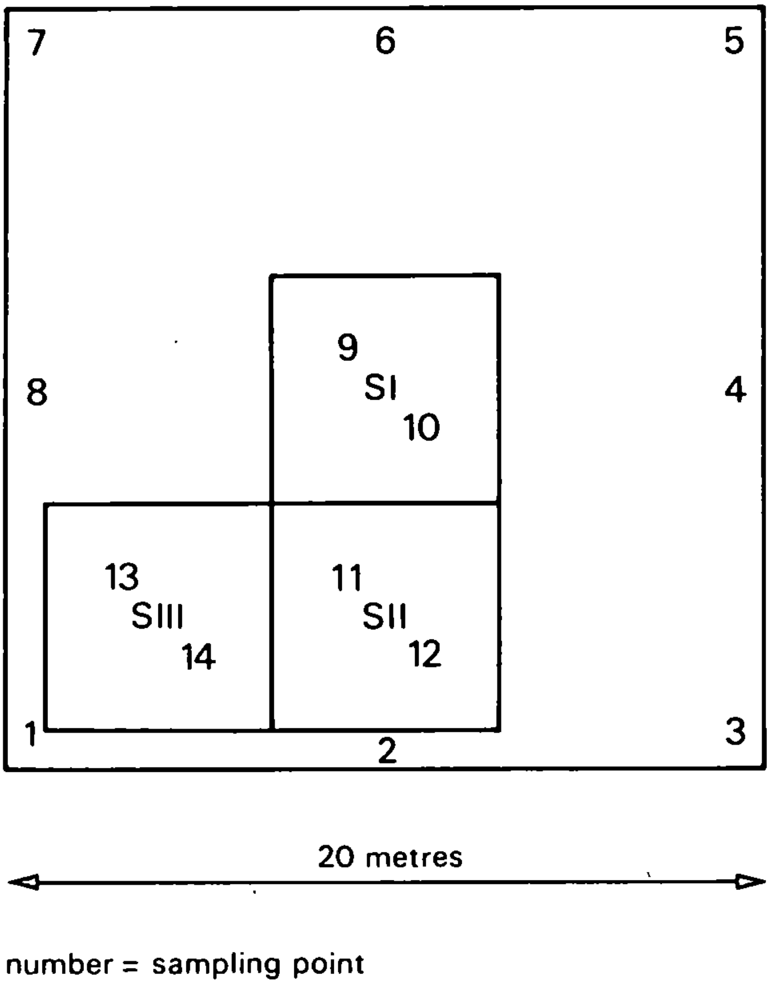


Figure 3.4b. Location of sub-quadrats within a $400m^2$ quadrat containing B - Plan sub-units for phases II, III and IV

the plants around the edge. Thus in phase II, a half-metre squared rectangular quadrat of aluminium dexion was employed (Plate 3.3.). Greig-Smith (1983) suggests that a rectangular quadrat avoids trampling and a larger number of smaller samples will give a better overall description of variation in the vegetation (Green, 1979).

3.4.2. Measures of abundance

> "The additional effort required for a visual estimate of abundance instead of a record of mere presence is (often) small ... This small effort produces more informative data, suitable for a greater variety of purposes." (Gauch, 1982: p. 52)

Although errors are made in visual estimation, generally the overall variability or noise in a sample is greater than that attributable to visual error, (Brown, 1954; Orloci, 1978). In comparing visual cover estimates with the data obtained from a point-quadrat frame, Sykes *et al.*, (1983) found that:

> "For most taxa considered here, (woodland ground flora species), the 90% confidence interval for an observer drawn at random spans a range of approximately + or - 10-20% cover of the mean value; the corresponding range for an observer repeating an estimate a few days later on the same quadrat is approximately + or - 5-15%. There is thus a worthwhile gain in precision from the use of a single observer." (Sykes *et al.*, 1983: p. 449)

Smartt *et al.*, (1974) found that frequency data were sufficiently similar to presence and absence data not to justify the extra time spent on collections while percentage cover estimates correlated well with weighted biomass. Some measure of abundance approximating to biomass is favoured by most ecologists (Smartt *et al.*, 1974). Direct estimates of cover using pin frames were too difficult and time-consuming especially in the densely vegetated areas. However, any extra accuracy gained would be lost in the analysis since results from multivariate analysis are not affected by difference in the data finer than those of a range between 0 and 10 (Hill, 1977; van der Maarel, 1979; Gauch, 1982).

Plate 3.3. Sampling quadrat used in phases II - IV

The Domin-Krajina cover-abundance estimation scale (Table 3.2.), which combines cover with abundance (Sykes et al, 1983) fulfilled the requirements for a measure of cover. Its applicability in forest communities is well proven (Mueller-Dombois and Ellenberg, 1974).

Table 3.2. The Domin-Krajina scale

		%
10	=	100%
9		75%
8	-	50 - 75%
7	-	33 - 50%
6	-	25 - 33%
5	-	10 - 25%
4	-	5 - 10%
3	-	1 - 5%
2		1%
1	-	seldom
+	-	solitary

3.4.3. Measurement of canopy closure - moosehorn measurements

In an effort to satisfy part of the second aim of this project, the quantification of environmental controls and in particular light, and to separate their effects from those of management and past history, a measure of canopy closure was made during this phase II survey in 1981. The degree of canopy closure controls the light climate on the ground. One of the primary effects of B - Plan appears to be its production of various sized openings in the canopy. A moosehorn canopy sampler was constructed and tested in the field (Plate 3.4.). (Garrison, 1949; Morrison and Yarranton, 1970). The grid inside the canopy sampler is divided into 100 sections and percentage cover is calculated by simply counting the number of squares in which canopy vegetation appears. A comparison of the moosehorn results with those of a sample light meter (Figure 3.5a and b), shows that although the

Plate 3.4. Moosehorn canopy sampler

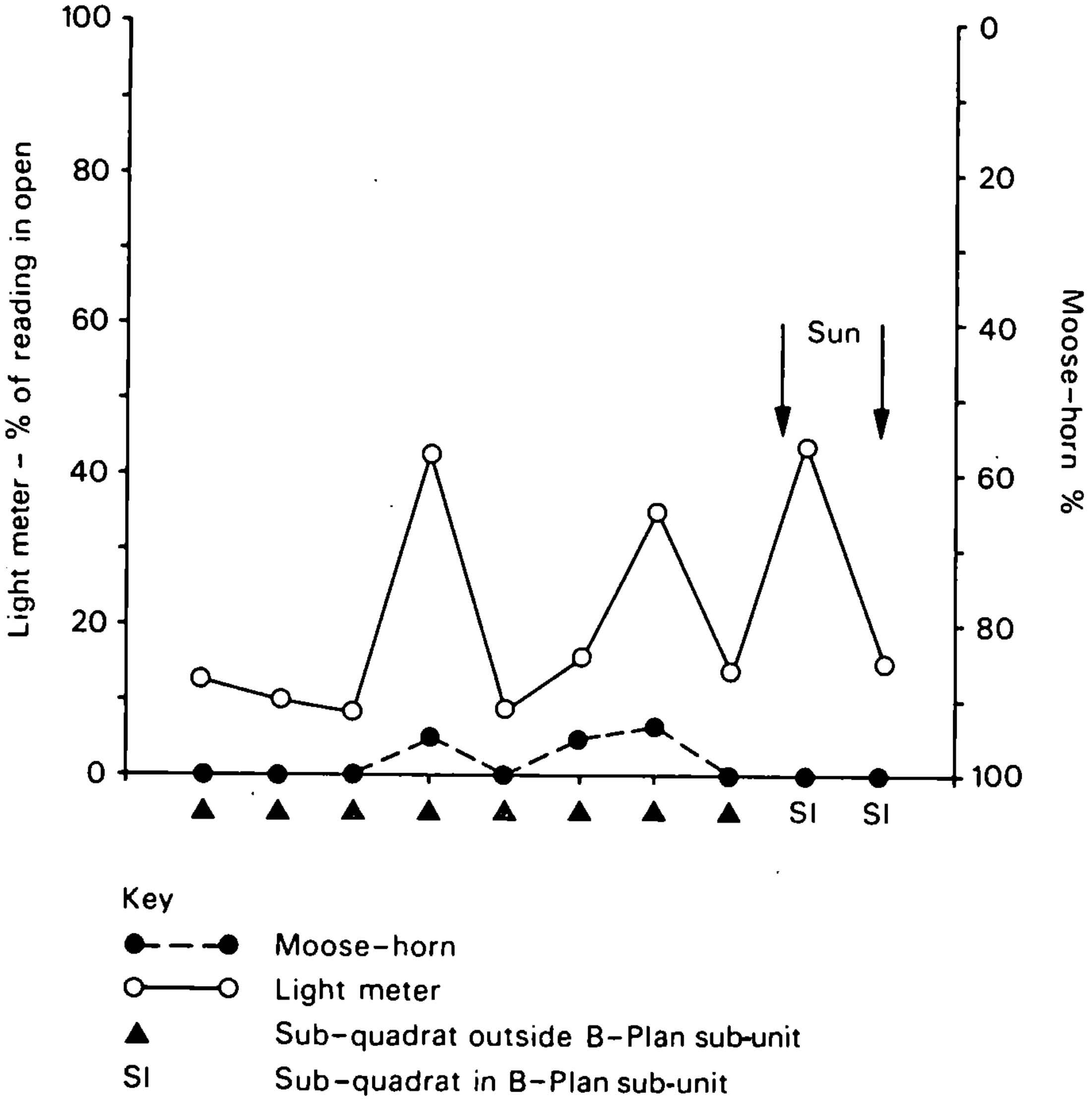


Figure 3.5a. Moosehorn readings compared to light meter readings under a *Fagus sylvatica* with *Larix* spp. canopy - quadrat 51

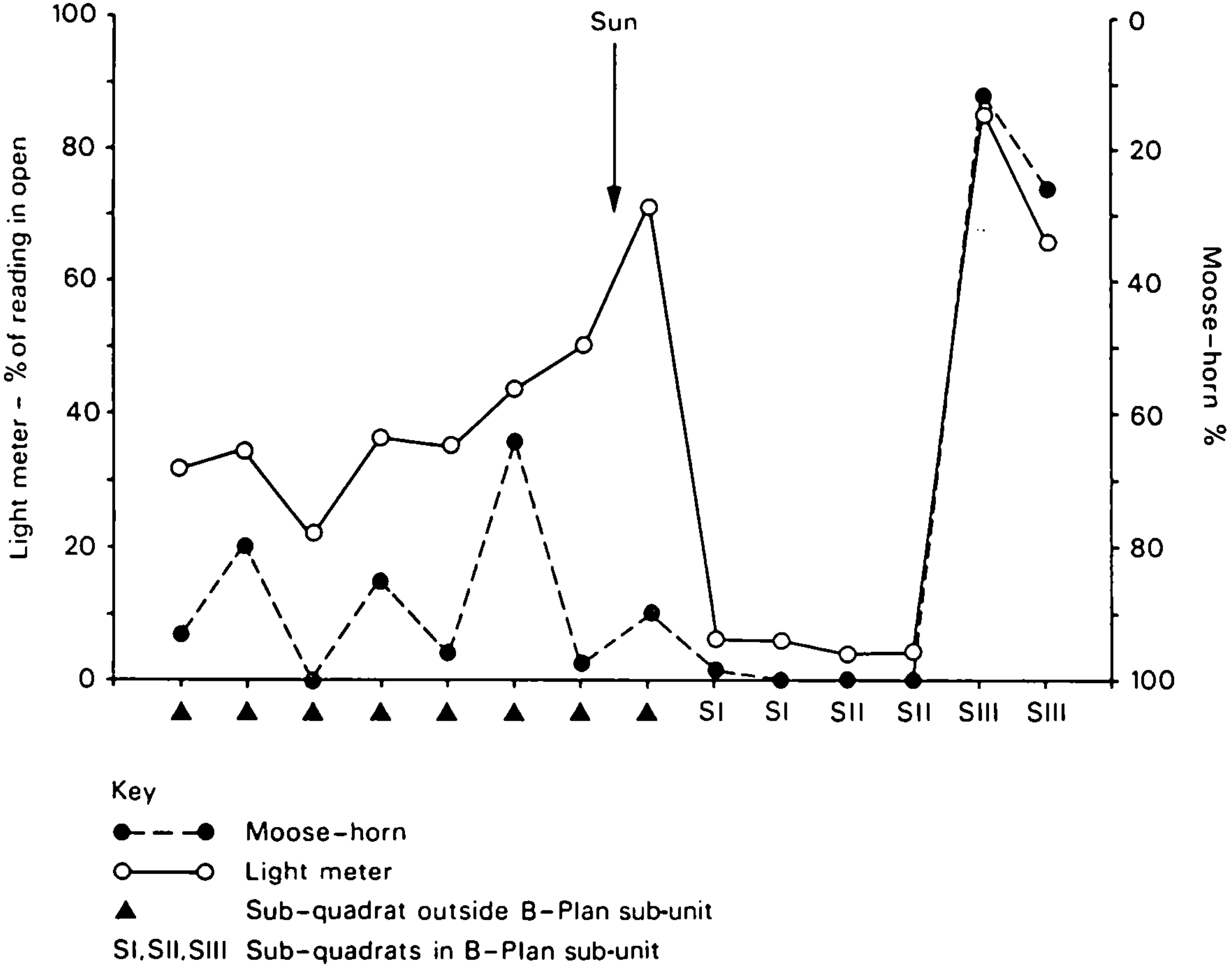


Figure 3.5b. Moosehorn readings compared to light meter readings under a *Quercus* x *rosacea* canopy with three B - Plan sub-units - quadrat 54

canopy sampler detects only major differences in canopy closure, the results correspond to those of the light meter. It is, however, particularly insensitive under a closed canopy (Figure 3.5a.). Figure 3.5b also illustrates the difficulties with light meter readings on days when the cloud conditions are not uniform.

3.5. Main survey - phase III - Shrub survey - 1982 and re-examination of ground flora in phase II quadrats

A detailed survey of the shrubs in 17 of the 20 selected quadrats was undertaken in 1982, to satisfy the first aim of the project by providing basic information on species and abundance and to determine how B - Plan affects the shrub layer.

3.5.1. Definition of shrubs

Shrubs do not receive much attention in vegetation surveys of Eurasian and North American forests because the canopies are one-layered with only a few scattered large shrubs, and the low growing shrubs are usually included in the ground flora (Larsen, 1980). Hence the height criteria used to define the understorey layer and the methods by which the dominance of this layer is assessed vary greatly in the literature. Table 3.3. illustrates this variation. Rowe (1959) divides the shrubs into three classes - less than one metre, one to three metres and greater than three metres. Ohmann(1973) groups tree seedlings with taller shrubs as individuals greater than 15cms. Like Gauch (1982) and Whittaker (1978), he then suggests measuring the diameter at the base of the shrubs as a measure of dominance. As an alternative to this, all three authors suggest cover estimates. Ohmann(1973) uses a line intercept method reading of linear cover along a tape. Williams (1971) feels that points and lines should not be used in survey work and that areas are more appropriate. Gauch (1982) and

Table 3.3. Criteria used for shrub/understorey surveys

Author	Forest Type	Height Criteria	Dominance measures
Rowe (1959)	temperate	1m; 1-3m; 3m.	--
Ohmarm (1973)	temperate	All woody plants 15cm but not part of the canopy	Diameter classes or cover (line intercept)
Gauch (1982) and Whittaker (1978)	temperate	--	Diameter at base or visual cover estimates
Bunce and Shaw (1973) and Bunce (1982)	temperate	--	Diameter at base
Borman and Buell (1964)	temperate	All woody plants 3.6m.	Cover (line intercept)
Küchler (1949)	tropical	1m = shrubs 1m = dwarf shrubs.	--
(1966)		0.1-0.5 = shrubs, 0.1m = dwarf shrubs.	
Mueller-Dombois and Ellenberg (1964)	temperate	30 or 50cms to 2 or 3m and 2 or 3m to 5m.	--

Whittaker (1978) propose visual cover estimates. Küchler (1949; 1966), working in tropical rain forests, used two different sets of height limits, the second a revision of the first (Table 3.3.). Mueller-Dombois and Ellenberg, (1974) feel the height classes for shrubs from 30 or 50cms to 5m, with a subdivision into two classes at either two or three metres and with a maximum herbaceous height of one metre are "commonly found convenient". These particular criteria suited the understorey layers under B - Plan and the shrubs were thus surveyed in the manner shown in Table 3.4.

Table 3.4. Criteria used for the shrub survey - 1982

Layer	Size criterion	Abundance measure
Upper	>2m; ≤ 5m in height	Basal area - cm^2
Lower	$\leqslant$ 2m in height	Total cover - m^2

3.5.2. The shrub survey

Between May and October 1982, the height and either cover or diameter at breast height were recorded for all woody individuals, including tree seedling and saplings in 17 of the selected 20 quadrats. Of the three other quadrats, quadrat 29 was previously omitted due to damage from mine waste runoff. Quadrat 38, as part of a newly planted Nothofagus plantation, was weeded frequently, thus severely inhibiting the shrub layer, and the lack of light under the dense even-aged plantation of quadrat 19, precluded the survival of any shrub layer. Both of these quadrats exhibited the effects of conventional management of the shrub layer.

Cover was estimated for all the individuals in the lower shrub layer using a metre rule and/or a tape measure. In the upper shrub layer, basal area was calculated from diameter breast height measurements. When dealing with coppice-like regrowth of species such as Quercus, Betula or Corylus, the number of stems was counted and the diameter at breast height of the largest stem was measured. From this, an estimate of basal area was calculated by multiplying the number of stems times the diameter of the largest stem and then dividing by two. This estimate of the total basal area of a multi-stemmed individual compared well with other records of multi-stemmed individuals, where all the stems were measured.

3.5.3. A second soil survey

The aim of this second soil survey was to confirm the information on soil properties gained in the pilot survey of phase I for the 20 quadrats selected at phase II. The effects of edaphic factors on the ground flora needed to be studied in order to separate soil effects from those of the light environment and the management and history.

On September 30th and October 1st, 1982 this final soil survey was conducted. Samples for pH and % soil moisture content were taken and analysed as in the earlier survey, but sampling points were more numerous being within one metre of every sub-quadrat for each of the 19 quadrats. Only one sample was collected between each of the two sub-quadrats in each B - Plan sub-unit (Figure 3.4b).

3.5.4. The ground flora survey

Once during the shrub survey, the ground flora of some of the quadrats in phase II was re-examined. These quadrats were the 11 (omitting quadrat 29) not included in phase IV. No significant changes were noticed, but two new species were recorded, Agrostis stolonifera and Hyacinthoides non-scripta.

3.6. Phase IV - light, seed bank and phenological studies on eight quadrats selected from phases II and III

In 1982, between April and October, the final part of the study was conducted. Eight quadrats were chosen for this more detailed survey, on the basis of the phytosociological analyses of the quantitative data collected in phase II. Certain ground flora species appeared to be associated with particular canopies and with particular B - Plan stages. Hence eight contrasting quadrats were selected from these groupings.

3.6.1. Selection of quadrats

Two *Pinus* spp. canopied quadrats 4 and 9, each with well developed B - Plan units, were chosen (Figure 3.1; Table 3.5.). Quadrats 4 and 9, although similar now, differ in their history. Quadrat 4 is on the site of an area that was almost certainly former heath and which was damaged during mining operations in the 1800's, while quadrat 9 is a continuously wooded site (Hamilton, pers. comm.), (Figure 1.5.). Quadrat 13 was chosen because it represented a deciduous canopy on a continuously wooded site (Figures 1.5. and 3.1.), with the largest number of B - Plan sub-units - five. Quadrats 52 and 54 also represented deciduous canopies but of a broadleaf, *Quercus*. Quadrat 52 appeared to be particularly interesting because it is on a continuously wooded site and is abandoned coppice with *Sorbus torminalis*, an indicator in eastern England of ancient woodland (Peterken, 1981), (Figures 1.5. and 3.1.). Quadrat 54, with a B - Plan unit, provided the only quadrat where the effects of an oak canopy on B - Plan could be examined. The only other representative of this rare type was quadrat 40, where the B - Plan unit had failed due to rabbit damage. Quadrats 55 and 56 represented the mature *Pseudotsuga* canopy under which the B - Plan units appear to be particularly successful (Table 3.5; Figure 3.1.). Finally, quadrat 14 with a *Picea sitchensis* canopy, was chosen because it clearly shows the effect of opening up a dense, dark canopy to introduce B - Plan (Plate 1.4.). The enhanced ground flora growth is clearly visible.

3.6.2. Measurement of light under the canopy

The aim of this first part of phase IV was to provide data on the light climate under B - Plan. During the phase II survey, the moosehorn canopy sampler was used to measure canopy closure, but was found to detect only gross differences in cover. Light meters have

Table 3.5. Eight quadrats selected for the detailed study in 1982

		B - Plan plot with planting date				
Quadrat	Canopy type	S I	S II	S III	S IV	S V
4	*Pinus* spp.	1976	1976			
9	*Pinus* spp.	1973	1980	1980		
13	*Larix* spp.	1962	1968	1973	1980	1980
14	*Picea sitchensis*	1973	1980	1980		
52	*Quercus x rosacea*	No B - Plan - abandoned coppice				
54	*Quercus x rosacea*	1961	1967	1973	1973	
55	*Pseudotsuga menziesii*	1961	1967	1973	1980	
56	*Pseudotsuga menziesii*	1961	1969	1973	1980	

also been used in other studies but measurement is always difficult because cloud and light conditions are never uniform. Constant fluctuations in both diffuse and direct light, even in overcast conditions make instantaneous measurements difficult and inaccurate (Anderson, 1964).

For this reason, direct measurement of light was rejected and hemispherical photographs were used to calculate both the diffuse and direct components of the global short wave radiation at each sub-quadrat within the eight selected quadrats. Pope and Lloyd (1975) stated that although on an annual basis 60% of the total radiation is diffuse, its "variable and unpredictable nature" and its dependence on climates where the prevailing climatic conditions tend more toward overcast conditions means that direct irradiation is of greater ecological significance. However, in the discussion following this paper, Evans suggests that comparisons of diffuse radiation within the same area are possible. Salminen et al., (1983) found a high correlation when direct radiation measurements were compared with indirect measurements of diffuse radiation using hemispherical photographs in overcast but not sunshine conditions.

A difficulty in using hemispherical photographs is that the resulting measurements are only composed of the short wavelengths. Gay and Knoerr (1975) showed that long wave scattered radiation in the infra-red is a dominant proportion of the forest radiation budget, particularly in the spring and autumn. This portion can be accounted for by estimation of 'sky view factors' (Oke, 1978; Proctor, 1980), or by the use of radiometers which measure both short and long wave radiation (Gay and Knoerr, 1975). However this was considered to be beyond the scope and intent of this study and although the hemispherical photographs do not take into account this scattered long wavelength radiation, they provide a good estimate of photosynthetically active radiation, 400-700mm, for both diffuse and direct light, when compared to the actual values averaged over a period of a month or longer (Anderson, 1971)..

Hemispherical photographs

Each month, from May until October (omitting September), hemispherical photographs were taken of the canopy over each sub-quadrat in the eight selected quadrats. Subsequent examination of the photos showed that in most, the change in cover between the end of May and subsequent months was not significant. Thus the latter were not analysed.

Hutchison and Matt (1977) comment that changes in a Liriodendron tulipifera stand in Tennessee the changes induced by leaf phenology are as great as the seasonal changes due to the variations in the declination of the sun. However, in the few cases where the change in closure was large, the photos for both May and August were analysed.

This was true particularly for the deciduous canopy in quadrat 54 (Figure 3.1.) and for several sub-quadrats, where Pteridium aquilinum created a low dense canopy after the May photo was taken. The Quercus canopy in quadrat 52, which is on a south-facing slope, had already reached its full expansion by the end of May.

A semi-fisheye lens (Hanimax) was used as a conventional fisheye lens was not available. Black and white HP5 film was employed and the speed upgraded in the developing. The photographs were printed with fairly high contrast. The semi-fisheye lens covered an angle of 150°. The loss of 15° close to the horizon is not as significant as might first appear, because Madgwick and Brumfield (1969) found that in a coniferous stand 99.6% of the cosine-corrected diffuse light came from a zone of sky within 70° of the zenith, with 98.4% in a hardwood stand.

The drawback in using this semi-fisheye lens is apparent when estimation of direct radiation is made using the solar track diagrams (Figure 3.6.). The December track is lost completely, as are several hours of each of the other tracks throughout the year. The percentage of the total daily radiation lost (calculated from figures obtained from the Meteorological Office station at Camborne) for one day per month or pairs of months represented by the solar tracks in Figure 3.6. is as follows:

Months	% lost
June 21st	2.0
May 22/July 22	1.5
April 21/August 22	2.5
March 22/September 22	9.0
February 20/October 22	11.0
January 20/November 22	22.5

These losses are relatively small in terms of the total direct radiation. For example, the total monthly figure for December is

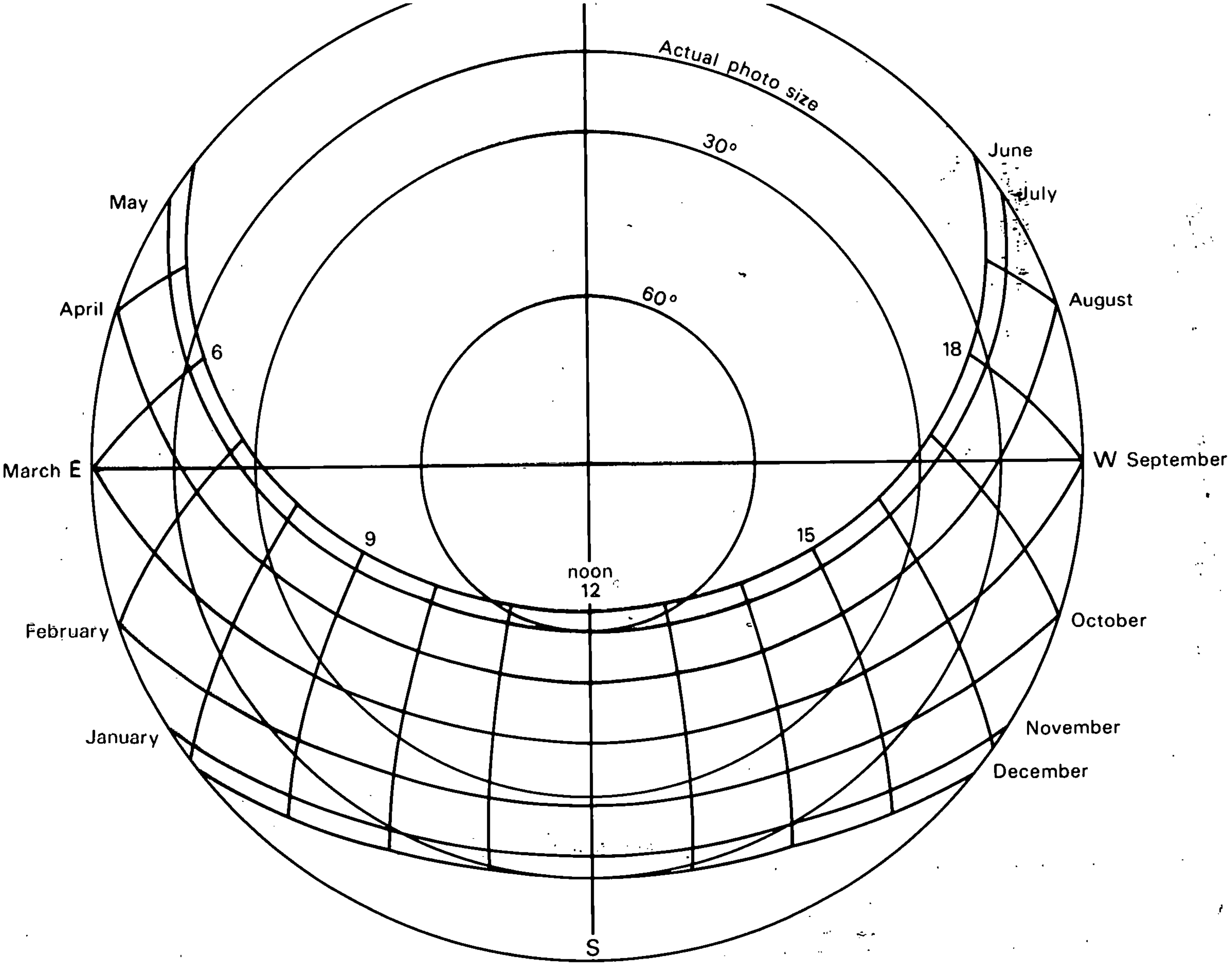


Figure 3.6. Solar track transparency for 50° 32'N

only 9% of that in June. The photos were therefore still acceptable for within-site comparisons, if not for absolute radiation value determinations.

In taking hemispherical photographs, levelling of the camera is important (Evans and Coombe, 1959). A tripod proved difficult to level and did not provide a firm base on which to rest the camera. A 180° rotating tripod was not available. Hence a 'bird table' arrangement was devised (Plate 3.5.). The table was attached to a one-metre high stake, which could be hammered into the same hole each month at the lower left-hand corner of each sub-quadrat. Using a spirit level, the top of the table could be made both firm and level by adjusting the stake in the ground. After the exposure and the delayed time release were set, the camera was then placed on the intersection of two perpendicular lines drawn on the top of the table. Each photograph included a marker pole indicating magnetic north. Adjustment for the 5 degree difference in 1982 between magnetic and true north was made in analysing the solar tracks. A compass was used to position the pole next to the 'bird table'.

Calculation of direct and diffuse radiation

Global and diffuse (direct = global - diffuse) irradiation data in milliwatts per square centimetre were available from the Meteorological Office's station at Camborne. The station is close to Tavistock Woodlands in latitude 50°13' and 50°32' respectively. The data were in the form of the monthly means per hour (LAT) for the years 1982 to 1984, the station having only commenced radiation readings in 1982. These mean values are close to what would be obtained over a period of many years for the specific dates used in the solar track diagrams (Weaver, Met Office, pers. comm.).

Plate 3.5. 'Bird table' used for taking hemispherical photographs

A solar track diagram was constructed to estimate direct light (Evans and Coombe, 1959; Anderson, 1964 and 1971; Proctor, 1980). The percentage of the track that was clear in each photograph was estimated using a clear overlay (Figure 3.6.). Then the total percent direct radiation per hour was calculated using the figures from the Camborne data to weight the percentage distribution on an hourly basis (Table 3.6.). The resulting percentages were summed for each track and then again summed for the seven monthly tracks, resulting in a composite annual site factor, a direct site index, to simplify comparison of the results. Pope and Lloyd (1975) used the real values in calculating a similar overall site radiation index.

Table 3.6. Hourly percent contribution to the total daily direct radiation per month calculated from the Meteorological Office Station at Camborne. Data for 1982-1984

Hours(LAT)	June	May/ July	April/ August	March/ September	February/ October	January/ November
6- 7	4.0	2.5	-	-	-	-
7- 8	6.0	5.0	4.5	-	-	-
8- 9	8.0	7.0	8.0	6.5	-	-
9-10	9.0	9.5	10.0	10.0	11.0	-
10-11	11.0	11.5	12.0	12.5	16.0	17.0
11-12	11.0	12.5	13.5	14.0	18.0	22.5
12-13	12.0	12.0	13.5	15.0	17.0	21.5
13-14	11.0	12.0	12.0	14.0	16.0	16.5
14-15	9.0	10.0	11.0	11.5	11.0	-
15-16	7.0	8.0	8.0	7.5	-	-
16-17	6.0	5.5	5.0	-	-	-
17-18	4.0	3.0	-	-	-	-

- = hours missing as a result of the 150° semi-fisheye photograph

Note: The values for pairs of months are averages of the two sets of measurements

Analysis of hemispherical photographs using a computerised visual image analysis system

Diffuse light was calculated using Anderson's (1971) grid. However instead of subjectively estimating the clear area in each section of the grid (which contributes 0.1% of the total diffuse light), a computerised image analysis method was employed.

> "Comparison of estimates of diffuse site factors obtained from each of three hemispherical photographs indicated large variations among six observers." (Madgwick and Brumfield, 1969: p. 537)

The computerised method was employed both to reduce these variations by providing an objective measure and to reduce the time taken to analyse each photograph. The time for analysis of each photograph was reduced from over an hour for the visual assessment, to less than fifteen minutes.

The computerised system involved using a "Microsight" program developed by Digihurst for an Ikegami video camera with a 16mm Cosmicar television lens and the BBC Acorn microcomputer (Plate 3.6.). With the camera focused on the photograph, the image is transmitted to the microcomputer, stored in digital form and re-presented on the computer screen. The camera then evaluates the degree of white versus black on each photograph in the form of screen pixels with over 12,000 per image (Plates 3.7. and 3.8.). The evaluation is controlled by a threshold value set between 1 and 260 and a contrast value set between 1 and 30. In a series of trials, a threshold value of 212 and a contrast value of 18 were found to be suitable for this study. A program routine then counts the area of white and the area of black on either side of the threshold (Plate 3.9.). The analyses were carried out in a room curtained from direct sunlight, using two 60 watt light bulbs on a photographic stand for illumination (Plate 3.6.). Some of the photographs differed in the degree of contrast, hence the camera

Plate 3.6. Visual image analysis system "Microsight" based on the BBC microcomputer used for calculating diffuse site factors

Plate 3.7. Hemispherical photograph - sub-quadrat 13 in May

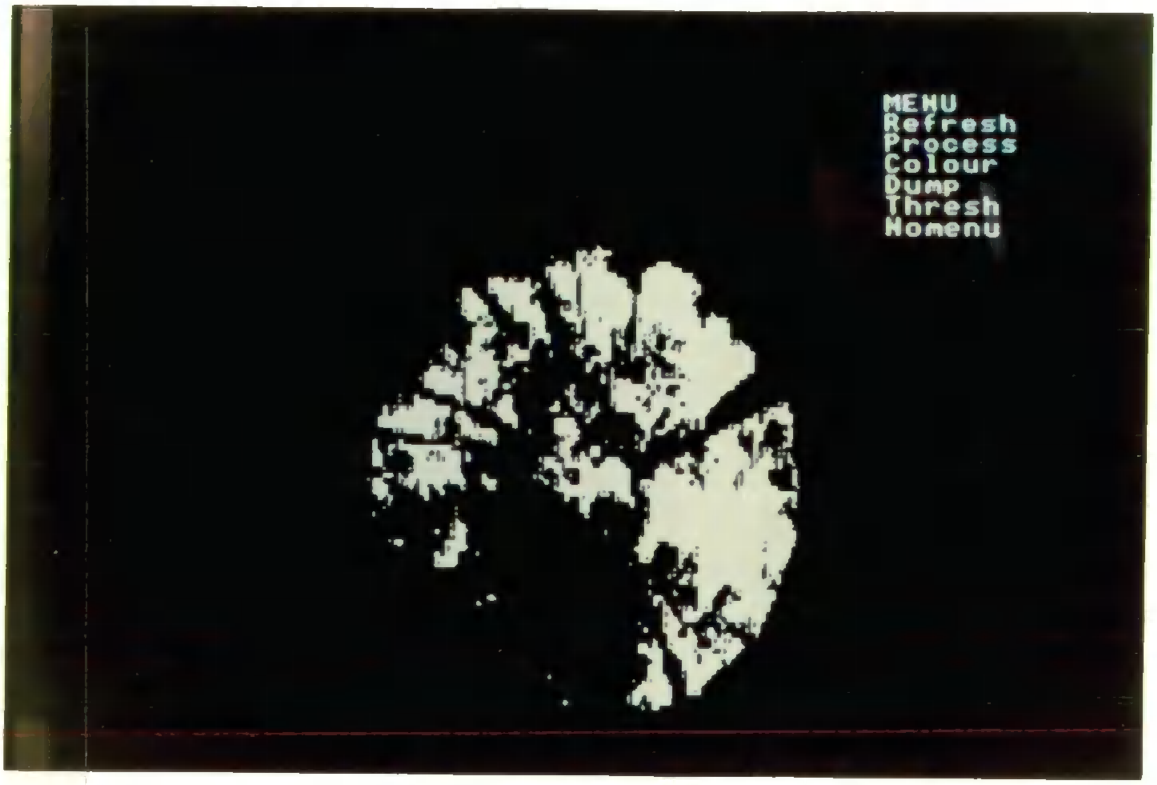


Plate 3.8. Screen image of hemispherical photograph in Plate 3.7.

```
AREA
W=02152
B=10421
X=
Y=

PERIM'
```

Plate 3.9. Generalized image showing pixel values for photograph in Plate 3.7.

aperture was adjusted until an image appeared on the microcomputer screen (Plate 3.8.) which closely approximated the actual photograph.

Eight matt black circular masks were constructed (Plates 3.10.-3.12) which combined several of Anderson's (1971) rings. Rings were combined to give similar photographic areas, thus minimising error in the determinations, while at the same time reducing the time taken for analysis. Table 3.7. shows the ring combinations, their areas and the percentage diffuse radiation contributions. The last two of Anderson's 26 rings were omitted to account for the difference between her 180° photograph and the 150° of the semi-fisheye lens photograph. The final ring (the 24th on Anderson's (1971) grid) reached to within 17° of the horizon, 2° of the semi-fisheye being lost to the analysis. The total area of the semi-fisheye photograph corresponded to a 95% contribution of total diffuse light.

Table 3.8. shows the screen pixel values of clear rings for each of the different aperture settings. The percentage diffuse light contributions for each ring in each photograph was calculated using these values. Five readings were taken and averaged for each ring because the "Microsight" readout fluctuated slightly about a mean value, although this fluctuation was very small in relation to overall accuracy. Finally, these percentage contribution values for each ring were summed, resulting in a diffuse site factor (Anderson, 1971) for each sub-quadrat.

An earlier attempt to minimize the time taken and to increase the accuracy of the analysis of the photographs using Anderson's grid was made using an Apple II micro-computer with a graphics tablet and software for area measurement (Plates 3.13.-3.15). A direct measure of the clear areas in mm^2 could be made by tracing around the area with the graphics tablet pen. Although this method was very accurate,

Plates 3.10. and 3.11. Two of the eight masks used for "Microsight" analysis

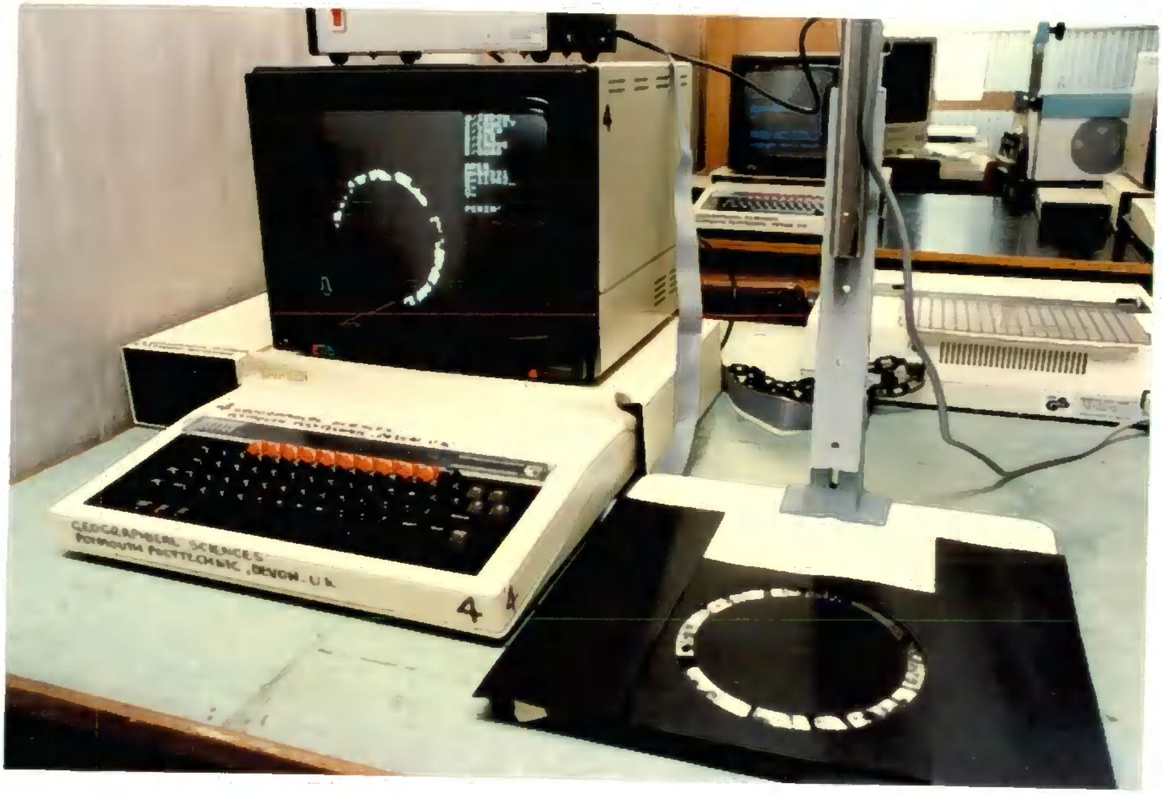


Plate 3.12. One of the eight masks used for "Microsight" analysis

Table 3.7. Anderson's (1971) rings for determination of diffuse radiation combined for "Microsight" analysis

Area in mm^2 of Anderson's grid rings	Combined ring numbers	Total % contribution per ring
10.2	1	5%
22.0		
130.7		
108.9		
136.6		
147.4		
507.9	2	15%
583.9		
575.4		
680.5	3	15%
622.3		
705.7		
770.1	4	15%
807.4		
867.7		
897.2	5	15%
986.6		
874.0		
1280.3	6	10%
1439.7		
1613.5	7	10%
1935.4		
2347.2	8	10%
3539.9		

Table 3.8. The mean values (for 10 determinations) measured in screen pixels using "Microsight" for clear rings

Ring numbers	% contribution to the total diffuse radiation	Total area of clear ring measured in screen pixels for each of the following camera apertures				
		2.0	4.0	0.6 of 5.6	between 5.6 & 8	8.0
1	5%	194	179	171	157	158
2	15	570	525	502	465	453
3	15	743	651	618	579	546
4	15	942	801	776	720	683
5	15	1046	869	824	735	657
6	10	1099	889	840	768	673
7	10	1254	1062	1002	892	799
8	10	1906	1645	1557	1453	1362

Plate 3.13. Apple II microcomputer with graphics tablet

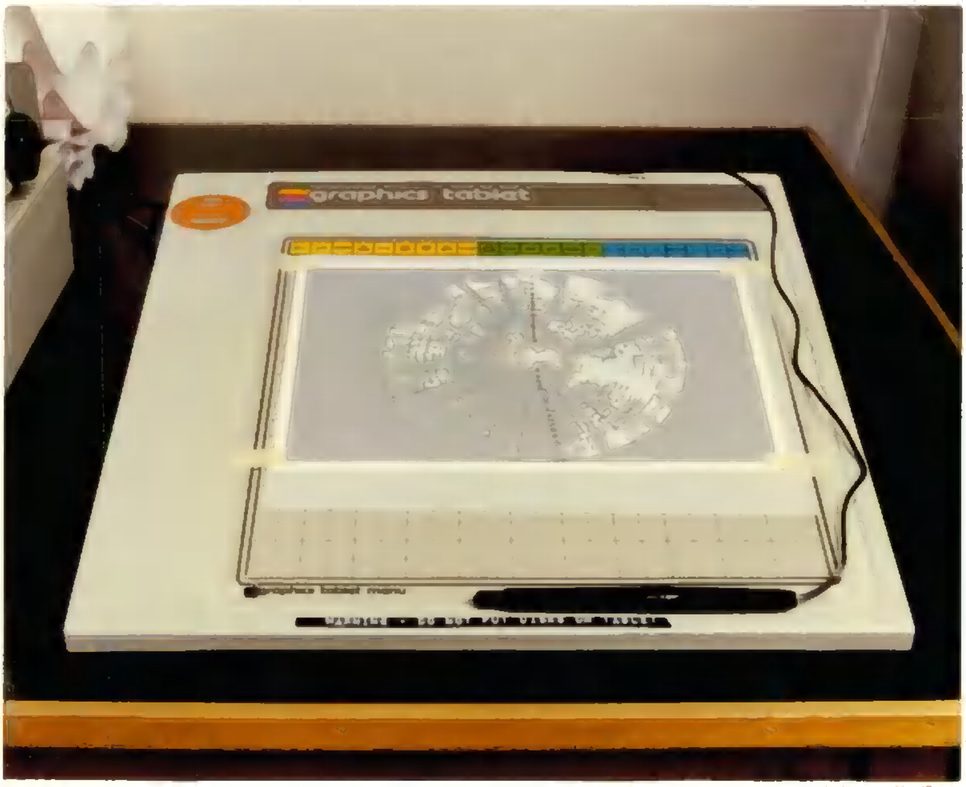


Plate 3.14. Apple II graphics tablet with hemispherical photograph and diffuse light grid

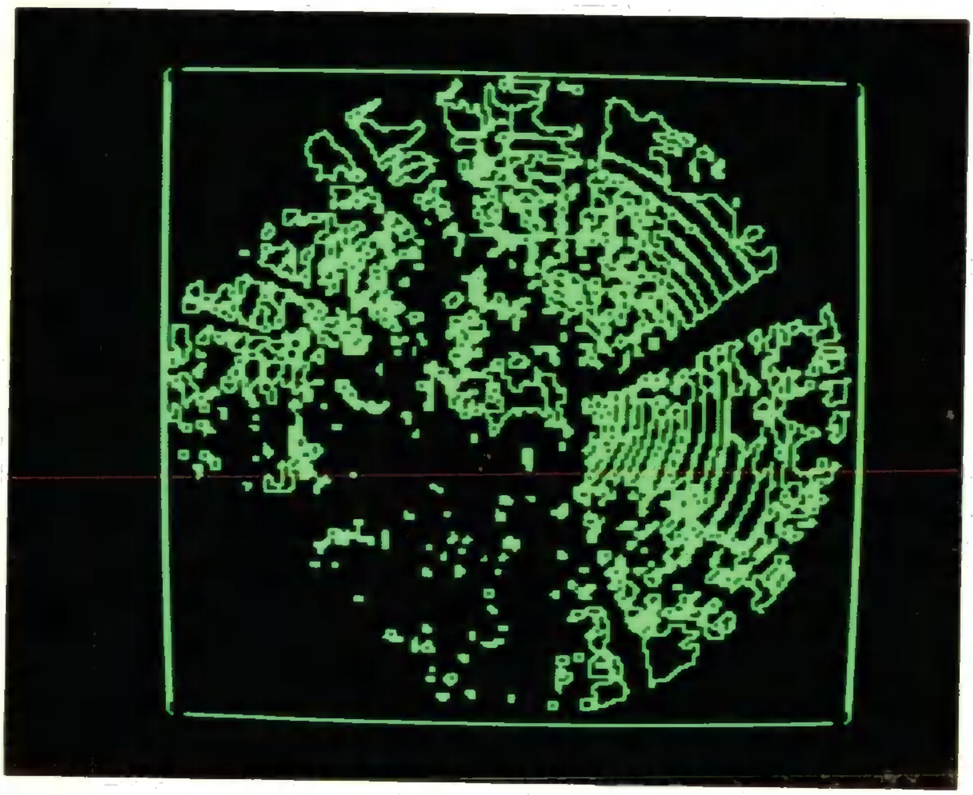


Plate 3.15. Screen image of tracings around open areas of hemispherical photograph and diffuse light grid

it proved too time consuming, taking over one hour per photograph. This degree of accuracy was also considered unnecessary in light of the inexactness of the photographs. Proctor (1980) stated that:

> "... the resolution limits of lens and film may severely restrict the accuracy of estimates under tree canopies ... A circle of confusion of 0.01mm on the film corresponds to 1cm among the leaves and twigs of a canopy 8m above the camera. This implies a large uncertainty of measurement even with the best lenses and whether the photographs are analysed visually or by some photoelectric method." (p. 363)

A comparison was made of this method with that of the "Microsight" image analysis system and the visual estimation methods (Table 3.9.). The visual method appears to have consistently higher values for diffuse light while the Apple II graphics tablet has the lowest values. The "Microsight" values fall inbetween.

Table 3.9. A comparison of three different analysis techniques for determining diffuse light (% of total in open) using semi-fisheye lens photographs

Quadrat-Sub-quadrat		Diffuse site factors		
		Apple II graphics tablet	BBC Acorn "Microsight"	Visual estimation
4(*Pinus*)	7	34%	43%	46%
56(*Pseudotsuga*)	2	20%	26%	30%
52(*Quercus*)	8	23%	28%	31%

3.6.3. Seed bank studies

The seed bank of a woodland predicts the potential response of the vegetation to present and future management, while at the same time reflecting the past history of the site. The aim of the seed bank survey was to provide this information about B - Plan management and to answer the questions posed in section 2.6.3.

Sampling

Between 24th and 29th April 1982, soil samples were collected approximately one metre away from each sub-quadrat within the eight selected quadrats (Table 3.5.). The sampling points were near each of the sub-quadrats numbered one to eight (Figure 3.4a). Only one sample was collected from each B - Plan sub-unit located halfway between the two sub-quadrats. A 16 x 16cm sample, five centimetres in depth, of the humus layer including the litter was taken with a spade. Litter was included because the aim of this first sample was to see which species were currently contributing to the seed bank. Many studies use a soil corer (Oosting and Humphreys, 1940; Brown and Oosterhuis, 1981), but the extremely stony nature of the soil and the strength required for this method made it impossible to use. Another sample of the same size was taken from the mineral soil just below the humus layer. The purpose in taking this second sample was to discover which species had survived in the seed bank from past ground floras. A large proportion of seed bank studies concentrate on samples from the mineral layer (Oosting and Humphreys, 1940; Olmsted and Curtis, 1947; Major and Pyott, 1966; Livingston and Allessio, 1968; Brown, 1981; Brown and Oosterhuis, 1981). Kellman (1970) and Thompson and Grime (1979) include litter samples. The results of these samples from the two horizons may be used to provide information on those species which could potentially appear in the ground flora after a unit has been cleared for B - Plan and the former coniferous canopy removed.

> "The practical significance of the viable seeds in the soil, however, lies not in their association with the past, but in their bearing on the plant communities likely to develop in the future." (Roberts, 1970: p. 25)

Four samples were also taken from quadrat 51, a dense beech canopy where the B - Plan units are failing and where there is little ground cover.

Germination experiments

The samples were air-dried after sieving (Olmstead and Curtis, 1947; Thompson and Grime, 1979). At the end of May (Brown and Oosterhuis, 1981), the soil was spread on a two centimetre bed of perlite (Kellman, 1970) in a 35 x 23.5cm plastic seed tray (Plate 3.16.). A number of studies have collected and germinated the seed bank on in the autumn (Oosting and Humphries, 1940; Olmstead and Curtis, 1947; Roberts and Dawkins, 1967). Livingston and Allessio (1968) had greater germination in their spring samples than in those from the autumn due to the requirement of stratification by many species. Once stones and roots had been removed, the volume of soil was measured and recorded before putting the soil in the trays. These volumes were extremely variable.

The 182 trays were placed at random on shelves constructed from dexion and covered with capillary matting in an 8 x 12 foot cold greenhouse (Plate 3.17.). An unheated greenhouse was used because these conditions would approximate to the natural light and temperature regime (Major and Pyott, 1966; Brown and Oosterhuis, 1981; Brown, 1981). Other studies have used controlled laboratory conditions or temperature and light controlled greenhouses (Olmstead and Curtis, 1942; Livingston and Allessio, 1968; Kellman, 1970), but these were not available for this study. The trays were moved every month following a random pattern to minimise variation in light distribution.

The trays were kept well watered and examined each month between June and October, when the seedlings were counted and identified using Chancellor (1966); Muller (1978). Any unidentified species were potted up and grown on to facilitate identification (Plate 3.18.). After the first seeds had germinated at the end of June, the trays were watered with a dilute solution of a standard fertilizer every

Plate 3.16. Seed tray used for seed bank germination tests

Plate 3.17. Greenhouse with seed bank germination test in progress

Plate 3.18. Unidentified seedlings potted up for later identification

two weeks to keep the seedlings growing for identification. Two control trays (Kellman, 1970) of sterile potting compost on a bed of perlite were included with the other 182 trays to collect any stray local air-borne seeds.

3.6.4. Phenological Studies

The aim of the phenological studies was to discover how certain species in the ground flora responded through the growing season to variation environmental factors controlled by the canopy and present management regime. Light is a primary factor affecting phenology (Harper, 1977; Al-Mufti et al. 1977; Mahall and Bormann, 1978; Fowler and Antonovics, 1981; Givnish, 1982).

From April until October 1982, the eight selected quadrats (Table 3.5.) were visited each month (except for September when most of the shrub survey was completed) to assess vegetative as well as the reproductive state of the ground flora.

To facilitate rapid recording of both a Domin-Krajina abundance number and the phenological stage a system was adapted from Persson (1975). Each species was given four numbers -

1) The Domin-Krajina number
2) A phenological number (Table 3.10.)
3) Six followed by i or f to indicate either the initial or final stage of the phenological number in 2)
4) If necessary number five to indicate if the vegetative parts remained from the previous winter.

Spaces were provided on the data sheet for each of these numbers (Figure 3.3a-d.). The other 11 quadrats were each visited only once in the season mainly in September as part of phase III and recorded in the same manner as the eight.

Table 3.10. Phenological stages and numbers (adapted from Persson, 1975)

Number	Description
1	Development of the current year's leaves
2	Flowering Stage
3	Fruit/seed ripening stage
4	Withering of vegetative parts
5	Photosynthesizing leaf parts dormant throughout the winter
6(i or f)	Initial and final stages of the above phases

CHAPTER 4. TREES AND SHRUBS

CHAPTER 4. TREES AND SHRUBS

4.1. Introduction

The tree, understorey and shrub studies in Blanchdown, Grenoven and Hangingcliff Woods were conducted over several years and in several stages. (Table 4.1.)

Phase I - The first tree survey - 1977-78

The first tree survey in 1977-78 was purely a study of the variation in canopy species. The results, based on presence and absence and summarising the main canopy types, provided the basis for sampling at the second stage. This was to be the stratified sampling of the vegetation under B - Plan, with recording of the tree canopy species, the understorey, shrub species and finally the ground flora.

Phase II - The second tree survey - 1981

This second tree survey was a refinement of the first survey. Data from the first phase I survey were used for 14 of the original 50 quadrats. Six new quadrats were also surveyed in 1981. In this second survey basal area was recorded to provide a more precise analysis of the canopy composition.

Phase III - The understorey - upper shrub layer and lower shrub layer surveys

The sampling of the understorey layers beneath the 20 quadrats (Table 3.1.) began the detailed main survey - phases III and IV of the vegetation under B - Plan.

4.2. Results from the first tree survey - 1977-78

4.2.1. Multivariate analyses

The presence/absence data for trees with a diameter at breast height greater than or equal to five centimetres were analysed by classification and ordination. Quantitative data were not used in this early pilot study. The ordination method used was detrended reciprocal averaging (DECORANA) (Hill, 1979b; Hill and Gauch, 1980) and the classification technique applied was Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979c). Analyses were run on the PRIME computer system at Plymouth Polytechnic using versions of the programs adapted by Kent (1980a,b). These techniques have now been shown to be as good as, if not better than, most other ordination and classification methods and are generally agreed to provide a very efficient means of summarising variation in floristic data sets (Kershaw and Looney, 1985). It is also now commonly accepted that 'complementary analysis' with both classification and ordination applied to the same data set gives the maximum information on community variation.

Table 4.1. The tree and shrub studies

	Year	Layer	Size criterion of layer	Number of quadrats	Type of analysis
Phase I	1978	Tree	≥5cm dbh	50	TWINSPAN and DECORANA on presence/absence
Phase II	1981	Tree	>5m height	20 (14 from 1978 +6 new)	TWINSPAN and DECORANA on summed basal area
Phase III	1982	Upper shrub layer	>2m and ≤5m height	15 (from the 20 in 1981)	TWINSPAN and DECORANA on summed basal area
Phase III	1982	Lower shrub layer	≤2m height	17 (from the 20 in 1981)	TWINSPAN and DECORANA on summed cover m^2

4.2.2. Classification of canopy tree species

Table 4.2. shows the results of this first tree survey and was compiled using the raw data on tree composition in conjunction with the results of TWINSPAN (Tables 4.2. and 4.3.) and DECORANA (Figures 4.1. and 4.2.). The original 50 randomly located quadrats divide into 10 canopy types. The major divisions were based on TWINSPAN groups. However because of the nature of presence/absence data, where small saplings are weighted the same as the canopy trees, the maximum height and maximum basal area were also used in the definition of canopy types. Ecologists determine dominance using basal area (Mueller-Dombois and Ellenberg, 1974), but many foresters use the crown height in relation to the overall height of the woodland strata to determine dominance (Shimwell, 1971).

The groupings from the species classification using TWINSPAN are presented in Table 4.3. The quadrat groups of Table 4.2. have been plotted on the first two axes of the DECORANA ordination in Figure 4.1., with the major types labelled and similarly, the species groups of Table 4.3. have been plotted on the first two axes of the DECORANA ordination in Figure 4.2. Using these diagrams, an interpretation of the 10 canopy types could be made.

4.2.3. The canopy species associations

The TWINSPAN classification divides the species into four main groups (Table 4.3.). The first two groups in Table 4.3. contain all the B - Plan species with the planted canopy conifers. The second two groups, 3 and 4 in Table 4.3., contain most of the naturally regenerated and native species.

