The dynamics of buried seed banks beneath woodlands,

with particular reference to Hypericum pulchrum.

By

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This study has examined the rate at which the seeds of certain species disappear from woodland soils, and whether the composition of the seed banks beneath stands of known age can be used to reveal management history. Associated with this is an investigation of the spatial distribution of the stored propagules.

A question arises as to whether species with long lived seeds can survive as buried seed long enough to take advantage of the opening of the canopy and soil disturbance resulting from the falling of old trees. Given the great life span of most trees, this is a strategy open only to species with exceptionally long lived seed banks. One such species is Hypericum pulchrum, which, as the seed bank surveys carried out in this study show, can exist as viable seeds beneath woodlands of great age in the Tavistock Woodland Estate in Devon.

Is this germination and reproduction on tree falls sufficient to maintain Hypericum in the seed bank indefinitely? To answer this question, a computer model was developed to examine the effect of various parameters on the survival time of a Hypericum seed bank beneath a simulated woodland. The model allowed prediction of both the mean density of buried seeds in a unit area, and the development of pattern within the seed bank. Analysis of the simulation results established that the dispersal of Hypericum was insufficient to maintain a seed bank by a "chain reaction" of windthrown reinforcement. The implications of this are discussed with respect to pioneer species within both temperate and tropical forests.
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SECTION 1

A survey of woodland seed banks in the Tamar Valley.

1.1 Introduction

The existence of a seed bank of shade intolerant species in the soil beneath the canopies of secondary woodlands has been established by the studies of Oosting & Humphries (1940) and Livingstone & Allessio (1968). These surveys have revealed that woodlands cover seed banks composed of species of previous successional states, or in the case of managed woodlands of species present at the site before planting. Moore & Wein (1977) and Brown & Oosterhuis (1981) have shown how both canopy species and management practice can also influence seed bank floristic composition.

With closure of the woodland canopy and the cessation of the seed input of excluded, shade intolerant plants, the density of viable propagules will decrease through the combined effects of premature germination, depletion of the seeds' stored reserves, fungal attack and predation (Moore & Wein 1977). Thus without further disturbance, the soil seed flora of woodland will revert to that of ancient forests, consisting of seeds carried in from external sources and the transient seed banks of shade tolerant species, viable for less than one year (Thompson & Grime 1979).
With increasing use of seed bank studies in the examination of the past vegetation of particular sites and the dynamics of existing communities, a knowledge of the spatial distributions of seed banks in the soil, and the rates at which changes occur would be valuable. This study was initiated with the aim of examining the spatial heterogeneity of the seed bank floras of the woodlands comprising the Tavistock Woodland Estate, Devon, England, with an emphasis on the developments taking place with increasing canopy age.
1.2 Site Descriptions.

The Tavistock Woodland Estate covers 900 hectares of woodland in the Tamar and Tavy valleys in Devon and Cornwall England (Figures 1 & 2). The Estate is now owned by the Earl of Bradford, but before 1956 was part of a much larger estate owned by the Russel family, Dukes of Bedford, obtained after the dissolution of the English Monastic orders in 1539.

Apart from the diversity of woodland ages and canopy types provided by this area the Tavistock Woodland Estate has one major advantage for seed bank studies. A continuous series of estate management records dating from the 16th century can be used to ascertain the management history of the majority of timber stands.

The historical ecology of the major coppice woods of this area is linked to the industrial archaeology of the Tamar Valley. During the 18th and 19th centuries the region was the site of one of the largest collections of copper mines in the country. Seams of copper ran through the valley sides from east to west and were excavated from a series of mine shafts, the remains of which can still be seen. Ore was shipped by barge from the docks at Morewellham and Calstock down the Tamar to Plymouth. The woodlands of the Tavistock and Cotehele Estates provided timber for local shipping, house building, mining and fuel. Smaller wood was stripped of its bark for use in the tanning trade.
Figure 1. A map of England showing the location of the study area in Figure 2.

Location of area covered by Figure 2.
Figure 2. A map showing the approximate locations of the woodland areas studied in this survey.
At the end of the 18th century the arrival of the railway led to the decline of the barge trade and along with closure of the mines in 1901 and the introduction of cheap chemicals into the tanning industry, led to the cessation of coppicing in the area in the early 1900's. In order to reclaim the mining areas Lord Bradford planted large areas with softwoods, following which there has been a gradual conversion of the remaining coppice areas to softwood.