Pinus nigra and *P. sylvestris* are classified together in group 2 (Table 4.3.) with *Larix* spp. This combination is a major planted

Table 4.2. The 10 canopy types recognised in the first tree survey

Canopy Types

Species	Quadrat Numbers (Figure 3.1.)
Major Types	
1. *Pinus spp.*	1,2,3,4,5,9,10,11,16,18,20,24,25,29,34,43.
2. *Quercus* x *rosacea*	26,28,33,37,42,45,48,50.
3. *Pseudotsuga menziesii*	7,12,30,31,36,39,44.
4. *Larix spp.* and *Pinus spp.*	6,15,21,22,23.
Minor Types	
5. *Picea sitchensis* and/or *Picea abies*	8,14,17.
6. *Larix spp.*	13,35,49.
7. *Quercus* x *rosacea* with *Larix spp.*	40,27.
8. *Quercus* x *rosacea* with planted *Fagus sylvatica*	32,47.
9. *Larix spp.* and *Fagus sylvatica*	46.
10. Mixed coniferous plantation	19

Table 4.3. 1978 Tree species groups from TWINSPAN species classification

GROUPS 1	2	3	4
Picea abies	*Larix* spp.	*Betula* x spp.	*Abies alba*
Sequoia sempervirens	*Pinus nigra*	*Carpinis betulus*	*Ilex aquifolium*
Fraxinus excelsior	*Pinus sylvestris*	*Picea sitchensis*	*Acer pseudoplatanus*
Corylus avellana		*Quercus* x *rosacea*	*Castanea sativa*
Nothofagus procera			*Quercus cerris*
Sorbus aucuparia			*Fagus sylvatica*
Pseudotsuga menziesii			
Thuja plicata			
Tsuga heterophylla			

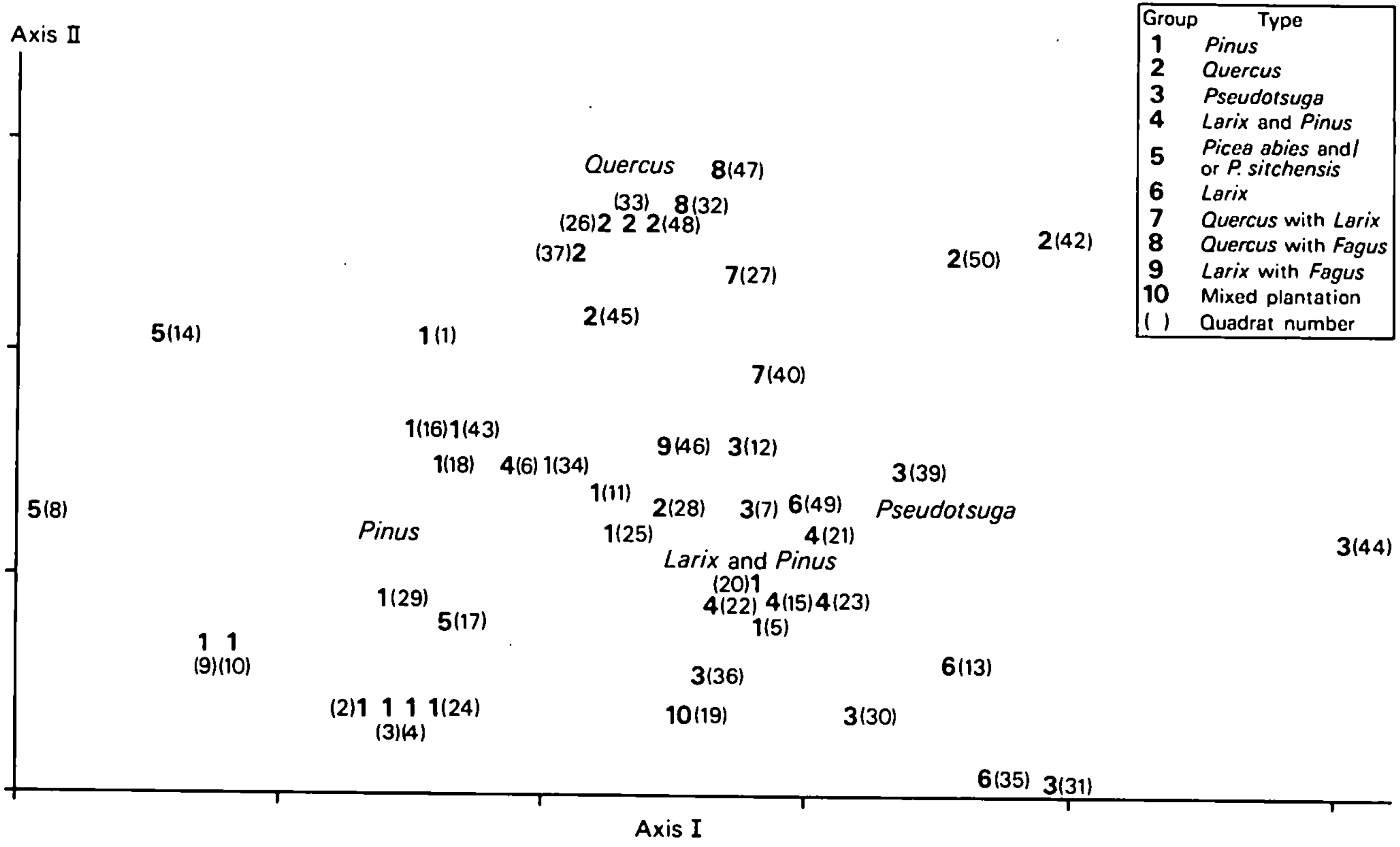


Figure 4.1. DECORANA site ordination of data from the phase I tree survey showing TWINSPAN groups and major canopy types

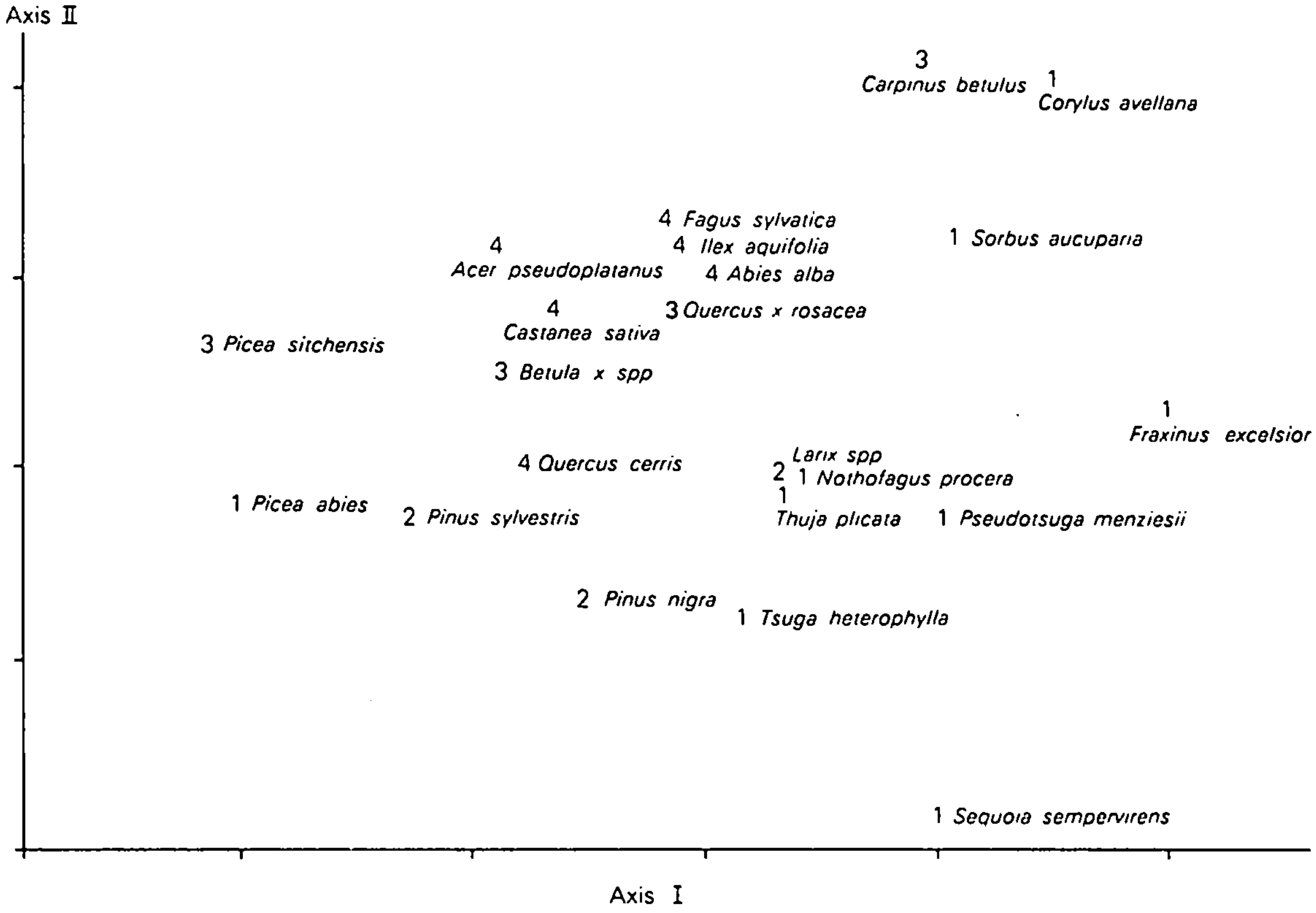


Figure 4.2. DECORANA species ordination of data from the phase I tree survey showing TWINSPAN groups and species names

canopy type. P. nigra and P. sylvestris is an even more common canopy association which was planted before the introduction of B - Plan. Both of these canopy associations are now frequently underplanted with B - Plan units. Pinus spp. are no longer planted in the Tavistock Woodlands Estate, as the yield class is only eight to ten in this part of Britain. This yield class is uneconomic compared to a species with a faster growth rate and hence a higher yield class such as Pseudotsuga, yield class 22 or 24 (Dyer, pers. comm.). These three species in group 2 occur near each other in the ordination (Figure 4.2.), although the groups overlap on the quadrat ordination (Figure 4.1.). Pseudotsuga menziesii, major canopy type (Table 4.2.) appears in combination with the other main B - Plan species, Tsuga and Thuja in group 1 of Table 4.3. They are a distinct sub-group of group 1 (Table 4.3.) and were classified together in line 3 of the species division of the TWINSPAN analysis. The other two B - Plan species - Sequoia sempervirens and Nothofagus procera also appear in group 1 (Table 4.3.). In general, the species of group 1 appear on the lower right hand side of the species ordination (Figure 4.2.).

Quercus x rosacea, which is another major canopy type (Table 4.2.), appears in group 3 of the species classification Table 4.3.[1] Much of the estate was covered by Quercus canopy until this century (Figure 1.5.). Thus it is the dominant canopy species in many quadrats, as well as being abundant as a naturally regenerating species under coniferous canopies.

Quercus and Betula in group 3 (Table 4.3.) are ordinated towards the centre of the species ordination (Figure 4.2.), which is reflection

[1] The taxonomic status of the oaks in Tavistock Woodlands is in doubt, and many are thought to be hybrids of Quercus robur and Quercus petraea (Wigston, pers. comm.). Thus, for the purposes of this study, all the oaks were classified under the hybrid name of Quercus x rosacea Bechst.

of their widespread distribution throughout the woodlands.[1] The other two species in group 3, *Picea sitchensis* and *Carpinus betulus*, are ordinated at two extremes (Figure 4.2.), a reflection of their limited distribution.

Group 4 (Table 4.3.) is a collection of primarily naturally regenerating species or those like *Fagus sylvatica* and *Castanea sativa*, that were planted in the past. This group of species is ordinated close together in Figure 4.2.

4.2.4. A description of the 10 canopy types

The TWINSPAN classification (Table 4.2.) divides the 48 quadrats into four main groups (1-4) and six minor groups (5-10). Quadrats 38 and 41, newly planted plantations with no canopies, were omitted. Overlap between canopy types is caused by the presence of B ÷ Plan species in most quadrats.

The major canopy types

Group 1

The *Pinus* spp. canopy type

The canopy types in order of frequency start with *Pinus* spp. with 16 quadrats (Table 4.2.). *Pinus sylvestris* is a preferential for group 1. *Pinus sylvestris* and *P. nigra* have been combined into one canopy type - *Pinus* spp. because both species have been planted by the estate in the same areas and are treated as one type of tree.

---

[1] The taxonomic status of many individuals of *Betula* on the estate presented difficulty. Recent chromosomal studies (Brown et al, 1982) show that there is evidence that *Betula pendula* and *B. pubescens* hybridize. In the field it became difficult to classify certain birch trees, their characteristics being of an intermediate nature, particularly leaf shape and degree of pubescence. The ecological requirements of both species are somewhat similar (Clapham *et al*, 1962; Harding, 1981). It was assumed for the purposes of this study that their ecological effect on the ground flora would be the same. Hence in the following analysis the two species are combined as *Betula* x spp.

They both have the same type of light canopy which encourages undergrowth (Hill and Stevens, 1981).

The DECORANA ordination (Figure 4.1.) shows clearly the *Pinus* spp. quadrats of groups 1 and 4. Quadrat 6 with a mixture of *Larix* spp. and *Pinus* spp. is ordinated with them, as is quadrat 17 with some *Pinus* spp. with *Picea abies*. Quadrats 5 and 20 are ordinated near a group of quadrats also having *Thuja* and *Tsuga* in B - Plan subunits. Quadrat 20 has *Nothofagus* as well.

Group 2

The *Quercus* x *rosacea* canopy type

The first TWINSPAN division separates those quadrats containing *Quercus* from those with predominantly coniferous species. The indicators for this group are *Quercus* and *Fagus*. Several quadrats in this group contain *Quercus* in mixture with *Larix* (group 7 - Table 4.2.) and in mixture with *Fagus* (group 8 - Table 4.2.).

The ordination (Figure 4.1.) shows clearly the quadrats with *Quercus* alone (group 2) or in combination (groups 7 and 8).

Group 3

The *Pseudotsuga menziesii* canopy type

Seven quadrats have pure *Pseudotsuga* canopies (Table 4.3.). *Pseudotsuga* is the TWINSPAN indicator for this group.

In the DECORANA ordination (Figure 4.1.) the quadrats with *Pseudotsuga* canopies are ordinated on the lower right-hand side. They tend to be intermingled with the *Larix* and/or *Pinus* quadrats because they all share the B - Plan species in common.

Group 4

The *Larix* spp. and *Pinus* spp. canopy type

Larix decidua, *L. kaempferi* and a hybrid of the two, *L.* x *eurolepis* have been planted throughout the estate in various combinations. Their ecological effect on the understorey and ground flora appears to be similar by virtue of being deciduous. Hence, to save sampling time no attempt was made to separate the species. All larch are listed as *Larix* spp. Five quadrats have *Larix* and *Pinus* quadrats (Table 4.2.).

In the DECORANA ordination (Figure 4.1.) the quadrats containing *Larix* and *Pinus* are grouped together. They are intermingled with several other quadrats with *Larix* and/or *Pinus*, and *Pseudotsuga* canopies because they all share the B - Plan species in common.

The minor canopy types

Group 5

The *Picea sitchensis* and/or *Picea abies* canopy type

Both *Picea sitchensis* and *Picea abies* were planted relatively infrequently in this part of the Tavistock Woodlands Estate. Hence only three quadrats have some combination of these species (Table 4.2.). Quadrat 14 is an even-aged *P. sitchensis* plantation with B - Plan plots. Quadrat 17 has predominantly *P. abies* but with some *Pinus* spp. Quadrat 8 has both species.

In the DECORANA ordination diagram (Figure 4.1.) 8 and 14 are ordinated together while 17 is within the *Pinus* spp. grouping.

Group 6

The *Larix* spp. canopy type

Three quadrats contain pure *Larix* spp. canopies - 13, 35 and 49. (Table 4.2.). They also contain B - Plan species. Consequently in the DECORANA ordination (Figure 4.1.) these quadrats are spread out in the *Larix*/*Pinus* space near other quadrats with B - Plan sub-units.

Group 7

The *Quercus* x *rosacea* with *Larix* spp. canopy type

In the early 1900's (Figure 1.5.) some of the estate was planted with a mixture of *Larix* spp. and *Quercus* x *rosacea*. Quadrats 40 and 27 on opposite extremities of the study area, are two remaining sites with this combination (Figure 4.2.).

In the DECORANA ordination diagram (Figure 4.1.) these two quadrats are ordinated as expected between the *Quercus* group and the *Larix* and/or *Pinus* groups.

Group 8

The *Quercus* x *rosacea* with planted *Fagus* *sylvatica* canopy type

Fagus appears to be planted with *Quercus* in only two quadrats, 32 and 47. The *Fagus* trees in these two are large, mature canopy trees. In contrast the *Fagus* in the understorey of other quadrats with *Quercus* canopies (Table 4.2.) appears to be naturally regenerated. *Fagus* can regenerate well under *Quercus*, however the reverse is not true (Tansley, 1968).

In the DECORANA ordination diagram (Figure 4.1.) these two quadrats with *Quercus* and *Fagus* are within the *Quercus* grouping.

Group 9

The *Larix* spp. with *Fagus* *sylvatica* canopy type

46 is the only quadrat with a *Larix* and *Fagus* canopy (Table 4.2.).

In the DECORANA ordination diagram (Figure 4.1.), this quadrat occurs in the centre between the four main canopy types. It has two Pinus sylvestris trees in a predominantly Larix and Fagus canopy, consequently it is positioned close to the quadrats containing both Larix and Pinus.

Group 10

Mixed coniferous plantation canopy type

Three quadrats are in this group 19, 38 and 41. 41 is the youngest plantation, a mixture of Pinus radiata and P. muricata with Nothofagus procera and N. obliqua. It was not included in the tree data because the trees being planted in 1975 were not of measurable size. Likewise the Thuja plicata and Nothofagus species in quadrat 38 planted in 1975 were not included in the tree survey. Quadrat 19 is a dense plantation of coniferous species including Pseudotsuga menziesii, Tsuga heterophylla, Pinus sylvestris, P. nigra and Picea abies planted in 1968. The trees were of a measurable size hence this was the only coniferous plantation included in the 1978 tree survey (Table 4.2.).

In the DECORANA ordination (Figure 4.1.) quadrat 19 is positioned at the bottom, a consequence of its very mixed canopy.

4.3. Results from the second tree survey - 1981

4.3.1. Selection of 20 special quadrats for the detailed study of B - Plan and the ground flora under different canopy types

Fourteen quadrats from the original 50 of the 1978 tree survey (Phase I) were selected using the canopy classification and ordination as well as those of the ground flora data (Chapter 5). However, six new subjectively selected quadrats were added to complement these 14. To avoid confusion, the original quadrat numbers from the first survey were retained for the first 14 quadrats. The six new quadrats were numbered from 51 to 56 (Table 4.4., Figure 3.1.). The 20 quadrats chosen were thus representatives of each of the major and minor canopy types.

Table 4.4. The 20 quadrats selected[1] for studies at phase II

Canopy types	Quadrat numbers
Major types	
1. *Pinus* spp.	4, 9, 29*
2. *Quercus* x *rosacea*	33, *52*, *53*, *54*
3. *Pseudotsuga menziesii*	44, *55*, *56*
4. *Larix* spp. and *Pinus* spp.	15, 23
Minor types	
5. *Picea abies* or *P. sitchensis*	14, 17
6. *Larix* spp.	13
7. *Quercus* x *rosacea* with *Larix* spp.	40
8. *Quercus* x *rosacea* with planted *Fagus sylvatica*	32
9. *Larix* spp. and *Fagus sylvatica*	*51*
10. Mixed plantations	19, 38

* Later rejected

[1] Underlined quadrats are new ones added after the initial 50 quadrats at Phase I.

The aim at this stage in the study was to provide a basis for sampling of the vegetation under B - Plan management with the purpose of determining those features of the ground flora which are conserved under B - Plan. A smaller number of quadrats were required to carry out the much more detailed ground flora, phenological, soil, light and seed bank studies, while at the same time covering all the canopy types as well as B - Plan sub-units of differing ages. Quadrats with unusual features such as the relics of past mine working were now rejected because of the additional variation which they would contain.

4.3.2. The major canopy quadrats selected for phases II and III (Table 4.4.; Figure 3.1.)

1. Pinus spp. - Quadrats 4, 9 and 29

Quadrats 4 and 9 of the original 50 quadrats in Phase I were selected as good representatives of this type of canopy. Both have well established B - Plan units at stages II and III (Plates 4.1. and 4.2.). Quadrat 29 was also initially selected because it represented a Pinus spp. canopy with B - Plan at stage I. However, further examination in the field showed that both the trees and ground flora were stunted by runoff from extensive mine waste deposits lying upslope from the site. Consequently 29 was eventually rejected after the field survey.

2. Quercus x rosacea - Quadrats 33, 52, 53 and 54

The Quercus grouping was less well defined in the ordination because there is a considerable degree of natural oak regeneration under many different canopy types (Figures 4.1. and 4.2.). Fagus sylvatica, which has been planted as well as naturally regenerating within Quercus stands, added further confusion. Quadrat 33 was selected because it has only a few Fagus individuals much dominated by a Quercus canopy. Three new Quercus quadrats - 52, 53 and 54, were added to the studies for phases II and III because no other suitable quadrats were found among original 50. Also, it was at this stage that the importance of the ground flora and also the seed banks under the former oak coppice woodland was realised. Quadrat 52 is an old coppice in part of what appears to be ancient semi-natural woodland. (Plate 4.3.) Quadrat 53 a pure Quercus stand, probably planted in 1916 (estate records), was also selected. This was a timber stand now abandoned and in contrast to quadrat 52 had been less disturbed (Wigston, pers. comm.).

Most Quercus sites are on the steepest slopes near the River Tamar. They are unsuitable for B - Plan development because

Plate 4.1. B - Plan sub-units in quadrat 4

Plate 4.2. B - Plan sub-units in quadrat 9

Plate 4.3. Relic oak coppice in quadrat 52

extraction is difficult. Hence few *Quercus* canopies have B - Plan units. However, quadrat 54 was chosen because it has a B - Plan unit at stage III under a *Quercus* canopy and was one of the few examples of this type (Plate 4.4.).

3. *Pseudotsuga menziesii* - Quadrats 44, 55 and 56

Quadrat 44 of the original 50 quadrats was chosen because it had B - Plan at stage III under a pure *Pseudotsuga* canopy (Table 4.4.). The other original quadrats with *Pseudotsuga* had inappropriate features. Quadrats 7 and 35 were too close to a ride, 12 bordered on oak coppice, and 31 did not have all of the B - Plan unit within the boundaries. Hence these quadrats were rejected and two new quadrats, 55 and 56, were selected (Table 4.4.). Both these were situated under mature *Pseudotsuga* canopies, where some of the first B - Plan units were planted in the early 1960's. The sub-units were at B - Plan stage IV (Plates 4.5. and 4.6.).

4. *Larix* spp. and *Pinus* spp. - Quadrats 15 and 23

Two good representatives of this group emerged from the original 50 quadrats - 15 and 23. They were ordinated closely at phase I (Figure 4.1.) and appeared in the same TWINSPAN group. Quadrat 15 contained a stage IV B - Plan sub-unit and 23 a stage I sub-unit.

4.3.3. The minor canopy quadrats selected for phases II and III

5. *Picea abies* or *P. sitchensis* - Quadrats 14 and 17

Quadrat 14 from the original 50 quadrats had a very dark *Picea sitchensis* canopy with B - Plan at stage III. These sub-units allowed light to reach the ground flora, which responded with abundant growth (Plate 1.4.). Quadrat 14 was chosen because it shows the marked contrast in the ground flora between dark monoculture plantations and the B - Plan units.

Plate 4.4. B - Plan sub-units in quadrat 54

Plate 4.5. B - Plan sub-units in quadrat 55

Plate 4.6. B - Plan sub-units in quadrat 56

Quadrat 17 was selected because it had a very mature B - Plan unit at stage V, as well as a dense spruce canopy of Picea abies with a few Pinus spp. trees (Table 4.4.).

6. Larix spp. - Quadrat 13

Very few of the stands in Tavistock Woodlands are of pure larch. Most have been inter-planted with Pinus spp. Quadrat 13, of the original 50, was chosen as the only good example of a light deciduous canopy of pure Larix spp. with a well-developed B - Plan unit at stage V (Table 4.4.) (Plate 4.7.).

7. Quercus x rosacea with Larix spp. - Quadrat 40

Quadrat 40 from the original 50 quadrats is the sole representative with a Quercus and Larix canopy. Hence it was chosen because in addition to representing this canopy type, it also has a B - Plan unit under a deciduous canopy.

8. Quercus x rosacea with planted Fagus sylvatica - Quadrat 32

Quadrat 32 from the original 50 represented this very minor canopy type (Table 4.4.). During the course of the study the canopy was felled to expand the adjoining 'Nothofagetum'. However the ground flora was sampled prior to and after the felling. The results were used to examine the immediate effect of clear-felling on the ground flora.

9. Larix spp. and Fagus sylvatica - Quadrat 51

Quadrat 46 with a Fagus canopy from the 1978 tree survey was rejected for further study because being sited randomly, part of the B - Plan unit fell outside the quadrat. A new quadrat - 51 - was substituted for 46. It has B - Plan at stage I (Plate 4.8.) and is also an example of B - Plan management that has been unsuccessful. The Tsuga heterophylla in the B - Plan unit is not thriving. The estate managers plan to fell the surrounding canopy to encourage the Tsuga (Dyer, pers. comm.).

Plate 4.7. B - Plan sub-units in quadrat 13

Plate 4.8. B - Plan sub-units in quadrat 51

10. Mixed plantations - Quadrats 19, 38 and 32

Two examples of even-aged plantations were included in the study for comparison with the uneven-aged B - Plan quadrats - 19 and 38. A third example - 32 - was added after its Quercus and Fagus canopy was felled in 1980. Quadrat 19 is older than 38. It has a dense canopy and is nearly impenetrable. Quadrat 38 was planted on the site of a Quercus coppice cleared in 1975 three years before the tree survey. Consequently the ground flora development was followed over a period of four years.

4.4. Survey and analysis of the canopy in the 20 selected quadrats at phase II

The canopy composition of the 19 specially selected quadrats for the phase II tree survey in 1981 were examined in detail. Quadrat 29 was omitted due to the effects of toxic mine waste. The aim of this survey analysis was to more clearly describe the various canopy types which could ultimately determine the understorey and ground flora layers. Species dominance was considered an important aspect of these relationships and thus was studied in detail.

> "The tree species which dominate a particular woodland have more influence of the total character of the ecosystem than do herbaceous plants of the field layer." (Ratcliffe, 1977: p. 14)

4.4.1. Field survey using summed basal area

To study the dominance of a particular canopy species, a quantitative measure was used for field survey. Basal area is used as an expression of dominance in both ecological and sylvicultural work (Lindsey et al., 1958; Shimwell, 1971; Greig-Smith, 1983). The total summed basal area of all the trees of one species in a quadrat was used.

The stems of multi-stemmed coppice trees were measured individually. For smaller multi-stemmed individuals only diameter at breast height of the largest stem was measured. From this, the basal area was calculated, multiplied by the total number of stems and then divided by two. This produced a reasonable estimate of the total basal area without having to expend an excessive amount of time in the field. Dead trees were not included.

In the phase I tree survey 1978, presence/absence data were collected for trees greater than five cms diameter at breast height. To describe the canopy and understorey layers better at phase II, height, rather than diameter was used to distinguish canopy trees from those of the upper shrub layer. The layers were recorded as follows:

Tree >5m
Upper shrubs >2m - $\leqslant 5$m
Lower shrubs $\leqslant 2$m

This change resulted in a few smaller individuals being included in the second tree survey which were not in the first. These were some naturally regenerated species growing either between units or at the edges of rackways thus escaping clearing. Some trees from B - Plan sub-units were also included. These inclusions did not have a significant effect on the quantitative analysis because their basal areas were small.

To further clarify the species relationships within the canopies, <u>Pseudotsuga</u> <u>menziesii</u> was divided into three types depending upon its origin. This reduced the overlap in the analysis between canopies containing <u>Pseudotsuga</u> of different types. The types are as follows:

1 - <u>Pseudotsuga</u> <u>menziesii</u> A - in plantations (usually pre-B - Plan)
2 - <u>Pseudotsuga</u> <u>menziesii</u> B - in B - Plan sub-units
3 - <u>Pseudotsuga</u> <u>menziesii</u> C - naturally regenerated

<u>Pseudotsuga</u> <u>menziesii</u> C was not yet tall enough to be included in the tree analysis, but it was included in both the upper and lower shrub layers (section 4.5.).

4.4.2. Canopy densities of the quadrats in the phase II tree survey

Bunce (1982) used summed basal area of all the trees in a 200m^2 quadrat to describe native woodland canopies as either dense, average or open. Table 4.5. shows the 19 quadrats in phase II in relation to these categories.

Table 4.5. Canopy densities of the quadrats in phase II tree survey 1981 (after Bunce, 1982)

Canopy description	Summed basal area m^2 (all species)	Quadrats
Dense	1.5400 - 1.0750	14,32,* 33,51,52,53
Average	1.0749 - 0.6090	4,9,13,17,19,23,40,44, 54,55,56
Open	0.6089 - 0.1420	15

* Quadrat 32 before felling

Ten quadrats, all with B - Plan, have average densities. The densest quadrats include all of the neglected Quercus canopies, 32,33,52,53, the Fagus and Larix canopy, 51, and the Picea sitchensis canopy 14. Quadrat 54 has a light canopy of Quercus with a B - Plan unit. This canopy was just dense enough to be included within the average class. Quadrat 19, which was a nearly impenetrable plantation, had only an average density because the tree trunks were still small, even though the canopy was completely closed. The only open canopy was in quadrat 15 with a B - Plan unit at stage IV. This quadrat also had Rhododendron ponticum covering a relatively large portion of its area. This excluded trees which would have contributed to a higher density.

4.4.3 Classification and ordination of the canopy data at phase II

Only 17 of the 20 quadrats were analysed using TWINSPAN and DECORANA in the phase II canopy survey. Quadrat 29 was eliminated from further study due to the adverse effect of runoff from toxic mine waste. Quadrat 38 was omitted because it had no distinct canopy and most of the trees were less than five metres tall. Finally, quadrat 32 was the *Quercus* and *Fagus* canopy felled after the phase I tree survey.

Using summed basal area, the pseudospecies cut levels for TWINSPAN had to be carefully chosen. The final values are shown in Table 4.6. Fewer species have summed basal areas per quadrat in the two largest cut levels 4 and 5. This is firstly because B - Plan management aims to follow the reversed J - curve for age versus size distribution (Figure 2.2), with many more smaller individuals of the recently introduced species such as *Tsuga* and *Thuja*. Secondly, the naturally regenerated species contribute greater variety to lower cut levels due to their smaller basal areas.

The quadrats from the TWINSPAN Table 4.7. can be divided in six groups as follows:

	Quadrats
1. *Larix* spp. with *Fagus* or *Quercus*	40,51
2. *Quercus* x *rosacea*	32,52,53
3. *Larix* spp. or *Larix* spp. with *Pinus* spp.	13,15,23,54
4. *Pinus* spp.	4,9,17,19
5. *Picea sitchensis*	14
6. *Pseudotsuga menziesii*	44,55,56

A quadrat ordination using DECORANA (Figure 4.3.) shows the relationships between these groups.

Group 1

The first group, *Larix* spp. with *Fagus* or *Quercus*, consists

Table 4.6. Pseudospecies cut levels for TWINSPAN analysis - second tree survey - phase II

Summed Basal Area (dm^2)	Pseudospecies cut level	Number of times a species has a summed basal area within cut level
0-0.20	1	29
0.21-1.00	2	30
1.01-5.00	3	31
5.01-25.00	4	15
25.01 +	5	18

of quadrats 40 and 51. The indicator for this group was Larix spp. Quadrat 40 has one Larix spp. tree within a Quercus canopy, a minor canopy type (Table 4.4.). Quercus was the dominant species. The ratio of Quercus to Larix by basal area was 8 to 1. The Larix in quadrat 51 was in combination with Fagus, a minor canopy type (Table 4.4.), in a ratio of 1 to 1. Quadrats 40 and 51 are classified with 33,52 and 53 in the second TWINSPAN division (see quadrat division line 2 Table 4.7.). Fagus sylvatica is the indicator for this five quadrat group. The Fagus in 40,33,52 and 53 appears to be naturally regenerated, whilst that in 51 is planted. Both quadrats 40 and 51 have poor B - Plan units which have been abandoned by the estate. In the DECORANA ordination diagram (Group 1 - Figure 4.3.), quadrat 40 appears as expected in the space between the Larix and Quercus canopy types. Quadrat 51 appears within the Larix canopy space.

Group 2

The second group (group 2 - Table 4.7. and Figure 4.3.) Quercus x rosacea, quadrats 33,52 and 53, is composed solely of quadrats in the major canopy type Quercus (Table 4.4.). These three quadrats have no B - Plan units. Larix spp., the indicator for quadrats 40 and 51, divides 33,52 and 53 from 40 and 51. A combination of Betula,

Table 4.7. TWINSPAN classification table - phase II -tree survey

```
Groups                1  2      3       4    5  6

                      1 1|  1 1|      1|       |  |1 1 1
                      0 2|9 3 4|3 5 8 5|1 2 6 7|4 |1 6 7

 1  BETU  XSPP        5 -|5 4 3|- - - 3|- - 1 2|3 |- - -     0 0 0
 3  FAGU  SYLV        2 5|4 4 3|- 1 - -|- - - -|- |- - -     0 0 0
14  QUER  XROS        5 -|5 5 5|1 - 3 5|- - 3 2|- |- 1 -     0 0 0
 2  CORY  AVEL        3 -|- - -|- - 3 -|- - - -|- |- - -     0 0 1
 6  LARI  XSPP        4 5|- - -|5 4 5 -|- - - -|- |- - -     0 0 1
11  PINU  SYLV        - -|- 4 4|- 5 - -|4 5 5 3|- |- - -     0 1 0
 8  PICE  ABIE        - -|- - -|- - - -|- - 5 2|- |- - -     0 1 1 0
 9  PICE  SITC        - -|- - -|- - - -|- - - -|5 |- - -     0 1 1 0
10  PINU  NIGR        - -|- - -|- - 5 -|5 - 3 2|- |- - -     0 1 1 0
16  SORB  AUCU        - -|- - -|2 2 - -|1 1 2 2|1 |- - -     0 1 1 0
 5  ILEX  AQUI        - -|- - -|2 - - -|- - - -|- |- - -     0 1 1 1
13  PSEU  MENB        - -|- - -|2 2 2 3|- - - -|- |- - -     0 1 1 1
17  THUJ  PLIC        2 -|- - -|- 4 2 3|1 - - -|- |- 3 3     1 0
18  TSUG  HETE        - -|- - -|3 1 2 3|- - 3 4|2 |2 3 3     1 0
 4  FRAX  EXCE        - -|- - -|- - - -|- - - -|- |3 - -     1 1
 7  NOTH  PROC        - -|- - -|- - 3 -|- - - -|- |- 4 3     1 1
12  PSEU  MENA        - -|- - -|- - - 4|- - - 3|- |5 5 5     1 1
15  SEQU  SEMP        - -|- - -|- - - -|- - - -|- |- - 4     1 1

                      0 0|0 0 0|0 0 0 0|0 0 0 0|0 |1 1 1
                      0 0|0 0 0|1 1 1 1|1 1 1 1|1 |
                      0 0|1 1 1|0 0 0 0|0 0 0 0|1 |
                           0 0 0 0|1 1 1 1
```

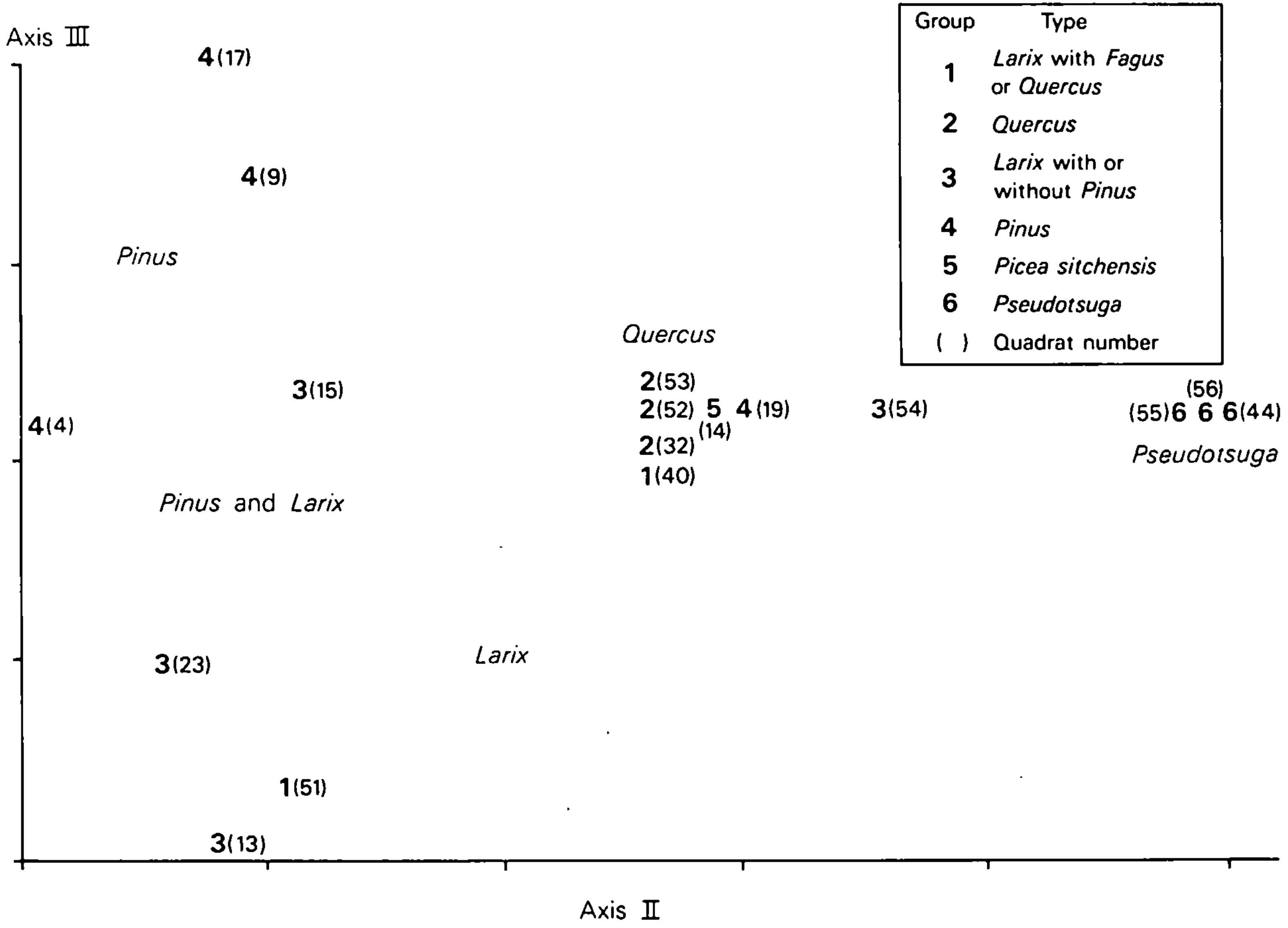


Figure 4.3. DECORANA site ordination of data from the phase II tree survey showing TWINSPAN groups and major canopy types

Fagus and Quercus are preferentials for this Quercus group. The group appears quite distinct on the ordination (Figure 4.3.) within the Quercus major canopy type space.

Group 3

The third group, Larix spp. or Larix spp. with Pinus spp., is less clearly defined. The group appears in the centre of the classification table (Table 4.7.) where the least differential quadrats are found (Hill, 1979c). The indicator for this group is Pseudotsuga menziesii B because all these quadrats have mature B - Plan sub-units with large Pseudotsuga trees. Larix spp. and Tsuga heterophylla are preferentials for this group. Quadrat 13 has the minor canopy type Larix spp., whilst 15 and 23 have the major canopy type Larix spp. and Pinus spp. Quadrat 54 with a Quercus canopy is classified with these three due to the Pseudotsuga in the B - Plan unit. On the ordination diagram (group 3 - Figure 4.3.), quadrat 13 appears in the minor canopy type Larix spp. Quadrats 15 and 23 are in the overlap space between Pinus and Larix, in the major canopy type space Pinus and Larix. Quadrat 54, with its Quercus canopy, appears in the Quercus space, but closer than the other Quercus quadrats to the Pseudotsuga space, because it has B - Plan species as well as one large Pseudotsuga menziesii left over from the rotation prior to the one in which the Quercus was planted.

Group 4

The fourth group, quadrats 4,9,17 and 19 all contain Pinus sylvestris and all but 9 have some P. nigra. There are no specific indicators for this group to separate it from quadrats 13 to 54, because Pseudotsuga menziesii B is the strong indicator for the latter group. Quadrats 4 and 9 have younger B - Plan units than 13,15,23 or 54. Pinus sylvestris, P. nigra and Sorbus aucuparia are preferentials for this Pinus group.

In the DECORANA ordination (group 4 - Table 4.7. and Figure 4.3.), quadrats 4,9 and 17 appear in the Pinus spp. canopy space. Quadrat 17 is at one extreme due to the Picea abies component of its canopy. Quadrat 19 is positioned in the middle of the ordination, a result of its great mixture of species. These include some naturally regenerated species which originated at the time of clear-felling and re-planting. These Betula, Quercus and Sorbus individuals have grown up with the coniferous trees planted in 1968. However, they are lagging behind in growth and are nearly over-topped by the coniferous species.

Group 5

The fifth group contains only quadrat number 14 (group 5 - Table 4.7. and Figure 4.3.). This is an unusual canopy type of Picea sitchensis, which is the indicator for this group. Quadrat 14 appeared as an outlier on the first ordination axis, causing a poor ordination on axes I x II and I x III. Hence the ordination used in Figure 4.3. is for II and III. In this plot, the relationships between the other quadrats and canopy types are well illustrated even though quadrat 14 is plotted in the centre of the ordination.

Group 6

The final group Pseudotsuga, quadrats 44,55 and 56, is a very distinct division in the TWINSPAN classification (Table 4.7.). These three quadrats separate out in the very first division. They all have B - Plan units under mature Pseudotsuga canopies. The indicator for the group is Pseudotsuga menziesii A. In the ordination, these three quadrats lie clearly at the right hand end of the second axis (Figure 4.3.).

4.5. Phase III - the shrub survey - 1982

Under the Bradford Plan, shrubs appear to benefit from the increased light and the reduction in competition from trees after clearing of a new sub-unit. They react with relatively abundant and diverse growth compared to shrubs under the even-aged plantations or under the abandoned coppice. As such, they are an important component of the woodland structure under B - Plan and need to be examined in detail.

The low productivity of shrubs under closed canopies means they cannot always recoup the energy expended in making their woody stems and as a result they die out (Givinish, 1982). Consequently large shrubs in Eurasian and North American forests are few and widely scattered (Larsen, 1980). Their scarcity means that they have received little attention in the literature and that there is no consensus in methods of treatment or of definition.

4.5.1. Defining shrubs

Bunce (1982) and Cameron (1980) define shrubs as:

> "... woody perennials that usually do not contribute to the canopy." (Bunce, 1982: p. 15)

The word 'usually' can cause confusion. For example, Sambucus niger, Ilex aquifolium, Corylus avellana and Salix spp. are cited as examples of shrubs by Packham and Harding (1982), Cameron (1980) and Bunce (1982). However, when these species become large enough to reach the canopy, Bunce (1982) lists them as trees. Ash and Barkham (1976) consider these species plus Crataegus monogyna and Fraxinus excelsior as trees, but count them as part of the field layer when they are smaller. In the same way, Norris and Barkham (1970) consider all species less than 91cms in height as part of the field layer, whether they are shrub, tree seedling or herb. Hence the criterion of size, rather than species, defines a shrub and this was the approach adopted here. Loucks (1962) also considers a multi-stemmed form important in classifying an individual as a shrub.

4.5.2. Field surveys of upper and lower shrub layers

The development of a working definition, incorporating height, was essential to enable an examination of the understorey layers. The decision was made to consider all those individuals having a woody, persistent stem, with either a multi-stemmed form or a single-stemmed growth form, as part of the shrub layer. Species like Rubus agg. and Lonicera periclymenum were excluded on the grounds that although they have a persistent woody stem, their form is neither shrub nor tree-like. Most of the understorey is less than two metres high due to the estate weeding operations. This was termed the lower shrub layer. Some individuals escape cutting back, particularly at the edge of rackways and rides or between units, where their growth does not interfere with the establishment of new sub-units. These individuals form an upper shrub layer up to and including those which are five metres in height. This layer is comparable to the height of the shrub layer in a regularly cut coppice - 2.6-3.2m (Rackham, 1980a). Meuller-Dombois and Ellenberg (1974) suggest the following height limits for the shrub layers:

Lower shrub layer - $>30\text{cm} \leqslant 2\text{m}$

Upper shrub layer - $>2\text{m} \leq 5\text{m}$

These limits were adopted for the lower and upper shrub layer survey in phase III 1982, but with the lower shrub layer including all individuals having a woody, persistent stem from small seedlings upwards.

The predominant growth form in the lower shrub layer was spreading and multi-stemmed, the result of frequent cutting. An estimate of cover, rather than basal area, was more appropriate. Hence cover in square metres was used for describing the lower shrub layer. A complete list of all the species in the lower shrub layer appears in Table 4.8. *Pseudotsuga menziesii* appears in the analysis as:

B - planted in B - Plan sub-units

C - naturally regenerated

Table 4.8. Lower shrub layer species

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1. *Acer pseudoplatanus* L.
2. *Betula pendula* Roth.
   Betula pubescens Ehrh.
3. *Castanea sativa* Mill.
4. *Corylus avellana* L.
5. *Crataegus monogyna* Jacq.
6. *Cytisus scoparius* (L.) Link
7. *Fagus sylvatica* L.
8. *Frangula alnus* Mill.
9. *Ilex aquifolium* L.
10. *Nothofagus procera* (Poepp. and Endl.; Oerst)
11. *Picea abies* (L.) Karst.
12. *Pinus sylvestris* L.
13. *Pseudotsuga menziesii* (Mirb.) Franco
14. *Prunus laurocerasus* L.
15. *Quercus cerris* L.
16. *Quercus* x *rosacea* Bechst.
17. *Rhododendron ponticum* L.
18. *Rosa canina* L.
19. *Salix cinerea* L.
20. *Sambucus nigra* L.
21. *Sorbus aucuparia* L.
22. *Thuja plicata* D. Don.
23. *Tsuga heterophylla* (Rafin.) Sarg.
24. *Ulex gallii* Planch.
25. *Viburnum opulus* L.

Nomenclature follows Ivimey-Cook (1984) and Mitchell (1974)

Cover estimates were less appropriate for the upper shrub layer, which was more tree-like in growth form. Hence this layer was treated in the same manner as the trees in the second tree survey. Basal area instead of cover was used as the quantitative measure of species dominance. A complete list of the species in the upper shrub layer appears in Table 4.9. *Pseudotsuga menziesii* appears in this layer as:

A - planted in plantation usually prior to 1960
B - planted in B - Plan sub-units
C - naturally regenerated.

4.5.3. The analyses of the lower and upper shrub layers - phase III - 1982

The lower shrub layer data for each species in each quadrat in the form of summed total cover (m^2) were analysed using TWINSPAN and DECORANA (Hill, 1979b,c) for the classification and ordination of 17 quadrats. Quadrats 19 and 38 were omitted, because quadrat 19 had no understorey under the dense plantation, while quadrat 38, a newly established plantation, was weeded frequently, thus suppressing shrub growth. The data ranged from 18% total quadrat cover for one species to less than 0.5%. Many species were represented by less than 0.5% total quadrat cover (Table 4.10.). This made it difficult to select pseudospecies cut levels for TWINSPAN which would adequately represent the range of species cover without giving too much weight to the rarer species. The dominant species with higher cover values appeared to represent more accurately the lower shrub layer of each quadrat, so the first pseudospecies cut level has many entries, while

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Table 4.9. Upper shrub layer species

1. *Betula pendula* Roth./ *Betula pubescens* Ehrh.
2. *Castanea sativa* Mill
3. *Corylus avellana* L.
4. *Crataegus monogyna* Jacq.
5. *Fagus sylvatica* L.
6. *Frangula alnus* Mill.
7. *Fraxinus excelsior* L.
8. *Ilex aquifolium* L.
9. *Picea abies* (L.) Karst.
10. *Pseudotsuga menziesii* (Mirb.) Franco
11. *Quercus* x *rosacea* Bechst.
12. *Salix cinerea* L.
13. *Sambucus nigra* L.
14. *Sequoia sempervirens* (D. Don) End.
15. *Sorbus aucuparia* L.
16. *Sorbus torminalis* (L). Crantz
17. *Thuja plicata* D. Don.
18. *Tsuga heterophylla* (Rafin.) Sarg.

Nomenclature follows Ivimey-Cook (1984) and Mitchell (1974)

Table 4.10. Lower shrub layer - total percentage cover by species

	Quadrat number																	% of quad. species occurs in
	4	9	13	14	15	17	23	32	33	40	44	51	52	53	54	55	56	
Acer pseu			+				+				1							18%
Betu pend/pube	18	11	1	1	+	2		1		1	+				+	+	+	71
Cast sati													+	+				12
Cyti scop										+								6
Cory avel		1					+	+		2	4				3	1	5	47
Crat mono			+												+			12
Fagu sylv		+			+	1	+	1	5	+		+	+	1	+		+	71
Fran alns	+																	6
Ilex aqui	+		1	+	+	+		3	7	+		+	2	+	1	+	+	82
Noth proc								2										6
Pinu spp.								+										6
Prun laur											+							6
Pseu men b			1		1	2									+	1	+	35
Pseu men c	+	+	+	+				1	+		+		1	1	+	+	+	71
Quer cerr	1	1				+										+		24
Quer xros	2	6	2	1	1	7	1	3	+	4	+	+	+	+	4	1	1	100
Rhod pont					7		6									1	+	24
Rosa cani												+						6
Sali cine	1	1			1			+										24
Samb nigr		+																6
Sorb acup	2	3	+	+	+	+	+	+	1	+			+	2	+	+		82
Thuj plic	+	+	1	1		+	+	+			+				+			53
Tsug hete	1	+		1	+		+				1							35
Ulex gall	5					+		+		+								24
Vibu opul						+	+					1				+	1	29
Pice abie															1			6
Total species	11	11	9	7	9	10	9	12	5	8	8	5	6	7	10	10	9	x̄ = 8.59, s.e. = 0.50
"Natural species"	9	9	7	5	7	8	7	10	5	8	6	5	6	7	8	9	8	x̄ = 7.29, s.e. = 0.37
Total % cover	31	24	7	4	10	13	8	12	13	7	6	2	4	5	8	4	7	x̄ = 9.71, s.e. = 1.82
Number of pseudospecies	25	23	13	16	15	18	13	24	12	14	13	6	10	12	17	15	14	x̄ = 15.29, s.e. = 1.21

mean % of quadrats a species occurs in = 33.15;

% ⩾ 0.50% rounded off; < 0.50 % recorded as +

each subsequent level has fewer (Table 4.11.). This gives more weight to the higher cover values.

The upper shrub layer data for each species in each quadrat in the form of summed total basal area (cm^2) were analysed using TWINSPAN and DECORANA (Hill, 1979b,c), providing a classification and ordination for 15 quadrats. Quadrats 14,19,32 and 38 were omitted. Quadrat 14 has no individuals within the upper shrub layer height limits. Quadrat 19 has no real lower or upper shrub layer under the even-aged plantation canopy, although there were several Betula in the ground flora analysis. Quadrat 32 was under the recently felled Quercus and Fagus canopy, which had been planted as an even-aged Nothofagus plantation. Quadrat 38, another slightly older even-aged plantation, also part of the 'Nothofagetum' had no upper or lower shrub layer due to constant weeding. The average canopy height was also under five metres. The data for the upper shrub layers ranged from one to $232cm^2$. The pseudospecies cut levels chosen appear in Table 4.12. As with the lower shrub layer, the emphasis is on the dominant species having the largest basal areas.

Table 4.11. The TWINSPAN pseudospecies cut levels for the lower shrub layer

Pseudospecies cut level	Total % Quadrat Cover	Actual cover-m^2	Number of entries
1	0 - 0.50	0.01 - 2.0	90
2	0.51 - 1.00	2.01 - 4.0	24
3	1.01 - 3.00	4.01 - 12.0	17
4	3.0+	12.01+	16

Table 4.12. The pseudospecies cut levels for the upper shrub layer

Pseudospecies Cut Level	Total Summed Basal Area/Species/ Quadrat (cm^2)	Number of Entries
1	0 - 10	29
2	11 - 30	25
3	31 - 70	15
4	70+	13

4.5.4. The shrub layer species associations

The lower shrub layer

The main species groups from the TWINSPAN classification (Table 4.13.) appear in Table 4.14.

Group 1 (Table 4.14.) consists of three species. Rhododendron and Viburnum occur under the more humid canopy of either Pseudotsuga menziesii or Larix spp. with either Pinus spp. or Fagus sylvatica. Group 2 (Table 4.14.) is a collection of naturally regenerated species found in quadrats with B - Plan units. It also includes Pseudotsuga planted in B - Plan sub-units. Group 3 (Table 4.14.) is composed of Betula spp. and Quercus x rosacea with the main B - Plan association of Thuja plicata and Tsuga heterophylla. Quercus is widespread in the understorey and with Betula colonizes openings created by B - Plan clearings. Hence these are grouped with the two B - Plan species. Group 4 (Table 4.14.) contains Fagus sylvatica and Ilex aquifolium. These two species which also appear together in the tree ordinations are a typical natural association. Both species can survive low light intensities (Harper, 1977; Newbold and Goldsmith, 1981). Group 5 (Table 4.14.) contains species requiring high light intensities to reproduce and thrive, naturally regenerated Pseudotsuga, Quercus cerris,

Table 4.13. TWINSPAN classification table - phase III - lower shrub layer

```
Groups                  1       2      3  4

                     11  1|1 11  |  |  11
                     27576|153534|12|8934

16  RHOD  PONT       -1442|------|--|----     000
17  ROSA  CANI       1----|------|--|----     000
25  VIBU  OPUL       22-11|-1----|--|----     000
 1  ACER  PSEU       ---1-|2---1-|--|----     00100
12  PSEU  MENB       -12-2|-3-12-|--|----     00100
 5  CRAT  MONG       -----|---11-|--|----     00101
 9  PRUN  LAUR       -----|1-----|--|----     00101
20  SARO  SCOP       -----|--1---|--|----     00101
 4  CORY  AVEL       -3-11|4-33--|-2|1---     0011
 2  BETU  XSPP       -11-1|132123|44|2---     01
15  QUER  XROS       12222|144432|34|4111     01
22  THUJ  PLIC       ---1-|11-122|11|1---     01
23  TSUG  HETE       --11-|2----3|21|----     01
 6  FAGU  SYLV       1111-|-211--|-1|3412     10
 8  ILEX  AQUI       111-1|-11231|1-|4431     10
13  PSEU  MENC       -1--1|1--111|11|2132     110
14  QUER  CERR       ----1|-1----|32|----     110
21  SORB  AUCU       --111|-11111|33|1213     110
24  ULEX  GALL       -----|-11---|4-|1---     110
 3  CAST  SATI       -----|------|--|--11     1110
10  NOTH  PROC       -----|------|--|3---     1110
11  PINU  SYLV       -----|------|--|1---     1110
26  PICE  ABIE       -----|------|--|---2     1110
 7  FRAN  ALNU       -----|------|1-|----     1111
18  SALI  CINE       -----|------|22|1---     1111
19  SAMB  NIGR       -----|------|-1|----     1111

                     00000|000000|11|1111
                     00000|111111|00|1111
                     00111|011111
                           00011
```

Table 4.14. The major lower shrub layer species groupings from the TWINSPAN classification (Table 4.13.)

Group 1	Group 2	Group 3
Rhododendron ponticum	Acer pseudoplatanus	Betula spp.
Rosa canina	Pseudotsuga menziesii B	Quercus x rosacea
Viburnum opulus	Crataegus monogyna	Thuja plicata
	Prunus laurocerasus	Tsuga heterophylla
	Cytisus scoparius	
	Corylus avellana	
Group 4	Group 5	Group 6
Fagus sylvatica	Pseudotsuga menziesii C	Castanea sativa
Ilex aquifolium	Quercus cerris	Nothofagus procera
	Sorbus aucuparia	Pinus sylvestris
	Ulex gallii	Picea abies
		Frangula alnus
		Salix cinerea
		Sambucus nigra

Sorbus aucuparia and Ulex gallii. This requirement is fulfilled by either the Pinus spp. or the deciduous Quercus canopies. Group 6 (Table 4.14.) contains a number of species of low frequency found under either the Pinus spp. or Quercus canopies.

The upper shrub layer

The main species groups from the TWINSPAN classification (Table 4.15.) appear in Table 4.16. Group 1, like group 6 in the lower shrub layer, consists of a number of species of low frequency under primarily coniferous canopies. Group 2 consists of three species (Table 4.16.). Fraxinus excelsior with only one occurrence and Corylus avellana, which is most abundant in sites which have been continuously wooded, quadrats 40,54,56,23 and 55. It was in these sites that B - Plan was first introduced in 1961. Hence the third species in this group Thuja plicata is now large enough to be included in the upper shrub layer. Group 3 consists of two species, Betula spp. and Castanea

Table 4.15. TWINSPAN classification table - phase III - upper shrub layer

```
Groups              1  2       3          4      5

                         1|1     1|      1|1 1
                    9|5 8 3|5 1 4 5 4|2 3 7 0|1 2

 4  CRAT  MONO      -|- - 1|- - - - -|- - - -|- -    0 0 0 0 0
 8  PICE  ABIE      -|4 - -|- - - - -|- - - -|- -    0 0 0 0 0
20  FRAN  ALNU      -|- 2 -|- - - - -|- - - -|- -    0 0 0 0 0
 9  PSEU  MENA      -|- - -|5 - - - -|- - - -|- -    0 0 0 0 1
15  SEQU  SEMP      -|- - -|- - 1 - 2|- - - -|- -    0 0 0 0 1
 3  CORY  AVEL      4|- 3 2|2 - - 2 1|- - - -|- -    0 0 0 1
 6  FRAX  EXCE      1|- - -|- - - - -|- - - -|- -    0 0 0 1
18  THUJ  PLIC      3|- 2 1|4 5 4 4 4|- - - -|- -    0 0 0 1
 1  BETU  XSPP      -|2 2 1|1 1 2 1 -|1 1 - -|- -    0 0 1
 2  CAST  SATI      4|- - -|- - - - -|- - - -|1 -    0 0 1
10  PSEU  MENB      -|1 - 3|2 - - - -|- 4 - -|- -    0 1
12  QUER  XROS      -|1 5 3|1 2 2 1 -|- 3 - -|2 2    0 1
19  TSUG  HETE      -|4 - 4|3 2 1 1 1|2 4 - 3|- -    0 1
 5  FAGU  SYLV      -|- - -|1 - 2 - 1|- - 1 -|3 2    1 0
13  SALI  CINE      -|- - -|- - 1 - -|2 - - -|- -    1 0
16  SORB  AUCU      1|2 - -|- 2 - 1 -|3 2 3 2|2 4    1 0
 7  ILEX  AQUI      -|- - -|- - - - -|- 4 3 1|- 2    1 1
11  PSEU  MENC      -|- - -|- - - - -|- - - -|2 2    1 1
14  SAMB  NIGR      1|- - -|- - - - -|- - - 3|- -    1 1
17  SORB  TORM      -|- - -|- - - - -|- - - -|1 -    1 1

                    0|0 0 0|0 0 0 0 0|1 1 1 1|1 1
                    0|1 1 1|1 1 1 1 1|0 0 0 0|1 1
                      0 0 0|1 1 1 1 1
                            0 1 1 1 1
```

Table 4.16. The major upper shrub layer species groupings from the TWINSPAN classification (Table 4.15.)

Group 1	Group 2	Group 3
Crataegus monogyna	*Corylus avellana*	*Betula* spp.
Picea abies	*Fraxinus excelsior*	*Castanea sativa*
Frangula alnus	*Thuja plicata*	
Pseudotsuga menziesii A		
Sequoia sempervirens		
Group 4	Group 5	Group 6
Pseudotsuga menziesii B	*Fagus sylvatica*	*Ilex aquifolium*
Quercus x *rosacea*	*Salix cinerea*	*Pseudotsuga menziesii* C
Tsuga heterophylla	*Sorbus aucuparia*	*Sambucus nigra*
		Sorbus torminalis

sativa (Table 4.16.). *Castanea* is of low frequency, while *Betula* is widespread in the upper shrub layer of most quadrats except for those with mature closed deciduous canopies, 33,51,52 and 53. Group 4 (Table 4.16.) is similar to group 3 of the lower shrub layer (Table 4.14.), with two B - Plan species, *Pseudotsuga menziesii* B and *Tsuga heterophylla* combined with *Quercus* x *rosacea*, which are abundant in B - Plan clearings. Group 5 also has three species (Table 4.16.). *Salix cinerea* is of low frequency, found under two light coniferous canopies, 9 and 15. *Fagus sylvatica*, which is tolerant of lower light intensities (Newbold and Goldsmith, 1981) survives under the darker coniferous canopies of quadrats 56 and 55, as well as under the light *Pinus* and *Larix* canopy of quadrat 15. *Fagus* is also found under the closed deciduous canopies of quadrats 33,52 and 53. It germinates best on sites without competing herbaceous vegetation or mosses, conditions afforded by the darker canopies. The tolerance of *Fagus* of low light intensities stems from the fact that, unlike *Quercus*, it does not etiolate in shade and hence is not susceptible to fungal attack. (Newbold and Goldsmith, 1981). Group 6 (Table 4.16.) is composed of four species. Two are of low frequency, - Sambucus nigra and Sorbus torminalis. Sorbus is found in old woods with a long continuous history (Willmot, 1977) and is used in eastern England as an indicator of ancient woodland (Peterken, 1974). It is found in quadrat 52, an abandoned oak coppice. The other two species, Ilex aquifolium and naturally regenerated Pseudotsuga menziesii C are both found under deciduous canopies. Both species colonize open sites and most probably regenerated many years ago, when the sites were cleared and are remnants of that time.

The upper shrub layer in Tavistock Woodland is less of a reflection of a natural vegetational response than of management. When these species become too large and interfere with the B - Plan units, they are removed. Those individuals remaining are primarily on the edges of rackways, units and rides.

4.5.5. The relationship between canopy type and shrub layer

The lower shrub layer

The relationship between the canopy types and the lower shrub layer is illustrated in the TWINSPAN classification (Table 4.13.). The quadrats of the major canopy types are divided into four TWINSPAN groups as follows:

Groups	Quadrats
1 - Mixture of species	51,56,15,23,55
2 - Mixture of species	44,17,40,54,13,14
3 - Pinus	4,9
4 - Quercus	32,33,52,53

The first two groups are mixtures of quadrats with different canopy types. Three quadrats in groups 1 and 2 are the Pseudotsuga menziesii quadrats 44,55 and 56. 44 and 55 are classified next to each other in the first division (Table 4.13.) but are separated at the second division. If the TWINSPAN table is regarded more as a continuum rather than as a series of independent groups (Gauch, 1982), then the shrubs of these quadrats are similar. Quadrat 56 appears in the same group with 44 and 55 in the first division, with 55 in the second division and is separated from 55 in the fourth division (Table 4.13.). In the DECORANA ordination, the position of these three quadrats is clear and they appear together in the major canopy type space - Pseudotsuga (Figure 4.4; groups 1 and 2).

Group 1 (Table 4.13.) includes the two quadrats of the major canopy type Larix and Pinus, quadrat 15 and 23. They are classified next to each other but with three other quadrats of different canopy types. However in the fourth division (Table 4.13.) they are separated out, together with quadrat 55 with Sorbus aucuparia as an indicator. Sorbus is a light demanding species and benefits from the lighter Larix and Pinus canopies of quadrats 15 and 23, as well as from the B - Plan clearing in quadrat 55. In the DECORANA ordination (Figure 4.4; group 1), 15 and 23 are a distinct group, although the rest of the quadrats in this group 1 are scattered.

Quadrats 17,40,13,14,51 and 54 do not exhibit particularly clear patterns in either the TWINSPAN or the DECORANA analyses (groups 1 and 2, Table 4.13. and Figure 4.4.). All but 51 appear, in the centre of the TWINSPAN table, where the less differential species are classified (Hill, 1979c). Quadrats 40 and 54 show some cohesiveness in that they are classified (group 2, Table 4.13.) and ordinated (central group 2, Figure 4.4.) closely. They both have Quercus in their canopies,

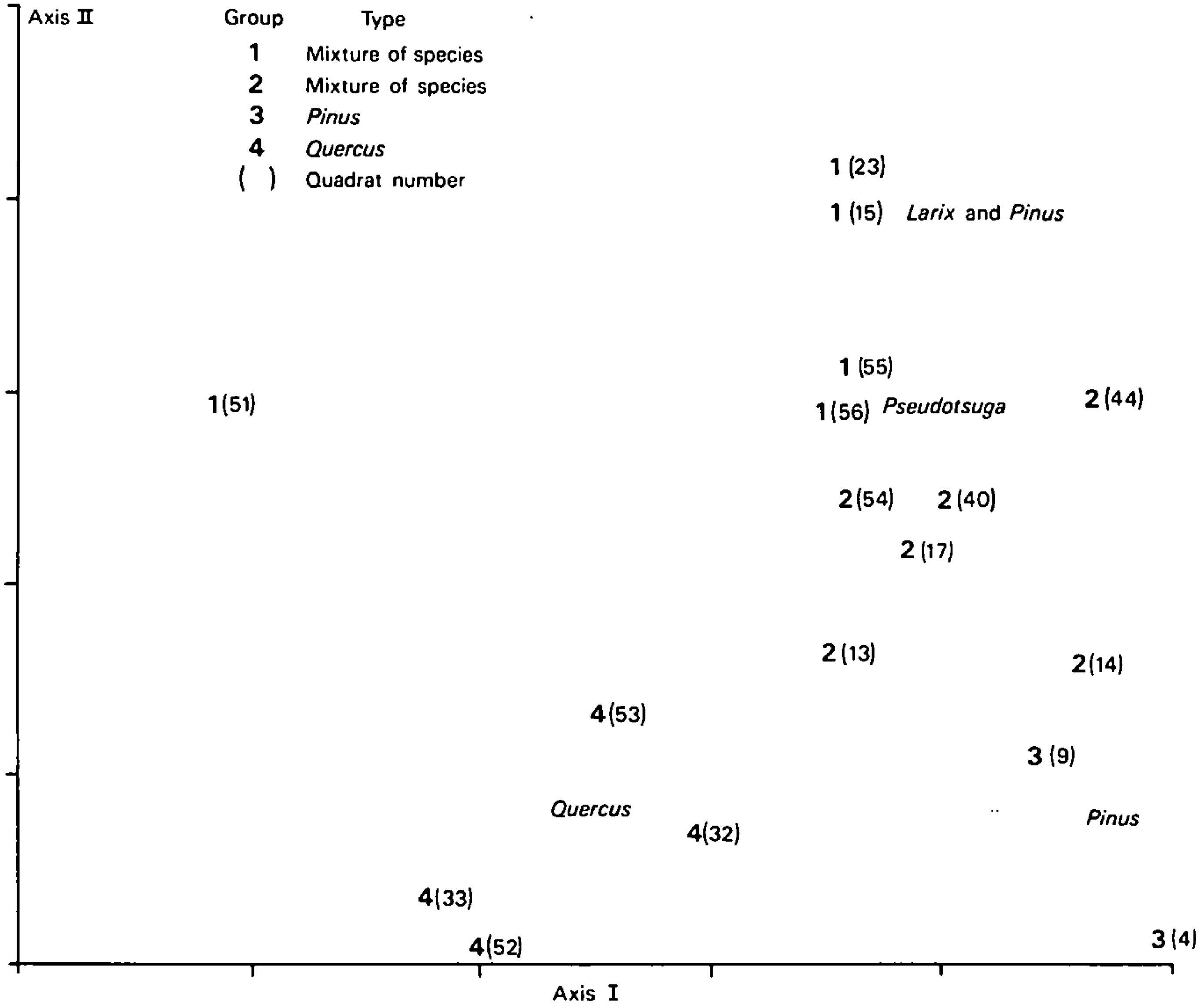

Figure 4.4. DECORANA site ordination of data from the phase III lower shrub layer survey showing TWINSPAN groups and major canopy types

with B - Plan units. The B - Plan trees in quadrat 40 were large enough to be included in the tree survey, so 40 is classified with 54, not on the basis of B - Plan, but on the similarities in the naturally regenerated understorey species. Quadrat 51 in group 1, with its sparse understorey appears on the extreme left side in both the classification and ordination (Table 4.13., Figure 4.4.).

The third and fourth site groups (Table 4.13.), include quadrats 4,9,32,33,52 and 33. In the first site division, these six are grouped together with Sorbus aucuparia, Salix cinerea and naturally regenerated Pseudotsuga as indicators. However in the third division (Table 4.13.), quadrats 4 and 9 become a distinct group 3. Quercus cerris is the indicator for this pair, Betula spp. with Tsuga heterophylla and Thuja plicata in the B - Plan units are preferentials. On the DECORANA ordination quadrats 4 and 9 appear together in the major canopy space - Pinus (group 3, Figure 4.4.).

TWINSPAN group 4 (Table 4.13.), consisting of the Quercus canopied quadrats 32,33,52 and 53 which is a major canopy type, is separated out clearly in the third site division. Naturally regenerated Pseudotsuga is the strongest preferential for this group. These quadrats appear as a distinct group in the DECORANA ordination (group 4, Figure 4.4.) in the Quercus major canopy type group space.

The upper shrub layer

The relationship between the canopy types and the species in the upper shrub layer is not as clear as it is with the lower shrub layer. This obscurity appears to be caused primarily by management operations removing the larger individuals of the upper layer when they interfere with the B - Plan units. This tends to reduce the majority of the understorey to two metres or less and selectively favours individuals growing at edges, allowing them to grow up into the upper shrub layer between two and five metres.

The quadrats of the upper shrub layer survey are divided into the following TWINSPAN groups (site groups, Table 4.15.):

Group	Quadrats
1 - Pseudotsuga	44
2 - Quercus with B - Plan	17,40,54
3 - Mixture of species	56,4,15,23,55
4 - Mixture of species	9,13,33,51
5 - Quercus	52,53

The first group 1 consists only of quadrat 44, an unusual quadrat with a Pseudotsuga canopy, shown on the extreme right of the DECORANA ordination (Figure 4.5.). Unlike the other Pseudotsuga quadrats, 55 and 56, this quadrat has an unusually high number of naturally regenerated species in the upper shrub layer. This undoubtedly stems from the management history of quadrat 44 where continual destruction of the B - Plan trees by rabbits resulted in B - Plan trees many years younger than the age of the B - Plan clearings. Hence the trees in the upper shrub layer have not yet interfered with the B -Plan sub-units and therefore have not been removed as they have in quadrats 55 and 56. These differences are again shown in the quadrat ordination (Figure 4.5.).

Group 2 consists of three quadrats, two of which are quadrats with predominantly Quercus canopies, with B - Plan units, quadrats 40 and 54. They are also classified together in the lower shrub layer analysis (Table 4.13.). Quercus is the indicator for this group which also includes quadrat 17, a Picea abies canopy with much Quercus regeneration in the B - Plan sub-units. In the DECORANA ordination the three quadrats in group 2 are scattered (Figure 4.5.).

The third and fourth groups (Table 4.15.) are mixtures of quadrats with different canopies. As in the lower shrub layer classification,

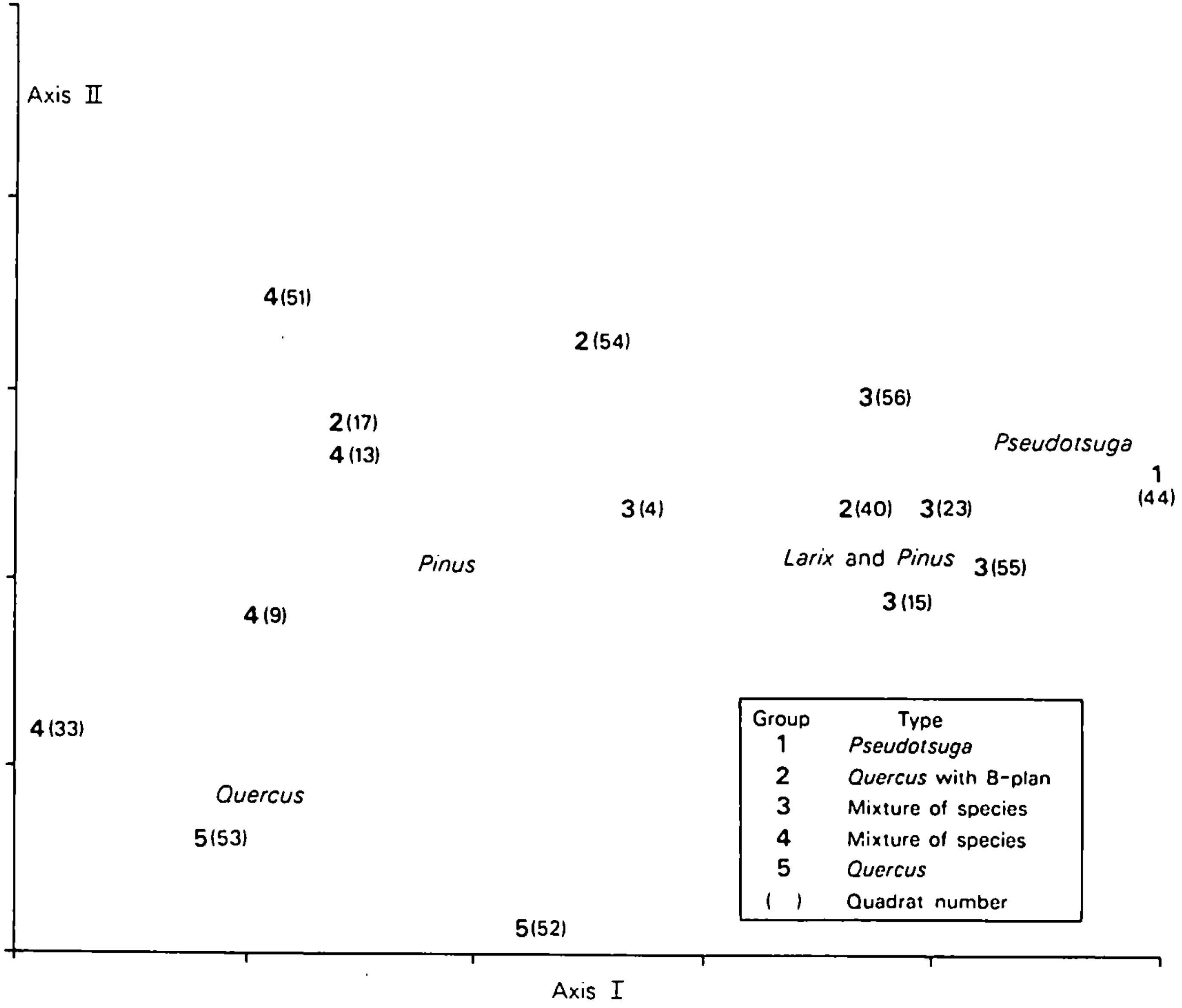

Figure 4.5. DECORANA site ordination of data from the phase III upper shrub layer survey showing TWINSPAN groups and major canopy types

(Table 4.13.), the two Larix and Pinus canopies quadrats 15 and 23 are classified together. They are also ordinated next to each other in Figure 4.5.(labelled Larix and Pinus). The other quadrats in the same group 3 appear near them in the ordination. The quadrats of group 4 (Table 4.15.) are widely spaced on the left-hand side of the ordination (Figure 4.5.).

The fifth group 5 is the Quercus canopied quadrats, 52 and 53. Like group 4 of the lower shrub layer (Table 4.13.), the indicator for this pair of quadrats is naturally regenerated Pseudotsuga. Fagus sylvatica, which regenerates naturally under the Quercus canopy is a strong preferential for group 5. In the ordination (group 5; Figure 4.5.), these two quadrats appear as a distinct group in the space labelled Quercus.. Although quadrat 33 is not grouped with 52 and 53 in the TWINSPAN Table 4.15., it is classified near them and appears as a member of group 4 but positioned near the Quercus space (Figure 4.5.).

4.5.6. The relationship of the shrubs with B - Plan management

In phase III there are more individuals in the lower shrub layer than in the upper layer, 147 versus 72. More low growing shrubs escape management cutting than do the larger upper layer shrubs, which interfere more frequently with B - Plan sub-units. As in regularly cut coppice, where the shrub layer is between 2.6 and 3.2m at the end of a 10 to 12 year rotation (Rackham, 1980a), the form and heights in the shrub layers are the result of management.

Quadrats with B - Plan units tend to be richer in shrub species and to have higher total cover values for these species than those without B - Plan units (Tables 4.10. and 4.15.). Two species of special ecological value are particularly abundant in quadrats with B - Plan units (section 4.5.4.). The first is Betula x spp., a soil-improving species (Dimbleby and Gill, 1955; Miles, 1981), (capable of supporting 229 insect species (Southwood, 1961).) The second is Quercus x rosacea, capable of supporting more insect species than any other native British tree, 284 species (Southwood, 1961).

Betula x spp.

Betula is present in 12 of 17 quadrats in the lower shrub layer survey and nine of 15 quadrats in the upper shrub layer survey. It is absent in both layers of the quadrats without B - Plan units (Tables 4.13. and 4.15.) and particularly abundant in the lower shrub layer in quadrats with B - Plan (Table 4.13.).

Betula is especially abundant throughout the lower shrub layers of the light Pinus canopied quadrats 4 and 9 (Table 4.10.). Unexpectedly, the darker Picea canopied quadrats 14 and 17, also have abundant Betula in the lower shrub layers (Table 4.13.). However instead of being distributed throughout the quadrat as in quadrats 4 and 9, the Betula in 14 and 17 is concentrated in and around B - Plan sub-units. 24 of the 28 small, single-stemmed new individuals in quadrat 14 are growing in B - Plan sub-units and 18 of the 30 in quadrat 17 are also in B - Plan sub-units.

The apparent affinity Betula has for B - Plan sub-units is explained by its ruderal strategy. Its seeds are unable to penetrate leaf litter because its radicle is small. Miles (1974) found that it needed at least $25cm^2$ of bare soil for establishment. Likewise its seedlings are light-demanding and shade intolerant (Harding, 1981). Hence B - Plan sub-unit clearings appear to satisfy the requirements for Betula seedling establishment by providing bare soil and sufficient light.

Quercus x rosacea

Quercus is present in all the quadrats of the lower shrub layer survey (Table 4.13.) and in 11 of the 15 in the upper shrub layer survey (Table 4.15.). It is a species intolerant of closed canopies (Newbold and Goldsmith, 1981). Hence it is particularly abundant in the lower shrub layer of those quadrats with B - Plan units classified in the centre of the TWINSPAN Table 4.13.

Likewise, in the upper shrub layer it is most abundant in some of the same quadrats, 17,40,15 and 13 (Table 4.15.). In quadrat 13 for example, the individuals in this upper shrub layer are in the form of small coppice stools growing near the edges of the older B - Plan sub-units. Their small diameters and growth form suggest that they were last cut when these sub-units were established in 1962. In contrast the seedling Quercus in the lower shrub layer of quadrat 13 is growing in the most recently established B - Plan sub-units.

The success of Quercus in B - Plan sub-units can be explained by its competitive strategy. It does not regenerate well under its own canopy. However it can compete well with grasses and other vegetation including Rubus agg. as the acorns have large reserves and a long taproot which enables it to reach the mineral soil thus avoiding competition with the shallower rooting herbs (Brotherton, 1973; Newbold and Goldsmith, 1981). Likewise its shoot can also elongate to out-compete the lower growing herbs. Under a canopy this etiolation is a disadvantage because the tall shoot is weaker and unlike in herbaceous vegetation, it never reaches a higher light level. Consequently Quercus is intolerant of shade. Thus B - Plan sub-unit clearings appear to provide sufficient light for seedling development, as well as for continuing growth of established individuals of Quercus in the upper shrub layer.

4.6. Trees and shrubs - a summary

1) In the canopy analysis 10 tree groupings emerged in the phase I tree survey of 50 randomly sited quadrats (Table 4.2.). These canopy types were confirmed and studied in more detail in the phase II tree survey of the 20 selected quadrats.
2) The shrub layer was studied in phase III by dividing it into upper and lower, this distinction being very much related to forestry management practice.
3) A distinct relationship between B - Plan management and the shrub layers emerged from the analysis of the phase III shrub survey. In addition to affecting the height of the shrub layers, B - Plan management encourages greater species diversity and abundance in the shrub layers in and around B - Plan units. Although shrubs are not useful for characterizing plant communities because they are easily affected by management (Rackham, 1980a), it is the management in Tavistock Woodlands that favours regeneration to two ecologically important species in the shrub layer, _Betula_ x spp. and _Quercus_ x _rosacea_.

CHAPTER 5. THE GROUND FLORA

CHAPTER 5. THE GROUND FLORA

5.1. Introduction

This chapter is primarily concerned with the first and major aim of the thesis, which was to examine the nature of the ground flora in early B - Plan units (stages I-V) and to compare the floristics under the Bradford Plan with those under other forest management types.

Disturbance and the ground flora

An important idea, which emerged during the early surveys, was that the herbaceous plants appear to respond well to the disturbances created and caused by B - Plan management. The response of herbs appeared to be more rapid than that of the shrubs which obviously need more time to establish themselves. Support for this idea comes from Givinish (1982: p. 367):

> "Herbs prosper ... in disturbed areas where the initially lower costs of support structure should give a short-lived advantage over woody plants that ultimately will overtop them."

Succession in time and space

A second concept of considerable significance to the ground flora under B - Plan is that of succession in the ground flora through the early B - Plan stages. Clearly, succession should occur in time, within each of the sub-units of a complete Bradford Plan unit. However, a very important part of the plan in ecological terms is that simultaneously, when the plan is fully implemented, succession is also represented in space within each B - Plan unit, with each successive sub-unit at one point in time representing the successional sequence in six-year intervals up to 54 years (Figure 1.1.).

A further very critical aspect of B - Plan therefore, is that the overall successional sequence which occurs under clear-fell forestry is recreated within individual B - Plan units in both time and space.

5.2. The ground flora surveys

The ground flora was surveyed in four phases representing increasing refinement of both methods and sampling. (Table 5.1.). The primary aim of first two surveys was to complete a phytosociological survey of the early stages of B - Plan, the results being an assessment of those aspects of the ground flora which are conserved and encouraged. In addition, those ecological variables of interest for conservation, cover,diversity and rarity were also studied.

A secondary aim was to quantify environmental factors, particularly edaphic and light conditions, and to study how the present management system and the past history has affected the ground flora. When the environmental controls are known, they can be separated from the effects of management and history.

This chapter is a description of the ground flora species and their associations under B - Plan management derived from the first two surveys and of how they relate to past history and management.

5.2.1. Phase I - 1979 ground flora survey

In the first survey, the 50 randomly located quadrats were sampled twice in and during the growing season. The second visit was made to check on any late species arrivals. The 10 $1m^2$ subquadrats (Figure 3.2.) in each $400m^2$ quadrat were examined for species presence/absence. For analysis by classification and ordination, the number of sub-quadrats in which a species appeared within each quadrat was totalled. For example, a species present in eight sub-quadrats out of 10 had 8 or 80% as a measure of abundance.

Table 5.1. The ground flora surveys

Phase I	- 1979	-	50 quadrats - 10 x $1m^2$ sub-quadrats per quadrat
Phase II	- 1981	-	20 quadrats - 8 to 18* x $\frac{1}{2}m^2$ sub-quadrats per quadrat
Phase III	- 1982	-	20 quadrats - 8 to 18* x $\frac{1}{2}m^2$ sub-quadrats per quadrat - re-check in August and September of the quadrats of phase II during the shrub survey
Phase IV	- 1982		8 quadrats - 8 to 18* x $\frac{1}{2}m^2$ sub-quadrats per quadrat - detailed studies of the ground flora in relation to light (Chapter 6), seed banks (Chapter 7) and phenology (Chapter 8).

* = a variable number of sub-quadrats per quadrat depending on the number of B - Plan sub-units

DECORANA uses this information directly. However, the TWINSPAN analysis required the following pseudospecies cut levels.

0 = $\leqslant$10%

1 = >10% and $\leqslant$20%

2 = >20% and $\leqslant$ 30%

3 = >30% and $\leqslant$ 40%

4 = >40%

These cut levels were chosen in order to avoid the over-weighting of dominance as is recommended in the manual (Hill, 1979c). Inclusion of too many higher cut levels over-weights the effect of dominance.

The aim was to identify possible species indicators and not the dominant species which, with abundance from British vegetation, often tend to mask information on species diversity and composition (Bunce, 1982).

> "The importance of the indicators is emphasised by this approach because of the high degree of similarity of the cover species in very dissimilar ecological conditions, a consequence of the limited number of dominants in ground vegetation in British woodlands." (Bunce, 1982: p. 39)

In phases II and III, the cut levels were closed to the default ones suggested by Hill (1979c) - 0,2,5,10, and 20% - because the data were collected using a Domin scale which has five levels of abundance between 0 and 20%.

5.2.2. A description of the main ground flora community types derived from TWINSPAN classification

The TWINSPAN classification (Table 5.2.), divides the 50 quadrats (Figure 5.1.) into five main groups as follows:

Group 1 - quadrats: 40,50,35,36,42,47

Group 2 - quadrats: 26,43,27,32,33,37,34,38

Group 3 - quadrats: 31,13,15,23,48,2,9,10,14,45,3,5,6,7,
12,19,24,25,28,39,11,20,21,30,22

Group 4 - quadrats: 17,1,4,18,46,8,16,29

Group 5 - quadrats: 41,44,49

Groups 1 and 2

These are composed mainly of quadrats with <u>Quercus</u> canopies. Nine out of the 14 in these groups have either <u>Quercus</u> alone or in combination. All are in areas that have been continuously coppiced or covered by a woodland canopy since the 1500's (Figures 1.5. and 5.1.).