1.2.1 Carthamartha Wood O.S Grid Ref 378 776

This wood was bought by the Duke of Bedford in 1870. The coppice was cleared in 1906 and replanted with a mixture of softwoods. It has been managed using the normal plantation forestry technique of thinning to control the growth rate of the trees.

The ground flora of the wood is dominated by either *Rubus fruticosus* or *Luzula sylvatica*. Each seems to form areas of complete monospecific cover in the thinned rows between the trees. This may be due to the ability of each species to exclude the other (in which case the first species present would form the ground vegetation), or to unknown physical and environmental factors. The only other species present in the ground flora of the area surveyed were *Oxalis acetosella* and *Hedera helix*. 
1.2.2 Morewellham Wood O.S Grid Ref 442 703

With the decline in the use of coppice as the major wood supply of the area, a section of this woodland was cleared in the 19th century to provide land for the cultivation of strawberries. This area was situated on the steep south facing slopes of the Tamar valley.

Over the past thirty years the area has been reafforested with a variety of softwood stands. The seed bank survey was carried out in an area replanted with Japanese larch (Larix leptolepis) 26 years before sampling. The ground flora consisted of a thick cover of Rubus fruticosus which provides a second canopy beneath the trees. The only species which can survive this double layer of shading are Galium aparine and Hyacinthoides non-scripta.

1.2.3 Blanchdown Wood O.S Grid Ref 420 730

This is the site of a secondary woodland planted on the mine spoil dumped from a disused copper mine. The site was also used in the early 19th century as a game reserve. The samples in this area were removed from a Beech plantation (Fagus sylvatica) planted in 1930. The ground vegetation was exceedingly sparse, composed only of Rubus fruticosus.
1.2.4 Wareham Wood O.S Grid Ref 390 780.

The tree cover of Wareham Wood is composed of approximately 20 hectares of old oak coppice (*Quercus spp.*) of various ages. Since the abandoning of the coppice management in the 19th century, areas have been felled for the use of the Estate, usually to be sold as firewood. Many are gradually being replaced with plantations, although it is hoped to leave a large area as a reserve. The removal of these areas has not been recorded in the management books so that stand ages were calculated using ring cores.

One feature throughout Wareham Wood is the absence of identifiable standard trees within the coppice. A series of decaying stumps that exhibited signs of felling indicated that the larger trees may have been removed and sold on abandonment of the coppice.

The ground flora of the area was composed of *Vaccinium myrtillus*, *Lonicera periclymenum*, *Rubus fruticosus*, *Oxalis acetosella*, *Pteridium aquilinum*, *Hedera helix*, and occasionally in the overgrown rides *Luzula sylvatica*. 
1.2.5 Greystone Wood O.S Grid Ref 363 795
Lifton Wood O.S Grid Ref 392 845

These coppice woodlands of stand age c50 yrs were situated to the north of the Tamar valley. They are two small areas of woodland which appear to have been abandoned at approximately the same time as Wareham Wood. The denser shading of the younger canopy excluded the majority of the ground flora with only *Rubus fruticosus* able to survive.

1.2.6 Warleigh Point O.S Grid Ref 448 610

This area of coppice and broad-leaved woodland is situated at the confluence of the rivers Tamar and Tavy to the north of Plymouth. The area is a nature reserve of 12.8 hectares that has been actively managed by coppicing. The reserve contains two stands of 5 and 20 yrs age which were used in this study. The ground flora beneath the canopy is composed of *Rubus fruticosus*, *Hyacinthoides non-scripta* and *Mercurialis perennis*.

1.2.7 Woodland Soils.

The woodlands studied in these surveys are situated on a slate and shale bedrock. These provide the parent materials for the soils above them which show little variation throughout all of the sampled stands. The structure is an Acid Brown Earth whose depth varies according to exposure. All are well drained with measured pH values between 3 and 4.
1.3 A review of previous seed bank survey techniques.

1.3.1 Extraction methods.

Investigations of the composition and density of seed banks have used a variety of techniques and tools for the extraction of a representative sample of soil. These fall into two categories.

i) Extraction by hand.