Table 5.2. TWINSPAN classification table - phase II ground flora survey

```
Groups          1      2              3               4     5
               45334424233333311 24  114     11222312233 1  14 1344
               00362763723740135362904533672945891010271406869149

 37 CALL VULO  -------------5-------2--5--25--22-24555725 53--   00000
  2 BLIN ACUT  --------------------------------2---------   000010
 27 DIPL ALBI  ------------2--2--------2--------- -225--25---   000010
 67 FEST TENU  ---------------------------------5-----------   000010
 70 MOLI CAER  -------------------2--2----------5-5---------   000010
 71 POAA ANNUA ----------------------------------------2----   000010
 84 QUER CERR  ----------------------------------------2----   000010
 95 PICE SITC  ---------------------------------------2-----   000010
 98 PINU SYLV  ----------------------------------------5----   000010
 16 PLEU SCHR  ---------------2-----------------------2-----   000011
 19 PSEU PURU  -------------------455--2--------------2--2----2-3   00010
  7 DICR SCOP  -----2---232---23-5--3---------3----223--3253----   000110
 17 POLY COMM  -------2--------32-5------------------------   000110
 99 PSEU MENS  ---2--------22------232----55--2-53--3----------   000110
105 ROTT SJUM  3--2----------322-------3--432332---2-2------2-----   000110
  4 BRAC VELU  -------------------------2-5-------------------   000111
 20 RHYN CONF  ----------------2-----2--------------------------   000111
 28 LEJE CAVI  -------------------------------3---------------   000111
 29 LEPI REPT  -------------------3----------------------------   000111
 42 GALI SAXA  ----------------------2-------------2-----------   000111
 55 SOLI VIRO  ---------------------------2--------------------   000111
 66 FEST RUBR  ------------------------2-----------------------   000111
 72 POAN EMOR  --------------------------------2---------------   000111
 76 CAST SATI  ------------------------------4-----------------   000111
 86 SALI CINE  ---------------------2----2---------------------   000111
 24 ULOT CRIS  ---233-----3------------------2-----------------   001000
 34 DRYO FILI  ----2--------------------------------------------   001000
 36 ANEM NEMO  33--2--------------------------------------------   001000
 48 LUZU SYLV  --------3----------------------------------------   001000
 63 DACT GLOM  ----------2--------------------------------------   001000
 75 CARP BETU  -2-----------------------------------------------   001000
 78 CRAT MONO  ------4------------------------------------------   001000
 88 VIBU OPUL  --3------3--22-----------------------------------   001000
  6 DICR CIRR  -4-----2--2--------------------4-----------------   001001
 11 HYPN FILI  -5-222325554-------23-3-2---------------2---2--3-----   001001
 25 CALY FISS  ------2-----------------------------------2---------   001001
 49 MELA PRAT  ----------5-22----5----------5----------------------   001001
103 BARE SOIL  ---22-53--5234-----------2-----25-----------3-------   001001
106 ROCK STON  --------4-2---3----------------------------3--------   001001
  9 HYPN CUPR  5-2----254--3------22---222--2---2-52---22-232-------   001010
 73 ACER PSEU  ------5-------------------------------------5--3-----   001010
 79 FRAN ALNU  2-----------------2-----------------------2--2-----   001010
 89 FAGU SYLV  --2--2---352222---3-------2-3--25--2-2-3--24---------   001010
 92 QUER XROB  2-22-22223245224-55342--5-555534524--3-52-55-2-------   001010
 14 MNIU HORN  2---2----------22--4---------2----------------------   001011
 83 RHOD PONT  ------5------------234-----------2---3--------------   001011
 10 HYPN ERIC  22-5--2-3455555-254555255555555554333525555555--5   001100
 12 HYPN RESU  5-4455555552-0----5555554544342352525-5555-545-3-   001100
 13 ISOP ELEO  ----33-53454---5---43-2--25223-352--32---5-43-4---2-   001100
 30 LOPH BICU  3245-2-5-5--3445-52-3552555455234333555555555-35   001100
104 BRAS LOOS  --55----22233-52-4--55-555552-5345---555----2---23   001101
 74 BETU XSPP  --24--------22------2-45-2542-252--------22334-4550--   00111
  5 DICR HETE  --22----233--3-2------------2222-----2-4----2333----23   01000
 77 CORY AVEL  2223425-2---22---3------------------2-2-----2--2-----22   01000
 81 ILEX AQUI  ------2-2553222-------2----32------------2-----------2-   01000
  8 EURH PRAE  44553--55--255-5-52555555555329445555553553445205 2   010010
 43 HEDE HELI  5552553455555555-5555555--55555-554535555-5--55055   010010
 46 LONI PERI  5555555-55555435-555554355-525-5555555-5-55555-5545   010010
 52 RUBU FRUT  5555555-5554555 5-555552555555-555555555555255-5055   010010
 58 VACC MYRT  -3-5-2-2-55-55-2-55-523---42-3-55-222-52---2-2-5--   010010
 62 AGRO CAPI  2------------2---4-4-3----32334-223-234-454345-2-522   010011
 18 POLY FORM  3-------2-----55-----------4--3---3--------------2---4   01010
 35 PTER AQUI  544--3--2-2-55---53-3---3352-555555555----3----535   01010
 87 SORB AUCU  --3-2-----22222-2--2-44--22-323-25232-------2-------43   01010
  3 BRAC RUTA  -------------------------3---------2--22--------------3-   01011
 38 CARE PILU  2-----------2--3-------2-------2--2---43334------3---5-2   01011
 57 ULEX GALL  -----------------------------------5---------5--------5--   01011
 31 ATHY FILI  -24242-----------2-2-2---2-3-------------------------3-   011
 44 HYPE PULC  2------------2--2------------------2---3-------------2-2   011
 47 LUZU PILO  5----------------3-52----------------------------------5--   011
 69 HOLC MOLL  33--5-------------------------------2-----------------5--   011
 32 BLEC SPIC  -23234-------33-4------------------2--------32-------455   100
 39 CHAM ANGU  ----------------2----------------------------------5-2   101
 41 EPIL ROSE  ----------------2---------------------------------------2   101
 56 TEUC SCOR  ---------3-2--2-------2--------------------------52-   101
 59 VERO OFFI  ----------------2-------------------------------------2--   101
 23 THUI TAMA  -----------------------2-------------------3-----------5   110
 33 DRYO DILI  2-3-2------------22----------------------24433-------55   110
 45 JUNC EFFU  ----------------2----------------------2---------------5--   11100
  1 ATRI UNDU  --------------------------------------------------------4-   111010
 15 PLAG DENT  ---------------------------------------------------------3   111010
 21 RHYT SQUA  -- ------------------------------------------------------5   111010
 22 RHYT TRIQ  ----- -------------------------------------------------2--   111010
 50 OXAL ACET  --------------------------------------------------------42   111010
 51 POTE EREC  -------------------------------------------------------2--   111010
 53 RUME CRIS  -------------------------------------------------------5--   111010
 54 SARO SCOP  -------------------------------------------------------5--   111010
 60 VIOL RIVI  -------------------------------------------------------2-2   111010
 61 AGRO CIOA  -------------------------------------------------------5--   111010
 64 DESC CAES  --------------------------------------------------------2-   111010
 82 PRUN AVIU  ---------------------------------------------------------2   111010
108 POLY AURA  --------------------------------------------------------3-   111010
109 CALY MUEL  --------------------------------------------------------2-   111010
 40 DIGI PURP  -----------------3-- -2----------------------------------525   111011
 68 HOLC LANA  ----------------2-2-- -------------------------------------525   111011
 65 DESC FLEX  ---------------------------------------4-----------5--   1111

               0000000000000000000000000000000000000000111
               0000000000001111111111111111111111111111111
               0000011111111000000000000000000000001111111
               0111100111111000011111111111111111100000011
                      000011011110000000000000000011111000001
                                0000011111111110000101111
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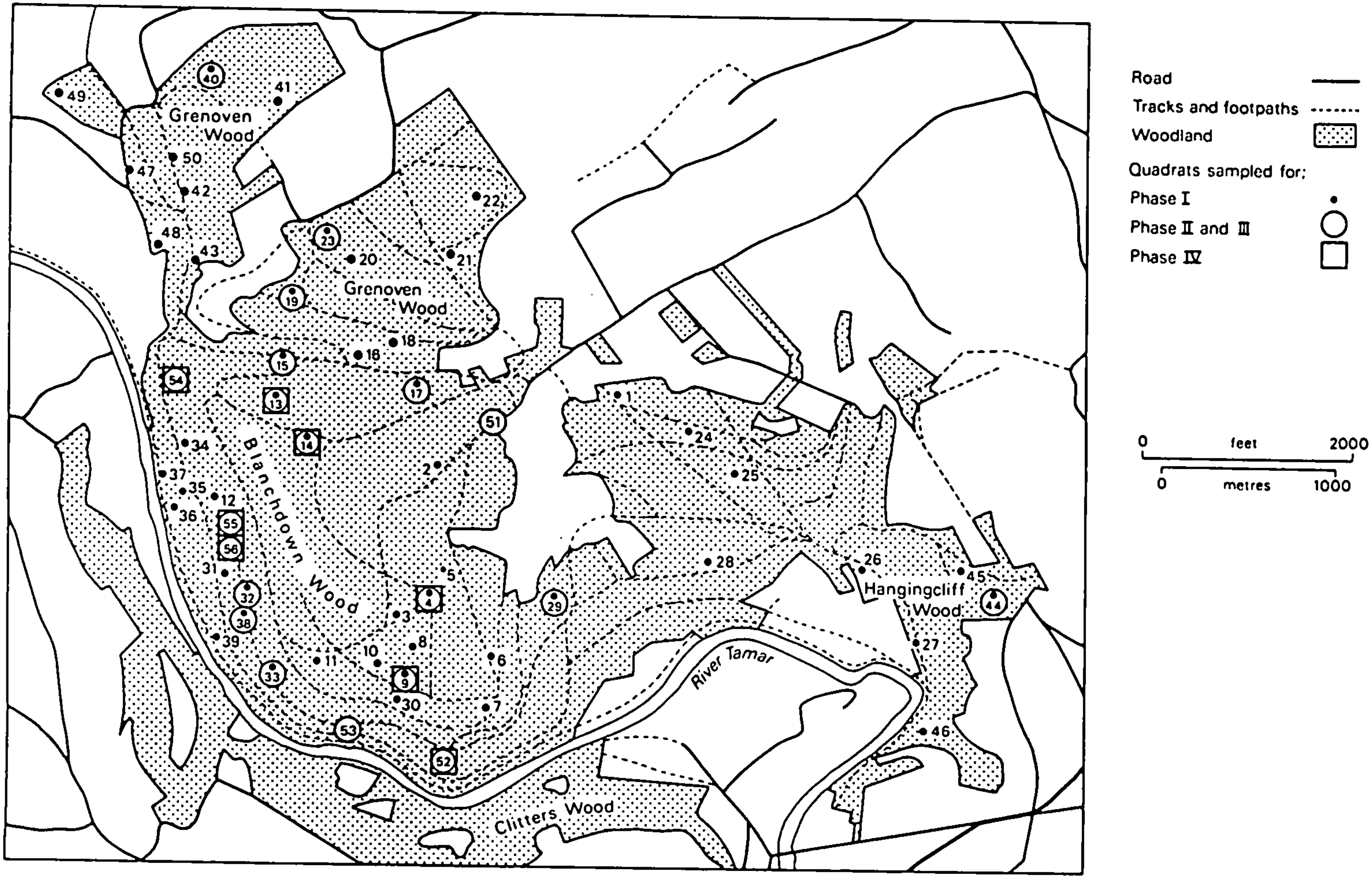

Figure 5.1. Location of quadrats in Blanchdown, Grenoven and Hangingcliff Woods

The indicators for these two groups are Corylus avellana and bare soil. The Corylus could well be a remnant of the coppice layer in a coppice with oak standards. Corylus has no strong natural colonizing ability and hence is most likely a result of past management (Peterken, 1974). The bare soil is the result of more rapid litter decomposition relative to that of the coniferous litter (Packham and Harding, 1982). Preferentials for these two groups include Dicranoweisia cirrata and Hypnum cupressiforme var. filiforme, associated species found in humid, shaded situations (Smith, 1978) as afforded by the mature, closed Quercus canopies.

Groups 1 and 2 are separated at a later division (Table 5.2.). The Quercus quadrats in group 1 are comprised of single-stemmed individuals and several with a mixture of other species in the under-storey. For example, quadrat 50 has a Quercus canopy that is single-stemmed with an under-storey of Carpinus betulus, which is in a multi-stemmed coppice form. Carpinus may have been planted with oak in an attempt to discourage epicormic growth on the Quercus (Dyer, pers. comm.). All quadrats but 47 in group 1 have B - Plan units. The quadrats in group 2 have both single-stemmed and multi-stemmed Quercus. Unlike the quadrats in group 1, Ilex aquifolium, an indicator, is abundant in the under-storey of group 2 quadrats. This species, which needs high light intensity to regenerate (Harper, 1977), most probably invaded quadrats 33 and 37 when the Quercus was last coppiced and remains overtopped by the oak, because it has a low compensation point.

Quadrat 27, with single-stemmed Quercus and a mixture of other species, including Larix and Abies alba, has Ilex in its under-storey probably because the patchwork of species of varied growth rates has provided light and time for Ilex to regenerate. Quadrat 32, with planted *Fagus* and *Quercus* with single stems, also has *Ilex* a typical associate of this canopy on acid soils (Brooks, 1980). Quadrats 27 and 26 are the only quadrats in group 2 with B - Plan. *Hypnum cupressiforme* var. *ericetorum* is the other indicator for group 2.

The indicator for group 1 is *Athyrium filix-femina* and the preferentials for group 1 include *Mnium hornum*, *Dryopteris dilitata*, *Anemone nemorosa*, *Ulota crispa* and *Holcus mollis*, all indicators of the damp, shaded conditions expected under the single-stemmed closed *Quercus* canopies (Smith, 1978; Rackham, 1980a; Sissingh, 1982). *Mnium hornum*, which is unable to emerge through litter (Packham and Harding, 1982) and the amount of bare soil, suggests that the litter turnover rate is quicker than under the coniferous canopies. The preferentials for group 2 include *Melampyrum pratense*, *Teucrium scorodonia* and *Carex pilulifera*. *Melampyrum* and *Teucrium* are light demanding (Sissingh, 1982). Both are coppice ground flora species which die out as the canopy closes (Packham and Harding, 1982). The *Carex* is a plant of woodland margins (Tansley, 1939), suggesting it, too is a light-demanding species. These species suggest that this set of group 2 quadrats are lighter than group 1, as would be expected of old, former coppice stands.

Groups 3 and 4

Group 3 is a large group consisting of quadrats that have been continuously wooded or either heath or farmland in the past. The canopies consist in the main, of coniferous species. This group is a transition group between the *Quercus* groups 1 and 2 and group 4, which was previously either heath or farmland on the upper plateau (Figures 1.5. and 5.1.). Groups 3 and 4 are separated from groups 1 and 2 by the group 3 and 4 indicators, *Agrostis capillaris*, Calluna vulgaris, Lophocolea spp., and Hypnum cupressiforme var. ericetorum. The Agrostis is the result of previous pasturing under the Quercus canopy (Tansley, 1968), the past coppice cycle or most probably a remnant of the heath or farmland that was afforested (Figures 1.5. and 5.1.). Agrostis is not present in seven of the 16 quadrats in groups 3 and 4 which have always been covered by a canopy, but is present in all but three of the 18 heath or farmland quadrats. The Agrostis may not survive as seed through a 50 year conifer rotation (Hill and Stevens, 1981), but in the quadrats of groups 3 and 4, it thrives under the light canopies of Larix and/or Pinus, as well as in B - Plan units. Calluna is, of course, a heathland species and as such is found in all the heathy quadrats of group 4, but it is also a characteristic coppicing plant of oak woods (Rackham, 1980a). It is killed by shade but remains in the seed bank (Rackham, 1980a). Hence it is not found in the Quercus groups 1 and 2. Calluna is however found in five quadrats out of a total of 16 covered by a canopy in group 3 and as such may be a product of clear-felling and replanting with a coniferous canopy or opening up of the canopy by B - Plan. Hypnum is associated in upland woods and heaths with Calluna (Watson, 1968) and although present throughout the Tavistock Woodlands, is particularly abundant in the former heathland area.

Group 3 is separated from group 4 in a later division of TWINSPAN (Table 5.2.). Pteridium aquilinum is the indicator for group 3. Pteridium was originally a woodland species (Tansley, 1939). Hence of the seven quadrats without Pteridium in group 3, two are on former heathland and two have Pseudotsuga canopies, which may have supressed the Pteridium prior to 1960. It survives the thicket stage of a dark canopy like Picea sitchensis, but dies out later (Hill, 1979a). Athyrium filix-femina, Dryopteris dilitata, *Carex pilulifera*, *Ilex aquifolium*, *Sorbus aucuparia*, *Vaccinium myrtillus* and naturally regenerated *Pseudotsuga menziesii* are all preferentials for group 3.

Group 4 consists of quadrats which are found only in areas that were formerly heath or farmland (Figures 1.5. and 5.1.). *Calluna vulgaris* and *Betula* spp. are indicators for this group separating it from group 3. Other heathland species including *Molinia caerulea*, *Agrostis capillaris* and *Frangula alnus* are the preferentials for this group. *Molinia* and *Calluna* are Bunce's (1982) indicators for peaty, podzolic soils either in the open or in woodland. *Frangula alnus* is one of the few shrubs found on podzolized soils in heathy oakwoods (Tansley, 1968) and with *Molinia* indicates soil moisture (Rackham, 1980a; Genssler, 1982). The canopies in group 4 are light. Six of the eight quadrats have either *Pinus* or *Larix* canopies. Quadrat 17 with a *Picea abies* canopy has some *Pinus* trees as well as a well developed B - Plan unit. Quadrat 8 has a dark canopy of *Picea abies* and *P. sitchensis* but has an opening in this created by a B - Plan unit.

Group 5

Group 5 is an unusual group of three quadrats, which is separated from the rest of the 50 quadrats in the first division (Table 5.2.). Quadrat 41 is a new plantation on a site that, which from historical records, appears to have always been wooded (Hamilton, pers. comm.). Quadrat 44 is a *Pseudotsuga* plantation with a B - Plan unit on what was formerly heath or farmland in 1750 but was recorded as plantation in 1835 (Figures 1.5. and 5.1.). Quadrat 49 now has a *Larix* canopy with some *Pseudotsuga* with B - Plan and is located in what is called Scrubtor Plantation, suggesting that this was an unwooded site which was afforested probably in the 1800's, when many such sites were planted (Rackham, 1976). The indicators for this group are Digitalis purpurea, Holcus lanatus, and Blechnum spicant. Chamerion angustifolium, Oxalis acetosella, Dryopteris dilatata and Viola riviniana are among the preferentials for this group. Digitalis, Dryopteris, Oxalis and Blechnum are Bunce's indicators for acid brown earths either on wooded or open sites. Holcus lanatus is ubiquitous on good soils (Tansley, 1968). Digitalis marks areas of enhanced fertility on acid soils where phosphate is not persistent (Rackham, 1980a). Oxalis, which avoids very acid soils (Tansley, 1939), shows a preference for base-rich soils, such as slopes whose acidic soil may be modified by run-off (Pigott, pers. comm.). Sambucus niger is in the shrub layer of quadrat 44 - another indicator of phosphate (Tansley, 1968; Harper, 1977; Rackham, 1980a). These species suggest that the soil under these three unusual quadrats may have increased fertility in common. All three border on farmland and quadrat 44 certainly may have been farmland in the 1700's and early 1800's. (Figures 1.5. and 5.1.) The increased fertility could be the result of liming, a practice prevalent on the acid soils in this area.

5.2.3. The species ordination

The general trend in the DECORANA species ordination (Figure 5.2.) from the bottom to the top is from shady, damp-loving woodland species to light-demanding heath species. A line has been drawn on the ordination which roughly separates these two vegetation types (Figure 5.2.).

The indicators for TWINSPAN groups 1 and 2, which separate them from groups 3 and 4, Corylus avellana and bare soil, fall below this line (Table 5.2.). Likewise the indicators for group 2 separating it from group 1, Ilex aquifolium and Hypnum cupressiforme

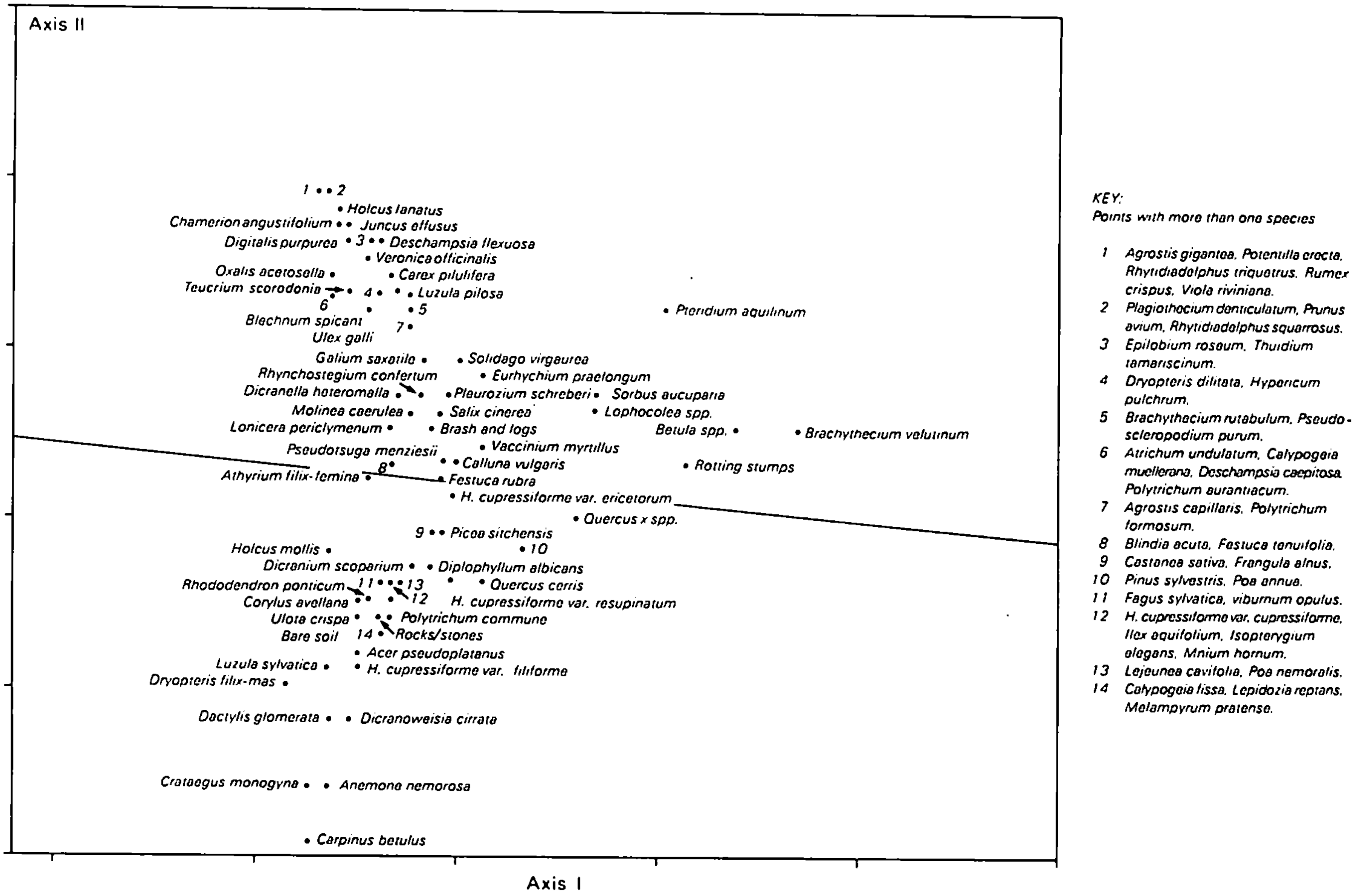

Figure 5.2. DECORANA species ordination of data from the 50 quadrats in the first survey - phase I

var. ericetorum are positioned below the line.

Five of the indicators and preferentials for group 1, Athyrium filix-femina, Mnium hornum, Anemone nemorosa, Ulota crispa, Holcus mollis are below the line grouped toward the left side. The sixth preference, Dryopteris dilitata, is positioned above the line with the heath species because it also shows a preference for the humid atmosphere under Pseudotsuga canopies as well as that under the old Quercus stands, in groups 1 and 2.

The preferentials separating group 2 from group 1 include Melampyrum pratense, which also falls below the line. However, two other preferentials for group 2, Teucrium scorodonia and Carex pilulifera, both with preferences for lighter habitats, are positioned with the upper group above the line. Teucrium is a coppice plant which is abundant two to five years after felling but absent later on (Packham and Harding, 1982), while Carex is a plant of woodland margins (Tansley, 1939) associated with a member of the coppice community, Solidago virgaurea (Rackham, 1980a).

The indicators for groups 3 and 4, separating them from groups 1 and 2 are Agrostis capillaris, Calluna vulgaris, Lophocolea spp. and Hypnum cupressiforme var. ericetorum. The first three are positioned above the line while Hypnum is just below the line. Although its growth is more luxuriant in the heathy quadrats, it is in nearly all the quadrats.

Pteridium aquilinum, on the far right of the ordination (Figure 5.2.), is the indicator for group 3, the transition group of quadrats sited on former heathland as well as on continuously wooded sites. Sorbus aucuparia and Vaccinium myrtillus are two preferentials for group 3 also on the right-hand side of the top group. Sorbus is characteristic of oakwood under-storeys (Rackham, 1980a). Many of the quadrats in group 3 are on former oakwood sites. *Vaccinium* is characteristic of heathy oakwoods on podzolic soils (Tansley, 1968). The rest of the preferentials for group 3 are mixed in with those for groups 4 and 5 due to the mixture of quadrats of different origins in group 3.

Calluna vulgaris, an indicator for group 4 the strictly heath sited group of quadrats, is positioned close to *Molinia caerulea*, a preferential for this group. These species are indicators of peaty, podzolic soil (Bunce, 1982). *Frangula alnus*, another preferential for group 4 is ordinated below the dividing line because it also favours damp woods as well as the heathy oakwoods (Rackham, 1980a). As expected, the position of the preferentials show less fidelity to the two vegetation types above and below the line because they have a less strong affinity for a group than do indicators (Hill, 1979c).

The species indicators for the unusual group 5, which separate it from all the other groups, are *Digitalis purpurea*, *Holcus lanatus* and *Blechnum spicant*. These, with some of the preferentials such as *Chamerion angustifolium*, *Oxalis acetosella*, *Dryopteris dilitata* and *Viola riviniana*, are all at the top of the ordination (Figure 5.2.) showing group 5 as a distinctly different association of quadrats.

Plants characteristic of the oak coppice community, *Anthoxanthum odoratum*, *Rumex acetosella*, *Digitalis purpurea*, *Calluna vulgaris*, *Galium saxatile*, *Solidago virgaurea*, *Luzula pilosa* and *Viola riviniana* are positioned above the line, with the more light demanding species (Rackham, 1980a). They tend to be found where the canopy is lighter due either to the canopy species *Pinus* and/or *Larix* or due to clearings for B - Plan.

Naturally regenerated Pseudotsuga is also in the top grouping because being a pioneer species, it favours a lighter environment (Hosie, 1969).

Quercus x rosacea is in the bottom vegetation type grouping, but positioned near the dividing line, as it does not regenerate well under its own canopy (Brotherton, 1973) and because it also favours the areas cleared for B - Plan.

Viburnum opulus and Frangula alnus, shrubs of damp woods, (Rackham, 1980a) are also found in the bottom group. Fagus sylvatica, which regenerates better under the protection of a canopy, is in the bottom group as well (Newbold and Goldsmith, 1981).

Although the system of primary woodland indicators used in Eastern England breaks down in the oceanic climate of the Southwest (Peterken, 1974), it is interesting to note that several primary woodland indicators, Anemone nemorosa, Luzula sylvatica and Melampyrum pratense are ordinated below the line, with the Quercus woodland species corresponding to groups 1 and 2 (Table 5.2.), the continuously wooded, Quercus-canopied quadrats.

5.2.4. The quadrat ordination

The division between the two main vegetation types which contribute to the present-day ground flora, heath and oak woodland, which was clearly defined by both TWINSPAN and the DECORANA species ordination is still present in the site ordinations (Figure 5.3.). The heath quadrats have been circled. Quadrat 19 was omitted from the ordination because it caused severe distortion in the first analysis. The quadrats in TWINSPAN groups 1 and 2 (Table 5.2.) are positioned in the bottom half of the ordination (Figure 5.3.). Those quadrats strictly on former heathland (group 4), are in the

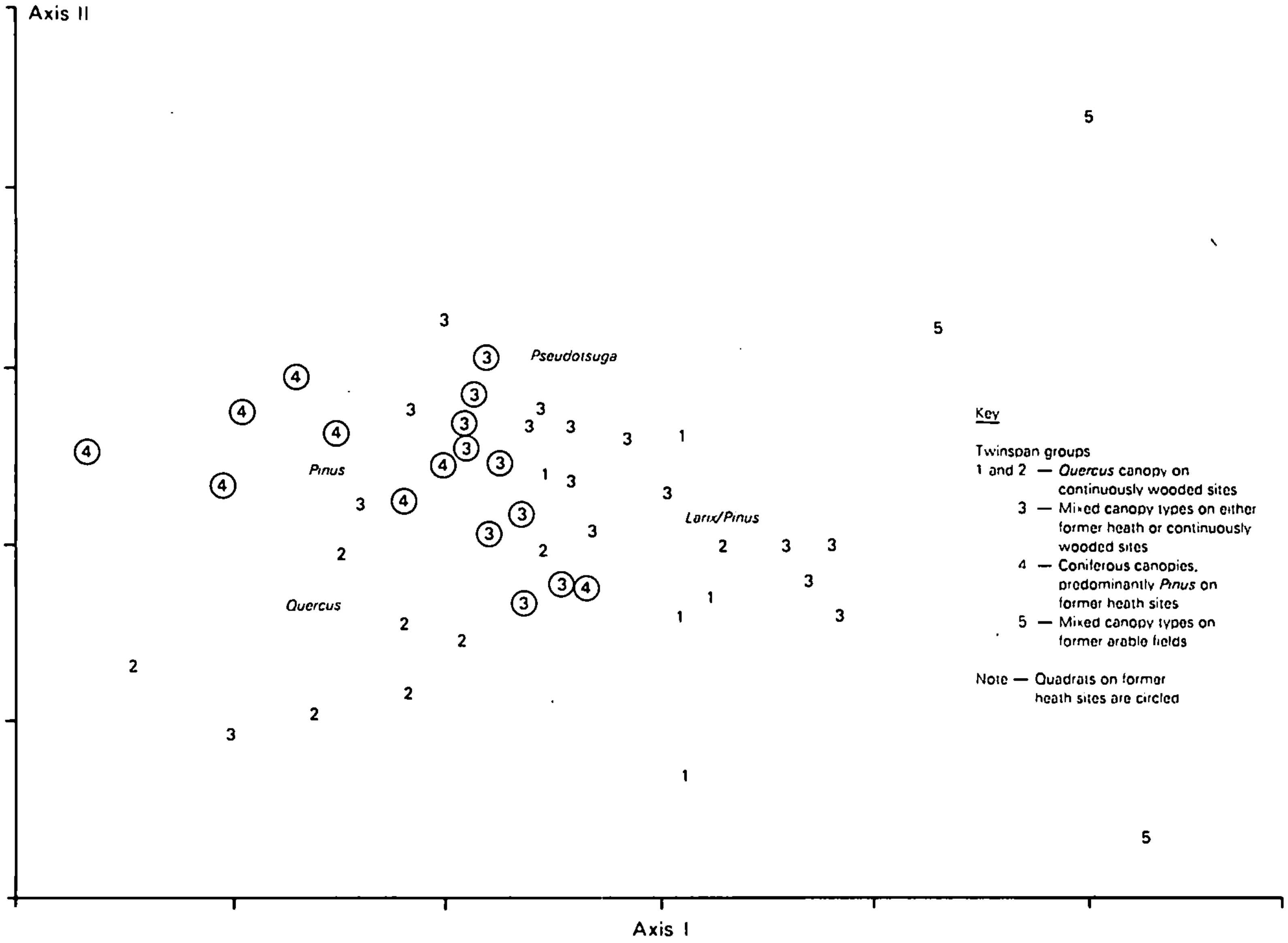

Figure 5.3. DECORANA site ordination of data from the 50 quadrats in the first survey - phase I showing TWINSPAN groups and major canopy types

upper left-hand corner, while those quadrats containing components of both communities (group 3), are in the middle, as would be anticipated. The major canopy types are also distinguishable on the ordination.

5.2.5. Discussion of the results of phase I and the selection of quadrats for phases II and III

Afforested heathland does not lose its heath species (Rackham, 1976).

> "... the present always depends upon the past, and the community of today is, at least in part, the consequence of the community of yesterday." (Salisbury in Sheail, 1982: p. 139)

This holds true for the heath in Blanchdown and its adjoining woods. However, there appears to be a change in the ground flora when coniferous canopies and B - Plan units replace Quercus canopies on continuously wooded sites. Group 3, the transition group between the continuously wooded, Quercus-canopied sites - groups 1 and 2 and the afforested heathland with coniferous canopies - group 4, illustrates this change. The indicators and preferentials for group 3 are intermixed with those of group 4 (Figure 5.2. - above the dividing line) and not with those of groups 1 and 2. These species are a mixture of some woodland species like Pteridium and Sorbus, heath species and coppice species.

The coppice species appear to be the result of the lighter canopies of Pinus and/or Larix, as well as the clearing for B - Plan. This effect is similar to coppice clearing. The woodland species are those like Pteridium and Sorbus which can tolerate the increased light intensities. The relationship between these two groups of species was described by Salisbury in 1923 and Sheail (1982).

> "... how coppicing affected the 'ebb and flow' of the two main components of a wood, namely the 'shade flora' and the 'marginal flora' (Salisbury, 1923). The relatively frequent and carefully regulated regeneration of the shrub layer under a coppicing regime highlighted in a particularly striking manner the dynamic inter-relationships that exist between the components of a plant community." (Sheail, 1982: p.138)

There is no change in the average number of species per quadrat from groups 1 and 2 through group 3 to group 4, the averages being:

Groups 1 and 2 - - 18.47
Group 3 - continuously wooded quadrats only - 17.94
- quadrats on former heathland only - 18.25
- both of the above together - 18.04
Group 4 - - 16.63

However, there is a shift in species type as well as species abundance. The shade loving species of groups 1 and 2 (Figure 5.2. - below the dividing line) become less abundant in favour of more light-demanding or tolerant species in those quadrats in group 3 which have had a continuous canopy for the past three hundred or more years (Figures 1.5. and 5.1.). In addition, there appears to be some tendency for indicators of brown podzolic and peaty podzolic soils (Bunce, 1982), as well as a more strictly heath species *Ulex gallii* to colonize these continuously canopied areas which have lost their *Quercus* canopies in favour of conifers and B - Plan. This also could seem true for the two bryophyte species. Those more indicative of open heathy places being more abundant in the relevant quadrats of group 3 (Watson, 1968).

This apparent vegetation shift may be due to a soil change which is the indirect result of replacing a deciduous oak canopy with a coniferous one. Although on acid soils such as in Tavistock Woodlands (Hogan, 1977) podzolic soils can form under *Quercus* and *Fagus* the rate of change is slower than with coniferous species

(Rackham, 1980a; Packham and Harding, 1982). Spruce and pine, in particular, acidify soil and accelerate podzolization (Miles, 1981). Pseudotsuga has less effect (Peterken, 1981). In addition, the soil under coppice cycles and presumably under B - Plan, is warmer earlier in the season. Hence the organic matter decays faster releasing mineral nutrients and nitrates and slightly acidifying the surface (Peterken, 1981).

Quadrats for phases II and III

Fourteen quadrats from the original were selected for further more intensive study. The emphasis was now on quadrats with well-developed B - Plan unitsunder a variety of canopies and not, as in phase I, on a random sample to gather information about the range of canopy types and the resultant ground flora. Table 5.3. shows the quadrats chosen for phases II and III.

In addition to meeting the above requirements, the quadrats were representative of the range of canopy vegetation types. Those from the 50 quadrats in phase I are spread over the TWINSPAN table, as well as throughout the DECORANA ordinations (Table 5.2.; Figure 5.3.). Where possible, replicates of a particular canopy type were chosen with the emphasis on the major canopy types (Table 5.3.). Although quadrats on former heath are less numerous than those on continuous canopies sites (19 versus 31), where possible, they were selected to provide a contrast to the same canopy on a continuously canopies site i.e. 4 with 9, and 44 with 55 and 56. The group of quadrats without B - Plan and still covered with a Quercus canopy were chosen in contrast to the other sites with B - Plan. Six new quadrats, numbered 51-56, were also added to the 14, to give a final total of 20. These were necessary to:

1) Avoid quadrats from the phase I group with unusual features such as relic mining work - quadrats 52 and 53

Table 5.3. The 20 quadrats chosen for phases II and III

Canopy type	Quadrat	History	Canopy age	B - Plan sub-units - year planted - stages				
				I	II	III	IV	V
Major types								
Pinus spp.	4	heath	1952	1976	1976			
	9		1952	1973	1980	1980		
	29	heath	1952	1980				
Quercus	33	c.w.+	1916	None				
	52	c.w.	1916	None				
	53	c.w.	1916	None				
Quercus with	40*	c.w.	1900	1961				
B - Plan	54	c.w.	1940	1961	1967	1973	1973	
Pseudotsuga	44	heath	1942	1964	1969	1974	1981	
	55	c.w.	1950	1961	1967	1973	1980	
	56	c.w.	1941	1961	1967	1973	1980	
Larix spp.	13	c.w.	1945	1962	1968	1973	1980	1980
with or without	15	c.w.	1942	1961	1967	1974	1979	
Pinus spp.	23	c.w.	1921	1961	1967	1973	1980	
Minor types								
Picea abies or	14	heath	1951	1973	1980	1980		
P. sitchensis	17	heath	1942	1962	1968	1974	1980	1980
Fagus and *Larix* spp.	51	heath	1930	1962				
Mixed	32	c.w.	cleared in 1981					
plantations	38	c.w.	cleared in 1975					
	19	c.w.	cleared in 1968					

\+ c.w. = continuously wooded

* Quadrat 40 has one *Larix* spp.

2) increase the sampling of B - Plan units - quadrats 54, 55 and 56.

3) increase the sampling of major canopy types - quadrats 52,53,54,55 and 56.

4) sample unusual canopies - quadrat 51.

Quadrat 32, with a Quercus and Fagus canopy, was felled in 1981 and hence was added to the mixed plantation group making a good sample of different aged plantations (Table 5.3.).

5.3. Phase II - 1981 ground flora survey

The aims of this more detailed survey were:

1) To examine to floristic composition of the early stages of B - Plan; to compare species composition with non-B - Plan sites and to look for similarities and differences between floristics under B - Plan and clear-fell systems.

2) To study species change through the early stages of B - Plan in both time and space.

5.3.1. Field survey

The sub-quadrats were sited as in Figure 3.4a,b, with the emphasis in sampling the B - Plan sub-units to determine those aspects of the ground flora conserved by this type of management. Where sub-units were adjoining and of the same age with the same planted conifer species, only two sub-quadrats were sited as in quadrats 9, stages II and III; 44, stages I and II, III and IV; 23, stages I and II; and 54, stages II and IV. These double sub-units were the result of:

1) a loss of the original trees in one sub-unit caused by rabbit damage as in quadrats 44 and 23. Hence, when the next sub-unit was cleared and planted six years later, new trees were also planted in the previous sub-unit.

2) the lack of adequate light under some canopies and on some sites for the trees of the first few sub-units in stages I to IV. Under these conditions, it has been estate practice to clear and plant two sub-units at the same time, for example in quadrat 54, stages II and IV.

Quadrat 40 had only one sub-quadrat because there were only two Thuja trees left in this stage I sub-unit. Hence the sub-quadrat was sited between them. Rabbit damage and the use of this deciduous wood for pheasant rearing resulted in no further B - Plan planting.

The reduction of sampling sites by the selection of the 20 special quadrats resulted in a reduction of the variety of habitats and hence a reduction of the total number of species from 1979 to 1981 (Table 5.4.). In 1979 96 species (bryophytes, ferns, herbs, grasses, and shrubs) were found in 50 x 400 m^2 quadrats using 500 sub-quadrats, while in 1981 68 species were identified in 20 x 400 m^2 quadrats using 244 sub-quadrats. Table 5.4. shows all the species in phases I - IV.

5.3.2. A description of the main ground flora community types in phase II derived from TWINSPAN classification

The TWINSPAN classification (Table 5.5.) divides the 244 sub-quadrats into seven major groups (Table 5.6.). The TWINSPAN table (Table 5.5.) shows that one species, Rubus fruticosus, is almost universally distributed within the Tavistock Woodlands. Other species with widespread distribution are Hedera helix and Lonicera

Table 5.4. Ground flora species recorded in phases I,II,III and IV

	Phase I 1979	Phase II 1981	Phase III 1982	Phase IV B - Plan only 8 quadrats
Mosses (after Smith, 1978) (*after Watson, 1968)				
1 *Atrichum undulatum* (Hedw.) P. Beauv.	+			
2 *Blindia acuta* (Hedw.)	+			
3 *Brachythecium rutabulum* (Hedw.)	+		+	+
4 *Brachythecium velutinum* (Hedw.)	+	+		
5 *Dicranella heteromalla* (Hedw.) Schimp.	+	+	+	+
6 *Dicranoweisia cirrata* (Hedw.) Milde	+	+	+	
7 *Dicranum scoparium* Hedw.	+	+	+	+
8 *Eurhynchium praelongum* (Hedw.)	+	+	+	+
9 *Eurhynchium striatum* (Hedw.) Schimp.			+	+
10 *Hypnum cupressiforme* Hedw.	+	+	+	
11 *H. cupressiforme* var. *ericetorum* B.,S. and G.*	+	+	+	+
12 *H. cupressiforme* var. *filiforme* Brid.*	+	+	+	+
13 *H. cupressiforme* var. *resupinatum* (Tayl.) Schimp.	+	+	+	+
14 *Isopterygium elegans* (Brid.) Lindb.	+	+	+	+
15 *Mnium hornum* Hedw.	+		+	+
16 *Plagiothecium denticulatum* (Hedw.)	+			
17 *Pleurozium schreberi* (Brid.) Mitt.	+			
18 *Polytrichum aurantiacum* Brid.	+			
19 *P. commune* Hedw.	+	+	+	
20 *P. formosum* Hedw.	+	+	+	+
21 *Pseudoscleropodium purum* (Hedw.) Fleisch.	+	+	+	+
22 *Rhynchostegium confertum* (Dicks.)	+		+	
23 *Rhytidiadelphus squarrosus* (Hedw.) Warnst.	+	+		
24 *R. triquetrus* (Hedw.) Warnst.	+	+	+	
25 *Thuidium tamariscinum* (Hedw.)	+	+	+	
26 *Ulota bruchii* Brid.			+	
27 *U. crispa* (Hedw.) Brid.	+		+	

Table 5.4. (Contd.)

	Phase I 1979	Phase II 1981	Phase III 1982	Phase IV B - Plan only 8 quadrats
Liverworts (after Watson, 1968)				
28 *Calypogeia fissa* (L.) Raddi	+			
29 *C. muellerana* (Schiffn.) K. Mull.	+		+	+
30 *Diplophyllum albicans* (L.) Dum.	+	+	+	
31 *Lejeunea cavifolia* (Ehrh.) Lindb.	+			
32 *Lepidozia reptans* (L.) Dum.	+			
33 *Lophocolea* spp.*	+	+	+	+
Ferns (after Ivimey-Cook, 1984)				
34 *Athyrium filix-femina* (L.) Roth	+	+	+	+
35 *Blechnum spicant* (L.) Roth	+	+	+	+
36 *Dryopteris dilatata* (Hoffm.) A. Gray	+	+	+	+
37 *D. filix-mas* (L.) Schott	+	+	+	+
38 *Pteridium aquilinum* (L.) Kuhn	+	+	+	+
Herbs (after Ivimey-Cook, 1984)				
39 *Anemone nemorosa* L.	+			
40 *Calluna vulgaris* (L.) Hull	+	+	+	+
41 *Carex pilulifera* L.	+	+	+	+
42 *Chamerion angustifolium* (L.) J. Holub.	+	+	+	+
43 *Digitalis purpurea* L.	+	+	+	+
44 *Epilobium roseum* Schreb.	+			
45 *Erica cinerea* L.	+	+	+	+
46 *Galium saxatile* L.	+	+	+	
47 *Hedera helix* L.	+	+	+	+
48 *Hyacinthoides non-scripta* (L.) Chouard ex Rothm.		+	+	+
49 *Hypericum pulchrum* L.	+	+	+	+
50 *Juncus effusus* L.	+	+	+	+

* *Lophocolea bidentata* (L.) Dum. or *Lophocolea cuspidata* (Nees) Limpr.

Table 5.4. (Contd.)

	Phase I 1979	Phase II 1981	Phase III 1982	Phase IV B - Plan only 8 quadrats
Herbs (Contd.) (after Ivimey-Cook, 1984)				
51 *Lonicera periclymenum* L.	+	+	+	+
52 *Luzula multiflora* (Retz.) Lej.		+	+	+
53 *L. pilosa* (L.) Willd.	+	+	+	+
54 *L. sylvatica* (Huds.) Gaud.	+		+	
55 *Melampyrum pratense* L.	+	+	+	+
56 *Oxalis acetocella* L.	+		+	
57 *Potentilla erecta* (L.) Rausch.	+			
58 *Rubus fruticosus* L. agg.	+	+	+	+
59 *Rumex crispus* L.	+			
60 *Solidago virgaurea* L.	+			
61 *Teucrium scorodonia* L.	+	+	+	+
62 *Vaccinium myrtillus* L.	+	+	+	+
63 *Veronica officinalis* L.	+	+	+	+
64 *Viola riviniana* Reichenb.	+	+	+	
Grasses (after Ivimey-Cook, 1984)				
65 *Agrostis capillaris* L.	+	+	+	+
66 *A. gigantea* Roth.	+			
67 *A. stolonifera* L.			+	+
68 *Anthoxanthum odoratum* L.		+	+	
69 *Dactylis glomerata* L.	+		+	+
70 *Deschampsia caespitosa* (L.) Beauv.	+	+	+	
71 *D. flexuosa* (L.) Trin.	+	+	+	+
72 *Festuca rubra* L.	+			
73 *F. tenuifolia* Sibth.	+			
74 *Holcus lanatus* L.	+	+	+	+
75 *H. mollis* L.	+	+	+	
76 *Molinia caerulea* (L.) Moench	+	+	+	+
77 *Poa annua* L.	+			
78 *P. nemoralis* L.	+			

Table 5.4. (Contd.)

	Phase I 1979	Phase II 1981	Phase III 1982	Phase IV B - Plan only 8 quadrats
Naturally regenerated trees (after Mitchell, 1974) (over-hanging less than one metre or rooted in sub-quadrat)				
79 *Acer pseudoplatanus* L.	+	+		
80 *Betula* spp.*	+	+	+	+
81 *Carpinus betulus* L.	+			
82 *Castanea sativa* Mill.	+	+		
83 *Corylus avellana* L.	+	+	+	
84 *Crataegus monogyna* Jacq.	+			
85 *Fagus sylvatica* L.	+	+	+	
86 *Ilex aquifolium* L.	+	+	+	+
87 *Picea sitchensis* (Bong.) Carr.	+			
88 *Pinus sylvestris* L.	+	+		
89 *Prunus avium* L.	+			
90 *Pseudotsuga menziesii* (Mirb.) Franco	+	+	+	
91 *Quercus cerris* L.	+	+	+	
92 *Q.* x *rosacea*	+	+	+	+
93 *Salix cinerea* L.	+			
94 *Sorbus aucuparia* L.	+	+	+	+
Shrubs (after Clapham *et al.*, 1962)				
95 *Frangula alnus* Mill.	+	+	+	
96 *Rhododendron ponticum* L.	+	+	+	+
97 *Sarothamnus scoparius* (L.) Wimmer	+	+		
98 *Ulex gallii* Planch	+	+	+	+
99 *Viburnum opulus* L.	+	+	+	

* *Betula pendula* Roth or *B. pubescens* Ehrh. or hybrids

Table 5.4. (Contd.)

	Phase I 1979	Phase II 1981	Phase III 1982	Phase IV B - Plan only 8 quadrats
B - Plan trees (after Mitchell, 1972)*				
100 *Nothofagus procera* (Poepp. and Endl.) Oerst.	+	+	+	+
101 *Thuja plicata* D. Don	+	+	+	+
102 *Tsuga heterophylla* (Raf.) Sarg.	+	+	+	+
Miscellaneous features				
103 Bare soil	+	+	+	+
104 Brash and logs	+	+	+	+
105 Rotting stumps	+	+	+	+
106 Rocks and stones	+	+	+	+

* B - Plan trees rooted or over-hanging sub-quadrats were not used in analyses due to their effect on ordering the naturally occurring species

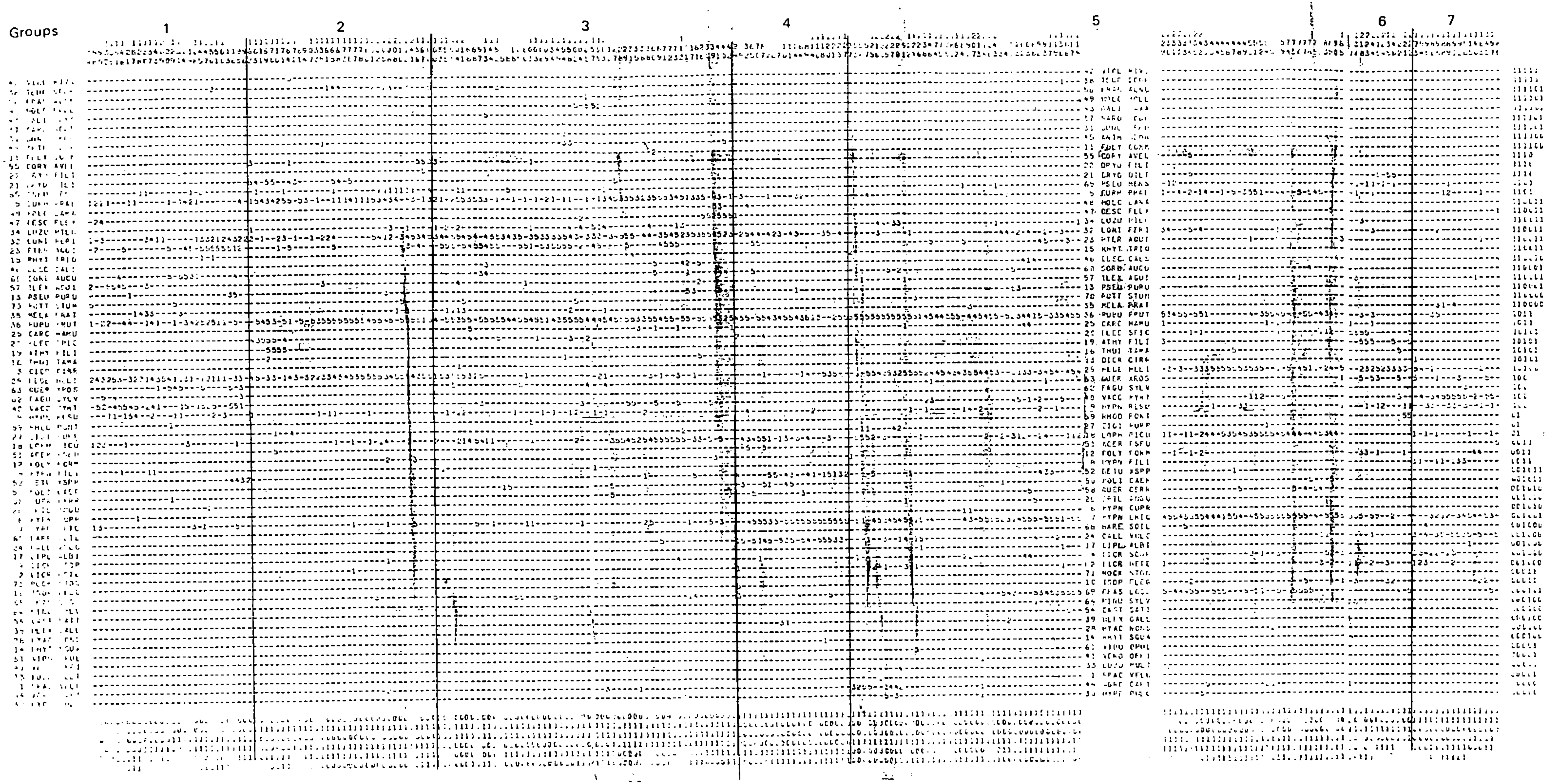

Table 5.5. TWINSPAN classification table - phase II - ground flora survey

Table 5.6. TWINSPAN classification groups phase II - 1981 (only the quadrats with two or more sub-quadrats in the group are included)

Group	Quadrat	% of sub-quadrats in group	Canopy type	Past history	Characterizing ground flora species (> 30% constancy by group)	% of all sub-quadrats containing species (% constancy by group)	Interesting associated species (Indicators/ preferentials)
1 Number of sub-quadrats in group 29	9	75%	*Pinus*	c.w.*	*Hedera helix*	86	*Sorbus aucuparia*
	32	63%	*Quercus* recently clear-felled	c.w.	*Vaccinium myrtillus*	66	*Quercus* x *rosacea*
					Rubus fruticosus	62	*Ilex aquifolium*
	38	63%	Mixed plantation	c.w.	*Lonicera periclymenum*	55	*Melampyrum pratense*
	33	50%	*Quercus*	c.w.	*Pteridium aquilium*	44	
	19	50%	Mixed plantation	c.w.	*Eurhynchium praelongum*	41	
					Hypnum cupressiforme var. *resupinatum*	35	
2 Number of sub-quadrats 33	44	92%	*Pseudotsuga*	heath	*Hedera helix*	91	*Teucrium scorodonia*
	54	50%	*Quercus*	c.w.	*Rubus fruticosus*	85	*Dryopteris filix-mas*
	51	50%	*Fagus* and *Larix*	heath	*Eurhynchium praelongum*	82	*Blechnum spicant*
	32	25%	*Quercus* recently clear-felled	c.w.	*Lonicera periclymenum*	58	*Athyrium filix-femina*
	23	21%			*Dryopteris dilitata*	33	
3 Number of sub-quadrats in group 54	13	78%	*Larix*	c.w.	*Rubus fruticosus*	94	*Luzula pilosa*
	40	78%	*Quercus* and *Larix*	c.w.	*Lonicera periclymenum*	89	
	23	71%	*Larix* and *Pinus*	c.w.	*Pteridium aquilinum*	82	
	15	50%	*Larix* and *Pinus*	c.w.	*Eurhynchium praelongum*	74	
	4	33%	*Pinus*	heath	*Lophocolea* spp.	52	
	54	29%	*Quercus*	c.w.	*Rhytidiadelphus triquetrus*	50	
	38	25%	Mixed plantation	c.w.			
	9	17%	*Pinus*	c.w.			

* c.w. = continuously wooded

Table 5.6. (Contd.)

Group	Quadrat	% of sub-quadrats in group	Canopy type	Past history	Characterizing ground flora species (> 30% constancy by group)	% of all sub-quadrats containing species (% constancy by group)	Interesting associated species (Indicators/ preferentials)
4 Number of sub-quadrats in group 22	29	50%	*Pinus*	heath	*Rubus fruticosus*	86	*Molinia caerulea*
	4	50%	*Pinus*	heath	*Hypnum cupressiforme* var. *ericetorum*	83	*Ulex gallii*
	15	31%	*Larix* and *Pinus*	c.w.	*Calluna vulgaris*	73	
	17	17%	*Picea abies*	heath	*Betula* spp.	59	
					Lonicera periclymenum	55	
					Lophocolea spp.	50	
5 Number of sub-quadrats in group 78	14	100%	*Picea sitchensis*	heath	*Hypnum cupressiforme* var. *ericetorum*	83	*Eurhynchium praelongum*
	56	69%	*Pseudotsuga*	c.w.	*Hedera helix*	80	*Vaccinium myrtillus*
	17	67%	*Picea abies*	heath	*Rubus fruticosus*	77	*Digitalis purpurea*
	55	63%	*Pseudotsuga*	c.w.	*Lophocolea* spp.	59	*Calluna vulgaris*
	51	50%	*Fagus* and *Larix*	heath	Brash/logs	41	*Agrostis capillaris*
	29	43%	*Pinus*	heath			
	52	38%	*Quercus*	c.w.			
	plus 5 other quadrats between 17 and 25%						
6 Number of sub-quadrats in group 12	55	38%	*Pseudotsuga*	c.w.	*Hedera helix*	75	*Dicranella heteromalla*
	56	25%	*Pseudotsuga*	c.w.	*Hypnum cupressiforme* var. *ericetorum*	50	*Isopterygium elegans*
					Athyrium filix-femina	42	
					Blechnum spicant	42	
					Hypnum cupressiforme var. *resupinatum*	42	
					Pseudotsuga menziesii	42	
					Polytrichum formosum	33	
					Dryopteris dilitata	42	

* c.w. = continuously wooded

Table 5.6. (Contd.)

Group	Quadrat	% of sub-quadrats in group	Canopy type	Past history	Characterizing ground flora species (> 30% constancy by group)	% of all sub-quadrats containing species (% constancy by group	Interesting associated species (Indicators/ preferentials)
7 Number of sub-quadrats in group 16	53	100%	*Quercus*	c.w.	*Vaccinium myrtillus*	69	*Melampyrum pratense*
	52	50%	*Quercus*	c.w.	*Calluna vulgaris*	63	*Quercus* x *rosacea*
	33	25%	*Quercus*	c.w.	*Hypnum cupressiforme* var. *ericetorum*	63	*Dicranum heteromalla*
					Dicranum scoparium	44	
					Hypnum cupressiforme var. *filiforme*	44	
					Hypnum cupressiforme var. *resupinatum*	44	

* c.w. = continuously wooded

periclymenum. Thus although these occur in Table 5.6. as characterising species with high abundance, they are not good indicators or preferentials. Figure 5.4. shows the 7 TWINSPAN groups plotted on the first two axes of the DECORANA quadrat ordination.

Group 1

Group 1 consists of sub-quadrats under relatively open canopies but which are not primarily deciduous (Table 5.6.). The indicators for this group are Vaccinium myrtillus, Hedera helix, Quercus x rosacea with the preferential, Ilex aquifolium, Melampyrum pratense and Sorbus aucuparia. These species indicate a lighter environment than that under the canopies of group 2. Quercus needs light and little competition if it is to regenerate (Newbold and Goldsmith, 1981), whilst Sorbus dies out under the darker established B - Plan units (Bird, 1983). Bracken (Pteridium aquilinum) is also found in 44% of all sub-quadrats and the presence of Melampyrum as a preferential is also important.

All of the sub-quadrats in this group are on continuously wooded sites (Table 5.6; Figure 1.5.). This group is clearly shown on the left-hand side of the quadrat ordination (Figure 5.4.).

Group 2

Group 2 consists of primarily sub-quadrats under deciduous canopies with B - Plan created disturbance (Table 5.6.). As in phase I, quadrat 44 is an anomaly in this group. The indicators for this group are Hedera helix, Dryopteris dilitata and Teucrium scorodonia. Hedera which is abundant in secondary and not primary woods, establishes itself at the first clearing of the original canopy and remains for centuries (Rackham, 1976). In Tavistock Woodlands, it seems to prefer the continuously wooded sites to the afforested heath, but because it is found to some degree on most sites it is best considered a 'ubiquitous' Tavistock Woodlands

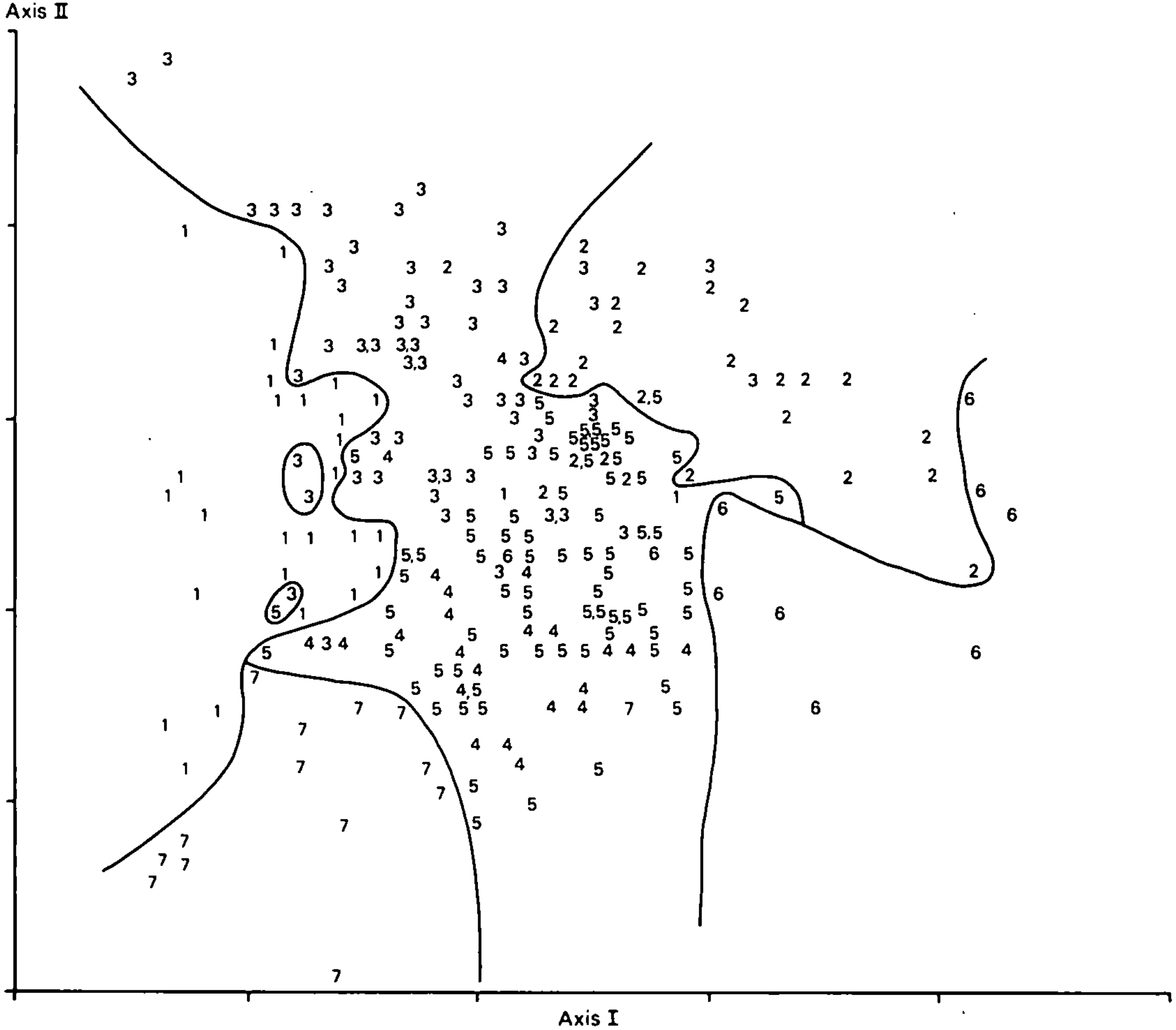

Figure 5.4. TWINSPAN group membership (Table 5.6.) plotted on the first two axes of the DECORANA ordination of 244 sub-quadrats of the phase II ground flora survey - 1981

species. *Dryopteris* is a common associate in woods with *Eurynchium praelongum* which is a shade-tolerant species (Watson, 1968; Myerscough, 1980). It is found in quadrats 44 and 51. The *Pseudotsuga* and *Fagus* with *Larix* canopies of these quadrats provide the shade and high relative moisture in the summer when it is needed by damp-loving species. The presence of *Blechnum spicant* and *Athyrium filix-femina* provide further evidence of the damp, shady habitat of this community type. Group 2 is clearly defined on the upper right of the ordination diagram (Figure 5.4.), grading into groups 3/5 on the one hand and group 6 on the other.

Groups 1 and 2 correspond to groups 1 and 2 of phase I (Table 5.2.) from which quadrats 40,38,32 and 33 were chosen for further study.

Dryopteris is a preferential for group 1 of phase I and group 2 of phase II. Quadrat 32 is interesting in that its sub-quadrats are classified in both groups. It was clear-felled just before sampling in 1981 so that the ground flora of several of its sub-quadrats reflects the past shady and damp deciduous broadleaved canopy belonging to group 2, while the ground flora of the remainder of the sub-quadrats is beginning to show a response to clearing and these are grouped with the open canopies of quadrats 38 and 9 (group 1).

Group 3

Group 3 consists of quadrats with primarily light *Larix* canopies either alone or in combination with other canopy species (Table 5.6.). The indicators for this group are *Lonicera periclymenum*, *Pteridium aquilinum*, *Lophocolea* spp. and one preferential *Luzula pilosa*. *Lonicera*, although widespread in Tavistock Woodlands, is less abundant in shaded places such as under abandoned *Quercus* canopies or in the older B - Plan sub-units (Table 5.5.). The same is true for *Pteridium*. Thus in this group 3, both species have responded to the light canopies, as well as to the disturbance and light created by B - Plan. *Luzula* is an indicator of primary woodland in Eastern England (Peterken, 1974), but is also an indicator of acid brown earth in the open or in woods (Bunce, 1982). The association of *Pteridium*, *Lonicera* and *Luzula* is part of a typical oak field layer (Tansley, 1939). Hence they are the relics of the past oak canopies typical of most of the sites in group 3. The *Lophocolea* appears to take advantage of the dense cover created by the *Pteridium* and *Lonicera* and grow well under this low lying canopy.

Group 4

Group 4 appears to consist primarily of quadrats on the afforested heath (Table 5.6.). It is comparable to group 4 in phase I (Table 5.2.). Three of the quadrats selected for the phase II study appear in both group fours - 29,4 and 17. The indicators for this phase II group 4 are *Calluna vulgaris*, *Betula* x spp., *Lonicera*, *Molinia caerulea* and *H*. *cupressiforme* var. *ericetorum*. *Calluna* is included in both group fours as a relict heath species and not as a component of the dwarf shrub layer in an oak coppice (Gimingham, 1960). *Betula* is a preferential for group 4 as in phase I. *Molinia* is a distinct heath species, and *Hypnum* is a heathland associate of *Calluna*. *Ulex gallii* is another heath associate found in two sub-quadrats.

Group 5

Group 5 is dominated by all the sub-quadrats of quadrat 14, the *Picea sitchensis* canopy, as well as over half of those under the *Picea abies* canopy in quadrat 17 and over half of those under the Pseudotsuga canopy of quadrat 56(Table 5.6.). In addition, there are 38% of the sub-quadrats of the Quercus-canopied quadrat 52 and a mixture of sub-quadrats from 8 other quadrats. This makes this group similar to the group 3 of phase I (Table 5.2.), which is the transition group between the oak canopied groups 1 and 2 and the heath group 4. Likewise this group 5 lies between the heathy quadrats of group 4 and the relic oak quadrats of group 7 (Table 5.5.). The indicators are brash and logs, Hedera helix and Lophocolea spp. and Eurhychium praelongum is a preferential. The brash and/or logs are a feature of the areas surrounding the B - Plan units - sub-quadrats 1 to 8. The unwanted products of sub-unit clearance as well as the lower branches removed from the young trees are left on the ground to decompose. Under the spruce canopies of quadrats 14 and 17 and the Pinus canopy of 9, this brash appears to take a considerable time to break down. Pines and spruces are well-known for the slow rate of organic matter decomposition of their tissue (Miles, 1981). Again as in group 3 phase II, the Lophocolea and the Eurhychium thrive under the shade created by the 'canopy' of brash. On the ordination diagram (Figure 5.4.), groups 3-5 occupy the central area and overlap considerably. There is, however, a gradient corresponding to the second axis with group 3 predominantly at the top, grading through group 4 to group 5 quadrats at the bottom.

Group 6

Group 6 is a small group of 12 sub-quadrats. It consists primarily of the older B - Plan sub-units stages I and II in quadrats 55 and 56, which have a sparse ground flora. This group is between the mixed transition group 5 and the relic oak group 7 suggesting that the ground flora under these older plots resembles that under the old overgrown oak. No such group appears in the classification in phase I because the B - Plan units were not sampled selectively. The indicators for the group are Athyrium filix-femina, Blechnum spicant and naturally regenerated Pseudotsuga menziesii with the preferentials Polytrichum formosum, Dryopteris dilitata, Quercus x rosacea and Isopterygium elegans. The ferns are indicators of increased air humidity (Sissingh, 1982) and Isopterigium is a shade-loving species (Smith, 1978). Polytrichum is abundant on well-drained soil (Smith, 1978) and can be an index of increased acidity especially in the open (Tansley, 1968). Athyrium, unlike Blechnum, is definitely a shade plant with a light compensation point of 300 to 500 lux (Packham and Harding, 1982). Group 6 quadrats are clearly separated in the bottom right of the quadrat ordination (Figure 5.4.).

Group 7

Group 7 is the overgrown Quercus community, quadrats 52,53 and 33 (Table 5.6.). Quadrats 33 and 52 are old coppice stands, while 53 appears to be an abandoned timber stand. The indicators for this group are Vaccinium myrtillus, Calluna vulgaris, Hypnum cupressiforme var. filiforme with the preferentials Dicranella heteromalla, Dicranium scoparium, Hypnum cupressiforme var. resupinatum, Melamypyrum pratense and Quercus x rosacea. Vaccinium is tolerant of the shade under the Quercus canopy but Calluna needs open places or breaks in the canopy such as that afforded by coppicing to thrive (Tansley, 1968). The Calluna in 52 is fairly sparse and is certainly not thriving. It is most likely a floral relic from the last clearing at the beginning of this century. However the Betula in quadrat 52 at 60 to 70 years old is coming to the end of its natural life span (Harding, 1981) and may be the cause of gaps in the canopy, allowing Calluna to grow. It is interesting that part of quadrat 33 is with the sub-quadrats of group 1 (Table

5.6.) but two sub-quadrats 5 and 7 are grouped here, perhaps because they are under gaps in the canopy and have responded accordingly. The H. cupressiforme var. resupinatum is an atlantic species found on trees bases as well as rocks and is tolerant of the light shade afforded by the oak canopies (Ratcliffe, 1968; Smith, 1978). Group 7 is another well-defined group on the ordination plot (Figure 5.4.).

5.3.3. Relationships between ground flora communities and environmental factors - soil moisture and canopy closure

Overall correlation with ordination axes

In order to determine the possible overriding influence of both soil moisture and canopy density on ground flora distribution, rank correlation coefficients were calculated between the first three axis scores from the DECORANA ordination and the values for % soil moisture and % of the canopy open (moosehorn) in each sub-quadrat. The resulting correlation matrix is presented in Table 5.7.

Although with the very large sample size, significant correlation coefficients have very low explanation, it is interesting that canopy closure just achieves significance on the first axis and both soil moisture and canopy closure are significant on the second. The interpretation of this was that light in relation to canopy closure could be a significant environmental factor and thus would merit further more detailed analysis, particularly since the rapid survey using moosehorn methods at this general survey stage had serious limitations with regard to accuracy.

The soil moisture variations are also understandable as a secondary gradient. However, in both cases, the percentage explanation is very low and other unmeasured sources of variation such as

Table 5.7. Rank correlation matrix between the first three 1981 ground flora ordination axes and % soil moisture and % of the canopy open (n = 214)

		Ground flora axes			%	% of the
		I	II	III	soil moisture	canopy open
Ground flora axes	I	-	0.07	0.04	0.05	-0.19
	II		-	-0.04	0.27	0.20
	III			-	-0.01	-0.11
% soil moisture					-	0.20
% of the canopy open						-

With n-2 degrees of freedom (214-2 = 212) a coefficient of±0.19 or above is significant at the 0.01 level (two-tailed test)

management both past and present presumably affect the ground flora. Also, the very large data set covering the wide range of canopy and woodland types tends to mask variation within particular community assemblages.

Soil moisture and canopy closure values by ground flora groups

In order to examine this idea further, means and standard errors were calculated for the % soil moisture and % of canopy open scores in each of the seven ground flora groups from the TWINSPAN analysis (Table 5.5.). Results are presented in Figure 5.5.

It is clear from Figure 5.5. that the % of soil moisture and the % of the canopy that is open for TWINSPAN groups 6 and 7 (Table 5.6.) are both significantly lower than the values for the other five groups. There appears to be two factors acting to reduce the

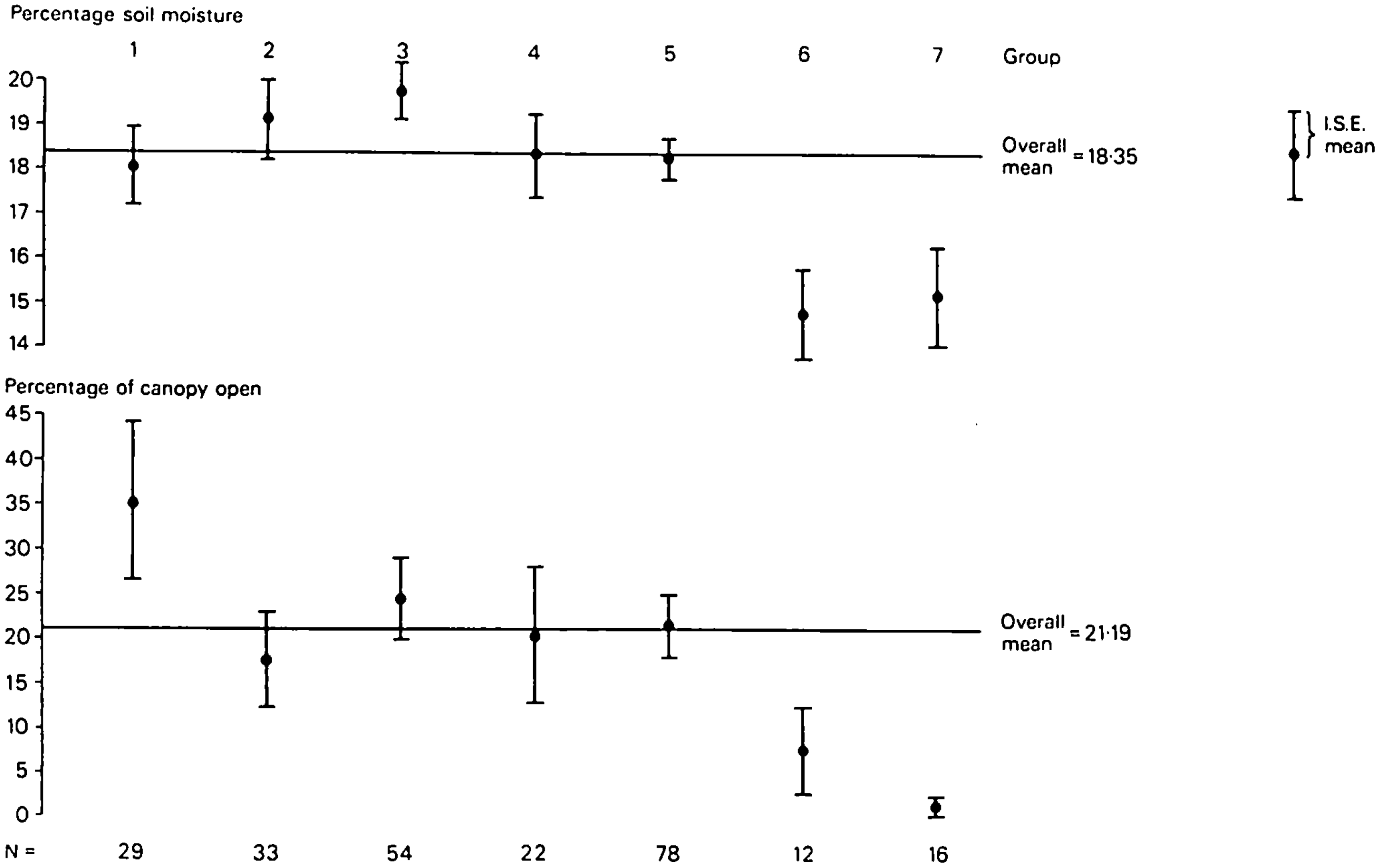

Figure 5.5. Means and standard errors of the % soil moisture and % of the canopy open scores in the seven ground flora groups from TWINSPAN analysis (Table 5.5.)

soil moisture in group 6, consisting primarily of sub-quadrats in the oldest B - Plan sub-units in quadrats 55 and 56 and in group 7, consisting of sub-quadrats in the relic Quercus stands of quadrats 33,52 and 53 (section 5.3.2.). These are:

a) the effect of slope;

b) the effect of rainfall interception by the canopy.

a) Slope

Both groups 6 and 7 have higher mean slopes than the mean for groups 1-5 combined; groups 1-5 = 13.4° (s.e.= 0.63), group 6 = 17.5° (s.e.=1.15), group 7 = 25.1° (s.e. = 0.91). The means of groups 1-5 and group 6 lie within the range of what Bunce (1982) considers a medium slope, 11-18°, while group 7 has a particularly steep mean slope in the high range, 19-26°. The run-off in the groups with higher mean slopes would be greater, thus reducing soil moisture.

b) Rainfall interception by the canopy

The sub-quadrats of groups 6 and 7 are under closed canopies for all or part of the year. The dense Thuja plicata, Tsuga heterophylla, Sequoia sempervirens and Pseudotsuga menziesii canopies in the older B - Plan sub-units of quadrats 55 and 56 intercept a considerable quantity of rainfall throughout the year. Any further rainfall reaching the ground, perhaps by stemflow, would be quickly utilized by the dense root systems. Hence canopy interception and absorption by roots, plus the effect of slope on run-off, would act to reduce the soil moisture in the sub-quadrats of group 6, (Figure 5.5.).

The Quercus x rosacea canopies over the sub-quadrats of group 7 would intercept rainfall for part of the year, from May until the autumn, but not as much over the entire year as the evergreen canopies of group 6. Therefore it appears that the effect of steep slopes on rainfall run-off must be more important than canopy interception in reducing the soil moisture in the sub-quadrats of group 7 (Figure 5.5.).

Although the sub-quadrats in the B - Plan sub-units of quadrats 55 and 56 in group 6 show a lower percentage soil moisture, the relative humidity within these sub-units appears to be high, as indicated by the presence of <u>Athyrium</u> <u>filix-femina</u>, <u>Blechnum</u> <u>spicant</u> and <u>Dryopteris</u> <u>dilitata</u> (section 5.3.2.). The dense canopies and close spacing of the trees reduces air movement. Consequently the water vapour from evapotranspiration is 'trapped' within the sub-unit.

5.3.4. The distribution of the B - Plan sub-quadrats

Approximately 34% of all the sub-quadrats in the phase II ground flora analysis were in B - Plan sub-units. However, the distribution of these sub-quadrats is not even throughout the TWINSPAN table (Table 5.5.). It is as follows:

		% within groups
Group 1	-	17%
Group 2	-	30%
Group 3	-	33%
Group 4	-	50%
Group 5	-	35%
Group 6	-	83%
Group 7	-	6%

Group 1 has less than average at 17%. As predicted by its indicators, these are the more open B - Plan sub-quadrats, sub-quadrat 9 of quadrat 9 = 9.9 (note: sub-quadrats will be referred to with first their quadrat number followed by the sub-quadrat number) planted in 1973 and sub-quadrat 23.9 also planted in 1973. The third sub-quadrat is also under a light canopy of <u>Quercus</u> and

Larix, sub-quadrat 40.9. It is the only sub-quadrat in a failed B - Plan unit with only two Thuja plicata trees. Being sited between them, the ground flora is subject to side-light, unlike the ground flora under a complete unit.

Group 2 has at 30% just below the expected distribution. The sub-quadrats are the older, darker one of quadrats 23,54 and 13 and all those of quadrat 44.

Group 3 with 33% has many of the more recently cleared sub-quadrats including several cleared in 1980 the year before phase II sampling. The average age of these sub-quadrats is 5.74 years. The luxuriant growth of Rubus and Lonicera, indicators for this group, is in response to the recent clearing.

Group 4 with 50% contains a large proportion of sub-quadrats sited on former heath sites that have been very recently cleared, for example, stages IV and V of quadrat 17 and all the stage I's of quadrat 29, all of which were cleared in 1980. All the sub-quadrats in 29,9 to 14, are all stage I's, the result of the randomly placed quadrat straddling three units. Hence this quadrat was over-sampled and was later abandoned.

Group 5, the large mixed transition group with slightly greater than the average complement of B - Plan sub-quadrats at 35%, contains all the sub-quadrats under the Picea sitchensis canopy on quadrat 14. These sub-quadrats show a clear response to clearing, with the growth of Agrostis capillaris, the only sub-quadrats in quadrat 14 where this species will grow. Likewise Digitalis purpurea responds to B - Plan clearing and is only found in group 5 in the sub-quadrats of quadrat 14. Sub-quadrat 14.9 is also stage III and not stage I as might be expected. Like quadrat 29, quadrat 14 was sited randomly and encompasses part of three units - unit 1 sub-quadrats

10 and 11 (stage I), and 12 and 13 (stage II); unit 2 sub-quadrats 14 and 15 (stage III); and unit 3 sub-quadrat 9 (stage III).

Group 6 has the highest percentage of B - Plan sub-quadrats with 83%. These were discussed earlier.

Group 7, the relic *Quercus*-canopied quadrats, has only one B - Plan sub-quadrat not really part of the group - sub-quadrat 13 of quadrat 17 (17.13). This odd quadrat is separated from group 7 in the seventh TWINSPAN division (Table 5.5.). It has several less frequent species such as *Acer pseudoplantanus*, *Quercus cerris*, *Deschampsia flexuosa*, and *D. caespitosa*. These are most likely to respond to both B - Plan disturbance and a high light environment created by clearing the stage V sub-unit of the unit directly above sub-quadrat 17.13, as well as by clearing for the stage V sub-unit directly below in 1980 for its own stage IV and stage V sub-units.

5.3.5. A description of the B - Plan sub-quadrats - the results of the analyses

The B - Plan sub-quadrats of phase II were classified separately using TWINSPAN (Table 5.8.) with cut levels of 0,2,5,10 and 20% (Hill, 1979c). A DECORANA ordination was also run on the same data and results for the first two axes of the quadrat ordination are presented in Figure 5.6. with TWINSPAN groups superimposed. The TWINSPAN classification divides the sub-quadrats into three main groups (Tables 5.8. and 5.9.).

Group 1

Group 1 is primarily composed of sub-quadrats on the former heathland (Table 5.9.), quadrats 29,51,17,14 and 4. It also contains a scattering of some other single sub-quadrats particularly the younger, lighter ones for example sub-quadrats 55.13,55.14,55.15, 55.16 and 56.16 cleared and planted in 1973 and 1980.

```
Groups                        1                                 2                        3
             344 3733  44555 22222223177755783661188111122333344446  2316665  4115678655574278 677
             8028677923131459012345533560343222357124912680123578981494016765746805904789167846902
27 DIGI PURP -------------------1-11---42-------------------------2----------------------1---------- 000000
15 RHYT TRIQ ------------------------2---------------------------------------------------------- 000001
17 DIPL ALBI --------------1---------------------------------------------------------------------- 000001
26 CHAM ANGU -5---------1----------------------------------------------------------------------- 000001
28 HYAC NONS --------------------2---------------------------------------------------------------- 000001
33 LUZU MULT ---------------------------4--------------------------------------------------------- 000001
39 ULEX CALL --------1---------------------------------------------------------------------------- 000001
44 AGRO CAPI ----------------5-22155-3442-------------1------------------------------------1------ 000001
52 BETU XSPP ---44---434-3-2-------------15------------1-------------------------------------------- 000001
61 VIBU OPUL --------------------------------5---------------------------------------------------- 000001
64 PINU SYLV -1----------------------------------------------------------------------------------- 000001
24 CALL VULG 54--1--4354435--------11---1----1-------------1--------5-51----------------------1---- 000010
50 MOLI CAER ------5545----------------------------------------------35----------------------------- 000010
 4 DICR SCOP ------2---------11-----5---------------------------1--4------------------------------------ 000011
46 DESC CAES 444-------------------------------------------------43---------------------------------- 000011
60 SORB AUCU ------------------1------5-2-------------------------4------------1------------------- 000011
 7 HYPN ERIC -555-55555555554555551-5-45444551---35555-2-55------------1-----4------2------535---- 0001
36 RUBU FRUT -1-4434555555151355555355555555555453555-3354555-1455554441555143225-----535----3---- 0001
18 LOPH BICU --43-1453-4--1-45555553------2------5-24525455555--51143551--1--1-------------------- 0010
30 HYPE PULC --------------------------3-----------5------------3------------------------------------ 0010
34 LUZU PILO -------------------------33----1-------4--------1--3-1---------------------------------- 0010
47 DESC FLEX 1---1-5----------------------------25-----------------------------55----------------- 0010
13 PSEU PURU ---1----------------------------------------------------------------13-------------------- 00110
45 ANTH ODOR ------------------------------------------------------------------5------------------ 00110
58 QUER CERR 4-------------------------------------------------------5-4--------------------------- 00110
23 PTER AQUI -------------------------------------------4555553--43-4----55---------------1------- 001110
38 TEUC SCOR ------------------------------------------------------3------------------------------ 001110
43 GALI SAXA ----------------------------------------------------5-------------------------------- 001110
48 HOLC LANA -----------------------------------53----------------------------------------------- 001110
70 ROTT STUM --------------------------------3----------------------------5-55---------------------- 001111
32 LONI PERI ---3-----4--4---------------1-----45544--4544545331244233-1-342-212311-----3-2--3---- 010
 5 EURH PRAE ---3-5----------41----4-------------331353235-5342453434551--5-1-1-1----4345-2-11---- 0110
25 CARE PILU ------------1------1----------------------3-5----1-----------------1----------1-1---- 0110
40 VACC MYRT ----------------2-----------------------1-------5--------------451---------------3--- 0110
 9 HYPN REBU ----------------------------1-------------2-----------------235-------------1-----112 0111
12 POLY FORM ------------------------1----------3-32--------------------------------3-----1-- 0111
35 MELA PRAT -----------------------------------------------------1-------3----------1------------ 0111
 2 DICR HETE ----1-2----3-----------------2--1-------------------------3--------------3-------112---- 10
10 ISOP ELEG ----514--------------------------------------------------------------32-------3----- 10
29 HEDE HELI ------41--45-5-355---52-5325553545---4333--32---3----5--1-2355131---353353313---233-2 10
69 BRAS LOOS -5-435-----------1-----------------------5----------------------------------------4-5- 10
51 ACER PSEU 5------5---------------------------------------------------------------5---------- 110
57 ILEX AQUI -----------1--------1-------------------------------------2---------------------3---- 1110
65 PSEU MENS -------------------------------1-----1---------------1-------11--------11--11--11---1 11110
16 THUI TAMA ------------------------------------------------------------------------------2-------5--- 111110
19 ATHY FILI ---------------------------------------------------------------------5-55555--5--5- 111110
20 BLEC SPIC ----2-24--------------1---------------1----44-----5------1--------------5545-55---5- 111110
21 DRYO DILI --------------------------------------------------------------------3-55-55---------- 111110
59 RHOD PONT ----------------------------------------------------------------------------------55- 111111
63 QUER XROS --------------------------------------------------------------------------------55--- 111111
71 ROCK STON -------------------------------------------------------------------------------4----- 111111

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Table 5.8. TWINSPAN classification table - phase II - ground flora survey - B - Plan sub-quadrats only

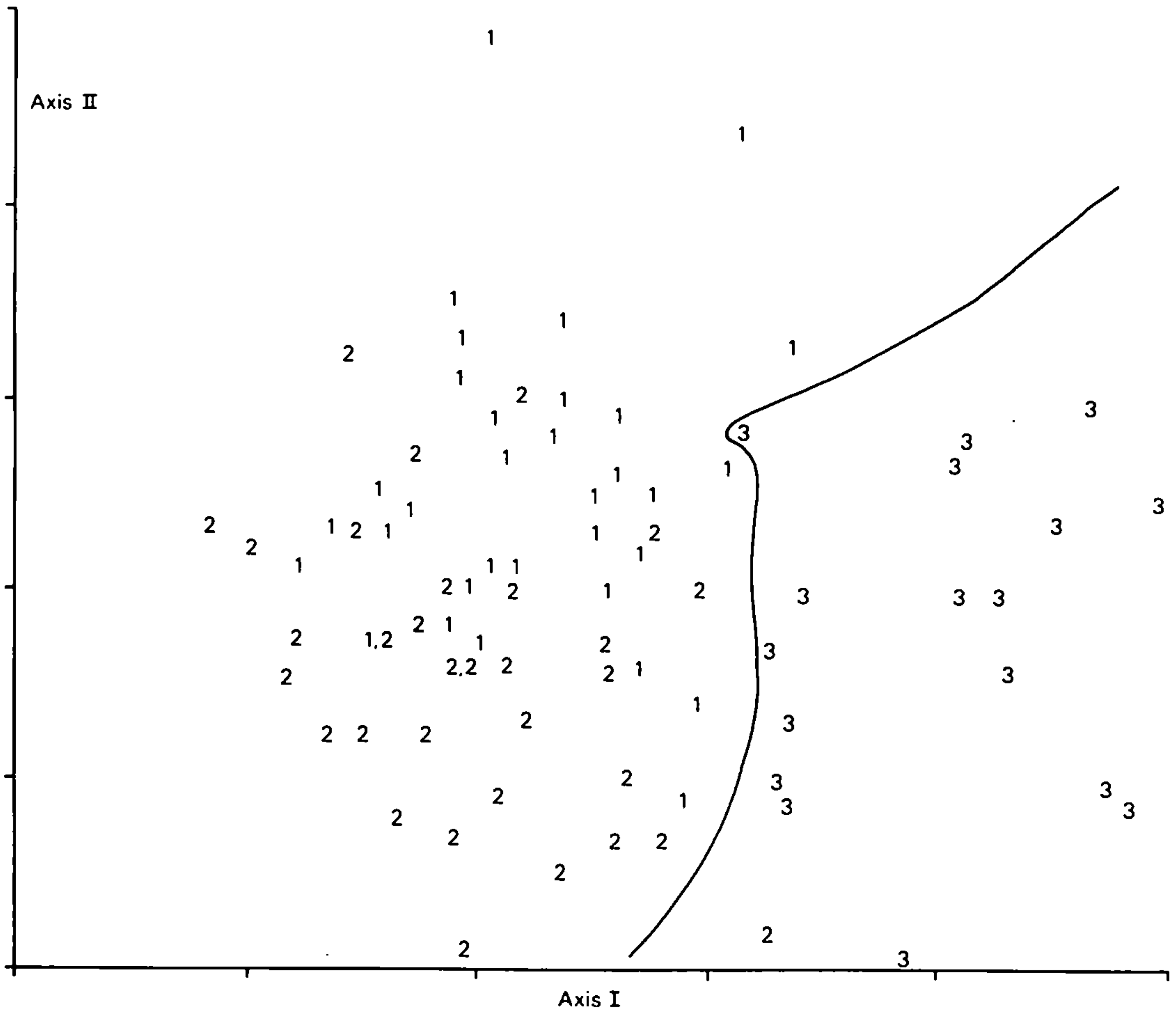

Figure 5.6. TWINSPAN group membership (Table 5.9.) plotted on the first two axes of the DECORANA ordination of 84 sub-quadrats in B - Plan sub-units of the phase II ground flora survey - 1981

Table 5.9. TWINSPAN classification groups - phase II - 1981 - B - Plan sub-quadrats only

Group	Quadrat	% of B - Plan sub-quadrats in group	Canopy type	Past history	Characterizing ground flora species (> 30% constancy by group)	% of all sub-quadrats containing species (% constancy by group)	Interesting associated species
1	29	100%	Pinus	heath	Rubus fruticosus	94	Brash/logs
Number of sub-quadrats 34	17	90%	Picea abies	heath	Hypnum cupressiforme	82	Digitalis purpurea
	14	86%	Picea sitchensis	heath	var. ericetorum		Molinia caerulea
	4	50%	Pinus	heath	Hedera helix	59	Betula x spp.
	55	50%	Pseudotsuga	c.w.*	Lophocolea spp.	50	
	51	50%	Fagus and Larix	heath	Calluna vulgaris	41	
	56	25%	Pseudotsuga	c.w.	Agrostis capillaris	30	
2	40	100%	Quercus and Larix	c.w.	Rubus fruticosus	94	Blechnum spicant
Number of sub-quadrats 33	15	88%	Pinus and Larix	c.w.	Lonicera periclymenum	82	Deschampsia flexuosa
	13	80%	Larix	c.w.	Eurhynchium praelongum	78	Hypnum cupressiforme
	23	67%	Pinus and Larix	c.w.	Lophocolea spp.	66	var. resupinatum
	9	50%	Pinus	c.w.	Hedera helix	49	Luzula pilosa
	54	50%	Quercus	c.w.	Pteridium aquilinum	36	Polytrichum formosum
	4	50%	Pinus	heath			Vaccinium myrtillus
	51	50%	Fagus and Larix	heath			
	56	25%	Pseudotsuga	c.w.			
3	44	100%	Pseudotsuga	heath	Hedera helix	76	Dicranella heteromalla
Number of sub-quadrats 17	55	50%	Pseudotsuga	c.w.	Athyrium filix-femina	47	Dryopteris dilitata
	56	50%	Pseudotsuga	c.w.	Thuidium tamariscinum	47	Hypnum cupressiforme
	54	33%	Quercus	c.w.	Blechum spicant	41	var. resupinatum
	23	33%	Larix and Pinus	c.w.	Eurhynchium praelongum	41	Lonicera periclymenum
					Pseudotsuga menziesii	41	

* c.w. = continuously wooded

The indicators for group 1 are Hypnum cupressiforme var. ericetorum, Calluna vulgaris, Hedera helix and Agrostis capillaris. Hypnum is in the fourth or greater cut level suggesting it is fairly abundant. This heathy species (Watson, 1968) is found throughout Tavistock Woodlands, but is particularly abundant in heathy open areas. It is associated with Calluna vulgaris in upland woods and heaths. Not surprisingly, with the ground flora similar to both Peterken's (1981) upland pedunculate oak wood flora and to heathland, Betula x spp. is one of the preferentials for group 1. This group is shown on the upper left-hand side of the ordination (Figure 5.6.). It overlaps with group 2.

Group 2

Group 2 consists of sub-quadrats found primarily on continuously wooded sites (Table 5.9.). The indicators for this group are Lonicera periclymenum, Eurhynchium praelongum and Pteridium aquilinum. The trend from group 1 to 2 appears to be of decreasing light. The two bryophyte indicators, H. cupressiforme var. ericetorum for group 1 and E. praelongum for group 2, indicate a gradient of decreasing light and increasing relative humidity from group 1 to group 2, (Gimingham and Birse, 1957). Unlike the indicators for group 1, both Pteridium and Lonicera stand moderate shade (Tansley, 1939). Pteridium is "largely if not primarily a woodland plant" which Tansley (1939) sees as part of a group of plants surviving on heath or grassland from previous woodland. Pteridium clones can live up to 80 years (Rackham, 1980a). Group 2 is positioned in the lower left-hand corner of the ordination (Figure 5.6.).

Group 3

Group 3 is distinctly different from groups 1 and 2. The sub-quadrats of group 3 are in the older B - Plan sub-units on both former heathland sites or continuously wooded sites (Table 5.9.).

The indicator for this group 3 is Athyrium filix-femina with the preferentials Blechnum spicant and Dryopteris dilitata, all three indicating high relative humidity (Sissingh, 1982). The third preferential is naturally regenerated Pseudotsuga which needs the light created by the B - Plan clearing to germinate but appears to be able to linger on under a shady canopy for a time. Group 3 is positioned on the right-hand side of the ordination (Figure 5.6.), clearly different from groups 1 and 2.

5.3.6. Age distribution of the B - Plan sub-quadrats in the analyses

Figure 5.7. shows the distribution of ages since clearing in the sub-quadrats located in the B - Plan sub-units in the three ground flora groups of the TWINSPAN classification (Tables 5.8. and 5.9.) and the DECORANA ordination (Figure 5.6.). Group 1 is composed predominantly of sub-quadrats in B - Plan sub-units cleared one year before the phase II survey, with a scattering of sub-quadrats in older sub-units. Similarly, group 2 is also composed mainly of sub-quadrats in the more recently cleared sub-units. The distinction between the two groups lies in the historical origin of the sites where the sub-quadrats are located. Group 1 sub-quadrats are on primarily heathland sites as indicated by some of the species in Table 5.9., while group 2 sub-quadrats are on continuously wooded sites. This distinction between groups 1 and 2 is not clear on the ordination axes I and II (Figure 5.6.), but lies on the third axis. In contrast to groups 1 and 2, group 3 is composed of sub-quadrats located in the older B - Plan sub-units (Figure 5.7.).

This pattern of distribution shows up clearly in the mean time since clearance for B - Plan sub-units of each of the three

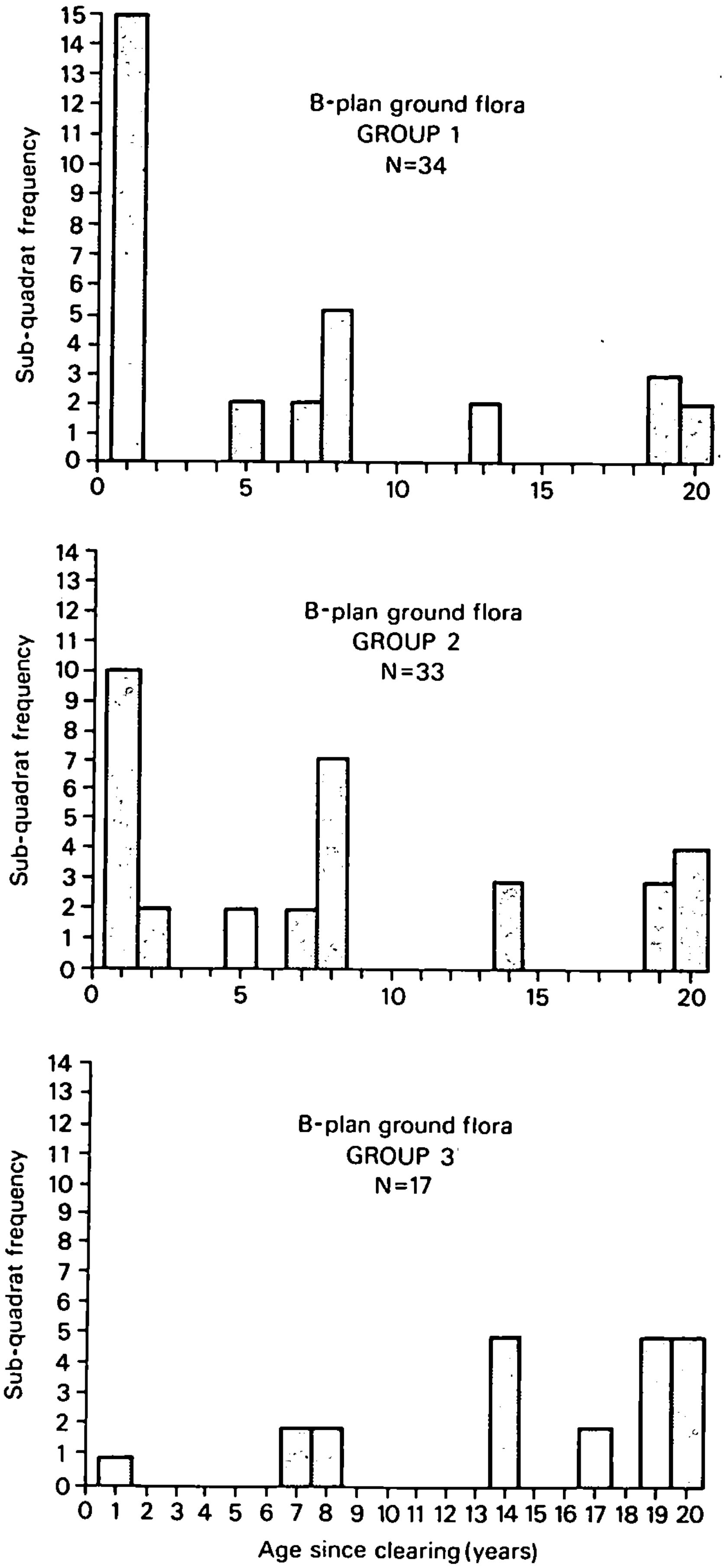

Figure 5.7. Distribution of ages since clearing in B - Plan sub-units in the three ground flora groups (Table 5.9.)

groups. Groups 1 and 2 have a similar means, 6.40 years (s.e. = 1.19) and 7.41 (s.e. = 1.12) respectively. Group 3 however, has a mean of 15.65 years (s.e. = 1.11). The values in group 3 are significantly different when tested with a Mann-Whitney U-test (two-tailed) from those in either group 1 or group 2, p = 0.0004 and p = 0.0090 respectively. Hence, as the B - Plan sub-units 'age', the ground flora community shows a marked change in composition and abundance.

5.3.7. Relationships between B - Plan sub-unit communities and environmental factors - soil moisture and canopy closure

Overall correlation with ordination axes

As with the entire data set from phase II (section 5.3.3.), rank correlation coefficients were calculated between the first three axis scores from the DECORANA ordination of the sub-quadrats located in B - Plan sub-units only and the values for % soil moisture and the % of the canopy open (moosehorn) in each sub-quadrat. The resulting correlation matrix is presented in Table 5.10.

Both canopy closure and soil moisture achieve significance on axis I only. As with the entire data set from phase II, soil moisture appears as a secondary gradient.

Soil moisture and canopy closure values by ground flora groups

The means and standard errors were calculated for the % soil moisture and the % of the canopy open scores in each of the three ground flora groups from the TWINSPAN analysis (Table 5.8.) of the sub-quadrats located in B - Plan sub-units only. Results are presented in Figure 5.8.

Table 5.10. Rank correlation matrix between the first three 1981 B - Plan ground flora ordination axes and % soil moisture and % of the canopy open (n = 84)

	Ground flora axes I	 II	 III	% soil moisture	% of the canopy open
I	-	-0.07	-0.28	-0.33	-0.43
II		-	0.21	0.28	0.19
III			-	0.13	0.20
% soil moisture				-	0.33
% of the canopy open					-

With n-2 degrees of freedom (84-2 = 82) a coefficient of ± 0.3 or above is significant at the 0.01 level (two-tailed test)

It is clear from Figure 5.8. that the % of soil moisture and the % of the canopy that is open in group 3 are both significantly lower than the same values for groups 1 and 2.

This pattern is similar to the results from the entire data set of phase II when groups 6 and 7 are compared to groups 1-5 (Figure 5.5.). However group 7, consisting of sub-quadrats in relic oak stands has been eliminated from this analysis of B - Plan sub-units only. Slope appeared to be more important in reducing soil moisture in group 7, while the effect of rainfall interception by the canopy was more important in group 6. Likewise, this rainfall interception by the dense coniferous canopies in the older B - Plan sub-units of group 3, appears to be more significant than the effect of slope in reducing soil moisture. The moosehorn readings were at or near

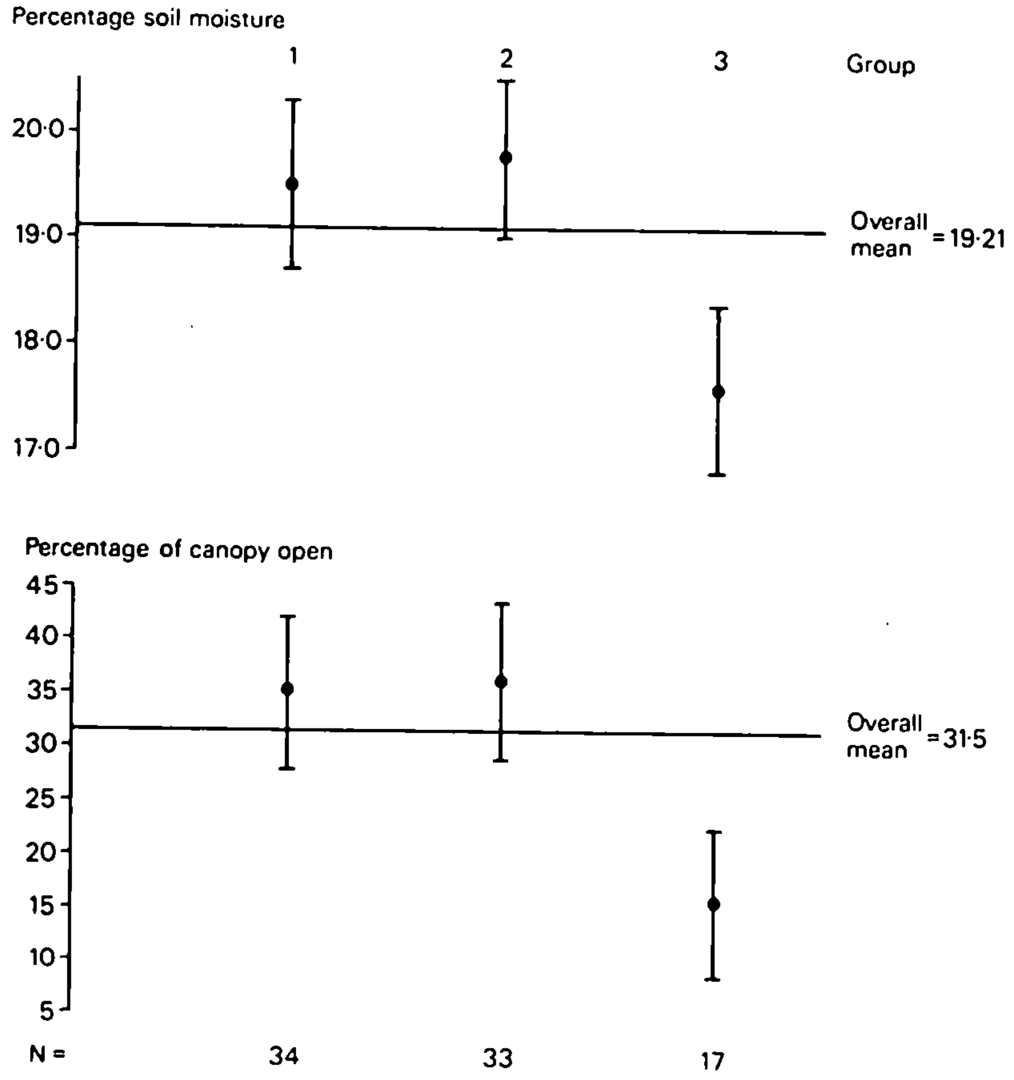

Figure 5.8. Means and standard errors of the % soil moisture and % of the canopy open scores in the three ground flora groups from TWINSPAN analysis (Table 5.9.)

0% showing no large canopy openings in group 3 in contrast to the higher values for groups 1 and 2 (Figure 5.8.). The mean slopes for groups 1 and 2, 12.84° (s.e. = 1.30) and 11.46° (s.e. = 1.56) respectively, are not significantly steeper than that of group 3, 16.25° (s.e. = 2.11). Hence the closing of the canopy as the B - Plan sub-units 'age' reduces soil moisture and available light. These environmental changes are reflected in the changes in the ground flora from groups 1 and 2 to group 3.

5.4. Successional changes under B - Plan

5.4.1. Changes in species number and abundance with increasing age of the B - Plan sub-units

Figures 5.9., 5.10., and 5.11. show the trend over time in B - Plan sub-units of:

a) the mean total number of species per sub-quadrat;

b) the mean abundance value (cover + frequency) per sub-quadrat;

c) the total abundance (summed cover + frequency) per sub-quadrat.

To calculate these abundance values, the Domin numbers were transformed using the system of Bannister (1966) to a combined cover + frequency value as follows:

Domin number	Transformed mean
+	0.04
1	0.20
2	0.40
3	0.90
4	2.60
5	3.00
6	3.90
7	4.60
8	5.90
9	7.40
10	8.40

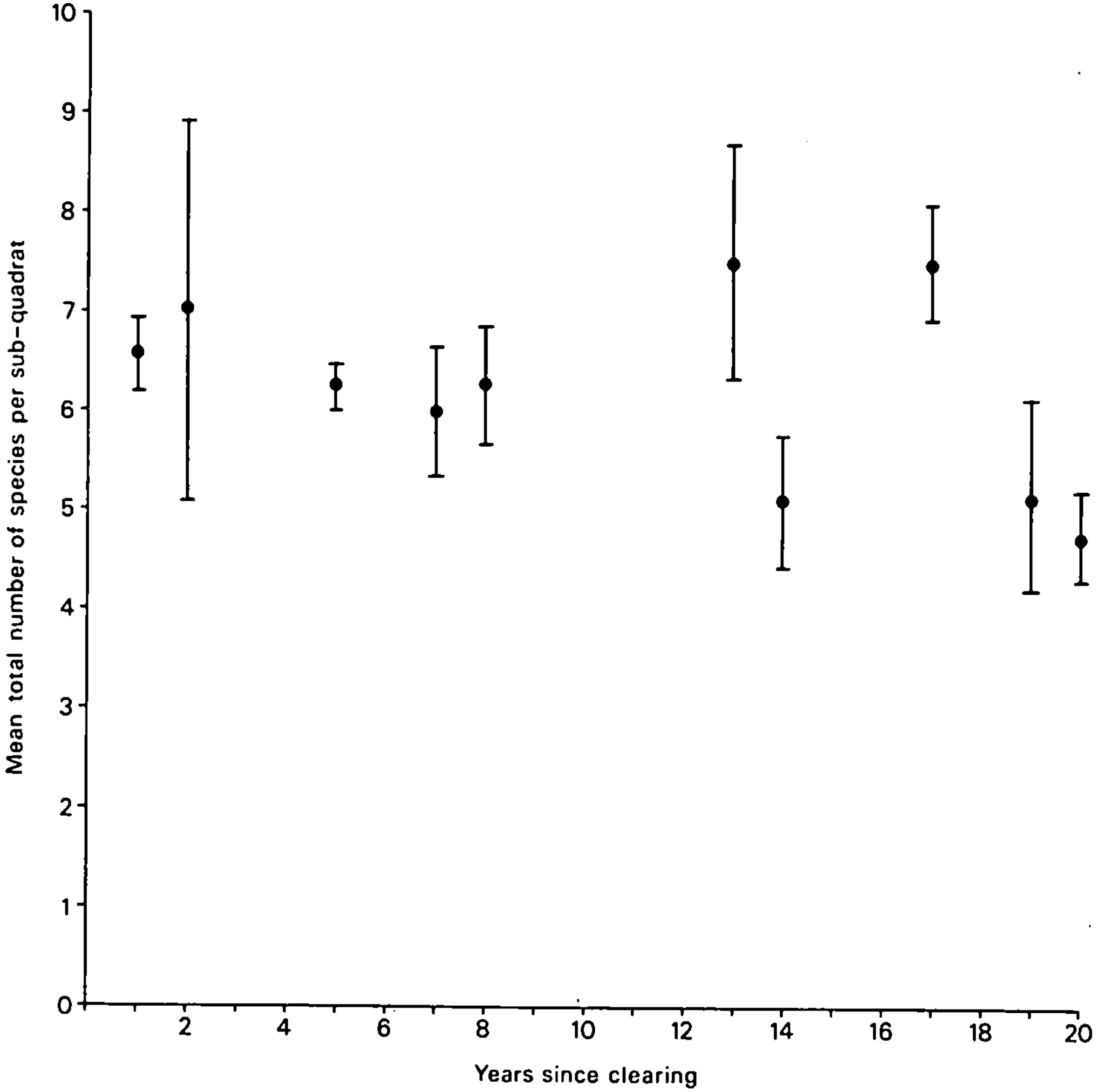

Figure 5.9. Mean total number of species per sub-quadrat and standard errors versus time since last clearing in B - Plan sub-units - phase II ground flora survey

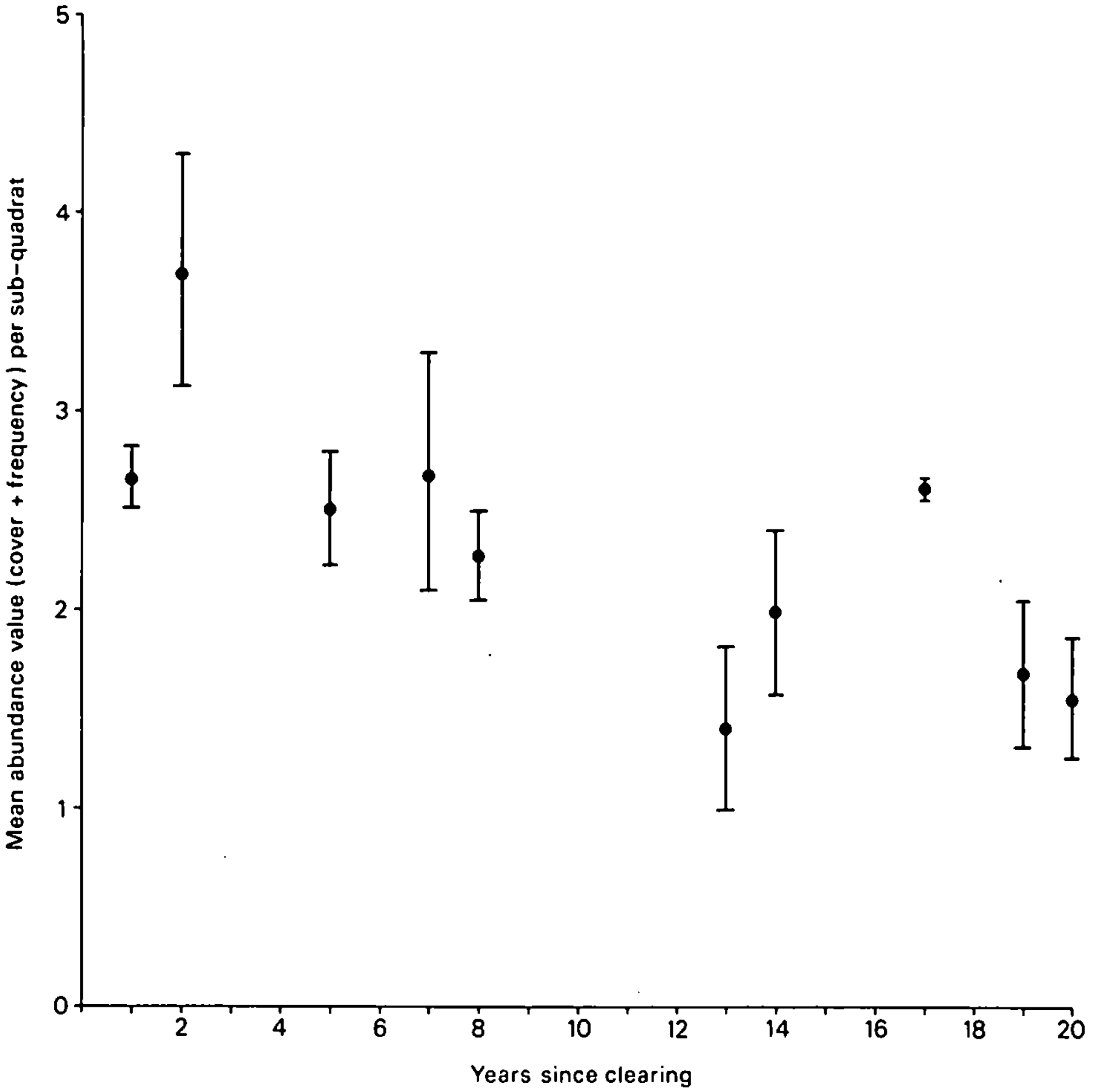

Figure 5.10. Mean abundance (combined cover + frequency after Bannister, 1966) per sub-quadrat and standard errors versus time since last clearing in B - Plan sub-units - phase II ground flora survey

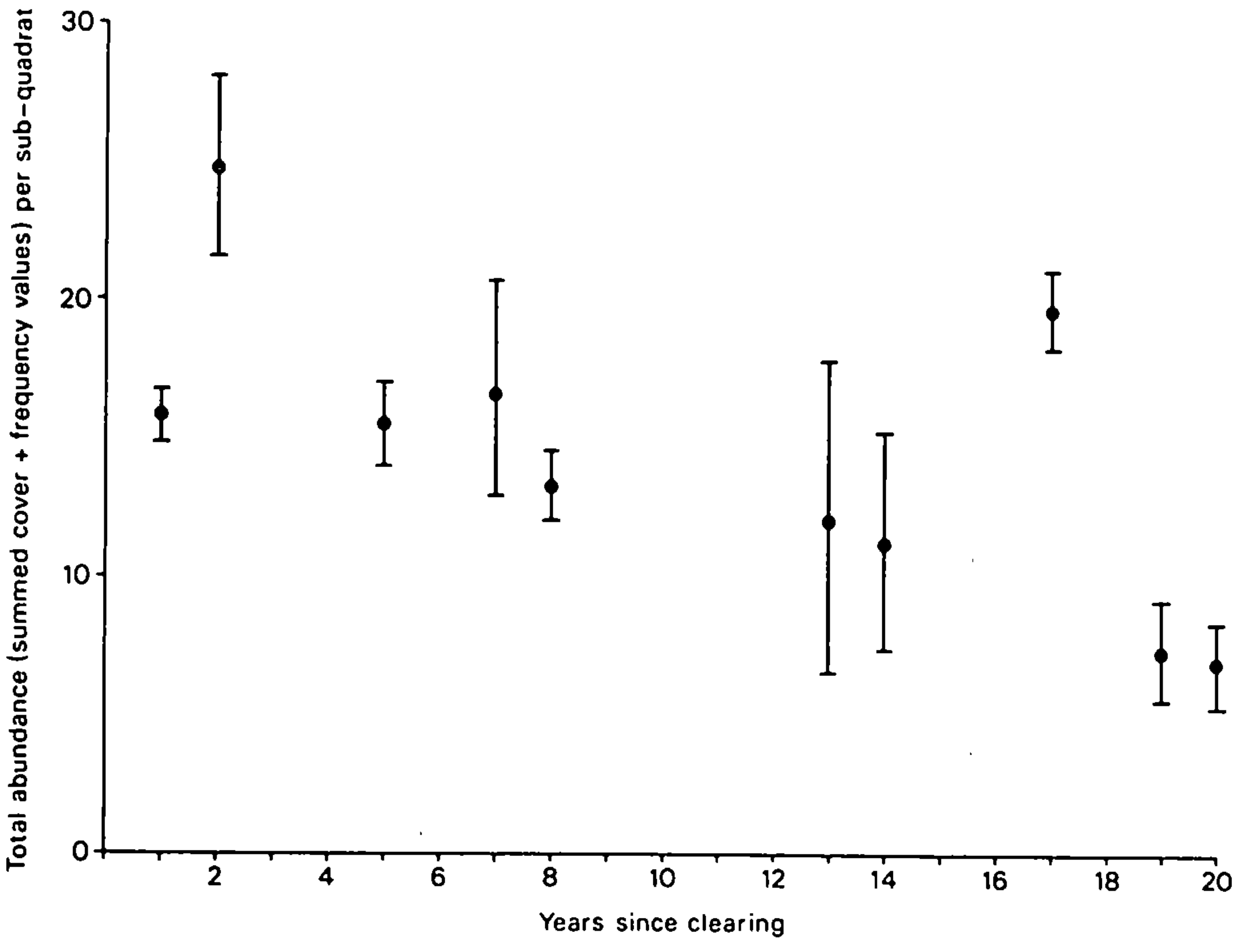

Figure 5.11. Total abundance (summed cover + frequency after Bannister, 1966) per sub-quadrat and standard errors versus time since last clearing in B - Plan sub-units - phase II ground flora survey

These transformations were used because when the Domin scale is used for cover and/or frequency the relationship is non-linear and is not appropriate for direct averaging (Grubb et al., 1982).

The species number and abundance values in Figures 5.9.-5.11. decrease with increasing time since the last clearing of the B - Plan sub-units. However, in all three graphs there is a rise between year one and two with the downward trend beginning at two years. This suggests that there is a lag of one year before the ground flora responds to clearing reaching its maximum abundance and diversity. Bormann and Likens (1979) describing their clear-cutting experiments state:

> "... biotic regulation of large losses of water and dissolved nutrients is established in three to five years after cutting, but losses may exceed those of an uncut forest for 10 to 20 years." (p. 162)

In Tavistock Woodlands, where the area cut is the equivalent to the loss of only one or two trees, the ground flora covers the ground after only one year. Hence, it is reasonable to suppose that water and nutrient losses are likely to be much less than in a clear-felled area. Gross particle erosion is controlled by dead organic matter in the forest floor, but after two years this control breaks down due to decomposition and mechanical factors. If revegetation has not taken place to exert control over the erosion, as in Bormann and Likens' experiment, where they kept the ground artificially bare, severe erosion can take place (Bormann and Likens, 1979).

In Figure 5.9. the difference between the values for species numbers at one + two years after clearing compared to those at 19 + 20 years is significantly different (p = 0.0083) using a one-tailed directional Mann-Whitney U-test.

The mean number of species is lower than expected in some quadrats soon after clearing, because when one species becomes particularly abundant, the number of species decreases due to the competition afforded by the aggressive species. This is particularly true for the grasses in quadrat 13, stages IV and V, where the mean and total abundance is greater than in the older sub-units, but the total number of species is lower. Pteridium has the same effect in quadrat 15 stages III and IV. Both the grass in quadrat 13, Deschampsia flexuosa and the Pteridium have been shown to have allelopathic effects on other plants (Rice, 1974). This may explain their competitive advantage. Likewise, in the oldest sub-units where ferns are dominant, the total abundance is higher than would be expected, as in quadrat 44 at 17 years (Figure 5.11.).

In Figure 5.9. at 13 and 17 years, the species numbers are not in line with the general trend. The higher values are caused partially by a higher number of bryophytes - four in 13.12 and five in 17.12, both at 13 years after clearing. At 17 years after clearing, there are only two sub-quadrats of this age, both in quadrat 44. Again, the unusually high species number is caused by the addition of ferns to the other species. Apart from the unusual ground flora in this quadrat, rabbit damage has killed most of the trees in these 17 year old sub-units, stages I and II. Hence many of the trees here have been replanted and lost several times. This has resulted in continual disturbance through planting, weeding and rabbits, thus increasing the number of species artificially.

In Figure 5.10. the trend is for the mean abundance value per sub-quadrat to decrease with time from the last clearing. The difference between the values at one + two years and those at 19 + 20 years is statistically significant ($p = 0.0004$) using a one-tailed directional Mann-Whitney U-test.

In Figure 5.11. the trend is again down and with a decrease in the mean total abundance (summed cover + frequency values) per quadrat over time since the last clearing. The difference between the values at one + two years and those at 19 + 20 years is statistically significant (p = 0.0010) using a one-tailed directional Mann-Whitney U-test.

5.4.2. Successional changes in species composition with increasing time since the last clearance of B - Plan sub-units

The first two groups of the TWINSPAN analysis of the B - Plan sub-quadrats (Table 5.8.) are not significantly different in time since last clearing from each other. However, they are significantly different from the third group. There also appears to be a successional species change over time. Table 5.11. shows this using the species present in 1981 survey in the B - Plan sub-units. The sub-units are divided into four age groups - 19-20, 12-14, 5-8 and 1-2 years after the clearing. Quadrats 32,38 and 19, which are even-aged plantations, are also included for comparison. The species list for quadrat 32 is taken from the 1982 data, the 1981 data were collected only six months after clearing. The list for quadrat 38 is a combination of 1981 and 1982 data - six and seven years after clearing. The sub-quadrats sampled in 1981 in quadrat 38 were different from those in 1982. The stakes in quadrat 38 were disturbed during weeding and brashing operations during this time. The species list for quadrat 19 was that recorded in 1981, which was exactly the same as that in 1982.

Many species in Table 5.11. appear to be relatively constant throughout the B - Plan cycle to date, other species appear abundantly after clearing a sub-unit then disappear after several years, while others linger on longer.

Table 5.11. Successional species changes in B - Plan sub-units - phase II ground flora survey

	Years since last clearing	19-20 years								12-14 years									5-8 years											1-2 years									
	Quadrat numbers:	56	55	54	51	40	17	15	13	56	55	54	44	23	19	17	15	13	56	55	54	38	23	17	15	14	13	9	4	56	55	44	32	23	17	15	14	13	9
Group 1 species	Hypn eric	+					+	+	+	+					+	+	+	+	+	+		+		+	+	+	+		+	+	+		+		+		+	+	+
	Loph bicu	+					+	+	+						+	+	+	+	+		+	+		+	+	+	+		+				+	+	+	+	+	+	+
	Rubu frut	+		+	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Eurh prae	+		+			+		+			+	+	+	+		+	+	+			+	+		+	+	+	+		+			+	+		+	+	+	+
	Hede heli		+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+	+	+		+		+	+	+		+		+	+		+	+	+		+
	Loni peri					+		+	+			+		+	+		+	+	+		+		+		+		+		+	+		+	+	+		+		+	+
	Dict hete	+					+	+		+						+														+			+		+				
	Ulex gall																												+										
	Dicr scop						+									+										+	+									+			
	Mela prat			+																	+																		
	Hypn resu		+			+					+				+			+			+	+						+					+						
	Poly form		+								+								+								+	+					+						
Group 2 species	Acer pseu												+											+															
	Thud tama												+																										
	Isop eleg	+								+						+																							
	Blec spic	+	+				+	+			+		+	+		+	+		+			+		+								+							
	Athy fili		+							+	+		+	+																+		+							
	Rhodo pont		+																																				
Group 3 species	Pseu mens	+								+	+								+		+	+								+		+	+						
	Agro capi							+	+									+		+						+	+				+		+				+		
	Ilex aqui	+							+													+											+		+		+		
	Pter aqui					+		+						+	+		+				+	+	+		+			+					+	+		+			
	Care pilu							+										+												+			+		+	+	+	+	
	Call vulg						+									+	+							+	+	+				+	+				+		+		
	Quer cerr						+																	+					+										

Table 5.11. (Contd.)

		Years since last clearing																																			
		19-20 years								12-14 years									5-8 years											1-2 years									
Quadrat numbers:		56	55	54	51	40	17	15	13	56	55	54	44	23	19	17	15	13	56	55	54	38	23	17	15	14	13	9	4	56	55	44	32	23	17	15	14	13	9
Group 4 species	Dryo dili									+			+																			+							
	Betu spp.														+	+		+											+						+				+
	Desc flex														+	+								+									+					+	
	Moli caer															+								+					+				+						
	Vacc myrt														+							+	+			+		+					+			+	+		+
	Quer xros														+							+						+		+			+						
	Sorb acup														+					+			+			+					+		+	+					
Group 5 species	Hype pulc																		+												+			+					
	Luzu pilo								+												+						+			+	+			+		+			
	Teuc scor																				+	+																	
	Rhyt triq																					+					+												
	Pseu puru																											+											+
	Desc caes																							+									+	+	+				
	Cham angu																					+															+		
	Fagu sylv																					+																	
	Junc effu																					+																	
Group 6 species	Digi purp												+																		+		+	+			+		
	Luzu mult																														+								
	Holc lana																																		+			+	
	Pinu sylv																																		+				
	Gali saxa																																	+					
	Hypn fili																																+						
	Anth odor																																+						
	Dicr cirr																																+						
	Hyac nons																																				+		
	Dryo fili																																+						

Group 1

The constant species include Hypnum cupressiforme var. ericetorum, Lophocolea spp., Rubus agg., Eurhychium praelongum, Hedera helix and Lonicera periclymenum. These species are present in most of the different aged sub-units, but their abundance decreases over time as the B - Plan canopy closes as in Figure 5.11.

Group 2

A second group of species are those that appear later in the cycle, after the first sub-units have been cleared (Table 5.11.). The fern Athyrium filix-femina appears more abundantly later in the cycle and thrives under the darker plots (section 8.2.3.). Likewise Blechnum spicant, although present under most conditions in Tavistock Woodland, becomes more frequent in the 12 to 14 year old sub-units and remains so through to 20 years after clearing.

Group 3

The third group of species responds to B - Plan clearing with luxuriant growth and remains through the four cycles in Table 5.11. However it becomes far less frequent and less abundant between 12 to 20 years. Calluna vulgaris and Carex pililifera are included in this group (section 8.2.2.). Calluna distribution correlates with light intensity (Chapter 6), it being able to tolerate a reduction down to 40% of light in the open (Gimingham, 1960). Under the lighter canopies such as Pinus in quadrat 4, Calluna is found under both the B - Plan sub-units, as well as under the main canopy. However, under the Pseudotsuga canopy and under the 19 to 20 year old sub-units, it slowly dies out although it may stay for several years. It also appears to be more frequent in the areas which were formerly heath. Carex pilulifera follows a similar pattern but seems less likely to remain under the main canopy (section 8.2.2.). For example, under the *Quercus* canopy of quadrat 32 before felling, it was not present, but 18 months after felling in 1982, it appeared in the ground flora. It appeared in many samples in the seed bank experiments (Chapter 7), as did *Calluna*.

Group 4

A further group lingers on through the 12 to 14 year stage but is shaded out by 19 to 20 years. These include *Quercus* x *rosacea*, *Betula* spp., *Sorbus aucuparia*, *Vaccinium myrtillus*, *Molinia caerulea* and *Deschampsia flexuosa* (Table 5.11.).

Quercus appears to germinate from seed and regenerate from old stools well in the new B - Plan clearings, as it competes well with other vegetation (Newbold and Goldsmith, 1981). It is less frequent under the main canopy but thrives on the edges of rackways and rides. Under the dark canopy of the 19 to 20 year old sub-units it appears to be completely shaded out due to its tendency to etiolate which renders it susceptible to fungal attack (Newbold and Goldsmith, 1981). *Betula* like *Quercus* is successful in recent clearings, on edges and under the light canopy of *Pinus*, as in quadrats 4 and 9. It appears to be shaded out by the canopy of the 19 to 20 year old B - Plan sub-units, (Table 5.11.). However, under the plantation thicket (quadrat 19), it is still present at 12 to 14 years, but is rapidly becoming overtopped by the conifers. *Sorbus* is another distinctly successional species in Tavistock Woodlands. Like *Betula*, it perishes under the canopy of the oldest B - Plan sub-units but is able to survive under lighter canopies and on edges. *Vaccinium* is not present in older B - Plan sub-units, but is present in most quadrats under the main canopies which are lighter than the 19 to 20 year old sub-units. *Molinia* dies out under the older B - Plan sub-units but is usually found under the canopy in the quadrats on former heathland. The presence of *Deschampsia flexuosa* depends on high light intensities, as it is a sun plant with a high compensation point (Packham and Harding, 1982). It dies out under the closed canopy of the 19 to 20 year old sub-units, but can be found lingering on under the main canopy, dependent on gaps for enough light.

Group 5

A fifth group of species, including several coppice species, colonize after clearing but remain for a longer time and usually disappear after 12 to 14 years (Table 5.11.). These include *Hypericum pulchrum*, *Luzula pilosa*, *Deschampsia caespitosa*, and *Chamerion angustifolium*. *Hypericum*, a coppice species, is not found under the main canopy in quadrat 23, only under the recently cleared B - Plan sub-units (sections 7.1. and 8.2.3.). In quadrat 55 and 56 it is found under the main canopy in several places particularly near the rackways where there is a gap in the canopy as well as in the recently cleared B - Plan sub-units. It is abundant in the seed bank (Chapter 7) and hence appears to remain there for many years until a site is cleared, whereupon it germinates. *Luzula*, a coppice species, is also abundant in the seed bank (Chapter 7) and appears to respond in a similar way to the *Hypericum*. *Deschampsia caespitosa*, although not frequent in Tavistock Woodlands, responds by appearing after clearing, dying out after eight years. It is found in a typical coppice seed bank (Rackham, 1980a), although found only in one sample taken in Tavistock Woodlands from quadrat 54. It can persist under deciduous canopies by maintaining a positive carbon balance before the canopy expands but not apparently under the coniferous canopy of B - Plan sub-units (Davy, 1980). It is found in the new clearing in quadrat 32, but not in the older plantation in quadrat 38, which adjoins it. *Chamerion* was found only in the

B - Plan stages II and IV of quadrat 17 in 1981. However, in 1982 it was found in the most recently cleared B - Plan sub-units of quadrat 14. Although this species can just survive in deep shade, due to its rhizomes (Tansley, 1968), it does not appear to be persistent under the coniferous canopy of either B - Plan or the surrounding canopy. Teucrium scorodonia appears in the B - Plan sub-units 5 to 8 years old and not in the earlier or later ones. It behaves as it does under traditional coppices being abundant two to five years after coppicing but not later (Packham and Harding, 1982).

Group 6

The ruderal species in group 6 colonizing just after clearing, but gone by the time the next B - Plan sub-units are cleared 5 to 8 years later, include Digitalis purpurea, Holcus lanatus, Anthoxanthum odoratum, and Hyacinthoides non-scripta (Table 5.11.). Digitalis is definitely an early successional species in B - Plan with a short life once the canopy begins to close. Of the five quadrats where it is found, it occurs only in the early B - Plan sub-unit in four of them (section 8.2.1. and Chapter 7). In the fifth, quadrat 44, it is under a 12 year old sub-unit which has suffered continual disturbance due to rabbit damage to the young trees resulting in several replacements of the trees and a continuously open site. Hyacinthoides, although it can survive deep shade (Tansley, 1968), is one of the vernal species which decreases as coniferous plantation replace deciduous woodland because it has only a moderate colonizing ability, (Peterken, 1981). In Tavistock Woodlands it is found primarily along the rides and has, in quadrat 14, appeared in the most recently cleared B - Plan sub-unit (Table 5.11. and Chapter 8). It is not found under the canopy of the adjoining eight year old B - Plan sub-units nor under the rest of the Picea sitchensis canopy in quadrat 14. Consequently, it appears to be like Digitalis in its response to canopy closure.

5.4.3. Successional changes with increasing time since the last clearance in even-aged plantations

The three even-aged plantations sampled quadrats, 19,32 and 38 also fit well into this successional pattern of Table 5.11. Similarly, the graphs of their mean species number, mean abundance values and total abundance(Figures 5.12., 5.13., 5.14.) follow the same downward trend as do the B - Plan in Figures 5.9., 5.10 and 5.11.

The values for both 1981 and 1982 for quadrats 19,32 and 39 have been graphed (Figures 5.12.-5.14.). As in the B - Plan sub-units, quadrat 32 exhibits a sharp rise in species numbers and abundance between one and two years after clearing. This is the result of a response time lag in the ground flora. However, unlike in the B - Plan sub-units there appears to be a sharper decrease in species numbers as the canopy closes. This is firstly, because there are more species present after clearing a larger area and secondly, because more light from the sides is available in the B - Plan sub-units to keep species numbers up (Chapter 6).

Table 5.12. shows the results of Mann-Whitney U-tests (one-tailed) applied to the data in Figures 5.12.-5.14. The differences are particularly significant for the average abundance values (Figure 5.13.) for most combinations of quadrats and sampling years.

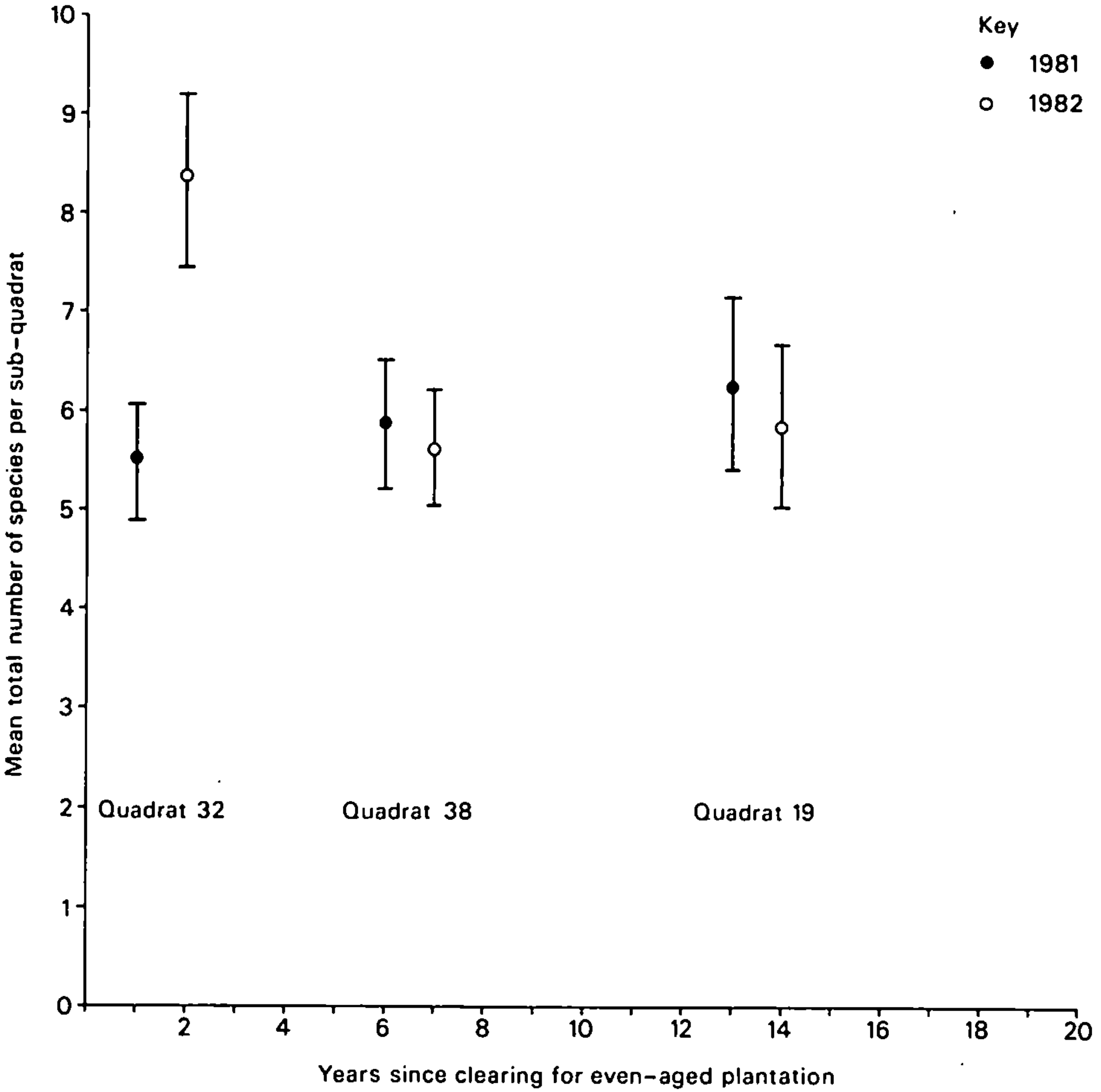

Figure 5.12. Mean total number of species per sub-quadrat and standard errors versus time since last clearing in even-aged plantations - quadrats 32, 38 and 19- phases II and III ground flora surveys

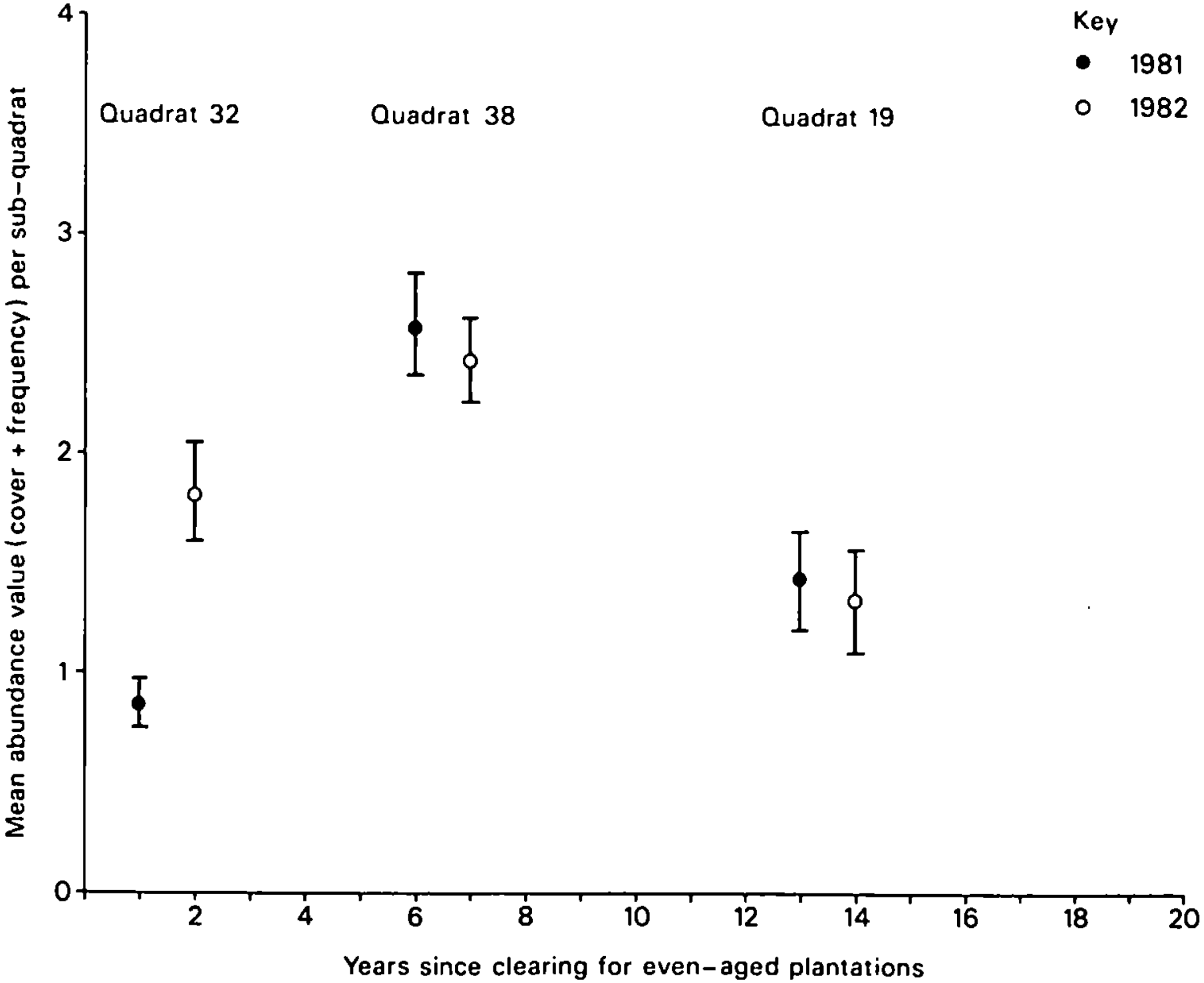

Figure 5.13. Mean abundance (combined cover + frequency after Bannister, 1966) per sub-quadrat and standard errors versus time since last clearing in even-aged plantations - quadrats 32, 38 and 19 - phases II and III ground flora surveys

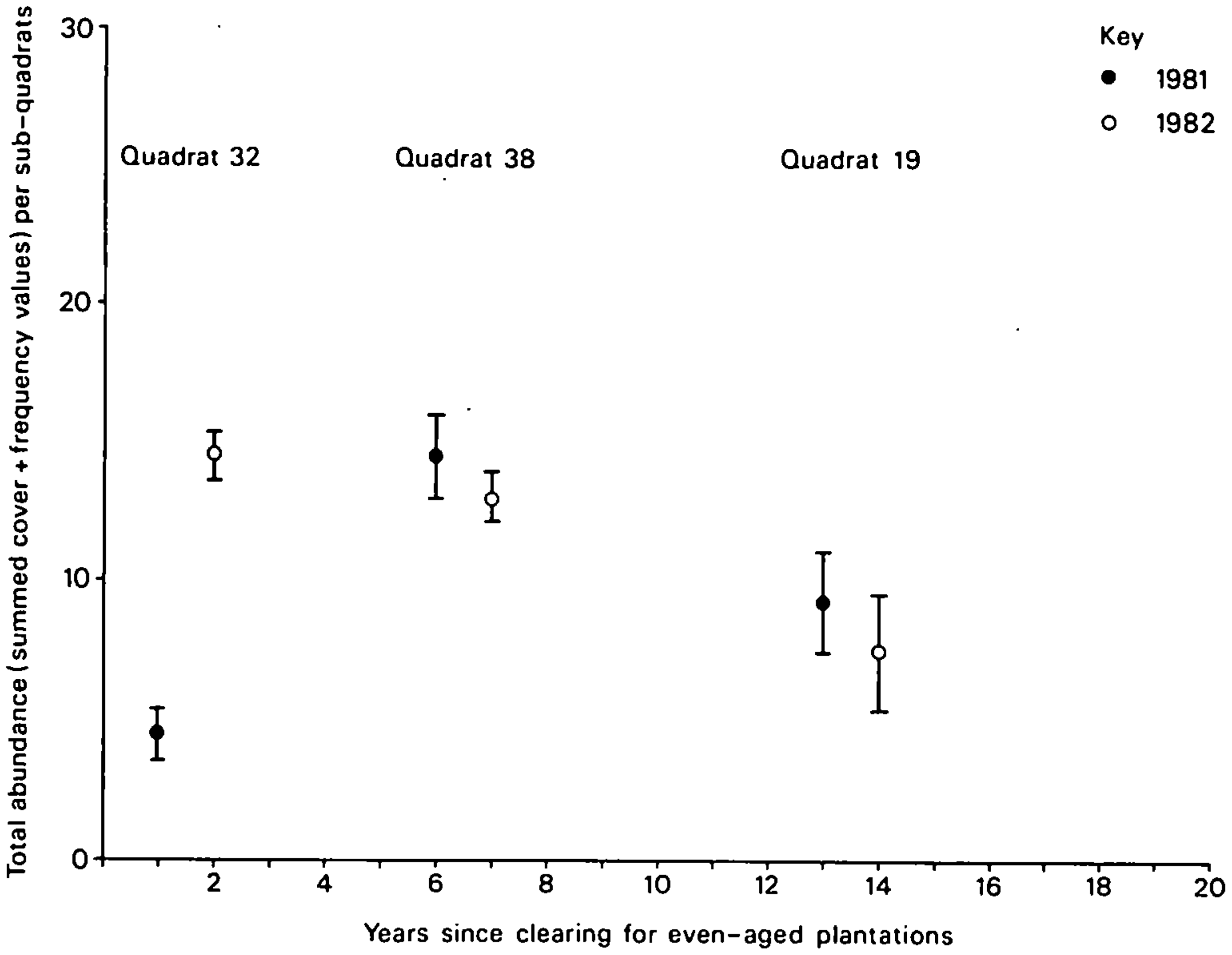

Figure 5.14. Total abundance (summed cover + frequency after Bannister, 1966) per sub-quadrat and standard errors versus time since last clearing in even-aged plantations - quadrats 32, 38 and 19 - phases II and III ground flora surveys

Table 5.12. Results of Mann-Whitney U-tests (one tailed - directional) on the values from Figures 5.12., 5.13. and 5.14. (only statistically significant results included)

Date set	Year data collected	Quadrats	Probability (p)
Species numbers per sub-quadrat	1982	32 and 38	0.0203
	1982	32 and 19	0.0464
Mean abundance values per sub-quadrat	1981	32 and 38	0.0005
	1981	32 and 19	0.0260
	1981	38 and 19	0.0037
	1982	32 and 38	0.0294
	1982	38 and 19	0.0027
Total abundance values per sub-quadrat	1981	32 and 38	0.0005
	1981	38 and 19	0.0416
	1982	32 and 19	0.0157
	1982	38 and 19	0.0294

5.5. The ground flora - a summary

1) Analysis of the phase I ground flora survey (50 quadrats) showed five main community types (section 5.2.2.). These types followed a vegetational gradient from damp, shade-loving plants to light-demanding heath species (section 5.2.3.).