These methods involve cutting of the turf, usually with a knife or machete, followed by the removal of the soil layers with a trowel (Olmstead & Curtis 1948, Marquis 1975). Although suitable for use in assessment of the composition and density of seed banks, this method is not suitable for the examination of the vertical distributions of seeds, because it allows contamination across the sampled layers.

ii) Removal of soil cores using an extraction tool.

This is the method used by the majority of seed bank studies. The dimensions of the instrument used range from the 1-3 inch diameter corer of Champness (1949), to the 30 x 30 cm square corer of Brown & Oosterhuis (1981). Soil cores extracted by this method can be divided horizontally into the required sampling depths with ease, reducing the errors associated with cross contamination.
The difficulties involved in handling large cores of soil and the statistical advantages derived from using large numbers of small cores to sample contagiously distributed populations, has led to the majority of workers increasing sample number rather than sample size. Thompson (1986) concluded that pattern within the seed bank cannot be established to within tolerable accuracy limits without removal of large numbers of soil cores (> 50), especially for the highly contagious distributions that he found within pasture seed banks.

Soil corers which have been used to assay seed banks range in sophistication from the golf cup cutters of Livingstone & Allessio (1936), to modifications of the samplers devised by Coile (1936), used for studying the physical properties of soil. The essential design criteria are ease of use and minimum compaction of the soil core if the vertical distribution of seeds is to be studied (Roberts 1981).

1.3.2 Sampling procedures.

The surveys of Oosting & Humphries (1940), Livingstone & Allessio (1968) and Brown & Oosterhuis (1981), in which the emphasis has been placed on the presence or absence of particular species, have involved consolidation of all samples removed from a single area into a unit from which sub-samples are taken. This results in values for the seed density which do not consider within site variation.
The introduction of statistical techniques in the analysis of sample results has led to an examination of the spatial distribution of seeds within the soil, by use of random samples (Champness 1949, Moore & Wein 1977, Hill & Stevens 1981); transects of soil cores (Kellman 1974, Symonides 1978); and grids of contiguous cores (Thompson 1986). Champness (1949) and Elliot (1977) have shown how the variation in sample densities measured for each species can be used to derive the number of samples required to obtain population density estimates within specific error limits.

However, owing to the contagious distributions exhibited by the majority of seed bank species and the low densities at which many are found, large numbers of samples are generally required to enable precision in density estimates. The difficulties involved in removal of a large volume of soil, as well as in the treatment used to assay the seed density, ensure that the majority of studies are still restricted to extraction of a manageable sample number, usually lower than the optimum (Whipple 1978, Thompson 1986). As Roberts (1981) states this may still be sufficient for predictions of sample densities to be made if the associated errors are included in the final conclusions.
1.3.3 Sample treatment.

A comprehensive survey of the literature concerning the techniques used for establishing the density of viable propagules within soil samples is given by Roberts (1981). The methods fall into two categories.

i) Extraction of the seeds from the soil.

Soil samples are washed in water or chemical solutions, or dried in order to break down the soil matrix. The seeds are then removed by floatation on solutions of various densities, in air flow apparatus, or by sieving.

The viability of the extracted seeds is then tested by inducing germination under controlled conditions, or by subjecting the seeds to a tetrazolium test.

ii) Germination of seeds from within the soil sample.

Samples are sieved to remove stones and plant debris. The remainder is placed in seed trays, usually within a cold greenhouse, and the seedlings which appear are then removed after identification. At regular intervals the soil is stirred to ensure that all seeds within the sample are subject to the germination inducing environment.
The first method has the advantage of extracting all seeds (although with increasing difficulty as seed size decreases), giving an exact measurement of density. However the determination of viability can be affected to a great extent by the operators skill at using the tetrazolium test, which is especially difficult for the small seeded species which tend to make up the largest proportion of seed banks; the method is therefore time consuming. In comparison with the densities that would germinate in the field this method will produce an overestimate of seedling density.