2) Analysis of the phase II ground flora survey (14 quadrats selected from phase I plus six new quadrats) resulted in six main community types (section 5.3.2.). The types, which now included samples in B - Plan sub-units, again showed the vegetational gradient in 1). The samples from the B - Plan sub-units showed an ordering along this gradient which was studied in detail in section 5.3.5.

3) The vegetational community gradient was shown to be correlated with canopy closure as a primary gradient and soil moisture as a secondary gradient (section 5.3.3.).

4) Analysis of the B - Plan sub-units from phase II showed three main community types related to both past history of sites and to the time since the sub-units were last cleared (sections 5.3.5. and 5.3.6.).

5) The vegetational community gradient in the B - Plan sub-units was shown also to be correlated with canopy closure and soil moisture (section 5.3.7.).

6) A clear pattern of successional change in species numbers and abundance, as well as species composition, emerged from the analysis of the B - Plan sub-units in phase II (sections 5.4.1. and 5.4.2.). This pattern was similar to that in three even-aged plantations (section 5.4.3.). However, the significant difference between the even-aged plantations and the B - Plan sub-units is that while the successional changes in the even-aged plantations occur over time only, those in the B - Plan sub-units occur in time and in space. The successional pattern over time is replicated within the $400m^2$ space of a single B - Plan unit by the $36m^2$ B - Plan sub-units cleared varying times since the beginning of the B - Plan management of Tavistock Woodlands in 1961.

CHAPTER 6. THE LIGHT CLIMATE UNDER B - PLAN MANAGEMENT

CHAPTER 6. THE LIGHT CLIMATE UNDER B - PLAN MANAGEMENT

6.1. Introduction

There are four components of the earth's radiation budget, which affect woodlands; global radiation (short wavelengths), long wave radiation and the re-radiation of both of these (Gay and Knoerr, 1975). The incoming global or total radiation is composed of direct radiation from the sun and diffuse radiation scattered by the earth's atmosphere. The incoming long wave radiation is emitted by atmospheric gases, especially water and carbon dioxide.

Transmission of global short wave radiation, which includes the photosynthetically active wavelengths, 400-700nm, is more affected by woodland canopies than the long wave radiation, whose transmission is affected by temperature (Anderson, 1964; Gay and Knoerr, 1975). The quality and quantity of the direct component of global radiation depends on the sun's position and canopy gaps and is attenuated most by the forest biomass at the top of the canopy. The composition of the diffuse component of global radiation depends mostly on sky condition, canopy gaps and canopy geometry and is modified as it passes through all layers in the canopy (Hutchison and Matt, 1977). As a result of this, the light reaching the forest floor is rich in green and near infra-red wavelengths, especially under dense broadleaf canopies. Coniferous canopies are less selective in their absorption of visible wavelengths. Consequently, the seasonal light trend under conifers is similar to that in the open, with seasonal maxima and minima corresponding to the solstices (Gay and Knoerr, 1975; Packham and Harding, 1982; Salminen et al., 1983). In contrast, deciduous canopies have been recognised as having a shade and a light phase, which was first described by Salisbury (1916). As a result, because the expanded canopy intercepts light in the spring and summer, the maximum seasonal radiation is in the early spring and the minimum is in the autumn (Hutchison and Matt, 1977). The pattern of this light attenuation depends on leaf area indices and the arrangement and angles of leaves. This changing pattern is important in woodland succession (Packham and Harding, 1982).

The long wavelengths, the far infra-red, are absorbed by leaves and dissipated as heat through increased transpiration and convection (Packham and Harding, 1982). Coniferous canopies have lower albedos than deciduous canopies. They are better at 'trapping' solar radiation (Gay and Knoerr, 1975).

The direct and diffuse components of global radiation can be estimated using hemispherical photographs (section 3.6.2.). They have been used in this study to examine the relationship between this part of the woodland radiation climate and the communities under B - Plan management.

6.2. Distribution of light under B - Plan management

6.2.1. Correlations between diffuse and direct light and vegetation

Pope and Lloyd (1975) found that their site radiation index, derived from estimates of direct radiation using hemispherical photographs, correlated well with aspect, soil moisture and certain qualitative aspects of species distribution. They suggested that further insight into the relationships between light and communities could be gained by correlating direct light estimates from hemispherical photographs with species abundance data such as frequency or cover.

Table 6.1. shows the results of Spearman's rank correlations between:

Table 6.1. Rank correlation matrix between the first three phase IV (August data) ground flora ordination axes and the moosehorn (% of canopy open), diffuse site factors and direct site indices for May and August, 1982 (n = 111)

			Ground flora axes I	II	III	% of canopy open	Diffuse site factor		Direct site indices	
Ground flora axes	I	May	-	-	-	-0.32	-0.62		-0.64	
		Aug	-	0.14	0.20	-0.36	-0.55		-0.61	
	II	May		-	-	0.26	0.59		-0.46	
		Aug		-	-0.11	0.28	0.61		-0.39	
	III	May			-	0.17	-0.34		-0.10	
		Aug			-	0.13	0.23		-0.23	
% of canopy open		May				-	0.72	May	0.57	May
							0.71	Aug	0.54	Aug
		Aug				-	0.74	May	0.61	May
							0.76	Aug	0.59	Aug
Diffuse site factor		May					-		0.76	May
									0.71	Aug
		Aug					-		0.72	May
									0.77	Aug
Direct site index		May							-	
		Aug							-	

With n-2 degrees of freedom (111-2 = 109) a coefficient of ± 0.25 or above is significant at the 0.01 level (two-tailed test)

1) the first three DECORANA ordination axes of the August phenological data from phase IV;

2) the moosehorn readings for May and August 1982 expressed as a % the canopy open,

3) the diffuse site factors for May and August (diffuse light under the canopy as a percentage of that in the open, after Anderson, 1964 - section 3.6.2.);

4) the direct site indices for May and August (percentage contribution of direct radiation in the open summed for all the six solar tracks, an adaptation of Pope and Lloyd's (1975) site radiation index - section 3.6.2.).

For these light estimates most of the August values are the same as those for May except under the deciduous canopy of quadrat 54 and in several other sub-quadrats where species like Pteridium aquilinum grew later in the season and necessitated the calculation of the August values as well.

All of the moosehorn and light values are significantly correlated with the first two ordination axes. However the values for diffuse and direct light show much higher correlation with the vegetation axis than do the moosehorn values. Undoubtedly this is because the moosehorn estimates the cover of only a small portion of the canopy immediately overhead emitting diffuse light and does not take into account the quantity of direct light reaching the site which is dependent on aspect as well as canopy closure.

The correlations for diffuse and direct light values decreases slightly from May to the August values. The reason for this slight decrease lies in the deciduous canopy of quadrat 54. There the ground flora flourished earlier in the season, when the canopy was less dense, resulting in the higher May values. By August the deciduous canopy was fully developed and the relationship between the ground flora axes and light is reduced.

6.2.2. Relationship between TWINSPAN classification groups and the DECORANA ordination light data

Using TWINSPAN to classify the August data from phase IV, the 111 sub-quadrats separated into six distinct groups (Table 6.2.).

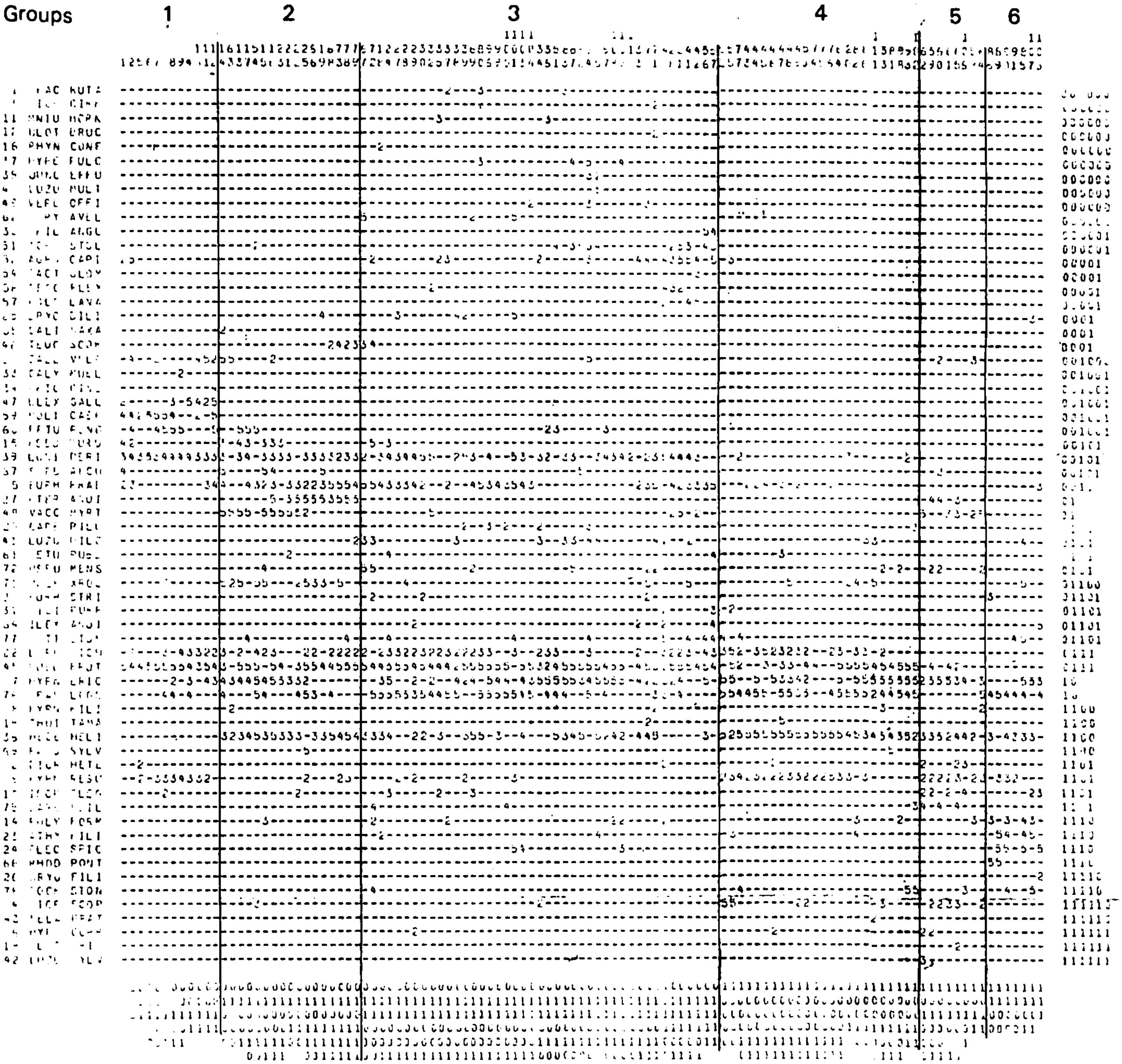

Table 6.2. TWINSPAN classification table - phase IV - ground flora survey - August data

Table 6.3. shows a summary of these groups with the main quadrats representative of each group, the past history of the quadrats, the indicators and preferentials, the mean diffuse site factors and the mean direct site indices.

The same data were also ordinated using DECORANA. Figure 6.1. shows the six TWINSPAN groups plotted on the ordination, axes I x II, as well as the sub-quadrat numbers. Figure 6.2. shows the same ordination with the diffuse site factors for each sub-quadrat and Figure 6.3. shows the direct site indices for each sub-quadrat. Figures 6.2. and 6.3. show the lighter sub-quadrats on the left side with the darker ones on the right side. This light-dark axis appears to run diagonally from the top left-hand corner to the bottom right-hand corner. The sub-quadrats with the average values are aggregated in the centre. This confirms the high correlation of light with the first axis of the ground flora data in Table 6.1.

Both the mean diffuse site factors and the mean direct site indices for each group decrease linearly from group 1 to group 6 (Table 6.3.). Table 6.4. shows that these differences between groups analysed with the Mann-Whitney U-test (two-tailed), are significant in most cases, between all but adjoining groups. It is apparent from these means that the vegetation in each sub-quadrat is closely related to the amount of short wave length radiation reaching the site.

Discussion of the main ground flora community types from the phase IV August data

Group 1

This group contains only sub-quadrats of quadrat 4 (Table 6.3.). It has the highest mean diffuse site factor and direct site index

Table 6.3. The main TWINSPAN groups emerging from the classification of the August data from phase IV (only those quadrats with two or more sub-quadrats in the group are included)

Group	Number of sub-quadrats	Quadrats	% of sub-quadrats from quadrat in group	Past history	Indicators in order importance with percentage constancy to group	Preferentials with percentage constancy to group	Mean diffuse site factor				Mean direct site index			
							May	(s.e.)	Aug	(s.e.)	May	(s.e.)	Aug	(s.e.)
1	12	4	100%	heath	*Molinea caerulea* 75% *Hypnum cupressiforme* var. *resupinatum* 67% *Ulex gallii* 50% *Betula pendula* 50%	*Calluna vulgaris* 42%	47	(3.93)	43	(4.21)	49	(3.83)	45	)3.04)
2	17	9	75%	c.w.*	*Pteridium aquilinum* 59% *Vaccinium myrtillus* 59% *Quercus* x *rosacea* 59% *Hedera helix* 94%	*Pseudoschleropodium purum* 35% *Teucrium scorodonia* 24% *Sorbus aucuparia* 24%	38	(3.58)	34	(3.33)	44	(2.34)	40	(2.52)
		54	36%											
3	43	13	94%	c.w.	*Agrostis capillaris* 30%	*Luzula pilosa* 26% *Agrostis stolonifera* 23% *Lonicera periclymenum* 70% Brash/logs 60%	33	(2.32)	31	(2.31)	37	(2.45)	34	(2.53)
		56	63%	c.w.										
		55	38%	c.w.										
		54	36%	c.w.										
		14	20%	heath										
		9	17%	c.w.										
4	24	14	73%	heath	Brash/logs 88% *Lophocolea* spp. 63% *Hedera helix* 100% *Rubus* agg. 71%	*Eurychium praelongum* 25%	26	(1.92)	26	(2.07)	28	(2.00)	27	(2.16)
		55	31%	c.w.										
		54	29%	c.w.										
		56	19%	c.w.										
5	8	52	88%	c.w.	*Vaccinium myrtillus* 63% *Isopterygium elegans* 50% *Pteridium aquilinum* 38%	*Dicranella heteromalla* 38% *Dicranium scoparium* 63% *Hypnum cupressiforme* var. *cupressiforme* 25% *Calluna vulgaris* 25% *Pseudotsuga menziesii* 38% Bare soil 38%	18	(2.57)	same as May		26	(2.86)	same as May	

* c.w. = continuously wooded

Table 6.3. (Contd.)

Group	Number of sub-quadrats	Quadrats	% of sub-quadrats from quadrat in group	Past history	Indicators in order importance with percentage constancy to group	Preferentials with percentage constancy to group	Mean diffuse site factor May (s.e.)	Mean diffuse site factor Aug (s.e.)	Mean direct site index May (s.e.)	Mean direct site index Aug(s.e.)
6	7	55 56	31% 13%	c.w. c.w.	*Blechnum spicant* 57% *Athyrium filix-femina* 57%	*Isopterygium elegans* 29% *Polytrichum formosum* 57% *Rhododendron ponticum* 29% Rotting stumps 29% Rocks/stones 29%	12 (2.53)	same as May	11 (2.29)	same as May

* c.w. = continuously wooded

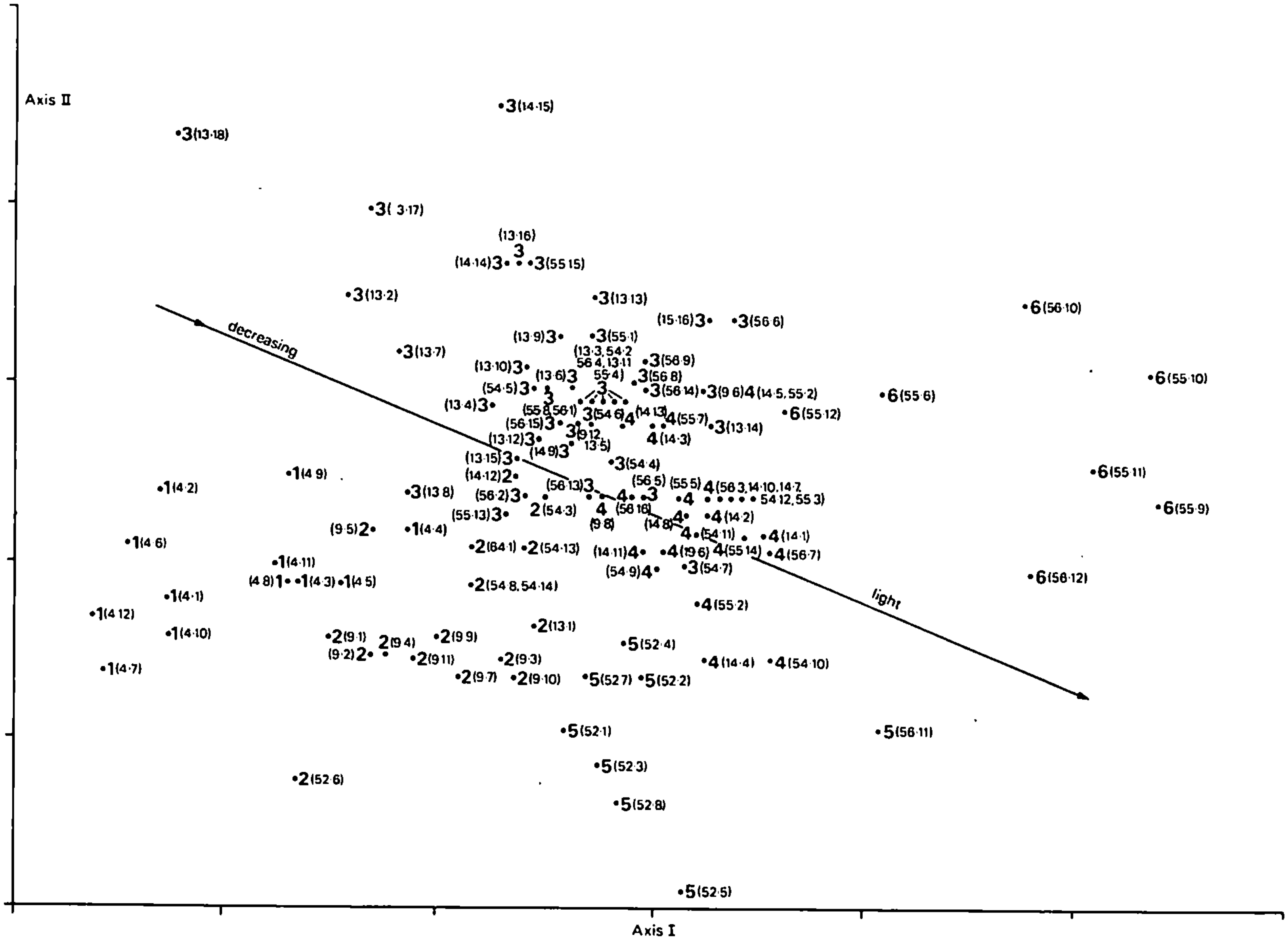

Figure 6.1. DECORANA site ordination of August data from the phase IV ground flora survey showing TWINSPAN groups (Table 6.3.) and sub-quadrat numbers

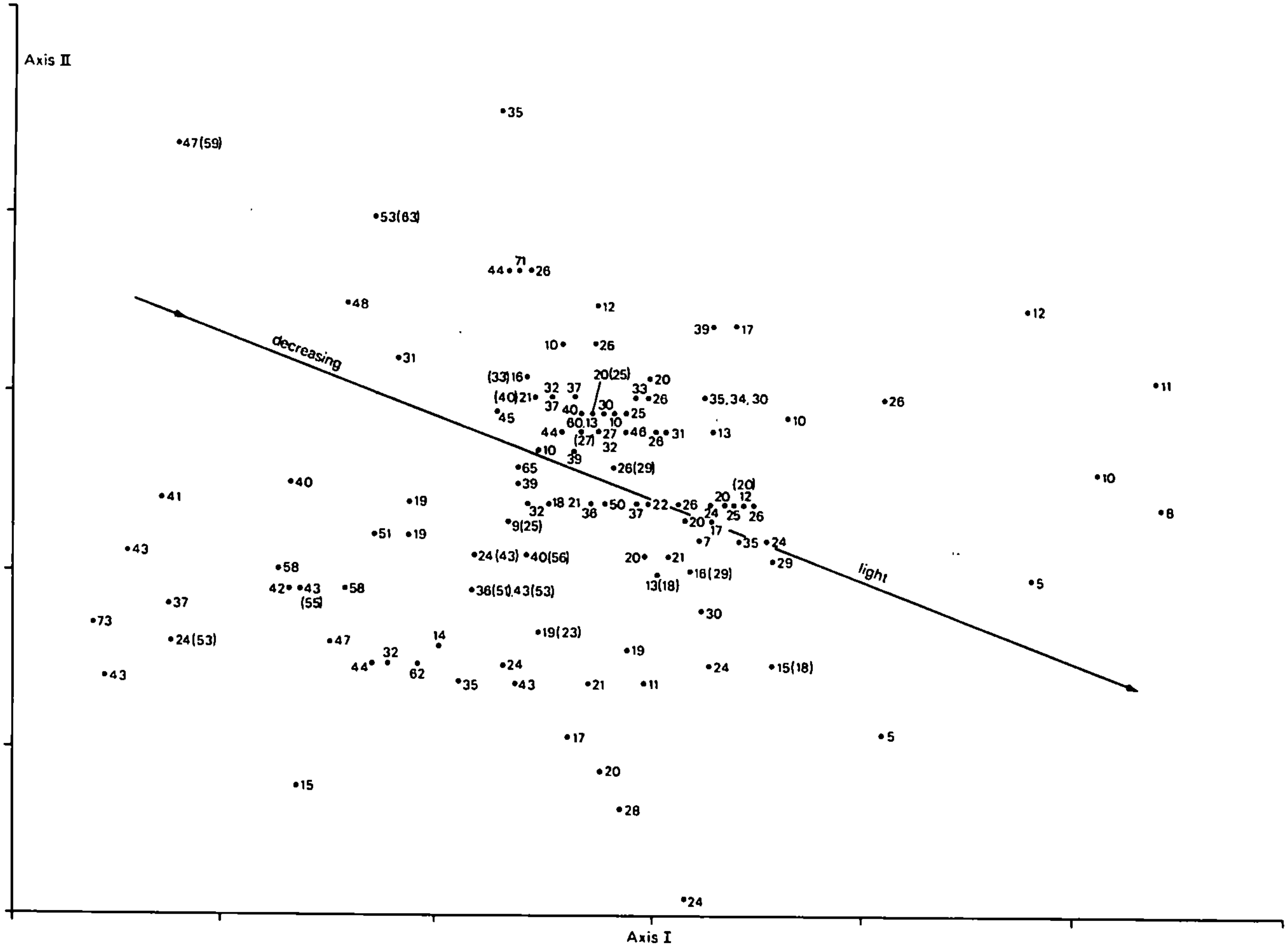

Figure 6.2. DECORANA site ordination of August data from the phase IV ground flora survey with the diffuse site factors for each sub-quadrat in Figure 6.1. (May values in brackets if different from August values)

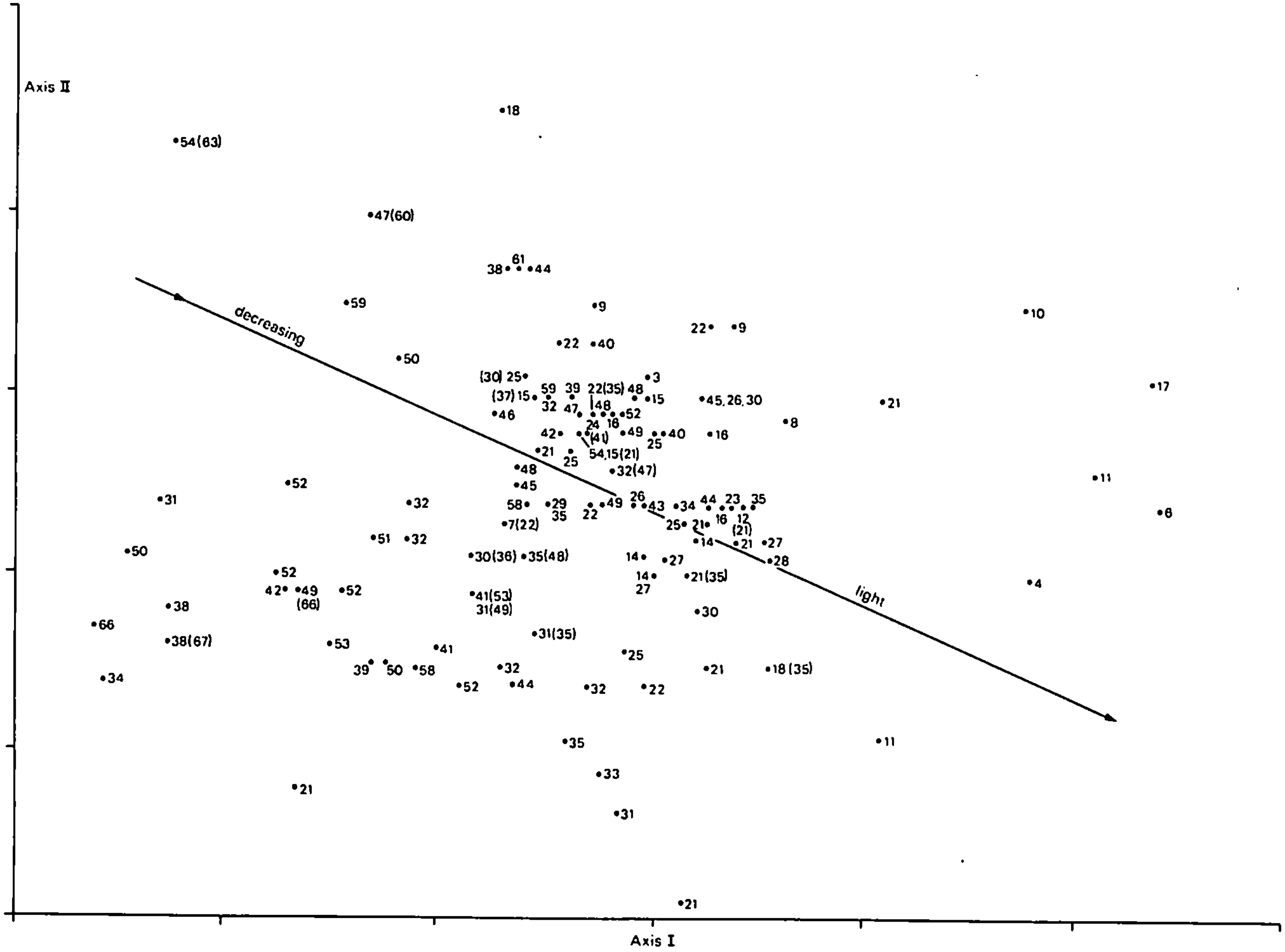

Figure 6.3. DECORANA site ordination of August data from the phase IV ground flora survey with the direct site indices for each sub-quadrat in Figure 6.1. (May values in brackets if different from August values)

of all the TWINSPAN groups. The values for both diffuse and direct light are significantly different from those in all the other groups except for group 2 (Table 6.4.).

As expected under a light Pinus canopy on former heathland, the indicators and preferential are light demanding heath species, - Molinea caerulea, Ulex gallii, Betula pendula[1] and Calluna vulgaris. Molinea caerulea, a typical heathland grass, occurs in the highest number of sub-quadrats in this group, 75%

Table 6.4. Comparisons of the diffuse site factors and direct site indices for the TWINSPAN groups of phase IV (August data) using Mann-Whitney U-test (two-tailed)

Groups		1	2	3	4	5
1	a	-	-	-	-	-
	b	-	-	-	-	-
2	a	n.s.	-	-	-	-
	b	n.s.	-	-	-	-
3	a	0.0118	n.s.	-	-	-
	b	0.0492	n.s.	-	-	-
4	a	0.0012	0.0487	n.s.	-	-
	b	0.0001	0.0003	n.s.	-	-
5	a	0.0114	0.0122	0.0259	n.s.	-
	b	0.0018	0.0122	n.s.	n.s.	-
6	a	0.0008	0.0080	0.0009	0.0027	n.s.
	b	0.0005	0.0002	0.0010	0.0008	0.0046

a = Diffuse site factors compared
b = Direct site indices compared
n.s. = not significant

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[1] An attempt was made in phase IV to separate Betula pendula and B. pubescens and their possible hybrids. The possible hybrids were classified as tending to one or the other species. No clear distribution pattern emerged.

On the site ordination (Figure 6.1.) group 1 is positioned on the extreme left-hand side, reflecting its distinct heathland vegetation, as well as its high light values shown in Figures 6.2. and 6.3.

Group 2

This group (Table 6.2.) is composed primarily of the sub-quadrats of quadrats 9 and 54. It has the second highest mean light values (Table 6.3.). Hence it contains, in addition to three sub-quadrats under the main canopy of quadrat 54, the two most recently cleared sub-quadrats, 54.13 and 54.14. This is a reflection of the abundant and diverse vegetation after B - Plan clearing has disturbed the soil and increased the quantity of light reaching the site. Both diffuse and direct light values in this group are significantly different from those of groups 4,5 and 6, but not from those of the adjoining groups 1 and 3 (Table 6.4.).

The indicators, (Table 6.3.) Pteridium aquilinum, Vaccinium myrtillus and Quercus x rosacea, are species characteristic of light oak woodland (Tansley, 1939; Bunce, 1982). The fourth indicator Hedera helix is characteristic of secondary woodland (Rackham, 1980a) which both 9 and 54 are sited in. Of the three preferentials (Table 6.3.), Teucrium scorodonia, is associated with the Pteridium on acid brown earths in woodland (Bunce, 1982). The moss Pseudoscleropodium purum, is associated with woodland clearings and Sorbus aucuparia prefers lighter canopied plantations such as Quercus, Fagus, and Larix (Anderson, 1979).

On the site ordination (Figure 6.1.) group 2 is a cohesive group on the left-hand side with the sites having higher light values (Figures 6.2. and 6.3.).

Group 3

As expected of a large mixed group, group 3 is in the centre of the TWINSPAN Table 6.2., where the least distinct sites are classified (Gauch, 1982). Unlike groups 1 or 2, it has more B - Plan sub-quadrats (49%) than the percentage of the total 111 sampled (42%). Group 3 contains nearly all of the sub-quadrats of quadrat 13 (Table 6.3.) and many of those in quadrat 56 including three in more recently cleared sub-units, 56.13, 56.14 and 56.15. Significantly, the only sub-quadrats of the dark Picea sitchensis canopies quadrat 14 in this group are those in recently cleared B - Plan sub-units, 14.9, 14.14 and 14.15. Both sets of light values for this group are significantly different from those of groups 1 and 6, but not from those of the adjoining groups 2 and 4 (Table 6.4.). The values of the diffuse site factors are significantly different from those of group 5, but not those of the direct site indices (Table 6.4.).

The single indicator for group 3 is Agrostis capillaris (Table 6.3.). This species is found in woods such as the site of quadrat 13, that were let for grazing in the past (Hamilton, pers. comm.; Tansley, 1968). A. capillaris probably has a persistent seed bank (Thompson and Grime, 1979) and hence responds well to B - Plan clearing in the numerous sub-quadrats in B - Plan sub-units in this group. Of the four preferentials (Table 6.3.), Luzula pilosa and Agrostis stolonifera are coppicing species that respond well to clearing (Tansley, 1939; Brown and Oosterhuis, 1981). Luzula was found to prefer sub-quadrats, particularly those in B - Plan sub-units with significantly greater diffuse site factors than others under the surrounding canopy. A. stolonifera was not recorded in phase II in the new B - Plan sub-units, cleared only the previous winter. However, by the second season, this species obviously had had time to respond to the clearing and was recorded in these sub-quadrats. The third preferential, Lonicera perclymenum, is an early successional species again responding to the light climate after clearing (Werner, 1979). Likewise, the fourth preferential is indicative of recent B - Plan clearing.

On the site ordination (Figure 6.1.) group 3 is positioned in the top centre, somewhat merged with groups 2 and 4 whose light values are not significantly different from those of group 3 (Table 6.4.). A distinct sub-group of group 3 occurs at the very top of the ordination (Figure 6.1.). The seven sub-quadrats, five of which are in recently cleared B - Plan sub-units, 13.16, 13.17, 13.18, 14.14 and 14.15, are separated out from group 3 in a lower division of the TWINSPAN classification (Table 6.2.). As expected they are the sub-quadrats with abundant A. capillaris, A. stolonifera and rotting stumps, the indicators for this sub-division of group 3. Several coppice species are preferentials for this sub-group including Luzula pilosa, Digitalis purpurea and Holcus lanatus (Rackham, 1980a; Brown and Oosterhuis, 1981). These sub-quadrats all have high diffuse site factors and high direct site indices (Figures 6.2. and 6.3.) again illustrating the effect of B - Plan on the light climate which in turn affects the ground flora community.

Group 4

This group is composed of the sub-quadrats under coniferous canopies, Picea sitchensis or Pseudotsuga menziesii, quadrats 14,55 and 56, as well as the sub-quadrats in the darker and older coniferous B - Plan sub-units, within the Quercus x rosacea canopy of quadrat 54, 54.9, 54.10, and 54.11. The mean diffuse and direct light values are midway between those of the extreme groups 1 and 6 (Table 6.3.) and significantly different from groups 1,2 and 6, but not from the adjoining groups 3 and 5, (Table 6.4.).

The indicators and preferentials (Table 6.3.), Lophocolea spp., Hedera helix, Rubus agg., and Eurhychium praelongum are all shade-tolerant but can grow in lighter sites as well (Watson, 1968; Brown and Oosterhuis, 1981). Eurhychium rapidly recolonizes after coppicing and as does Lophocolea heterophylla on left-over brash (Steele and Welch, 1973).

On the site ordination (Figure 6.1.) group 4 is positioned in the middle of the light gradient of increasing light and the resulting increased vegetational response (Figures 6.2. and 6.3.).

Group 5

This group is very distinctive in that it consists mainly of the sub-quadrats of quadrat 52, the relic oak coppice, with only one other sub-quadrat that in an older B - Plan sub-units, 56.11 (Tables 6.2. and 6.3.). These sub-quadrats have the second darkest light climate (Table 6.3.) and both sets of diffuse and direct light figures are significantly different from those of groups 1 and 2 (Table 6.4.). Only the diffuse site factors are significantly different from those in group 3 and the direct site indices from those in group 6 (Table 6.4.). There is no significant difference between group 5 and group 4 (Table 6.4.). This might be expected as group 5 was part of group 4 in an earlier TWINSPAN division (Table 6.2.).

The indicators for group 5, Vaccinium myrtillus, Isopterygium elegans and Pteridium aquilinum (Table 6.3.) are all woodland species that can tolerate some shade (Tansley, 1968; Smith, 1978). However, both Vaccinium and Pteridium are very sparse in quadrat 52. The six preferentials include three shade-tolerant mosses found in woodland (Watson, 1968), Dicranella heteromalla, Dicranium scoparium, and Hypnum cupressiforme var. cupressiforme (Table 6.3.). The fourth preferential, Pseudotsuga menziesii (Table 6.3.) is present as small individuals most likely originating from the time when the site was last coppiced as Pseudotsuga needs considerable light for regeneration, being a pioneer species (Hosie, 1969). They have remained in a suppressed state since then, able to take advantage of higher light levels only when the oak canopy is devoid of leaves. Likewise another preferential species, Calluna vulgaris (Table 6.3.) is probably remnant from the last coppicing around 1916. The final preferential bare soil (Table 6.3.) is a result of the slope, 26°, and the lack of significant ground cover.

On the site ordination (Figure 6.1.), the sub-quadrats of group 5 are positioned at the bottom right-hand corner, with other sub-quadrats having low diffuse site factors and low direct site indices (Figures 6.2. and 6.3.).

Group 6

This final TWINSPAN group of seven sub-quadrats (Table 6.2.) contains those allocated in the oldest and darkest B - Plan sub-units of quadrats 55 and 56 (Table 6.3.), as well as on sub-quadrat under the main canopy, 56.6.

The diffuse site factors and the direct site indices for this group are all significantly different from those of the other groups, except for the diffuse site factors of group 5 (Table 6.4.). The direct site indices of group 5 and of group 6 could be expected to be different as quadrat 52 is south-southwest facing and quadrats 55 and 56 are nearly west facing. However, the diffuse light levels might be similar as both the Quercus and the coniferous Pseudotsuga canopies in the B - Plan sub-units are closed in August.

The indicators for group 6 are both shade-tolerant ferns, Blechnum spicant and Athyrium filix-femina (Table 6.3.). Athyrium is especially tolerant of shade stress, having a low compensation point (Packham and Harding, 1982), as well as the ability to produce spores under low light conditions (section 8.2.3.). However, because it can also grow in light conditions, the diffuse site factors for the sub-quadrats where it is found are not significantly different from the values of those under the surrounding canopy (section 8.2.3.). Of the five preferentials, (Table 6.3.), three are also shade tolerant woodland species, _Isopterygium_ _elegans_, _Polytrichum_ _formosum_ and _Rhododendron_ _ponticum_ (Clapham _et_ _al_., 1962; Watson, 1968). The fourth preferential, rotting stumps, is the remnant of the previous canopy cleared 20 years before. The rocks and stones are the result of the slope, 19°, with little ground cover facilitating the exposure of surface rocks.

The sub-quadrats of group 6 are positioned on the extreme right-hand side of the ordination (Figure 6.1.) as might be expected of those sites with little light and sparse ground flora (Figures 6.2. and 6.3.).

6.3. The light climate under B - Plan management - a summary

Four clear gradients emerged from these TWINSPAN and DECORANA analyses:

a) light;

b) canopy type;

c) time since last B - Plan sub-unit clearing;

d) community gradient from the most to the least light-demanding species;

Taken together these four provide a clear indication of the importance of variation in the light climate under B - Plan.

a) Light

In both the TWINSPAN classification and the DECORANA ordination, a distinct gradient of decreasing light emerged. The mean diffuse site factors and the mean direct site indices for each of the six TWINSPAN groups decreases significantly from group 1 to group 6 (Tables 6.3. and 6.4.). This gradient is also observed in the ordering of the sub-quadrats in the DECORANA ordination. A line drawn from the upper left-hand corner to the lower right-hand corner corresponds to this gradient of decreasing light (Figures 6.1.-6.3.).

b) Canopy type

The main canopy types in the TWINSPAN classification change from the light *Pinus* canopies, in groups 1 and 2, through the open deciduous canopies of *Quercus* and *Larix* in groups 2 and 3, the darker *Picea sitchensis* and *Pseudotsuga menziesii* canopies of group 4, the closed *Quercus* x *rosacea* canopy of group 5 and finally to the very dark *Tsuga heterophylla* and *Thuja plicata* canopies in the oldest B - Plan sub-units.

This trend follows that of relative illumination (diffuse site factor measured on a grey day as a percentage of the simultaneous reading in the open) described by Hill and Hays (1978) under 43 year old even-aged plantation crops. The value under a *Pinus* canopy was 50% and that under *Picea sitchensis* 7%. Hill (1979a) places *Tsuga* canopies after the *P. sitchensis* as the darkest of all crops, *Larix* spp. as comparable to *Pinus* and *Pseudotsuga*, fitting in between *Pinus* and *P. sitchensis*. Hill and Hays (1978) present diffuse light values of 50% under pine corresponding closely to those of quadrats 4,9 and 13, for the mean diffuse site factor under the main canopy, shown on Table 6.5. Those under the *Pseudotsuga* and *P. sitchensis* are correspondingly less (Table 6.5.).

Table 6.5. Mean diffuse site factors and direct site indices (May-August where applicable) compared to the time since last clearing of site where sub-quadrats located; a = mean diffuse site factor, b = mean direct site index

Quadrats			Years since clearing													
			2	6	9	14	15	20	21	30	31	32	37	41	42	66
4	a	May		56						42						
	a	Aug		49						41						
	b	May		59						43						
	b	Aug		52						41						
9	a	May	61		29					40						
	b	May	56		42					47						
13	a	May	65		13	10		22					34			
	a	Aug	59		-	-		13					32			
	b	May	58		13	18		26					41			
	b	Aug	53		-	-		24					40			
14	a	May	41		20						24					
	b	May	35		15						25					
52	a	May														19
	b	May														28
54	a	May			55		14		18						35	
	a	Aug			42		10		14						24	
	b	May			47		18		31						40	
	b	Aug			33		13		16						27	
55	a	May	33		30		10		10			28				
	a	Aug	-		22		-		-			-				
	b	May	33		21		10		12			36				
	b	Aug	-		14		-		-			-				
56	a	May	41		31		5		16					27		
	b	May	34		18		7		7					36		

The Pinus canopies quadrats are further separated on the basis of past history in both the classification and ordination and hence occur as distinct groups in both (Table 6.3. and Figure 6.1.). In contrast, the effect of the dark P. sitchensis in quadrat 14 appears to have supressed the effect of its heathland origin by shading out the light demanding heath species. Hence, quadrat 14 is grouped with the continuously wooded sites (Table 6.3; Figure 6.1.).

c) Time since last B - Plan sub-unit clearing

The mean time since the sub-quadrats in the B - Plan sub-units were last cleared for each of the TWINSPAN groups is as follows:

group	mean time in years	(s.e.)
1	5.00	(0.00)
2	6.67	(1.48)
3	7.70	(1.53)
4	11.33	(2.32)
5	15.00	(0.00)
6	18.00	(1.34)

As a result, the youngest sub-quadrats in B - Plan sub-units are classified on the right-hand side of the Table with a gradient of increasing time since last clearing to the oldest sub-quadrats in the oldest B - Plan sub-units. This is reproduced in the ordination and corresponds to the diagonal light gradient line (Figures 6.1. to 6.3.).

Table 6.5. shows the mean diffuse site factor and the mean direct site index compared to the time since last clearing of the sites where the sub-quadrats were located. For the sub-quadrats in B - Plan sub-units, between 2 and 21 years, the trend is from high to low light values (Table 6.5.) for each of the quadrats. Thereafter, in the sub-quadrats under the main canopy cleared 30 to 42 years before the hemispherical photos were taken in 1982, the light values increase. Obviously these values under the main canopy cannot be separated from the effects of B - Plan management. Therefore

they do not correspond to the lower values under even-aged plantations of comparable age, 30 years being the darkest phase in an even-aged conifer rotation after which thinning increases the light environment (Hill, 1979a). These establishment and thicket phases correspond to the older B - Plan sub-units where the light values are the lowest between 9 to 21 years after clearing.

The light values (Table 6.5.), with few exceptions, are high enough to support a bryophyte community, which will not survive below 2-9% relative illumination, as well as a vascular plant community which will not survive below 10-20% (Hill and Hays, 1978).

This downward trend of light with increasing time since last clearing in the B - Plan sub-units corresponds to the same trend of decreasing species numbers and abundances shown in Figures 5.9. to 5.11 as well as to that of the successional trend in the seed bank of fewer species in common between the seed bank and the ground flora with increasing time since the last disturbance shown in Table 7.1. and Figure 7.3.

d) Community gradient

Finally, the vegetational response to this light gradient corresponds well to the change in the indicators and preferential for each TWINSPAN group from 1 to 6. The trend from light-demanding to shade-bearing species is as follows (Table 6.3.):

Group 1 - the extremely light-demanding heathland species - including Molinea caerulea, Ulex gallii, Betula pendula and Calluna vulgaris.

Group 2 - the woodland species benefitting from an open light wood - including Pteridium aquilinum, Vaccinium myrtillus, Quercus x rosacea and Hedera helix.

Group 3 - the coppicing species and species responding quickly to clearing disturbance - including Agrostis capillaris, A. stolonifera, Luzula pilosa, Digitalis purpurea, Holcus lanatus and Chamerion augustifolium.

Groups 4 and 5 - the woodland species able to bear some shade - including Lophocolea spp., Hedera helix, Rubus agg., Vaccinium myrtillus and Eurhychium praelongum.

Group 6 - the true shade tolerant species - including Athyrium filix-femina and Blechnum spicant.

The most important conclusion from this part of the study is that light is highly correlated with vegetational gradients and B - Plan management. This changing pattern of light does not occur over a long period of time, as with a 54 year conifer rotation, but is replicated in space in the mosaic of the differing light climates of each B - Plan unit. Hence the possibility exists for plants and in particular woodland species, to find a suitable refuge during the course of a rotation. Hill (1979a) states that this is not possible during the dark establishment and thicket stages of an even-aged conifer rotation.

CHAPTER 7. THE SEED BANK - PAST AND FUTURE DIVERSITY

CHAPTER 7. THE SEED BANK - PAST AND FUTURE DIVERSITY

7.1. Introduction

The majority of seed bank studies have been conducted in arable land rather than in woodlands (Thompson and Grime, 1979; Brown and Oosterhuis, 1981). In general, seed banks have been relatively under-researched. This is, in part, due to the experimental difficulties involved in the collection and germination of seeds and also to the practical difficulties in obtaining enough samples for the results to be analysed for statistical significance (Major and Pyott, 1966). Furthermore, the indigenous seed bank in woodlands has often been thought to be less important in determining potential ground flora diversity than immigration by wind or more especially animal transport (Olmstead and Curtis, 1947). Ash and Barkham tentatively suggested, as recently as 1976, that the indigenous seed bank "may obviate the need for subsequent immigration of propagules for the establishment of plants new to the site" (p. 697). Brown and Oosterhuis (1981) in their study of buried seed in coppice woods finally concluded:

> "... that the main reservoir of propagules for the floristic recovery of coppice areas by marginal species resides in their soils, rather than in the form of plants in the neighbouring open areas." (p. 35)

One consequence of the paucity of seed bank studies is the conflicting information on individual species behaviour in seed banks.

Germination of seeds from the Tavistock Woodlands seed banks following B - Plan sub-unit clearing can be described as a homeostatic mechanism to prevent the degradation of the ecosystem.

> "The mechanism(s) by which germination of buried seeds is synchronized with disturbance of the ecosystem represents one of the paramount control features in ecosystem dynamics; in a sense, it initiates a homeostatic response held in reserve for just such an occasion." (Bormann and Likens, 1979: p. 111)

The seed bank in Tavistock Woodlands reflects past management and also has predictive value for future diversity. Therefore to understand the plant community completely, it is necessary to know the potential competitors for the future (Major and Pyott, 1966).

Inclusion of a species in a persistent seed bank is part of the competitive strategy for this species. The strategy of seed dormancy in a seed bank allows seedlings to avoid the 'potentially damaging effects' of established plants (Thompson and Grime, 1979).

Seed banks have been divided by Thompson and Grime (1979) into four different types. This is a useful way to understand and characterize the seed bank strategies of some of the species in Tavistock Woodlands. Type I consists of species with transient seed banks present only during the summer in which the seeds are released. Germination then takes place in the same autumn. Many common grasses are included in this group. Type II includes those species which also have a transient seed bank but whose seeds, released in the summer, are dormant over the following winter and require stratification (chilling) before germination in the early spring. Many shade-tolerant woodland species such as Hyacynthoides non-scripta have this type of seed bank. Types III and IV consist of species with persistent seed banks and these two types differ only in the proportion of seeds entering the seed bank. In species belonging to the type III seed bank, many of the seeds germinate immediately after release, but others become part of the persistent seed bank. In species belonging to type IV, only a few of the seeds germinate after release, while the majority enter the persistent seed bank.

Many of the species in types III and IV are light-demanding species of open habitats and can therefore be expected to have a light requirement for germination and to be inhibited from germination by darkness (Grime and Jarvis, 1975). Species characteristic of oak coppices, which comprise a significant part of the ground flora in Tavistock Woodlands, are included in seed bank types III and IV. They are species such as Calluna vulgaris, Carex pilulifera, Digitalis purpurea, Galium saxatile, Holcus mollis, Hypericum pulchrum, Juncus effusus, Melampyrum pratense and Teucrium scorodonia all found more frequently in B - Plan sub-units (Table 8.1.). (Rackham, 1980a; Brown and Oosterhuis, 1981; Packham and Harding, 1982.) Many of these tend to have small seeds which are therefore easily buried in the litter and subsequently incorporated in the mineral soil probably by invertebrate activity and rain water percolation (Howard and Ashton, 1967; Harper, 1977). When the soil is disturbed and the buried seed surfaces, germination can take place if certain light requirements are met. For germination, the ratio of red to far red must approach that of daylight (1:1 - 1:2) and not the much lower ratio under a canopy (Roberts, 1972). Far red light is selectively transmitted through canopies. This red:far red ratio affects the equilibrium of the two forms of phytochrome found in plants. One current theory, now being investigated, is that the phytochrome alters the permeability of the seed membrane and hence has a direct effect on germinability (Lambton, 1982). In contrast to these light-demanding coppice species, true woodland species able to bear some shade, with transient type II seed banks, will germinate under conditions of low levels of red and green light and do not need the high intensity red light treatment necessary for germination in the light-demanding species like Juncus (Grime and Jarvis, 1975). These woodland species have a chilling requirement for germination but will germinate in light or dark and hence are not incorporated into persistent seed banks (Grime et al, 1981).

7.1.1. The phase IV seed bank study

The methods used in this study (Chapter 3), which sampled the soil of the phase IV quadrats only once in 1982, meant that a complete quantitative analysis was not possible. This was firstly, because the numbers of seeds of many species fluctuate in their ability to germinate throughout the year on a monthly basis (Thompson and Grime, 1979). Secondly, the contagious distribution of most seeds, excluding those with wind-borne seeds, around a mother plant, results in a high variance between samples, and an impracticably large number of samples would have been necessary for statistical reliability (Major and Pyott, 1966). However, it is possible to examine general spatial distribtuions of seeds within the study site with respect to B - Plan sub-units, as well as within the soil and to examine successional trends within the B - Plan sub-units and under the main canopies. The end of April was chosen as the best time for sampling, as the seed bank would include species in the persistent seed bank, as well as many of the shade-tolerant woodland species with seed bank type II, whose innate or acquired dormancy needs to be broken by winter stratification (Roberts, 1972).

The samples were collected from the 13th to the 29th of April 1982. After air drying and dark storage, they were placed in the seed trays on June 6th (Plate 3.16.) and by the 12th of June the first seedlings had appeared. As in Hill and Stevens (1981) study of forest plantations, the majority of the seedlings had emerged within one month of being placed in the greenhouse (Plate 3.17.). The greenhouse was considered suitable for providing optimum conditions for most species to germinate and that those not doing so would probably not germinate in the less than optimum field conditions (Hill and Stevens, 1981). Brown and Oosterhuis (1981), in their study of coppice seed banks, stated that conditions after coppice felling would approximate to those in the greenhouse sufficiently to make the results of this type of germination test valid. These conditions are light, warmth and moisture, soil disturbance, fluctuating temperatures and an increased nitrate level. Coppice cutting can result in diurnal soil temperature fluctuations of up to 10° (Ash and Barkham, 1976). The effect of B - Plan clearing is probably similar to coppicing but more limited in extent. Soil temperature differences of 3-4° were measured between the soil under mature B - Plan sub-units and that under recently cleared sub-units. Light obviously increased (Chapter 6), with both coppice clearing and B - Plan clearing. As in clear-fell forestry, it could be expected that the nitrate (NO_3-N) levels increase temporarily under B - Plan (Bormann and Likens, 1979). Bormann and Likens suggest that these increased nitrogen levels might be a stimulus to the high levels of seed germination after a clear-felling. However, after B - Plan clearing, the ground flora does not appear to respond with as abundant growth as after a clear-fell, suggesting that the soil disturbance and resultant enhanced nitrogen levels are limited. Coppice, and to a lesser extent B - Plan extraction and replanting, create local soil disturbance. Moisture under B - Plan and, in the southwest generally, is probably not as limiting a factor as Brown and Oosterhuis (1981) suggest it might be under coppice clearings. B - Plan sub-units are small and seedlings within them are afforded protection from wind dessication by the surrounding trees.

The emerging seedlings were identified using Chancellor (1966) and Muller (1978). When the trays became too crowded, seedlings were removed after identification. Unidentified seedlings were potted up (Plate 3.18.) and allowed to grow on until a positive identification could be made, in some cases until the following year. Epilobium sp., Taraxacum spp. and Senecio vulgaris seedlings germinated in the control trays and in several of the study trays. This contamination resulted from wind-borne seeds from a field adjoining the greenhouse site. These species were eliminated from the study. Several samples from quadrat 51, which was not part of phase IV, were taken. The sparse ground flora under this predominantly Fagus sylvatica canopy consisted almost entirely of Hedera helix and hence the aim was to see what type of seed bank might exist under the very dark 52 year old beech canopy. The germination experiment was not continued until the following season, apart from the species allowed to grow on for identification. It was felt that the qualitative results would not be appreciably affected by continuation. Brown and Oosterhuis (1981) found that for the most part only more of the same species germinated in the second year of their study and their results from the first year were not changed by the inclusion of the second year's results.

7.2. Seed bank succession

Seed banks of disturbed habitats tend to be large and similar in species composition to the current ground flora (Fenner, 1985). Those of relatively stable habitats, such as unexploited forests tend to be much smaller (Whipple, 1978) and to bear less relationship to the current ground flora. The nature of B - Plan management creates small localized disturbances of varying ages with the species number in the seed bank and in the ground flora varying with age. (Figure 5.9.).

As the ground flora in a forest develops after a disturbance, the species differences between it and the seed bank increase (Oosting and Humphreys, 1940; Livingston and Allessio, 1968; Thompson and Grime, 1979; Hall and Swaine, 1980; Fenner, 1985). Livingston and Allessio (1968), in their study of a series of successional forest sites, found that all but the youngest sites had more species in the seed bank than in the ground flora. Figure 7.1. shows a summary of their results (from Fenner, 1985).

The results of the seed bank germination test in this study show similar trends. Figure 7.2. shows the mean number of species in the ground flora for sub-quadrats of a similar age and the mean number of species for the corresponding soil germination test samples versus time since the last clearing either for B - Plan sub-units or for pre-B - Plan clear-felling. The mean values for the number of species in the seed bank are either the same or higher than those of the ground flora (Figure 7.2.), except in one case. As in Livingston and Allessio's (1968) study, the least mature site, in this case the most recently cleared B - Plan sub-units had more species in the ground flora than in the seed bank.

The number of species common to both the seed bank and the ground flora also decreases over time. Hall and Swain (1980) found that in mature forest soils in Ghana, some sites had as little as 5% of species common to both ground flora and seed bank. Figure 7.3. shows a similar trend in Tavistock Woodlands. The time elapsed since the area sampled was last cleared is compared to the percentage of species common to both the seed bank and the ground flora expressed as a mean percentage of the combined species list. Some years have more than one sample (Figure 7.3.). Quadrat 52 (Figure 7.3.- *) plotted on the end of the graph was probably last disturbed by coppicing around 1916 (estate records).

The significance of these results for B - Plan management, illustrated by Figures 7.2. and 7.3., lies in the fact that these differences do not occur in a series of different, geographically

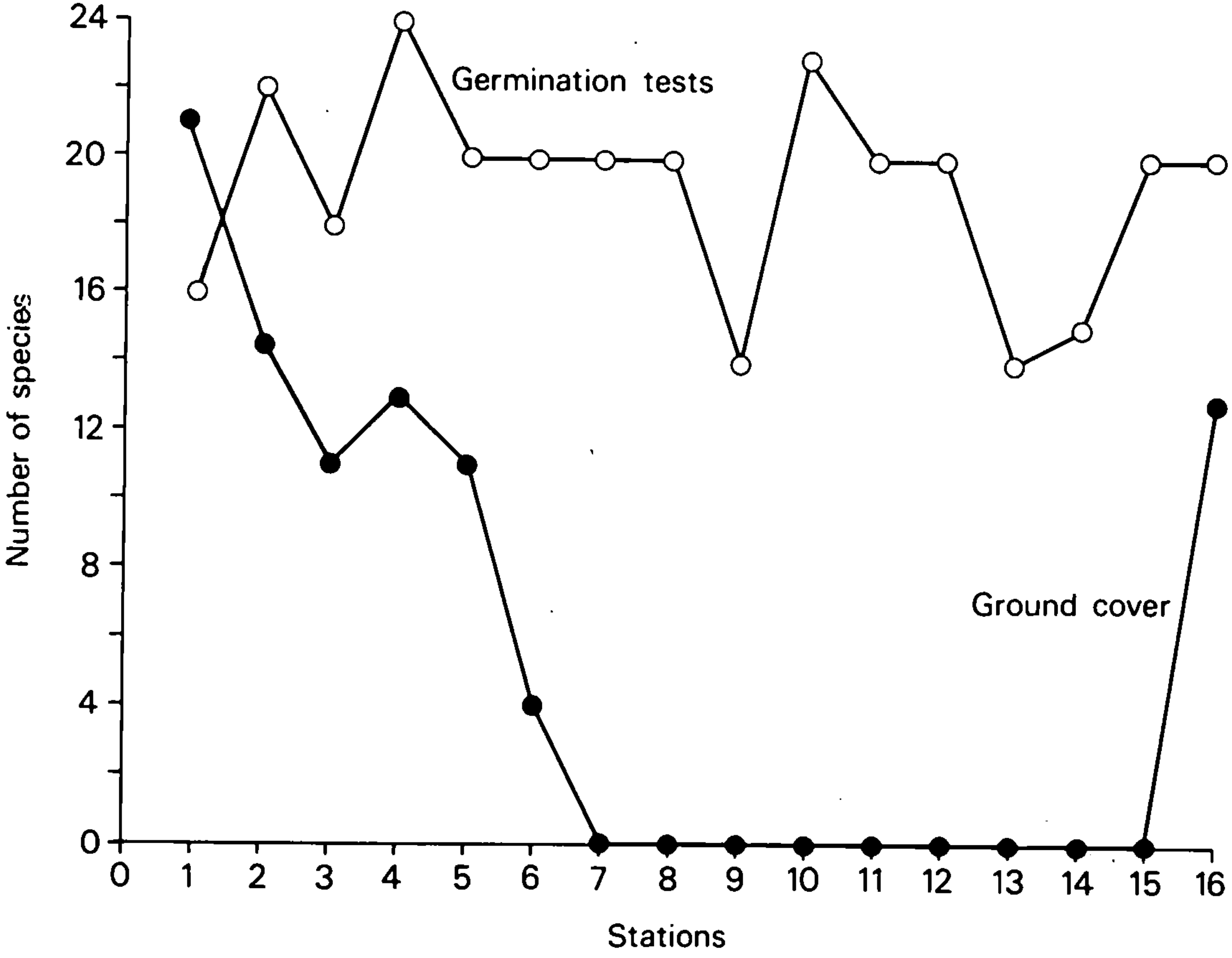

Figure 7.1. A series of forests sites of increasing successional maturity - species numbers in seed bank and in ground flora (after Livingston and Allessio, 1968 in Fenner, 1985)

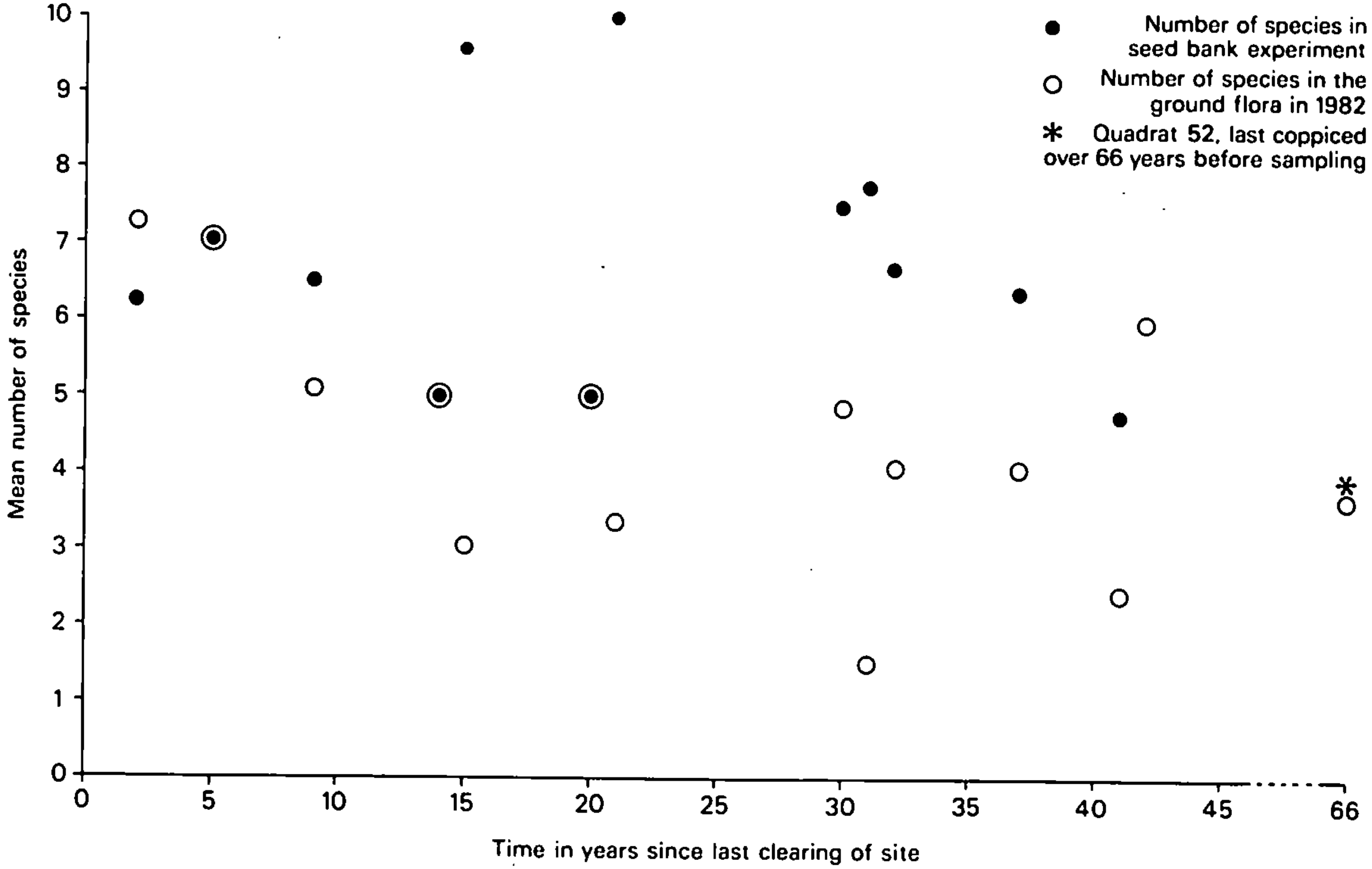

Figure 7.2. The mean number of species in the ground flora for sub-quadrats of a similar age and the mean number of species for the corresponding seed bank soil sample versus time since the last clearing either for B - Plan sub-units or for pre-B - Plan clear-felling

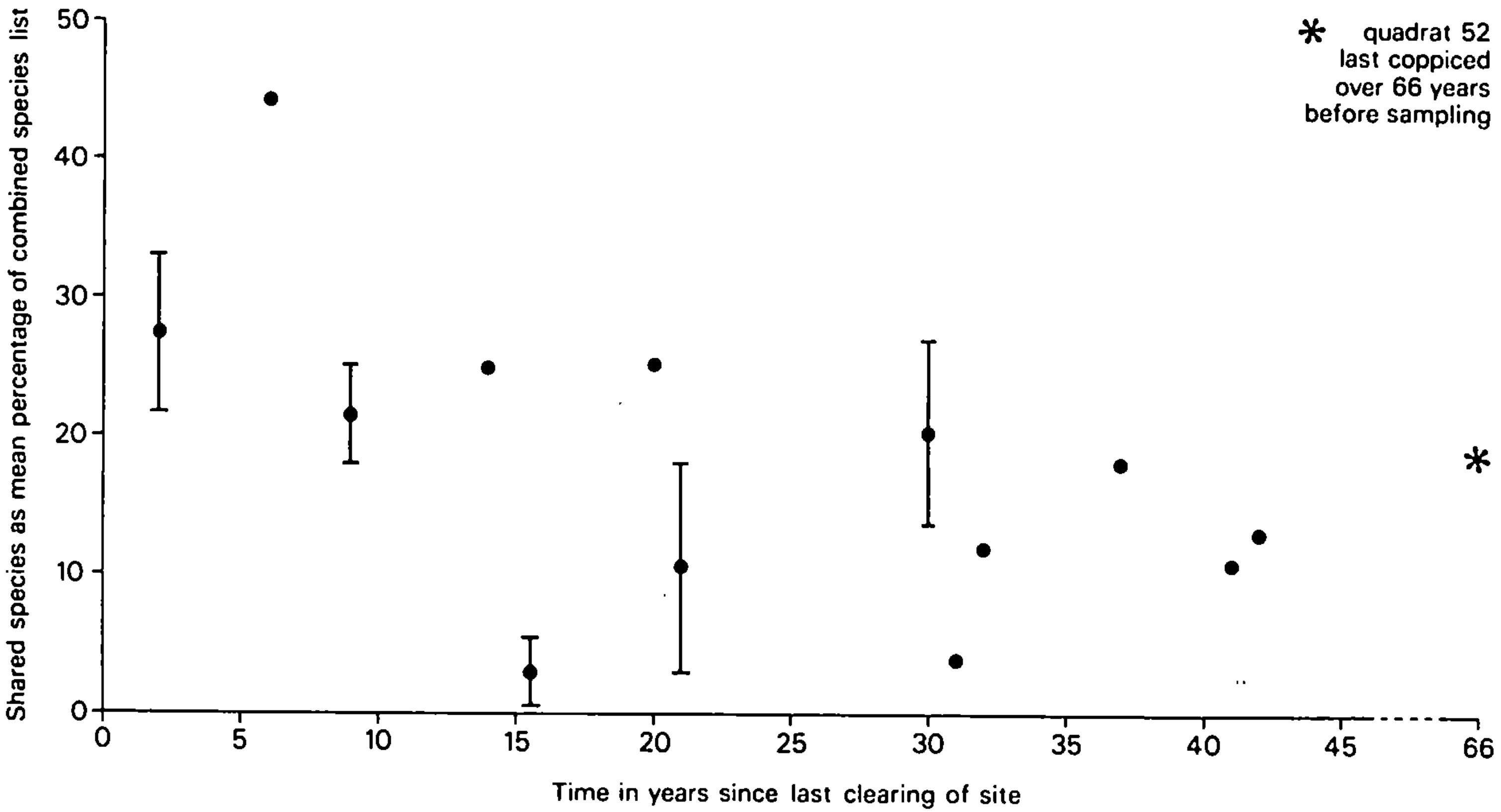

Figure 7.3. The number of species common to both the seed bank and the ground flora (expressed as a mean percentage of the combined species list) versus time since the last clearing either for B - Plan sub-units or for pre-B - Plan clear-felling

separated sites of increasing successional maturity, as in Livingston and Allessio's (1968) or Oostings and Humphrey's (1940) studies, but rather within the small $400m^2$ sampling quadrats of this study. Table 7.1. shows the shared species in the ground flora and seed bank as a % of the combined list for each quadrat, compared with age since the last disturbance. It is obvious from looking at any one single quadrat in Table 7.1., that this successional trend is replicated within this confined $400m^2$ space. This is in contrast to the usual changing successional pattern in the forest, where the seed bank reaches any one stage at only one point in time and not as in B - Plan many stages at the same time. Most of the stages, from the very youngest to nearly the oldest (42 years), are represented in one $400m^2$ quadrat at one point in time under B - Plan management combined with the remains of the previously clear-felled canopies. It will be interesting to see if this successional trend continues as B - Plan approaches the complete 54 year rotation.

That it is possible to replicate this pattern of local successions in these small areas, lies in the fact that the greater part of a buried seed bank is local and is not the result of immigration (Brown and Oosterhuis, 1981). Brown and Oosterhuis (1981) found no correlation between seedling species numbers and individual seedling numbers and the distance to the nearest ride in coppice woodland. For non-wind-borne seeds, effective dispersal is only a few metres from the parent plant (Hill and Stevens, 1981). Forestry operations may disperse some seed in mud on machinery and forestry worker's boots (Hill and Stevens, 1981) and some seed may immigrate from outside, but only in very low numbers, which do not have a significant effect on the community (Kellman, 1970).

Table 7.1. Species common to both ground flora and seed bank expressed as a percentage of combined list compared to the time since area (from which soil seed bank was taken) was last disturbed either by clear-felling or by B - Plan clearing

	Years since clearing													
Quadrats	2	6	9	14	15	20	21	30	31	32	37	41	42	66
4		44%						27%						
9	25%		27%					14%						
13	36%		25%	25%		25%					18%			
14	23%		11%						4%					
52														19%
54			13%		8%		7%						13%	
55	43%		22%		0%		0%			12%				
56	11%		33%		0%		25%					11%		

7.3. Distribution of seed bank species within quadrats and within B - Plan sub-units - past diversity

Tables 7.2.-7.9. show, for each quadrat, the number of seedlings of each species germinating from the soil samples for both the 0 - 5cm (h) layer and the 5 - 10cm (m) layer. Those species not occurring in the ground flora of that quadrat are followed by an asterisk (*).

Quadrat 4

Table 7.2. shows the species developing from the soil samples taken from quadrat 4. Nine of these (Table 7.2.- *) do not occur in the ground flora surveyed in phases I - III. Seven of these occur solely in the soil samples taken from near the first eight sub-quadrats located in the area largely undisturbed by the B - Plan sub-units. This area was last clear-felled in 1952. The seedlings of these seven species are few in number and are most probably the seed bank resulting from the 1952 clearing. Six of these - Carex pilulifera, Galium saxatile, Hypericum pulchrum, Juncus effusus, Rumex obtusifolia and Veronica officinalis are light-demanding,

Table 7.2. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats of quadrat 4

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																				
Agrostis capillaris			1		1	5		12			3	7			7		2		7	1
Agrostis stolonifera	8	24	9	1	14	2	34						8	5			2	1	4	7
Betula spp.		1		1			1		1		2									
Calluna vulgaris	26	15	17	7	49	4	109	23	65		47	5	46	6	51	10	26	2	40	18
*Carex binervis**					2															
*Carex pilulifera**											5									
*Galium saxatile**											3									
*Holcus lanatus**					1															
*Hypericum pulchrum**	4	3		1							1	7								
*Juncus effusus**			67	15	1						1					1			4	
Molinea caerulea			2	1	48	1	1		5		18		6	1	13	2	3		1	
Rubus spp.	13	26	23	5	12	3	27	9	9	2	13	1	2	2	4	1	4	1	3	
*Rumex obtusifolia**					1															
Ulex gallii	4	8	8		4		13	4	13	1	9	1			20	3	18		26	5
*Vaccinium myrtillus**		1																		
*Veronica officinalis**	6																			

* = species not occurring in ground flora

seed bank type III/IV species known to exist in coppice seed banks for at least 30 to 40 years (Brown and Oosterhuis, 1981). The seventh species is Holcus lanatus, a species tolerant of some shaded locations, but only represented in this seed bank by one individual. The seeds of this species are considered by Thompson and Grime (1979) to be included in seed bank type III, where many of the seeds germinate soon after release. Like many of the grasses, these seeds are dark germinated. However, some seeds become part of the persistent seed bank. The competitive strategy of Holcus is four-fold. First, some of its seeds can germinate immediately and develop if they reach a suitable substrate. Second, other seeds can become part of the persistent seed bank, waiting for suitable conditions to occur. Third, it can spread vegetatively. Fourth, it can tolerate some shade-induced stress and remain in situ after other species have succumbed.

The eighth species to occur in the seed bank of the first eight sub-quadrats, but not in the ground flora is Carex binervis (Table 7.2.). Although not in the ground flora, it occurs abundantly in the rides and hence could be transported from the rides in mud during management operations. Hill and Stevens (1981) found this species in the seed bank and not the ground flora of a 30 year-old conifer plantation, suggesting that it has a persistent seed bank.

The ninth species to occur in the seed bank of the first eight sub-quadrats but not in the ground flora is Vaccinium myrtillus (Table 7.2.). Hill and Stevens (1981) suggest that the seeds of Vaccinium, transported by birds, are short-lived because they never found them in the mineral layer. However, earlier, Hill (1979a) felt that the seed was long-lived in the mineral soil on afforested upland sites. The one individual in quadrat 4 germinated from the mineral layer.

Of these nine species in the seed bank and not in the ground flora of quadrat 4, only Juncus effusus occurs in the B - Plan sub-units (Table 7.2.).

The two species in the ground flora but not emerging in the germination tests were Erica cinerea and Lonicera periclymenum. The ground flora cover of Erica is very low and hence seeds from this species would not be easily detected in the seed bank with so few soil samples. Brown and Oosterhuis (1981) also found Lonicera in the ground flora of coppice woods but not in the seed bank. Werner (1979) suggests that clonal habit correlated well with long-distance dispersing seeds and relatively short longevity in the seed bank. Lonicera's strategy, as an early successional woody plant, is to cover as much space as possible with both vegetative growth and seed dispersal, when the competition is lower immediately after clearing (Werner, 1979). In addition, larger seeds like those of Lonicera survive less well in seed banks (Hill, 1979a). However, the main reason for the lack of Lonicera seedlings in any of the quadrats, may be the fact that it was not found to flower anywhere under B - Plan sub-units or under the main canopy. It appears that the species needs larger clearings, such as those occurring when the site was clear-felled 30 years before.

Quadrat 9

Table 7.3. shows the species germinating from the soil samples taken from quadrat 9. Nine of these species do not occur in any of the ground flora surveys, phases I - III (Table 7.3. - *). Six of these occur only in the samples from the first eight sub-quadrats located in the area largely undisturbed by the B - Plan sub-units. This area was last clear-felled in 1952. As in quadrat 4

Table 7.3. Species and numbers of ssedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats of quadrat 9

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																				
Agrostis capillaris*										2	5							1		
Agrostis stolonifera*	3	8	1	2	2		4	2	1	2	3	4	3	9	9		3		4	
Betula spp.	2		7	7	5		2	1	1		5	5	1		2		8	1	3	
Carex pilulifera	26	6	22	6	10	19	33	3	3	13	5	6	9	7	6	3	1	1	47	7
Calluna vulgaris	31	10	76	66	40	10	87	26	23	18	16	22	12	7	2	4	13	12	126	11
Deschampsia caespitosa*										1										
Digitalis purpurea*								1												
Galium saxatile					9	4				4	3									
Hypericum pulchrum									1	5	8	10			1					
Juncus bufonius*	2																			
Juncus effusus*										1	1		2							
Ranunculus repens*						1														
Rubus spp.	16	4	2		5	4	28		3	12	9	12	2	4	3	3	3		8	2
Rumex acetosella*														1						
Ulex gallii*							1			1										
Vaccinium myrtillus				1	3		1											2		

* species not occurring in ground flora

these seedlings, which developed in low numbers from the soil samples, are probably the seed bank remnants of the ground flora, resulting from the clear-fell thirty years before. They include many light-demanding, seed bank persistent, coppice species such as *Agrostis stolonifera*, *Digitalis purpurea*, *Juncus bufonius*, and *Rumex acetosella* (Rackham, 1980a; Brown and Oosterhuis, 1981).

Two species in this group of six, occurring only in the seed bank and only in the first eight sub-quadrats, are species tolerant of some shade (Brown and Oosterhuis, 1981). One, *Ranunculus repens*, is known to occur in large numbers in persistent seed banks (Odum, 1965; Sarukhán, 1974). The other, *Deschampsia caespitosa*, was found in low numbers in coppice seed banks (Brown and Oosterhuis, 1981). Thompson and Grime,(1979) classify it in seed bank type III.

The longevity of two of the species in the group of nine is in doubt in the literature. Livingston and Allessio (1968) suggest that *Rumex acetosella* persists for 80 years in the seed bank while Hill and Stevens, (1981) suggest it is shorter lived, 10 to 20 years. Thompson and Grime (1979) state that the second species, *Agrostis capillaris* has a large persistent seed bank, while Hill and Stevens (1981) state that it probably does not persist an entire conifer rotation and is dead in the seed bank after 45 years. In quadrat 9, both species appear to have survived in the seed bank for at least 30 years.

Only *Agrostis capillaris* and *Agrostis stolonifera*, in this group of nine species in the seed bank, occur in the B - Plan sub-units (Table 7.3 .). The species in the ground flora and not in the seed bank are *Hedera helix*, *Lonicera periclymenum*, *Athyrium filix-femina* and *Dryopteris dilatata*. Like *Lonicera*, *Hedera* does not flower under the canopy or under B - Plan sub-units. Likewise, it does not appear to have a persistent seed bank. Its seeds appear to be germinable soon after shedding, but rapidly lose viability after storage (Grime *et al*, 1981). *Athyrium* did develop in one soil sample taken from quadrat 55. *Dryopteris*, being very shade tolerant, is 'the only vascular plant to achieve appreciable cover in the later stages of British conifer rotations' (Hill, 1979a). Hence, *Dryopteris* already has a strong competitive advantage and does not need a seed bank storage facility. This may also apply to *Athyrium*. However, there is little information about ferns available in the seed bank literature.

Quadrat 13

Table 7.4. shows the results of the germination tests from quadrat 13. Six of these species (Table 7.4. - *) did not occur in the ground flora in phases I - III, fewer than in quadrats 4 and 9. Three of these occur solely in the samples from under the main canopy in the area last clear-felled in 1945. As in quadrats 4 and 9, these three species are the seed bank remains of this felling. The species, *Calluna vulgaris*, *Chenopodium album* and *Luzula multiflora* only developed in very low numbers from the seed bank (Table 7.4.). *Calluna* is a coppice species intolerant of shade, spending most of the coppice cycle in the seed bank (Rackham, 1980a). *Chenopodium* is a species of arable, disturbed sites and is known to be extremely long-lived in the seed bank. Odum (1965) found viable seed of this species thought to be 1,000 years old.

Little is known of the germination characteristics of *Luzula multiflora*. However, this perennial shows a high percentage of germination in the dark and 'no strong evidence' of a light requirement for germination (Grime *et al*, 1981), suggesting that, if it is a part of the persistent seed bank, its frequency would be low,

TABLE 7.4. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats in quadrat 13

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12		13-14		15-16		17-18	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																										
Agrostis capillaris	1		20	15		2	8	3	25	5	2	1	39	11	28	5	35	13			8	3	20	4	3	
Agrostis stolonifera	6					1		4	2	1					1				104	17	3				13	
Betula spp.							1						1	1	1				3							
Calluna vulgaris*	3																									
Carex pilulifera	1	4	1	21			1			16			6		1		8		1		1		1			
Chenopodium album*	1																									
Digitalis purpurea	10	50	2	110	80	117	120	81	131	100	11	8	65	22	28	10	105	50	200	104	29	55	61	41	24	10
Holcus lanatus													2										1		8	
Hypericum pulchrum*		1												1		2	3	6				7		2		1
Juncus effusus*	5	22							8				1										1			
Luzula multiflora*												1														
Luzula pilosa				1	2	1																				
Rubus agg.	18	2		29	31	5	10	3	7	11	23	9	8		9	2	3		6		12	2	6		2	
Vaccinium myrtillus	6													1												
Veronica officinalis*																					1					

* = species not occurring in ground flora

as the results in quadrat 13 suggest.

The other three species in the seed bank only, are in both the undisturbed area of sub-quadrats 1 to 8 and in the B - Plan sub-units. They are light-demanding, coppice species with persistent seed banks, Hypericum pulchrum, Juncus effusus and Veronica officinalis (Rackham, 1980a; Brown and Oosterhuis, 1981) and would be expected in quadrat 13 which is on a continuously wooded site, formerly coppice (Figure 1.5.).

Digitalis, present in the ground flora in sub-quadrats 15 and 16, which was cut back in the course of weeding operations in 1982, appears not to have yet been able to replenish the seed bank in those quadrats (Table 7.4.). The numbers of germinable seeds in this seed bank are reduced because the B - Plan disturbance caused the seeds to be exposed on the soil surface thus stimulating germination. However, although many seeds probably germinated, few developed into mature plants and hence the seed bank was diminished. The plants in this sub-unit were probably able to flower in 1983, delayed seed production increasing plant longevity (Harper, 1977). In contrast the older B - Plan sub-units have much larger numbers of germinable seeds (Table 7.4. - sub-quadrats 9-10 and 11-12) due to the fact that the Digitalis developed in these sub-units just after B - Plan clearing 20 years ago. The mature plants were then able to replenish the seed bank and then perish on seed production.

Betula spp. germinated in low numbers in this quadrat probably because there are few large seed producing trees nearby. Its seeds belong in the type II seed bank type, persistent only over the winter. Thus any seedlings developing will be of recent seed origin (Thompson and Grime, 1979; Hill, 1979a).

Species in the ground flora and not in the seed bank are *Dryopteris dilatata*, *Hedera helix*, *Lonicera periclymenum*, *Pteridium aquilinum*, *Ilex aquifolium*, *Pseudotsuga menziesii*, *Quercus* x *rosacea*, *Fagus sylvatica* and *Deschampsia flexuosa*. *Dryopteris*, *Hedera* and *Lonicera* are not in the seed bank for the reasons mentioned earlier. *Pteridium*, with its extensive rhizome systems, has no need for a seed bank strategy. The tree species, like other heavy seeded species, survive less well in the seed bank (Fenner, 1985). *Pseudotsuga* seedlings are always from seed of recent origin (Hill, 1979a). *Deschampsia* appears not to have a persistent seed bank and its success in colonizing after a clear-fell depends on the remaining individuals surviving a conifer rotation (Hill, 1979a; Hill and Stevens, 1981).

Quadrat 14

Table 7.5. shows the results of the germination tests from quadrat 14. As expected under the dark *Picea sitchensis* canopy, with a sparse ground flora, many species occur in the seed bank and not in the ground flora, nine altogether (Table 7.5. - *). Three other light-demanding species *Carex piliulifera*, *Calluna vulgaris* and *Vaccinium myrtillus* occurred in the ground flora in phases I and II but appeared to be shaded out by the time the ground flora was sampled in phase III. Of the previous nine species in the seed bank, only four were particularly light-demanding coppice species expected in a persistent seed bank (Rackham, 1980a; Brown and Oosterhuis, 1981). A fifth species, *Luzula pilosa*, is a species somewhat tolerant of shade which persists in the coppice seed bank at low densities (Brown and Oosterhuis, 1981). A sixth species, *Molinea caerulea*, is a heathland remnant and is an indicator of this site's heathland origin (Figure 1.5.).

Table 7.5. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats in quadrat 14

Sub-quadrats	1		2		3		4		5		6		7		8		9		10-11		12-13		14-15	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																								
Agrostis capillaris	4	5		10	4	13	8	6	7	3	23	10	6	5	3	12	5	1	17	5	24	7	2	7
Agrostis stolonifera	4	7	2		3		14	13	4	6	7	4	17	11	8	3	5	27		3	9	9	30	9
Betula spp.	1	3	3		3		1		4	2	7		8		13	1	3		1	1	2	2	3	
Calluna vulgaris					1	2			41	9			2			8	3		1					
Carex pilulifera							4	1					1						1	1	1			
*Chenopodium album**							1		1															
*Deschampsia flexuosa**						9																		
Digitalis purpurea	3	10	17	25	6	17	26	45	16	23	11	11	7	5	12	18	6	6		3	114	69	41	80
*Galium saxatile**													1											
Holcus lanatus																			1				1	
*Hypericum pulchrum**	1				2	11			1	2	3	1	2		2	1					16	10		16
*Juncus effusus**			8	4						1				2			8	3						
*Luzula multiflora**									2															
*Luzula pilosa**														1										
*Molinea caerulea**																		3						
Rubus agg.	2	4	2	1		2	3	1	5	3	13	2	3		2	3	3	2		2	5	2	2	1
Vaccinium myrtillus																					1			
*Veronica officinalis**									4	2														

* = species not occurring in ground flora

Of these nine species in the seed bank and not in the ground flora, five occur only in the samples from the area unaffected by B - Plan last clear-felled in 1951.

Six species occur in the ground flora and not in the seed bank of phases I - III, Athyrium filix-feminia, Hedera helix, Ilex aquifolium, Pseudotsuga menziesii, Quercus x rosacea and Hyacinthoides non-scripta.

The reasons for the non-appearance of the first five have been discussed earlier. The sixth, Hyacinthoides was in the ground flora in phase III in the two year old B - Plan sub-unit. It flowered during the sampling period. This is a shade-tolerant woodland plant that can only survive a coppice rotation in the ground flora, as it has transient seed bank of the type II kind (Thompson and Grime, 1979; Brown and Oosterhuis, 1981). Hence, remnants from the last clear-fell in 1951, probably survived under the spruce canopy and were then able to take advantage of the light created by B - Plan clearing, to flower in 1982. The fact that it did not appear in the germination tests is explained by two reasons. First, it only first flowered and seeded in 1982, after the seed bank soil samples had been collected. Second, it has only a transient seed bank and is only germinable for a very short time in early spring, after the winter chilling requirement has been satisfied (Thompson and Grime, 1979). The soil sample may have been taken after this transient phase ended.

Quadrat 51

Only six soil samples were taken from this quadrat as it was not officially part of phase IV. This site planted in 1930 with Fagus sylvatica, was at the centre of mining operations for many years, well into the beginning of this century (Figure 1.5.). Thus, it is not surprising that two species of disturbed arable and grassland sites germinated from these samples, Lotus corniculatus and Anagalis arvensis. Anaglis was found to survive at least 55 years in the seed bank (Odum, 1965).

Quadrat 52

Table 7.6. shows the results of the germination tests from quadrat 52. Only three light-demanding coppice species occur in the seed bank of this relic oak coppice and not in the existing ground flora, Carex pilulifera, Hypericum pulchrum and Juncus effusus. As expected in this site, which could be described as semi-natural ancient woodland, (Kirby et aL, 1984) most of the coppice species have disappeared from both the ground flora and the seed bank.
In the Brown and Oosterhuis (1981) study of neglected coppice seed banks the 'limits of seed survival were not reached' 30 to 40 years after the last cutting. However, the site of quadrat 52 was probably last coppiced in 1916 (estate records), 66 years before the germination tests. Unlike the coppices studied by Brown and Oosterhuis (1981), where the potential for ground flora recovery existed in the seed bank, in this coppice, the seed bank has deteriorated nearly to the point of no return. Brown (1981) suggests that species losses are greater in coppices planted with conifer plantations, than in remaining neglected coppice. However, this does not appear to be the case in Tavistock Woodlands, where the coppice species occur more frequently in the ground flora and seed bank of the B - Plan sub-units than in the ground flora and seed bank of the neglected coppice. Hill (1979a)makes the point that neglected coppice ground flora does not have the advantage of a thinning at 30 years as in a conifer plantation, when Pinus and Larix plantations on afforested sites can have a 'complete vascular flora'.

Table 7.6. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats in quadrat 52

Sub-quadrats	1		2		3		4		5		6		7		8	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																
Betula spp.	13		3				3		2		9		2		29	3
Calluna vulgaris	89	82	73	3	96	41	12	21	10	19	115	44	25	60	4	63
*Carex pilulifera**																2
*Hypericum pulchrum**															1	
*Juncus effusus**				1												
Luzula sylvatica									14	2						
Rubus agg.			2				1		8	3	1	1	2	3		
Vaccinium myrtillus	1		3		2				9		16		5		1	

* = species not occurring in ground flora

Evidence from other studies in temperate forest suggests that original seed from early successional communities disappears after 100 years and there may still be a large seed bank after 50 years (Hill and Stevens, 1981). It appears that in quadrat 52, the seed bank has already begun a downward deterioration.

Among the species in the ground flora, but not in the seed bank, *Pteridium aquilinum*, *Hedera helix*, *Sorbus aucuparia*, *Quercus* x *rosacea* and *Pseudotsuga menziesii* is also included one shade-bearing woodland plant, *Melampyrum pratense*, which behaves as a coppicing plant with luxuriant growth after felling (Packham and Harding, 1982). Brown and Oosterhuis (1981) suggest that it has poor seed dispersal attributed to ants (Ridley, 1930) and that being a shade-tolerant species, like *Hyacinthoides non-scripta*, it does not require the competitive strategy of a persistent seed bank. *Melampyrum* appears to need a canopy cover of less than 50% for abundant regeneration (Warren, pers. comm.). It occurs in the ground flora of quadrats 54 and 56 in recent B - Plan sub-units.

Quadrat 54

Table 7.7. shows the results of the germination tests from quadrat 54. 14 species occur in the seed bank but not in the ground flora (Table 7.7. - *). Most of these are the light-demanding coppice plants *Agrostis stolonifera*, *Calluna vulgaris*, *Digitalis purpurea*, *Hypericum humifusum*, *Hypericum pulchrum*, *Juncus effusus* and *Juncus bufonius* (Thompson and Grime, 1979; Rackham, 1980a; Brown and Oosterhuis, 1981). Included also in this group of 14, are other oak woodland species like *Vaccinium myrtillus*, one species tolerant of some shade, *Luzula sylvatica* and two species tolerant of deep shade, *Moehringia trinervia* and *Viola riviniana* (Brown and Oosterhuis, 1981). *Moehringia* is an oak woodland shade species but persists in the seed bank for a 'few decades' (Brown and Oosterhuis, 1981).

Table 7.7. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m) taken from near each of the sub-quadrats in quadrat 54

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12		13-14	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																						
Agrostis capillaris	2	2	10	13	13	12	18	16	5	5	18	13	13	6	6	7	21	53	14	14	9	16
Agrostis stolonifera*																	6	55				
Betula spp.	3	1	3	1	5	9	6	2	15	4	11		13	2	10	2	13	2	10	6	4	
Calluna vulgaris*							7	5														
Carex pilulifera*	8	4	6	1			3	2	5	7		4			1	2		4	6	4		3
Digitalis purpurea*	42	40	24	20	19	16	5	16	21	32	24	17	11	7	22	14	1	3	41	34	31	46
Hypericum humifusum*								1													3	
Hypericum pulchrum*	6	8	2	2	4	3	17	14	31	22	32	21	15	11	5	3	35	24	8	9	15	21
Juncus bufonius*																1						
Juncus effusus*															13	4			1			
Luzula multiflora*	1	1					6		2		7						10	17	2	2		
Luzula pilosa	2		2		1		1	1	2			2			1		5		4		4	2
Luzula sylvatica*										1		4	1									
Moehringia trinervia*																	1					
Rubus agg.	6	4	4	4	3	6	12	2	2		6	4	7	2	1	5	5	2	9	2	20	1
Teucrium scorodonia			1		2		2				1				2		1			1	1	1
Ulex gallii*			1			1		1														
Vaccinium myrtillus*															1		2					
Veronica officinalis							8	9	7	15				1			13	3			9	6
Viola riviniana*									1		1			1	1		7	1	1			

* = species not occurring in ground flora

Viola is present in the ground flora of quadrat 54 but was not sampled in the sub-quadrats, as it occurs very infrequently. As expected of a species with the competitive advantage of shade tolerance, it is reputed to be a type II seed bank species with a transient seed bank whose winter dormancy is broken by stratification (Thompson and Grime, 1979; Brown and Oosterhuis, 1981). The seed bank soil sampling at the end of April obviously collected this seed when it was in its germinable phase.

Most of these 14 species occur in both the seed bank of the undisturbed area last clear-felled in 1940 and replanted with oak (Table 7.7.), as well as in the B - Plan sub-units.

Pteridium aquilinum, Hedera helix, Lonicera periclymenum, Quercus x rosacea, Pseudotsuga menziesii and Melampyrum pratense occur in the ground flora and not in the seed bank. As mentioned earlier Melampyrum occurs in the recently cleared B - Plan sub-units.

Quadrat 55

Table 7.8. shows the results of the germination tests from quadrat 55. In this quadrat, in contrast to quadrats 4,9,14 and 54, it is particularly striking that only three species occur in the seed bank that are not in the ground flora (Table 7.8. - *). It might be expected that under this dark Pseudotsuga canopy more species would be lost to both the seed bank and the ground flora, than in the lighter deciduous canopies for example quadrats 13 or 54.

The light-demanding, coppice species Calluna vulgaris, Carex pilulifera, Digitalis purpurea, Hypericum pulchrum, and Juncus effusus, as well as the more shade bearing oak field layer species Rubus agg. and Luzula pilosa, occur in both the seed bank and in the ground flora. They occur in both the seed banks and the ground flora under

Table 7.8. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats in quadrat 55

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12		13-14		15-16	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																								
Agrostis capillaris														1		1	1		6		2	1		
Agrostis stolonifera		1									1	2	1				1	1	34	21			24	9
Athyrium filix-femina							42																	
Betula spp.	3		6		1		3		4		2	2	4			1	6	3	9	1	2	5	4	1
Calluna vulgaris		1										1		2	4		1	1	3				17	6
Carex pilulifera		1	1									3	3				1	1	5	2	2		5	4
Digitalis purpurea	15	7	80	27	11	8			43	63	209	80	2	2	8	6	121	24		2	41	6	2	1
*Holcus lanatus**																	1							
Hypericum pulchrum	4	5				1		1	1		2	1	6	2	1		2	2	4		3	1	10	4
Juncus effusus	1	44		1							2	1	70	37			1		8	3				
Luzula multiflora													1			1								
Luzula pilosa									1		1	1								1			1	
Rubus agg.	2		5		5	1	7	3	2	1	8	8			4		3	1	7	1	1		1	1
*Teucrium scorodonia**																			1					
*Vaccinium myrtillus**				1																				
Veronica officinalis							1				2	1												

* = species not occurring in ground flora

the main canopy, which was last clear-felled in 1950, as well as in the recently cleared B - Plan sub-units. Digitalis, Juncus and Luzula multiflora occur only in the newest B - Plan sub-unit. The older B - Plan sub-units do not have these species.

Athyrium filix-femina in the ground flora of both new and older B - Plan sub-units as well as under the main canopy, developed from the soil sample taken from near sub-quadrat 55.4. (Table 7.8.)

As in the other quadrats, Hedera helix, Lonicera periclymenum, Pseudotsuga menziesii, Fagus sylvatica and Quercus x rosacea are in the ground flora and not in the seed bank. Seed from the surrounding Pseudotsuga canopy is available, as the species freely regenerates naturally in the B - Plan clearings and in the rackways. Obviously its germination requirements were not met in the greenhouse. There is also Rhododendron ponticum in the ground flora but as this species is cut back frequently, in an effort to eradicate it, the remaining individuals did not flower during the phase III and IV surveys and hence no seed was produced.

Quadrat 56

Table 7.9. shows the results of the germination tests in quadrat 56. Six species occur in the seed bank and not in the ground flora surveyed in phases II and III. (Table 7.9. - *) Only two of these are light-demanding, coppice species with persistent seed banks, Digitalis purpurea and Juncus effusus. Two other species in this group of six are well represented in the rides upslope of quadrat 56, Carex binervis and Ulex gallii and as mentioned earlier could easily be transported by forestry working. Luzula multiflora is not in the ground flora of this particular quadrat but it is growing in this part of the wood.

Table 7.9. Species and numbers of seedlings germinating from soil samples, 0-5cm (h) and 5-10cm (m), taken from near each of the sub-quadrats in quadrat 56

Sub-quadrats	1		2		3		4		5		6		7		8		9-10		11-12		13-14		15-16	
Soil layer	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m
Species																								
*Agrostis capillaris**	1															1								
Betula spp.	6		9		3	2	4				3				3		4		4	1			1	
Calluna vulgaris	4	13	1						1		1			1										
*Carex binervis**					20	5													1					
*Digitalis purpurea**	40	31	136	88	72	24	18	1	4		25	16	12	8	5	4	77	3	21	9	145	25	84	27
Hypericum pulchrum	1	4	6	9	1				4	1	1	2	2		13	6	35	5		1		2	2	
*Juncus effusus**			1		1		1										1		1					
*Luzula multiflora**																				1				
Rubus agg.	4	2	8	2	8	3							3	1	10	3	2	1	5	1	5	1	6	1
*Ulex gallii**								1																
Veronica officinalis																	3							

* = species not occurring in ground flora

The light-demanding coppice species with persistent seed banks that occur in both the ground flora and in the seed bank are Calluna vulgaris, and Hypericum pulchrum, as does the woodland species Veronica officinalis. Luzula pilosa and Carex pilulifera also occur in the ground flora and not in the seed bank.

Of the six species in the seed bank and not in the ground flora, all but Ulex and Agrostis capillaris occur under the main canopy, last clear-felled in 1941, as well as in B - Plan sub-units.

Athyrium filix-femina, Blechnum spicant, Dryopteris dilitata, Hedera helix, Ilex aquifolium, Lonicera periclymenum and Pseudotsuga menziesii occur in the ground flora and not in the seed bank tests.

7.3.1. Discussion of the seed bank species distribution - a summary

Seed distribution in relation to depth

The distribution of seeds in the soil with respect to depth, of the species currently in the ground flora is roughly as would be expected for all the quadrats. The majority of the seedlings of current ground flora species developed from seed in the upper layer, which included the litter. However, the species no longer in the ground flora but in the persistent seed bank could be expected to be found only in the lower mineral layer. This was not the case for most quadrats, probably because the sampling method was imperfect. Contamination undoubtedly occurred with the use of a spade for sampling.

Seed banks under B - Plan management

Many of the light-demanding, coppice species with persistent seed banks occur more frequently in the ground flora of B - Plan sub-units (Table 8.1.). However the seed bank study showed firstly, that a further number of this kind of species occurred in the seed bank but not in the ground flora. Secondly, some B - Plan sub-quadrats appeared to have depleted seed banks when compared to the seed bank under the surrounding canopy. Thirdly, quadrat 55 is exceptional because many of these light-demanding, coppice species occur in the seed bank as well as in the ground flora and the seed bank of the B - Plan sub-units is nearly as rich as that under the surrounding canopy.

These three points emerging from the seed bank study are discussed in further detail below.

1 - Coppice species in the seed bank but not in the ground flora

Quadrats 4,9,14 and 54 have the largest number of species in the seed bank which do not occur in the ground flora. Table 7.10. shows the distribution of species numbers in the seed bank and not in the ground flora. This result could be explained if the species still present in the seed bank are no longer in the ground flora because the canopy is now closed and does not provide enough light. Contrary to this suggestion, two of the quadrats with the highest number of species in the seed bank that are not in the ground flora, quadrats 4 and 9, have the highest percentage contributions of both diffuse and direct light (Figures 6.1. to 6. 3 .). Therefore, it is more probably that the past history of the sites have depleted in some way the ground flora as well as the seed bank. For example quadrat 4, which has the lowest number of species in the ground flora, (Table 7.10.) was formerly heathland and was certainly affected in the last century by the nearby arsenic works. In addition, although the seed bank has nine species not in the ground flora (Table 7.10.), these species generally occur in low numbers (Table 7.2.) suggesting that the seed bank is also depleted. However, the past forestry management history may well be even more significant in the depletion of both ground flora and

Table 7.10. Distribution of species numbers for those species occurring in the seed bank and not in the ground flora, between samples from near B - Plan and non-B - Plan sub-quadrats

Quadrat	Total number of species in ground flora	Total number of species in seed bank and not in ground flora occurring in samples from all the sub-quadrats	Of the total number of species in seed bank and not in ground flora, the number occurring in samples from B - Plan sub-quadrats only
4	10	9	2
9	14	9	3
13	19	6	3
14	16	8	3
52	10	3	-
54	13	14	11
55	19	3	2
56	14	6	4

seed bank species. Below is a brief history of the management of the phase IV quadrats (estate records; Hamilton, pers. comm.):

Quadrat 4 - heath prior to 1813, planted with conifers (Pinus spp.) from 1813 to the present canopy

Quadrat 9 - coppice until 1862, planted with conifers (Pinus spp.) from 1862 to the present canopy

Quadrat 13 - coppice with grazing until 1903, planted with conifers (Pinus spp.) to the present canopy

Quadrat 14 - heath prior to 1813, planted with conifers (Pinus spp.) to the present canopy

Quadrat 54 - coppice until 1914, planted with Pseudotsuga menziesii in 1914 then with the present canopy Quercus x rosacea in 1940.

Quadrat 55 - coppice until 1950, planted with Pseudotsuga menziesii in 1950 which is still the present canopy

Quadrat 56 - coppice until 1941, planted with Pseudotsuga menziesii in 1941 which is still the present canopy

As is apparent from the above histories, those quadrats which have had coniferous canopies for at least 120 years or more, quadrats 4,9 and 14, show this discrepancy between the seed bank and the ground flora. Likewise those quadrats with oak coppice until relatively recently, quadrats 13,55 and 56, show less of a difference between the seed bank and the ground flora (Table 7.10.). Quadrat 54 is the exception having had an oak canopy until 1914. However the oak was replaced with Pseudotsuga and not Pinus. The darker Pseudotsuga canopy may have affected the ground flora and the seed bank more rapidly than a lighter Pinus canopy.

2 - Depletion of seed bank in B - Plan sub-units

Quadrats 4,9,13 and 14 show the most marked difference between the seed bank in the B - Plan sub-units and that under the surrounding canopy (Table 7.10.). There are several possible explanations for this.

Firstly, the seed bank sampling was weighted in favour of samples from under the main canopy, 16, in contrast to as few as four and a maximum of ten from the B - Plan sub-units. The results of the germination tests were very variable and hence fewer samples from the B - Plan sub-units meant that lower numbers of species would be detected in this set of samples.

Secondly, in the light or deciduous canopies of quadrats 4,9, 13 and 54 the ground flora was probably well-developed when the first B - Plan sub-units and rackways were cleared. Thus, when the buried seed was exposed through soil disturbance, the already high light intensities and temperature fluctuations stimulated germination. However, the established ground flora, including Pteridium aquilinum, Rubus agg., Molinea caerulea and other grasses, confronted these newly germinated seeds with immediate competition. Consequently, many did not develop, depleting the B - Plan sub-unit seed banks. By the time B - Plan was introduced into the darker quadrats, 56 and especially 55, the ground flora and its competitive ability were already reduced by the Pseudotsuga canopy. As a result, the germinating seeds were able to develop in the increased light, without excessive competition from an already established ground flora.

3 - Quadrat 55, the exception

Quadrat 55 is exceptional because many species, including coppice species, occur in the seed bank as well as in the ground flora and the seed bank of the B - Plan sub-units does not appear to be depleted (Table 7.10.). This is the most significant result of the seed bank study. This quadrat, unlike the others, has been able to retain a wider complement of coppice species in the seed bank and in the ground flora in spite of a Pseudotsuga canopy. It appears that the implementation of B - Plan in this site in 1961 conserved the coppice species. The species were most probably present in the seed bank until 1950, and then after clear-felling, in both the seed bank and the ground flora. Consequently, the potential for ground flora recovery exists in quadrat 55 under a dark coniferous canopy species, while it has diminished in the relic oak coppice, quadrat 52 (Table 7.10.).

The finding that the seed bank changes, like those in the ground flora, are successional in nature and that a series of successional changes can co-exist in space as well as in time, is also particularly significant to the assessment of the conservation value of B - Plan management.

CHAPTER 8. TEMPORAL AND SPATIAL PATTERNS - PHENOLOGICAL ASPECTS OF SELECTED GROUND FLORA SPECIES

CHAPTER 8. TEMPORAL AND SPATIAL PATTERNS - PHENOLOGICAL ASPECTS OF SELECTED GROUND FLORA SPECIES

8.1. Introduction

> "Indirect evidence that plants within a population interfere with each other comes from a study of changing pattern of individuals within a succession." (Harper, 1977: p. 726)

The succession of species within B - Plan sub-units was examined in Chapter 5. As the sub-units age, the environment appears to become more stressful, a direct effect of the growing trees reducing the amount of light available to the ground flora and competing with it for other resources, such as soil nutrients. Hence the species composition changes and the number of species as well as the total abundance decreases (Figures 5.9.-5.11.). These changes are all taking place within an 18 x 18m square B - Plan unit, resulting in a mosaic of different successional stages in space. The temporal pattern, or phenology of a community, as well as being a mechanism for increasing diversity (Grubb, 1977), can also act to reduce the interference between plants.

> "A separation in the timing of growth is equivalent to a separation in resource use if the resource is one whose use is dependent upon frequent removal, not storage."
> (Fowler and Antonovics, 1981: p. 838)

In dense communities, this 'infliction of hardships on neighbours' (Harper, 1977) is important, while in sparse communities, interference is not obvious (Grubb et al., 1982). The newly cleared B - Plan sub-units would appear to belong to the former category, while the older sub-units belong to the latter.

The species within these B - Plan communities can be divided into several subsets, based on their competitive, as well as phenological strategies. Set 1 are the highly competitive, successful species present throughout much of the B - Plan cycle. They owe their excellent competitive ability to their shrubby growth form with persistent stems and roots. These have been referred to as the 'ubiquitous' Tavistock Woodlands species and include Hedera helix, Lonicera periclymenum and Rubus agg. Set 2 are the ruderal species dependent on B - Plan clearing for the necessary disturbance needed for establishment, soon dying out as conditions become less favourable. These species include Digitalis purpurea and Chamerion angustifolium. Set 3 consists of species which appear to be of lesser competitive ability than group 1, but which can remain in B - Plan sub-units much longer than set 2 species. They tend to be present where initial B - Plan management has reduced the dominance of the 'ubiquitous' species by clearing and weeding. The species in set 3 include many of the species more frequently found in B - Plan sub-units than elsewhere in the study site. They appear in Table 5.11. as some of the successional B - Plan species, colonizing sub-units after clearing and remaining for several stages. These species can be divided into sub-sets of differing phenological strategies after Fowler and Antonovics, (1981):

1) Cool season species - evergreen or semi-evergreen species, which can exploit warm temperatures outside the warm growing season and also tend to be stress tolerant (Al-Mufti et al., 1977; Mahall and Bormann, 1978).
2) Warm season species - species with a distinct growing season, winter dormancy, and a short phenological cycle to exploit optimum growth conditions.

Species in the cool season group include Blechnum spicant, Carex pilulifera, Dryopteris dilitata and Luzula pilosa. Those in the warm season group include Athyrium filix-femina, Hyacynthoides non-scripta, Hypericum pulchrum and Melampyrum pratense.

It is not possible to demonstrate conclusively the existence of competition between species through a determination of actual versus virtual niche breadth, without experiments involving removal of competing species or by artificially manipulating scarce resources (Colwell and Futuyma, 1971). However, the partitioning of resource space over time by the species in B - Plan sub-units can be illustrated indirectly by examining competitive phenological strategies. Phenological diagrams (Figure 8.1.) as well as calculations of percentage similarity (Whittaker, 1975; Fowler and Antonovics, 1981) have been used in examining species in groups 2 and 3.

Percentage or proportional similarity can be used to compare the relative competitive 'robustness' of two species over a certain period of time. For each species in the relevant B - Plan subquadrats, the monthly proportion of the total cover (total = 1) was calculated. Then the arithmetic difference between pairs of species month by month was summed and inserted in the formula below to calculate proportional similarity. The species in the equation are species a and species b.

$$PS\ ab = 1 - 0.5\ (\sum /Pa - Pb/ \quad)$$

To calculate these values the Domin values were converted into mean cover values as follows:

Domin number	Mean cover (%)
+	.25
1	.50
2	1.00
3	3.00
4	7.50
5	17.50
6	29.00

Domin number	Mean cover (%)
7	41.50
8	62.50
9	85.00
10	100.00

Unlike the indicator species analysis used in Chapter 5, where species of low cover values were important in characterizing a community or where both frequency and cover were important in examining successional changes over time (Bannister, 1966) direct cover values are used here to examine each species' competitive phenology.

8.2. Species chosen for analysis

Of those species in groups 2 and 3 which appear in Table 5. 11. as possible successional B - Plan species, only some are more frequently found in B - Plan sub-quadrats than elsewhere under the main canopy. Table 8.1. was compiled using the data from the 19 quadrats when they were sampled for phase III in the period between August to September 1982. These also appear as successional species in Table 5. 11. Of these species, only some are present in a significant number of sub-quadrats to be suitable for further examination. For example, Hyacynthoides non-scripta although found under B - Plan,only occurred in one sub-quadrat. Likewise, Ulex gallii appears to favour B - Plan sub-quadrats, but only occurs in quadrat 4. Hence Digitalis purpurea is the one ruderal from set 2 chosen. Betula app. another ruderal was also more frequently found in B - Plan sub-quadrats, but it has already been discussed in Chapter 4. Carex pilulifera, Dryopteris dilitata and Luzula pilosa were chosen from the cool season, semi-evergreen sub-set of set 3. Athyrium filix-femina and Hypericum pulchrum were chosen

Figure 8.1. - Phenological patterns in some sub-quadrats for selected species for the 1982 season

Key
(Number shows main quadrat number followed by sub-quadrat number)

/ / / / = Development and growth of current year's leaves
▬▬▬ = Flowering (when at least 50% of the buds have opened)
I I I I I = Fruiting (when at least 50% of the potential seeds/fruit have developed
△ △ △ = Withering (when at least 50% of plant shows signs of dying)
● ● ● ● ● = When for some species leaves remain intact during winter

If a particular stage of development is regarded as well established on a sampling date, i.e. 75% of the new buds have opened or over 75% of the potential seed pods are developed, the stage is recorded as in the middle phase.

If only 50% or less of either the leaves, flowers or seed are well-developed, the stage is recorded as the initial stage.

If nearly all of the potential leaves, flowers or seed are nearly 100% developed or in the case of decay nearly all the leaves are showing some sign of decay, the phase was recorded as final.

To illustrate this, as well as the time lapse between monthly samples (or in the case of a two-month sampling gap between August and October); gaps have been left in the bars of the following phenological diagrams. These illustrate:

(A) Large gap before a new phenophase shows this new phase was already in its final stage when the plant/s were sampled or that a stage was so short it was not recorded.

(B) Small gap before a new phenophase shows this new phase was already in its middle stage when the plant/s were sampled.

(C) No gap between the previous phenophase and the new phase shows this new phase was in its initial stage when the plant/s were sampled.

* Note some species only appear in sub-quadrat later in season.

Figure 8.1. - continued

seedling
no over wintering fronds
seedling
no seed
*cut back
no seed set
*in bud

Figure 8.1. - continued

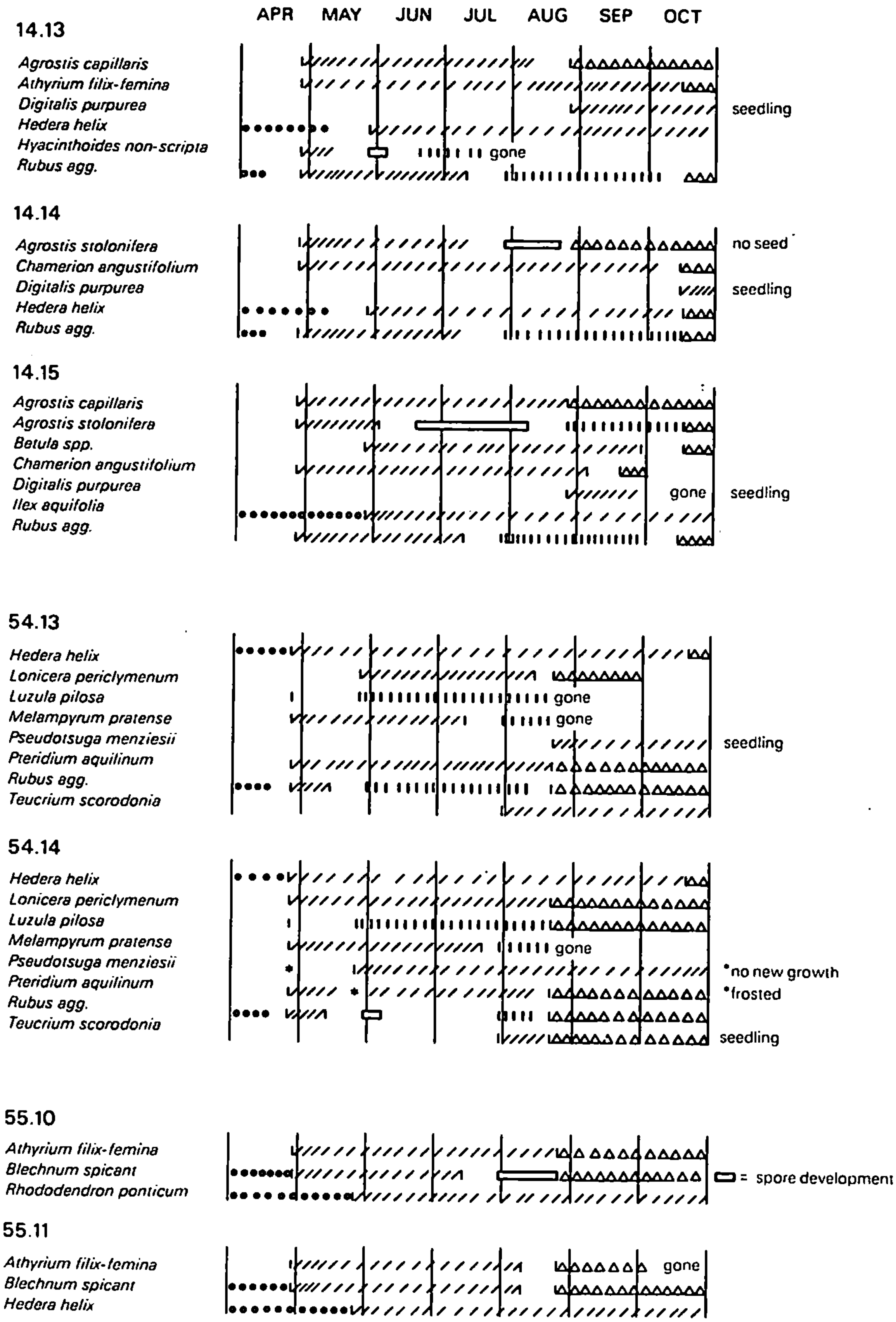

Figure 8.1. - continued

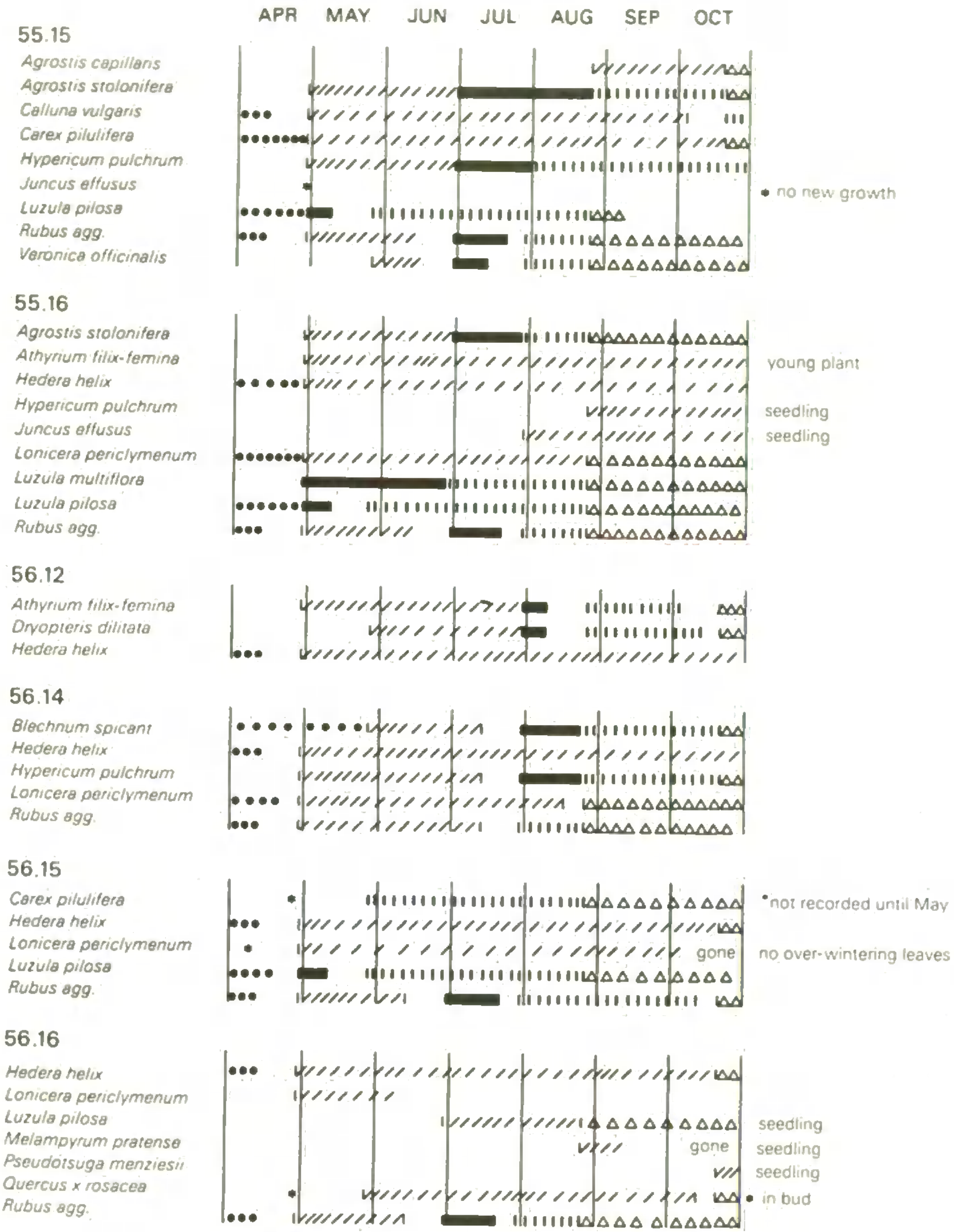

Table 8.1. Percentage frequency (of the total number of sub-quadrats where present) in B - Plan sub-quadrats versus non-B - Plan sub-quadrats of selected species in phase III from Table 5.11.

Species	Percentage frequency in B - Plan sub-quadrats	Percentage frequency in non-B - Plan sub-quadrats
Athyrium filix-femina	73	27
Betula spp.	55	45
Carex pilulifera	44	56
Deschampsia flexuosa	33	67
Digitalis purpurea	50	50
Dryopteris dilitata	35	65
*Hyacinthoides non-scripta**	100	0
Hypericum pulchrum	44	56
Luzula pilosa	46	54
*Melampyrum pratense**	18	82
Molinea caerulea	42	58
Quercus x *rosacea*	21	79
Sorbus aucuparia	18	82
Teucrium scorodonia	18	82
Ulex gallii	38	62
Vaccinium myrtillus	14	86

* 1981 - Phase II figures used because these vernal species were nearly gone when the 19 quadrats were sampled in phase III in August-September

Note: - Of the total 230 sub-quadrats sampled in phases II and III, 34% were B - Plan and 66% were non-B - Plan from the warm season sub-set of set 3. Table 8.2. shows the percentage frequency of these species in the eight special quadrats of phase IV. The following discussion of these species is based on these eight quadrats.

Table 8.2. Percentage frequency (of the total number of sub-quadrats where present) in B - Plan sub-quadrats versus non-B - Plan sub-quadrats in the eight special quadrats in phase IV

Species	Percentage frequency in B - Plan sub-quadrats	Percentage frequency in non-B - Plan sub-quadrats
Athyrium filix-femina	63	37
Carex pilulifera	67	33
Digitalis purpurea	100	0
Dryopteris dilitata	50	50
Hypericum pulchrum	60	40
Luzula pilosa	59	41

Note: Of the total 111 sub-quadrats sampled in phase IV, 42% were B - Plan and 58% were non-B - Plan

8.2.1. Set 2 species - ruderals

Digitalis purpurea

Digitalis purpurea is a ruderal species whose biennial habit is really the phenology of a winter germinating annual, making growth in late autumn and completing its life cycle in the spring of the second year, with the production of seeds resulting in the death of the plant. If the flowering shoot is damaged and no seeds are produced, the plant can delay seed production another season (Harper, 1977).

Digitalis is found only in recently cleared B - Plan sub-units in phase IV (Table 8.2.). In the eight special quadrats of phase IV, it is found in four B - Plan sub-quadrats, associated more frequently with the 'ubiquitous' B - Plan species Rubus agg. as well as with Agrostis capillaris, A. stolonifera, Chamerion angustifolium and Ilex aquifolium (Table 8.3.). It does not appear to be particularly associated with the other two 'ubiquitous' B - Plan species Hedera helix and Lonicera periclymenium. Table 8.3. shows the percent occurrence of these species in the sub-quadrats with Digitalis, compared to the percent occurrence of these species in all the 111 sub-quadrats of the eight special quadrats. They are light demanders like Digitalis. A. capillaris and Digitalis belong to Bunce's (1982) indicators of acid brown earths in the open or in woodland. Chamerion, like Digitalis is an opportunistic species associated with disturbance.

Table 8.3. Percentage frequency of occurrence of some species in the sub-quadrats with Digitalis purpurea compared to the percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special quadrats in phase IV

Species	Percentage frequency in the four sub-quadrats where Digitalis occurs	Percentage frequency in the total 111 sub-quadrats
Agrostis capillaris	75	14
A. stolonifera	50	10
Chamerion angustifolium	50	10
Hedera helix	50	67
Ilex aquifolium	50	5
Lonicera periclymenum	25	55
Rubus agg.	100	81

Digitalis occurs in four sub-quadrats cleared two years before sampling, 13.16, 14.13, 14.14, and 14.15. Figure 8.1. illustrates the phenology of species in these sub-quadrats. In three of the sub-quadrats it appears as seedlings later in the season to overwinter. In 13.16, it was in its second year of growth and was cut back before any seed was set, hence it will survive into a third season.

Digitalis is distinctly a plant of light habitats. Hence the diffuse site factors for the four sub-quadrats with Digitalis, May mean = 51% and August mean = 49%, are significantly higher (p = 0.0073 and 0.0093 respectively), than the factors for the eight non-B - Plan sub-quadrats of quadrats 13 and 14, May mean = 29% and August mean = 28%, using a one-tailed directional Mann-Whitney U-test. The direct site indices for the four sub-quadrats with Digitalis, May mean = 46% and August mean = 44%, are higher but not significantly so, than the indices for the non-B - Plan sub-quadrats of quadrats 13 and 14, May mean = 33% and August mean = 32%.

The competitive advantage of Digitalis lies primarily in its seed bank and not in the ability to remain for any length of time in the ground flora. Its small seeds are poorly dispersed in space, but well dispersed in time, due to their longevity in the soil (Harper, 1977), being dark-inhibited to reduce their chance of germinating while buried (Cresswell and Grime, 1981). Hence, although Digitalis is not abundant in the ground flora, it is particularly abundant in the seed bank of Tavistock Woodlands, occurring in 116 of a total of 160 samples with, in some cases, over 200 seedlings, it occurs in the seed bank of all quadrats but 4 and 52. This enables it to respond rapidly to local disturbance with dense population growth (Harper, 1977). It is interesting to compare this competitive strategy to that of its associate Chamerion. Unlike Digitalis, Chamerion seeds rapidly lose viability after two years in the soil (Thompson and Grime, 1979), but this lack of competitive advantage is compensated for by its ability to remain in a vegetative state up to 27 years (Myerscough, 1980) and by its having seed well dispersed in space by the wind. A second competitive advantage is the ability of *Digitalis* to prolong its life cycle, if the flowering spike is damaged. A comparison of the competitive phenologies shows that the percentage similarly of *Digitalis* paired to with cool and with warm season species is not significantly different, because *Digitalis* occurs only as a seedling late in the season in three of the four sub-quadrats.

The distribution and population levels of *Digitalis* are not particularly affected by B - Plan management in so far as the species is able to survive the dark 35 years stage of an even-aged conifer rotation (Hill, 1979a). However B - Plan management means that at any one point in time, *Digitalis* will be present in several different stages of its life cycle:

1) in the seed bank;
2) as seedlings;
3) as over-wintering rosettes;
4) as flowering and seed producing plants.

This is unlike the all or nothing situation in an even-aged rotation where *Digitalis* is very abundant in the ground flora just after clear-felling and then disappears and becomes part of the seed bank for most of the remaining rotation.

8.2.2. Set 3 species - cool season sub-set

Carex pilulifera

Carex pilulifera, a species of grassy or heathy places, which is sometimes found in open woods (Jermy and Tutin, 1968) is described by Salisbury (1924) as a less frequent species of woodland margins.

It is a semi-evergreen with some over-wintering leaves (Jermy and Tutin, 1968) with a rosette leaf arrangement resulting in higher leaf temperatures and hence the ability to utilize light throughout the year for photosythetic production, whenever temperatures permit (Packham and Harding, 1982).

C. pilulifera is found more frequently in B - Plan sub-quadrats in phases III and IV (Tables 8.1. and 8.2.). In the eight special quadrats of phase IV, it is found in six sub-quadrats, four of which are in B - Plan sub-units. In these sub-quadrats, it is more frequently associated with *Agrostis capillaris*, *Rubus* agg. and *Luzula pilosa* and not especially associated with *Hedera helix* or *Lonicera periclymenum*. Table 8.4. shows the percentage frequency of occurrence of species found with *C. pilulifera*, compared to their percentage frequency of occurrence in all the 111 sub-quadrats. It is present only once with *Agrostis stolonifera*, *Calluna vulgaris*, *Dryopteris dilitata*, *Juncus effusus* and *Holcus lanatus*. *C. pilulifera*, with *Luzula* and *A. capillaris* is among Bunce's (1982) group of indicators for acid brown earths in the open or in woodland.

C. pilulifera is found in three B - Plan sub-quadrats cleared two years before sampling, 13.15, 55.15 and 56.15. It is present in only one older B - Plan sub-unit, 13.10, cleared 20 years before sampling. Figure 8.1. shows the seasonal phenology for *C. pilulifera* in these four sub-quadrats for the 1982 season. Where it is an immature plant in newly cleared sites, 13.15, and 55.15, it does not flower. Flowering is delayed in 13.10 to July and the plants rapidly begin to decay in August. It exhibits a vernal phenological pattern flowering in May in 56.15 (Figure 8.1.). It appears to be restricted to the sites which have a history of continuous woodland - quadrats 13,55 and 56, but it does not appear

Table 8.4. Percentage frequency of occurrence of some species in those sub-quadrats with Carex pilulifera compared to the percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special sub-quadrats in phase IV

Species	Percentage frequency in the total six sub-quadrats where *C. pilulifera* occurs	Percentage frequency in the four B - Plan sub-quadrats where *C. pilulifera* occurs	Percentage frequency in the total 111 sub-quadrats
Agrostis capillaris	50	75	14
Hedera helix	50	50	67
Lonicera periclymenum	67	50	55
Luzula pilosa	50	75	15
Rubus agg.	100	100	81

in the over-mature coppice of quadrat 52.

The diffuse site factors for the eight non-B - Plan sub-quadrats of the three quadrats where *C. pilulifera* is present (minus the values for the two sub-quadrats in this group with *C. pilulifera*) for both May (mean = 30%) and August (mean = 30%), are lower, but not significantly so, than the values for the six sub-quadrats where *C. pilulifera* occurs, May (mean = 38%) and August (mean = 35%). The direct site indices used in a similar calculation for both May and August show that the trend is the same, but again not statistically significant.

C. pilulifera has the competitive advantages of semi-evergreeness and vernal growth and flowering. Where it is present in the recently cleared sub-quadrats, it competes with up to nine other species including the aggressive 'ubiquitous' *Rubus* and several grasses. All these species are able to occupy this one small space partly because differing phenological strategies reduce niche overlap and thus reduce competition. These differing strategies range from seedlings, summer - green grasses like *Agrostis* spp., warm season species like *Veronica officinalis* and *Hypericum pulchrum* to the semi-evergreen or evergreens like *Carex*, *Luzula*, *Calluna vulgaris* and *Juncus effusus*. In the older B - Plan sub-unit, sub-quadrat 13.10, only five species remain. *C. pilulifera* is able to survive here because it has a higher diffuse light level in May, 33% than its pair, 13.9, 10%, although the level decreases to 16% by August. The amount of light reaching this sub-unit is greater because it is on the edge of the unit near the recent clearings for 13.17 and 13.18. Hence *C. pilulifera* is benefitting from edge effects created by B - Plan management, but the suggestion is that it is growing on the limits of its tolerance here because it flowers late and decays early.

C. pilulifera is more similar in its competitive strategy to the semi-evergreen or evergreen species like *Hedera* and less to the summer-green species like *Veronica*. The percentage similarities of *C. pilulifera* when compared with cool season species, mean = 81%, are significantly higher (p = 0.0421) than the percentage similarities when compared with the warm season species, mean = 60%, using a one-tailed directional Mann-Whitney U-test.

The phenological strategy of semi-evergreeness of *C. pilulifera* and vernal growth, appear to allow it to compete successfully in B - Plan sub-units. There is some suggestion that it dies out as the sub-units age, but it is abundant in the seed bank (Chapter 7) and as such can exploit the constantly moving pattern of new clearings adjacent to the old ones created by B - Plan management, when conditions become too stressful under the maturing canopies of older B - Plan sub-units.

Dryopteris dilatata

Dryopteris dilatata is a perennial species, sometimes with sub-persistent, semi-evergreen fronds (Clapham et al, 1962), thus giving it some photosynthetic advantage in the early spring. Like Athyrium filix-femina, it is a shade-tolerant species.

Dryopteris does not appear to be found more frequently in the B - Plan sub-quadrats of the 19 quadrats in phases II and III (Table 8.1.). However in the 111 sub-quadrats of the eight special quadrats of phase IV, it is found margainally more frequently than expected in the B - Plan sub-quadrats (Table 8.2.). Of these six sub-quadrats, half of them are in B - Plan sub-units. It is not found together with any species more than once in these six except for the 'ubiquitous' species Hedera helix, Lonicera periclymenum and Rubus agg. Of these three, it only appears to be associated with Lonicera (Table 8.5.). With Lonicera, Dryopteris is among the group of Bunce's (1982) indicators for woodland with acid brown earths.

The three B - Plan sub-quadrats where Dryopteris occurs were cleared varying times before sampling, 13.5 - two years, 13.14 - nine years and 56.12 - 15 years. Figure 8.1. shows the phenological patterns for these sub-quadrats in the 1982 season. The fronds are only persistent over the winter in 13.14. In 13.15 Dryopteris had no over-wintering fronds in the spring and it did not produce spores (Figure 8.1.) suggesting that this was an immature plant resulting from the recent B - Plan clearing.

It appears that like Athyrium, Dryopteris can colonize new B - Plan sites. Likewise, because of its tolerance of a wide range of differing light environments, from 65% diffuse and 48% direct light in 13.15, down to 5% diffuse and 4% direct in 56.12, it can remain in B - Plan sub-units for many years and possibly throughout the entire B - Plan rotation. It is even capable of reproduction under the low light conditions (5% - diffuse site factor) in 56.12 (Figure 8.1.). Dryopteris was one of the three remaining species of vascular plants under a 43 year-old Forestry Commission *Picea sitchensis* plantation (Hill and Hays, 1978). The factors

Table 8.5. Percentage frequency of occurrence of some species in those sub-quadrats with Dryopteris dilitata compared to percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special quadrats of phase IV

Species	Percentage frequency in the total six sub-quadrats where Dryopteris occurs	Percentage frequency in the three B - Plan sub-quadrats where Dryopteris occurs	Percentage frequency in the total 111 sub-quadrats
Hedera helix	50	67	67
Lonicera periclymenum	83	67	55
Rubus agg.	67	67	81

of both diffuse and direct light in the six sub-quadrats where it occurs are not significantly different (Mann-Whitney U - test) from the light factors in the other non-B - Plan sub-quadrats without Dryopteris in the same quadrats. This is as expected in a plant with a wide tolerance of differing light intensities.

Like Athyrium, the competitive advantage of Dryopteris lies in its ability to tolerate a range of light intensities and to linger in B - Plan units long after other species have succumbed. The number of species decrease uniformly with increasing maturity of the B - Plan sub-units, 13.15 - two years - seven species, 13.14 - nine years - four species and 56.12 - 15 years - three species. Where it appears in a new site like 13.15, it grows with species of differing phenological strategies thus acting to reduce the competitive pressure on each one and increase the number of niches in space. In 13.15 there are seedlings of *Carex pilulifera* and *Holcus lanatus*, semi-evergreen and evergreens like *Lonicera* and *Hedera*, and a grass which died out in May, *Agrostis capillaris*. The *Rubus* was kept under control in this sub-unit by estate weeding of it during 1981-1982. When the species number in 56.12 has decreased to three, the remaining individuals of *Athyrium*, *Dryopteris* and *Hedera* are sparse and well-spaced out. As with *Athyrium*, the suggestion with *Dryopteris* is that success depends not on short term inter-specific competition, but rather on the ability to tolerate long term stress.

As expected in a species which can either exhibit cool season phenologies with persistent fronds or only warm season growth, the percentage similarities for *Dryopteris* paired with cool season and with warm season species using Mann-Whitney U-test are not significantly different.

Distribution of *Dryopteris* does not appear to be particularly affected by B - Plan management, because the species can even survive an even-aged conifer rotation (Hill and Hays, 1978). This explains why it is only present with slightly greater frequency in B - Plan sub-units.

Luzula pilosa

Luzula pilosa is a member of the oak field layer (Tansley, 1939) and is an indicator of primary woodland in eastern England

(Peterken, 1974). It is tolerant of some shade (Brown and Oosterhuis, 1981) and is a perennial, semi-evergreen, thus having a photosynthetic advantage in early spring, when light levels are less than that of full summer light. In the early spring, leaf temperature limits photosynthesis. However in species like Carex pilulifera and Luzula where the already green leaves are arranged in a rosette, this maximizes leaf temperature and makes possible the utilization of the light early in spring, (Givinish, 1982). Mahall and Bormann (1978) suggest that semi-evergreens are capable of considerable net photosynthesis during the summer shade phase as well as under a dark coniferous canopy due to their low compensation points.

Luzula is found more frequently (when compared to the total percent of B - Plan versus non-B - Plan sub-quadrats) in the B - Plan sub-quadrats in phases III and IV (Tables 8.1. and 8.2.). In the eight special quadrats of phase IV, it is found in 17 sub-quadrats, ten of which are B - Plan. In these sub-quadrats, it is more frequently in association with the 'ubiquitous' Tavistock Woodlands species, Lonicera periclymenum and Rubus agg; as well as with Agrostis capillaris, A. stolonifera, Carex pilulifera, Digitalis purpurea, Hypericum pulchrum, Melampyrum pratense and Teucrium scorodonia. It appears to be less frequently associated with Hedera helix, another 'ubiquitous' Tavistock Woodlands species. Table 8.6. shows the percentage occurrence of these species in all 111 sub-quadrats of the eight special quadrats. These coppice species are Bunce's (1982) indicators of acid, brown earths in woodland or in the open. They are light-demanding and hence some of them are typical coppicing plants, i.e. Teucrium, Melampyrum and Digitalis (Rackham, 1980a; Packham and Harding, 1982).

Table 8.6. Percentage frequency of occurrence of some species in those sub-quadrats with *Luzula pilosa* compared to percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special quadrats in phase IV

Species	Percentage frequency in the total 17 sub-quadrats where *Luzula* occurs	Percentage frequency in the ten B - Plan sub-quadrats where *Luzula* occurs	Percentage frequency in the total 111 sub-quadrats
Agrostis capillaris	35	50	14
A. stolonifera	24	30	10
Carex pilulifera	18	30	5
Digitalis purpurea	6	10	4
Hedera helix	71	50	67
Hypericum pulchrum	18	20	5
Lonicera periclymenum	82	90	55
Melampyrum pratense	18	30	11
Rubus agg.	94	100	81
Teucrium scorodonia	29	20	4

Luzula is found in six B - Plan sub-quadrats which were cleared two years before the 1982 sampling - 13.16, 13.17, 55.15, 55.16, 56.15 and 56.16. It is also present in three sub-quadrats cleared nine years before sampling - 13.14, 54.13 and 54.14. The only older B - Plan sub-quadrat where it is found is 13.10 which was cleared 20 years before sampling. Figure 8.1. shows the seasonal phenology of *Luzula* in these sub-quadrats for the 1982 season. Where it is found under a closed canopy as in 13.10, 54.2 and 55.4, it does not flower. Of the other six non-B - Plan sub-quadrats where Luzula is found, four are under the light deciduous canopy in quadrat 54. Of the remaining two, sub-quadrat 55.8 is under a light canopy adjoining a ride and 55.6 like 55.4 is under a dark canopy, but unlike 55.4, Luzula does flower here. Luzula is completely absent from quadrat 52, the overgrown coppice.

The diffuse light factors for the non-B - Plan sub-quadrats of the four quadrats where Luzula occurs (minus the values for the seven sub-quadrats in this group with Luzula) for both May (mean = 31%) and August (mean = 28%), are significantly lower when examined using the Mann-Whitney U-test - one-tailed (p = 0.0335 and 0.0396 respectively) than the values for the 17 sub-quadrats where Luzula occurs, May (mean = 39%) and August (mean = 36%). Hence the presence of Luzula is definitely influenced by diffuse light. There was no significant difference between the two groups above using the direct site indices in the same calculation.

In addition to having the competitive advantage of evergreeness, Luzula adopts a vernal competitive strategy and flowers as early as April and forms seed in at least 50% of the flowers as early as May (Figure 8.1.). By the end of August, it shows some signs of decay. Luzula is present in recently cleared sub-quadrats with many other species, and is able to remain in the sub-unit up to nine years after clearing, when the maximum number of species is eight with a mean of 6.67. In the only sub-quadrat where Luzula has remained until 20 years after clearing, only five species remain.

Luzula is more similar in its competitive strategy to evergreen species and less to the summer-green species. The percentage similarities of Luzula paired with semi-evergreen or evergreen species are greater than that of Luzula paired with summer-green species including Rubus agg., Lonicera and the grasses, means = 71% versus 63%. This result is similar to that obtained by Fowler and Antonovics (1981) when they compared the phenological strategies of two temporal guilds of competing grassland species, cool season versus warm season. Cool season species paired with other cool season species showed a higher mean percentage similarity to that of the mean of pairs of cool with warm. The differences in this study are not statistically significant for Luzula, using a Mann-Whitney U-test, probably because there are too few samples. In addition, seedlings like Pseudotsuga menziesii appear late in the season and as a result have a low percentage similarity, while the adult of the species has a similar strategy to Luzula and hence a high percentage similarity. When some of the late season occurring seedlings such as Pseudotsuga are omitted from the calculation the difference between the two, (means = 80% and 68%) becomes statistically significant, p = 0.0412 using a one-tailed Mann-Whitney U-test. However, the general trend is similar to Fowler and Antonovics' (1981) results. Table 8.7. shows this trend. The mean percentage similarity of Luzula paired with each of the other species in the ten B - Plan sub-quadrats, 65%, roughly divides all the species into the two groups of differing competitive strategies.

Luzula's phenological strategy of semi-evergreeness and vernal growth appear to allow it to compete very successfully with many others including with very aggressive species like Rubus. The reduction in light under a closed canopy is the primary factor in finally limiting the growth and ultimately the presence of Luzula. Had the entire study site been covered by a continuous, closed canopy and not B - Plan such as that in the mature B - Plan sub-quadrats or even the closed but deciduous canopy in quadrat 52, the distribution of Luzula would be severely limited.

Table 8.7. Mean percentage similarity of Luzula pilosa paired with the other species in the ten B - Plan sub-quadrats where Luzula occurs

Mean percentage similarity	Species	
100	Dryopteris dilitata	
93	Ilex aquifolium	
84	Calluna vulgaris	
84	Agrostis stolonifera	
77	Carex pilulifera	Species with predominantly cool season strategies (>65% similarity)
76	Juncus effusus	
75	Hedera helix	
75	Veronica officinalis	
74	Quercus x rosacea	
73	Rubus agg.	
70	Agrostis capillaris	
70	Luzula multiflora	
66	Holcus lanatus	
64	Athyrium filix-femina	
62	Pteridium aquilinum	
59	Teucrium scorodonia	Species with predominantly warm season strategies (<65% similarity)
54	Lonicera periclymenum	
53	Hypericum pulchrum	
41	Melampyrum pratense	
33	Deschampsia flexuosa	
33	Pseudotsuga menziesii	
14	Digitalis purpurea	

8.2.3. Set 3 species - warm season sub-set

Athyrium filix-femina

Athyrium filix-femina, a perennial, is common in damp, shady situations (Hyde and Wade, 1962). It has a low light compensation point between 300 and 500 lux and as such is a shade plant (Packham and Harding, 1982). It is one of Bunce's (1982) indicators of gleyed brown earths, in the open or in woodlands.

Athyrium is found more frequently in the B - Plan sub-quadrats of phases III and IV (Tables 8.1. and 8.2.). In the eight special quadrats of phase IV, it is found in eight sub-quadrats, five of which are located in B - Plan sub-units. Of the species selected for closer examination, it is second only to *Digitalis purpurea* in its preference for B - Plan units. In these quadrats, it is found more frequently than not in association with the 'ubiquitous' Tavistock Woodlands species *Hedera helix*, as well as with *Blechnum spicant* (Table 8.8.). *Blechnum spicant* and *Athyrium* are used in continental forestry as indicators of high relative humidity (Sissingh, 1982). *Athyrium* could well be associated with *Dryopteris dilitata* and *Rhododendron ponticum*, but as these species only occur once in sub-quadrats with *Athyrium*, it is not possible to prove this. It does not appear to have any particular affinity with the other two 'ubiquitous' Tavistock Woodlands species *Lonicera* or *Rubus*. (Table 8.8.)

Athyrium is growing in two B - Plan sub-quadrats cleared two years before the sampling in 1982, 55.16 and 14.13. In 55.16 it appears as a young plant in April (Figure 8.1.). It is abundant in the seed bank of this quadrat, 42 individuals being derived from one soil sample. Hence, the *Athyrium* in 55.16 is probably a result of the new clearing. However, the plant in 14.13 is mature and as such could well be a remnant of the previous closed canopy of *Picea sitchensis*, or a plant from the clearing two years before. It does not appear anythwere else in quadrat 14. Hill and Hays (1978) conclude that few vascular ground flora species survive the thicket stage of *P. sitchensis*, except sparse *Dryopteris dilitata*, *Deschampsia flexuosa* and *Vaccinium myrtillus*. This suggests it is a result of the recent clearing.

The other three B - Plan sub-quadrats where *Athyrium* is growing are older than these previous two and have few species remaining

Table 8.8. Percentage frequency of occurrence of some species in those sub-quadrats with Athyrium filix-femina compared to percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special quadrats in phase IV

Species	Percentage frequency in the total eight sub-quadrats where Athyrium occurs	Percentage frequency in the five B - Plan sub-quadrats where Athyrium occurs	Percentage frequency in the total 111 sub-quadrats
Blechnum spicant	38	40	6
Dryopteris dilitata	13	20	5
Hedera helix	88	80	67
Lonicera periclymenum	25	20	55
Rhododendron ponticum	13	20	2
Rubus agg.	50	40	81

in the ground flora. 55.11 and 56.12 were cleared 14 years before sampling and 55.10 was cleared 20 years before sampling. Figure 8.1. shows the 1982 seasonal phenology for the species in these B - Plan sub-quadrats. Athyrium produces spores in only two of the eight sub-quadrats, 55.6 and 56.12. 56.12 has the lowest diffuse light factor (of the total in the open) recorded, 5%. 55.6 at 26%, is similar to the mean value for the eight sub-quadrats, 25%. Obviously Athyrium does not need to depend on high light levels for reproduction.

Athyrium 'germinated' well under the bright but humid conditions of the greenhouse, as well as under those of a newly cleared B - Plan sub-unit. It appears to have a preference for the more uniformly stable and moist conditions of a short-needled coniferous canopy. Only once in phase IV does it occur under the direr, more open Pinus canopy in sub-quadrat 9.6. It appears to be tolerant of a range of diffuse light intensities from 5% to 46%. The diffuse site factors for May, mean = 24.75% (no different values for August) in sub-quadrats with Athyrium are not significantly lower than the diffuse site factors for the sub-quadrats of the four quadrats (minus those sub-quadrats with Athyrium), where Athyrium is present, mean = 29.69%, using one-tailed Mann-Whitney U-test. However, the direct site indices when used in the same way, shows that the values in sub-quadrats with Athyrium, mean = 26%, are significantly lower (p = 0.0398) than the values of the relevant sub-quadrats without Athyrium, mean = 37%.

Athyrium's competitive advantage lies in its ability to tolerate this range of light intensities and to linger in the B - Plan sub-quadrats long after other species have died out due to its low compensation point. In Tavistock Woodlands it is strictly a warm season plant, its fronds unfurling in April and dying back in the autumn (Figure 8.1.). Under the closed canopies of 55.10 and 55.11, it begins to die back by the end of August and in 55.11, it is gone by the third week in October. In the open, 55.16, it lingers on and shows no signs of decay at the end of October (Figure 8.1.). In the two recently cleared sub-quadrats, 14.13 and 55.16 there are six and nine species present, respectively. In the sub-quadrats cleared 14 years before, 55.11 and 56.12 the number of species had decreased to three and remains at this level to 20 years after clearing in 55.10. It does not appear to be a competitively 'robust' species as it appears to 'avoid' growing with the more aggressive species like Lonicera and Rubus (Table 8.8.). Where it appears in new sites, 14.13, and 55.16, (Figure 8.1.) it is competing with species of differing phenological strategies which could act to reduce the competitive pressure on the Athyrium. The species in 14.13 include a grass, Agrostis capillaris; a vernal species, Hyacinthoides non-scripta; a seedling of a summer-green species, Digitalis purpurea; and an evergreen species, Hedera and Rubus. Likewise in 55.16, where it is a young plant, two other species are seedlings new to the site, Hypericum pulchrum and Juncus effusus. Two others are semi-evergreen, vernal species, Luzula multiflora and L. pilosa and one is an evergreen, Hedera. There is also a summer-green grass, A. stolonifera. The aggressive Rubus and Lonicera are also present but kept in check by the estate practice of weeding annually in the first two years of sub-unit establishment.

When the species number in the sub-quadrat has decreased to three, the remaining individuals are sparse, spread apart and semi- or completely evergreen, Blechnum, Dryopteris, Hedera and Rhododendron. The suggestion here is that success depends not on short term inter-specific competition, but rather in the ability to tolerate long term stress either with an evergreen strategy and hence the ability to take advantage of any favourable growth conditions over the whole year or with the ability to tolerate extremely low light just during the growing season and to even reproduce under these conditions. The fact the Athyrium dies back earlier under these conditions and is gone by October in 55.11, suggests it will eventually disappear here, unless subsequent B - Plan clearing increases the side-light to this sub-unit.

The percentage similarities of Athyrium paired with species having either semi-evergreen or evergreen phenological strategies, mean = 78%, are significantly greater, using a one-tailed Mann-

Whitney U-test, (p = 0.0028) than *Athyrium* paired with vernal and summer-green species including *Rubus*, *Lonicera* and the grasses, mean = 54%. This is due to the tendency of *Athyrium* to unfurl its fronds in April and maintain more or less the same cover throughout the growing season, in a similar manner to the semi-evergreen or evergreen species. Along with *Athyrium*, many of these species have the similar competitive advantage of low compensation points.

The distribution of *Athyrium* in Tavistock Woodlands appears to be directly controlled by B - Plan management, primarily because it is able to exploit the protection and high relative humidity afforded by the small gaps within a continuous canopy. Its strategy of stress tolerance, rather than evergreeness, or ruderal or vernal growth means that it can maintain a foothold longer in a site than species with these other three strategies. When conditions become too stressful as with the closing of the B - Plan canopy, *Athyrium* can re-establish itself in the more favourable conditions of new adjacent, more open B - Plan sub-units, because it appears to have the ability to reproduce under low light conditions.

Hypericum pulchrum

Hypericum pulchrum is a warm season perennial coppice species which is long-lived in the seed bank (Grubb, 1977; Rackham, 1980a). It is characteristic of highly acid soils in woodland or rough grassland (Tansley, 1968).

Hypericum is found more frequently in the B - Plan sub-quadrats of the 19 quadrats of phase III, as well as in the B - Plan sub-quadrats of the eight special quadrats of phase IV (Tables 8.1. and 8.2.). It is found here in five sub-quadrats, three of which are in B - Plan sub-units. Of the three 'ubiquitous' B - Plan species, *Hypericum* is strongly associated with *Rubus* and *Hedera* and not very strongly with *Lonicera* (Table 8.9.). It is also associated with *Agrostis stolonifera*, *Juncus effusus* and *Luzula pilosa* (Table 8.9.). *Hypericum* is found once with *Blechnum spicant* and once with *Agrostis capillaris*. These two species with *Luzula* and *Hypericum* are among Bunce's (1982) indicators of acid brown earths in the open or in woodland.

Table 8.9. Percentage frequency of occurrence of some species in those sub-quadrats with *Hypericum pulchrum* compared to percentage frequency of occurrence of these species in all the 111 sub-quadrats of the eight special quadrats in phase IV.

Species	Percentage frequency in the total five sub-quadrats where *Hypericum* occurs	Percentage frequency in the three B - Plan sub-quadrats where *Hypericum* occurs	Percentage frequency in the total 111 sub-quadrats
Agrostis stolonifera	60	67	10
Hedera helix	80	67	67
Juncus effusus	40	67	2
Lonicera periclymenum	60	67	55
Luzula pilosa	60	67	15
Rubus agg.	100	100	81

The three B - Plan sub-quadrats where *Hypericum* is found are fairly newly cleared, 55.15 and 55.16 were cleared two years before sampling, and 56.14 was cleared nine years before sampling. Figure 8.1. shows the phenological patterns for these sub-quadrats for the 1982 season. In 55.16 *Hypericum* appears as a seedling in August. It flowers in the open of 55.15 earlier (in June) than in the nine year old clearing of 56.14. Likewise, it also shows no signs of deterioration in the open of 55.15 by the end of October, but it does in the more closed sub-quadrat 56.14. As expected in a plant found in both woodland and open grasslands, the factors of both diffuse and direct light in the five sub-quadrats where it occurs are not significantly different from those of the non-B - Plan sub-quadrats without Hypericum in quadrats 55 and 56. It does not occur in any sub-quadrat with particularly low or high light values, either diffuse or direct, hence probably does not have as wide a light tolerance as Athyrium filix-femina or Dryopteris dilitata or need light levels as high as Digitalis purpurea, Carex pilulifera or Luzula.

Hypericum appears to be able to establish itself in new B - Plan clearings and remain at least up to nine years after clearing. Where it occurs under the main canopy in 55.1 and 55.8, it is on the edge of a rackway where it could be affected by the forestry operations. There is the suggestion that like Digitalis, the competitive advantage of Hypericum lies in its seed bank. It is found in 88 of the total 160 samples in the seed bank study and in every quadrat. Like Digitalis, its seeds could well be dark inhibited (Fenner, 1985) to allow them to become part of the persistent seed bank. Hypericum thus has the potential to respond to B - Plan clearings, but with less intensity than Digitalis because of the lower numbers in the seed bank, a maximum of 37 individuals occurred in a sample. Thompson and Grime (1979) group species into four groups on the basis of their behaviour in the seed bank (Section 7.1.). The suggestion is that Hypericum belongs to group III, in which most seeds germinate after shedding, but some become incorporated into the persistent seed bank. Group IV is a variation of group III only in degree (Section 7.1.). Most seeds shed in this group become incorporated in the persistent seed bank. Although Thompson and Grime classify Digitalis in group III, the suggestion from Tavistock Woodlands is that it would better fit into the group IV category. To make up for the lower numbers of viable seed in the seed bank compared to Digitalis, Hypericum appears to be capable of remaining in the ground flora for a longer period of time, up to nine years in 56.14 (Table 5.11.).

Where Hypericum is in the recently cleared sub-units, it grows with eight different species, at nine years after clearing with four species, and under the main canopy with up to six different species. The species it occurs with exhibit varying phenological patterns (Figure 8.1.), a result of the tendency to reduce competition in space. Hypericum's slender, straggley habit, growing up to 60cm, gives it the potential to grow up and around aggressive species like Rubus to reach the light, a competitive advantage that other light demanding rosette-forming species like Luzula or Carex do not have.

The distribution of Hypericum in space and time appears to be affected by B - Plan management. It occurs in the ground flora particularly in places that have, in the recent past, been affected by management disturbance. In addition, although it survives in the seed bank up to 41 years after a clear-fell in quadrat 56, the numbers are much lower than those in the younger B - Plan sub-units. Likewise under the over-mature coppice of quadrat 52 there is only one individual in the seed bank samples. It seems that between 40 to 60 years Hypericum decays rapidly in the seed bank and therefore may not be able to survive a 55 year even-aged conifer rotation in any great numbers. However, Hill and Stevens (1981) found a few seeds of Hypericum spp. in an old plantation seed bank that may have been there over 100 years. The continual clearing of B - Plan management would no doubt serve to regularly replenish the distribution of Hypericum in time.

8.3. Temporal and spatial patterns - a summary

The species in B - Plan communities were divided into several sets and sub-sets based on their competitive and phenological strategies.

Set 1 - Highly competitive shrubby species - the 'ubiquitous' Tavistock Woodlands species

Set 2 - Ruderal species

Set 3 - Perennial species of lesser competitive ability

Sub-set 1 - Cool season species

Sub-set 2 - Warm season species

Many species in sets 2 and 3 were more frequently found in B - Plan sub-units. Six of these more frequent species Athyrium filix-femina, Carex pilulifera, Digitalis purpurea, Dryopteris dilitata, Hypericum pulchrum and Luzula pilosa were selected and examined in detail.

Particularly significant about most of these six species was the finding that B - Plan management appears to affect their distribution in time and space. Firstly, continual clearings of varying ages enable ruderal species to exist in both time and space in various life stages. Secondly, the distribution of species in time, like those of oak coppice which rely on seed bank strategies, is enhanced under B - Plan management by the provision of continual opportunities for seed bank replenishment. Thirdly, B - Plan provides a constantly moving pattern in space of suitable niches for stress susceptible species to exploit.

CHAPTER 9. DISCUSSION AND CONCLUSIONS

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9.1. Introduction

The prime aim of this thesis was the evaluation of the ecological and conservation interest of the ground flora under the early stages of the Bradford-Hutt continuous canopy system of forestry management - B - Plan. To achieve this aim, four distinct objectives were defined. The following is a discussion of each of these objectives, the extent to which this study has fulfilled each of them and the areas where a need for further study has been identified.

9.2. Objective 1 - Determination of the floristic composition of the ground flora under B - Plan stages I - V and comparison with adjacent areas of clear-fell forestry

The phase I tree survey (Figures 1.4. and 3.1.) revealed ten different canopy types (section 4.2.2.). Analysis of the ground flora under these types in phase I (section 5.2.2.) showed that the differences in community composition were primarily a reflection of past history and management, with three major groups being identified:

a) those on former heathland;

b) those on continuously wooded sites still relic oak coppice;

c) those on a mixture of sites of both heathland and woodland origins.

The historical origin of the sites was reflected in a vegetational community gradient from shady, damp-loving woodland species to drier, light-demanding heathland species (Figure 5.2.).

In phase II, these ten major canopy types were surveyed with the emphasis on sampling of the ground flora in B - Plan sub-units. When the results were analysed (section 5.3.2.), the community gradient apparent at phase I was revealed again. This gradient was examined further and found to be correlated with two underlying environmental gradients; light, as measured by canopy closure (moosehorn) and soil moisture (section 5.3.3.). Further analysis at phase II of only the sub-quadrats in B - Plan sub-units showed that these environmental and vegetational gradients were also related to the age and maturity of the B - Plan sub-units (sections 5.3.6. and 5.3.7.).

The changes in vegetational communities along these environmental gradients were shown to be of a qualitative nature (in phase II), and certain groups of ground flora species were found to be associated with B - Plan sub-units of differing ages since clearing (Table 5.11.). These qualitative changes were also quantitative in nature, in terms of decreasing species numbers and abundance with increasing successional maturity of the B - Plan sub-units (Figures 5.9.-5.11.). These changes were found to be similar to the successional changes in three even-aged plantations of differing ages (Figures 5.12-5.14, section 5.4.3.). The most significant difference between the changes in the B - Plan sub-units compared to those in the even-aged plantations was that the changes in the sub-units occurred in space as well as time, while those in the plantations occurred only over time.

Many of the successional species revealed in phase II (Table 5.11.) were found to occur more frequently in B - Plan sub-units than under the adjacent clear-fell canopies. These were investigated further under objective 4 and results were presented in Chapter 8.

Although the species diversity was not expected to be high on the acid soils of the Tavistock Woodlands, the B - Plan management system is able to maintain this diversity within the mosaic of sub-unit clearings.

In a theoretical discussion of diversity and stability, Orians (1975) suggests that this spatial heterogeneity of the environment leads to stability. Heterogeneity acts as a buffer to produce long term stability (Whittaker, 1975; Margalef, 1975).

B - Plan clearing at six-yearly intervals through the 54 year cycle in adjacent 6 x 6m sub-units provides gaps for random colonization and encourages the natural successional sequences, so that species form all successional stages can contribute to diversity, as shown in Chapters 5 and 8. Horn (1974) states that some degree of disturbance is needed for a system to realize its maximum potential diversity.

Diversity and stability depend not on each other, but on external properties of the ecosystem and environmental stability (Margalef, 1975). Stability also depends on environmental predictability (Pielou, 1975) and acts through its effect on the availability of resources (Whittaker, 1972). The stratification of space and time of B - Plan trees helps to provide a degree of environmental stability by reducing the effects of extreme climatic events, i.e. frost, drought and wind (Pielou, 1975). In the Tavistock Woodlands, the heterogenity of species and habitat is enforced, creating a mixed age structure that Bormann and Likens (1979) refer to as the "shifting mosaic steady state", characteristic of an ageing and more diverse forest. Whittaker (1972) compared this type of forest canopy favourably with that of a closed canopy, evergreen forest, the former having a mosaic of shade, sun and soil resulting in greater species diversity.

Pielou (1975) describes a substrate - patchiness effect which reduces the competition between species. A species will not compete with another occupying a different substrate (or micro-habitat).

As a result, a greater number of species can co-exist in the same area. This substrate - patchiness is greatest in a sequence of successional habitats such as is present in both space and time under B - Plan management. Here species can reach their greatest numbers (Whitmore, 1982). The cycle in B - Plan can also be likened to the concept of cyclic regeneration described by Watt (1947).

The rackways and rides in Tavistock Woodlands are a separate community, whose ground flora contributes to diversity and ecological interest. These merit further study which would contribute to a better understanding of conservation value under the B - Plan system.

The shrubs surveyed at phase III showed that, although the diversity and structure of both the upper and lower shrub layers is strongly affected by B - Plan management, this management favourably influences the regeneration of two ecologically important species, Betula spp. and Quercus x rosacea (section 4.5.6.).

In summary, the initial objective of the thesis, the study of ground flora under the first five stages of B - Plan has been achieved. The overall results indicate that B - Plan conserves the ground flora and maintains ecological interest through the cycle to date. Further study of the ground flora at the end of the 54-year cycle would clearly be extremely valuable. In addition to examining the further changes in existing sub-units, the changes of the ground flora in new sub-units cleared over the next 25 years would prove very interesting, particularly when compared with those already studied.

Another important idea would be a study of B - Plan after full implementation of the system in the long term over 2-3 rotations (100-150 years). One of the major problems of studies in woodlands is the long time scale needed to study ecological change. The ground flora under a 100-year old B - Plan system could be significantly different to that found in this survey of the early stages.

9.3. Objective 2 - Examination of the environmental controls affecting floristic composition under early B - Plan and in particular to study light as an ecological factor

The vegetational communities under B - Plan management studied in phases I and II can be arranged along a gradient correlated with both canopy closure as a primary gradient and soil moisture as a secondary gradient. The primary gradient of light, as represented by canopy closure and its effects on the ground flora were then examined in more detail. Hemispherical photographs were used at phase IV as an indirect measure of both diffuse and direct light (Chapter 6).

The results of analysis of the photographs from the sub-quadrats in phase IV showed that both diffuse and direct light were highly correlated with the vegetational community gradient (section 6.2.1.). The community gradient from light-demanding, heathland species to shady, damp-loving species, as represented by the indicators and preferentials from the classification groups of phase IV (Table 6.3.), is a reflection of a slow decrease in quantity of diffuse and direct light through B - Plan stages.

The recently cleared B - Plan sub-units, with the highest number and abundance of species, received higher light intensities; while the closed canopy of the older sub-units, with the sparsest ground flora, received the lowest light intensities. Thus the changing pattern of light reaching the ground under B - Plan management is the prime factor controlling the mosaic of successional communities within areas under B - Plan management.

The problems and limitations of studying the light environment in woodlands were discussed in Chapters 3 and 6. Good relative values for short wavelength radiation were obtained from the analysis of hemispherical photographs enabling relative differences under B - Plan stages to be measured and compared with ground flora variation.

However, there are several ways in which the light studies could be improved. Firstly, a 180° fisheye lens would give still greater accuracy particularly for direct light measurements. Secondly, for more detailed assessment of the light climate under deciduous canopies, the taking of photographs throughout the year would be a substantial improvement.

9.4. Objective 3 - Seed bank studies

As part of the detailed examination of B - Plan management in phase IV, the seed bank was studied to discover:

a) if the species in the seed bank were the same as those in the ground flora;

b) whether any of the former oak coppice species, not in the ground flora, were still in the seed bank;

c) whether the seed bank was a reflection of past management. If so, this could have implications for future diversity;

d) can study of the seed bank be used as the basis for value judgments about the conservation/potential of B - Plan?

Discussion

a) Some species in the seed bank were the same as in the ground flora. However, an increasing difference between the seed bank and the ground flora with increasing maturity of B - Plan sub-units was observed. This is similar to the successional pattern over time in natural forests (Figures 7.1.-7.3.). However, under B - Plan management, successional change takes place in time as well as in a very small unit of space, 20 x 20m, while the successional changes in natural forests take place only in time over large geographically separated areas.

b) Some of the former oak coppice species not present in the ground flora were present in the seed bank of certain quadrats. The most significant finding of this part of the seed bank study was that one quadrat, number 55, had been able to retain a wider complement of coppice species in both the seed bank and the ground flora despite the presence of a Pseudotsuga menziesii canopy. The implementation of B - Plan into this canopy in 1961 appears to have conserved the oak coppice ground flora assemblage which was, at that time, only in the seed bank.

c) The seed bank is a reflection of past management. Coniferization early in the 1800's appears to have had an adverse affect on the seed bank in some sites (section 7.3.1.). This is in marked contrast to the conservation of the seed bank and the ground flora in quadrat 55 which was a relic oak coppice until 1950. The implication of this is that once coniferization has proceeded beyond several rotations, any species of former oak coppice seed banks are seriously reduced.

d) Two results of the seed bank study are particularly significant in judging favourably the conservation based merits of B - Plan. Firstly, the presence under B - Plan management of successional trends similar to those in natural forest successions but replicated in space as well as time. Secondly, the fact that in one quadrat the coppice species have been retained under B - Plan management in spite of coniferization and in contrast to the depleted seed bank of the relic oak coppice in quadrat 52.

There were several limitations to the seed bank study. Firstly, the sampling method was imperfect and hence distribution of seed in relation to depth was not studied. This could have yielded more information about past management. Secondly, a quantitative study of the seed bank, concentrating on B - Plan areas like the site of quadrat 55, compared to other continuously wooded sites which were coniferized in the 1800's, would add the further information necessary for a full assessment of the ecological benefits of B - Plan.

9.5. Objective 4 - Analysis of certain aspects of the phenology of the ground flora

The detailed phenological studies described in Chapter 8 on selected species from the successional sequences under B - Plan (Table 5.11.) and found more frequently in B - Plan sub-units, were revealed to be extremely diverse in their competitive strategies. This diversity was expressed in terms of phenology, their ability to tolerate stress and in their seed bank behaviour. This appeared to be particularly true of the species in the recently cleared B - Plan sub-units. Here, the species diversity and abundance was high, resulting in increased competition. These selected species also appear to be affected by B - Plan management in terms of their distribution in both time and in space.

The phenological studies could be improved further if the communities were sampled bi-monthly throughout the year and percentage similarities were computed for those data. These more detailed data are vital if the percentage similarity approach to phenological study is to be used to best effect.

9.6. Conclusions

A number of economic, production and ecological advantages have been claimed for selection-based forestry management systems (Chapters 1 and 2). This study has shown that B - Plan management as a form of 'creative conservation' (O'Connor, 1974), creates ecological interest and diversity in both space and in time with a mosaic of sub-units of differing successional maturity. The system also creates the potential for future diversity in the seed bank, all within the confines of commercial forestry management. This creation of a heterogeneous environment, similar to the traditional coppice with standards, is suggested by Peterken (1981) as essential for conservation-conscious woodland management.

Although this thesis has concentrated on the ground flora under B - Plan, there is evidence that B - Plan may also conserve other components of the ecosystem. Small scale surveys by the R.S.P.B. have indicated increased ornithological interest (Smart, pers. comm.; Smart and Andrews, 1985) and also increased entomological interest as is demonstrated by the recording of the Heath Fritillery in B - Plan areas during 1985 (Warren, 1984).

Ecological and landscape advantages clearly exist in the B - Plan approach to forestry management. However, balancing these against the economic arguments for and against clear-fell systems has been and probably always will be extremely difficult.

9.6.1. The future of B - Plan management in the Tavistock Woodlands Estate

With the death of the 6th Earl of Bradford in 1981, the estate was forced for tax reasons to realize some of its assets. Consequently, the decision was made to increase felling of the mature canopy surrounding established B - Plan units in places where extraction was difficult;

on steep slopes and where large, over-mature trees, planted in the 1920's, were damaging the new plantings during extraction. As a result, the area of the estate under B - Plan management has been reduced from 50% to 25%.

B - Plan is still viewed as a sound management system by the estate managers, but present financial constraints on the 7th Earl mean that, although the 25% of the estate still under B - Plan will remain so, no new areas will be taken into the system for the foreseeable future (Dyer, pers. comm.). There are two primary reasons for these present financial restrictions on B - Plan. Firstly, the taxation schedule in woodlands does not favour a system like B - Plan. The estate gains much greater financial advantage under schedule D for replanting after clear-felling then under schedule B, which currently applies to B - Plan management. However, the estate management is negotiating with the inland revenue office for a more favourable tax concession for B - Plan management. If a more favourable tax concession is granted than the area under B - Plan management may once again increase. Secondly, although the production and economic advantages of B - Plan are likely to be greater in the future, when all nine sub-units are planted and the first final crop trees are harvested, the costs of establishing B - Plan within the optimum-aged 15 to 20 year old plantation cannot be borne by the estate at the present time (Dyer, pers. comm.). If left even-aged, these plantations will begin to bring in much needed revenue to the estate with the first substantial thinnings at 30 years.

Thus, it is the present economic climate in forestry and not the merits or failings of the B - Plan management system which threatens its continuation. Garfitt (1986) feels that the economic system of net discounted revenue, where the tree growth rates are compared with the artificial interest rates applicable in industry, is not appropriate in forestry. The cost of re-stocking should be charged on the old crop at harvest time. This would remove the economic constraints, forcing foresters to plant quick-growing conifers and would encourage longer rotations in attractive woodlands producing high quality timber, similar to the mixed selection forests on the continent. Broadleaves would no longer be viewed as uneconomic.

The current attitude toward forestry as an agribusiness, as manifested in the woodland tax schedule favouring clear-felling and in the application of net discounted revenue favouring short-term financial gain must change. Only then will forestry management systems like the Bradford-Hutt system of continuous canopy forestry, with it's careful husbandry of woodlands as a trust for the future, gain the financial support it needs to be more widely accepted.

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