The advantages of the second method are the reduction in effort required for the survey, ease of seedling as opposed to seed identification, and if conditions are kept as close as possible to those of the field, a better estimate of the densities likely to arise in the natural environment. Criticisms of the method are the amount of space required for the assay, the delay in obtaining results and the fact that conditions may not stimulate germination of all species. Roberts (1981) has suggested that a combination of the two methods may provide a suitable solution. Choice of the technique to be used, as with the number of samples to be extracted, is dependent on available resources of both time and space.
1.4 Sample extraction and treatment.

1.4.1 The soil corer.

All samples were removed from the woodlands using a sledge hammer and a soil corer designed specifically for this survey. The corer was produced from a length of steel piping with internal diameter 10 cm and a wall thickness of 0.5 cm (Figure 3a). The base of the pipe was sharpened to provide a cutting edge, and two 0.5 cm holes were drilled across a diameter at the top, so that a handle could be attached. To protect the corer edges from the blows of the sledge hammer and distribute the force evenly over the cutting edge, a 2 cm thick countersunk steel lid was placed on to the top of the cylinder before striking with the hammer.

Removal from the soil was achieved by attaching the handle to the holes in the upper rim. A plunger similar to that of a syringe (Figure 3c) was then used to push the sample out from the corer. In a few cases the soil moisture content prevented the application of sufficient force to remove the core by this method. A screw threaded plunger (Figure 3d), fitted to the holes drilled for the handle, removed all "stubborn" cores.
Figure 3. The soil corer and extraction tools used to remove seed bank samples.
1.4.2 Sampling procedure.

Prior to coring loose leaves and twigs were removed from the position to be sampled. The corer was then placed on the soil and driven vertically into the ground using the sledge hammer. The handle was attached, and the corer slowly withdrawn.

After scraping the excess soil from the outside of the corer, the unit was placed inside a tight fitting plastic bag and the plunger was then used to push the sample from the corer. During this process the plastic bag was supported by a half section of plastic drain pipe, preventing the sample from breaking up. The plastic bag was then wrapped tightly around the sample and bound with sellotape to keep the unit together. All samples were then packed upright in carrying trays to prevent damage during transport.

All samples were removed during the months from November to February of each sampling year. Samples were processed within one week of removal from the woodland and during this period they were stored in the carrying trays in the polythene tunnel used for the germination treatment.
1.4.3 Sample treatment.

Samples were processed using one of two methods selected according to the number of cores removed in the experiment.

i) Soil washing

Cores from the depth experiments (see page 34), which analysed a relatively small number of samples with an emphasis on the accuracy of the separation of soil layers, were treated with a soil washing apparatus. This was developed from the seed blower developed at Sheffield (Whatley 1984), used to separate seeds from chaff. The blower uses a variable speed electric fan to create a current of air within a vertical column into which the seeds and chaff are placed. Variations of air speed allow the lighter chaff to be removed from the seeds.

Replacing the air blowing fan with a water jet produces an apparatus which will separate the light organic matter from the heavier mineral soil (Figure 4).

Soil samples were treated chemically using the technique developed by Malone (1967), but at a dilution of four times. This solution strength was found to be sufficient to disrupt the chemical bonding of the soil matrix and allow extraction of the organic matter. The slurry produced by this technique was placed in the base of the washing apparatus and the system sealed. A water jet created by the pressure from a laboratory tap disturbs the slurry and produces a revolving column of water. Lighter particles are lifted by the force of the rising water and settle.
Figure 4. The soil washing apparatus used to remove seeds from soil samples.
at the level where the force of the water and gravitational pull are balanced. This sets up a graded column of particle sizes. The flow rate can then be adjusted to lift the lighter organic matter over the top of the column, to be caught in the removable sieve. The waste water with suspended soil passes through the sieve and out of the waste pipe.

The collected seeds and organic matter were either hand sorted beneath a microscope or laid on a 5 cm layer of sterile sand in pots in a cold greenhouse. The pots were watered from below by felt matting attached to a continuous drip feed system. This reduction of the volume of the treated soils allows more samples to be subjected to rigorously controlled germination conditions if required.

Tests for the effect of both the chemical treatment and the washing technique, using the seeds in untreated soil as a control, showed no significant change in germination or survivorship of seedlings.

Trials also showed that hand sorting for the larger seeded species eg Rumex spp. and Rubus fruticosus, gave almost 100% success in recovery. Smaller seeds were less successfully recovered, with the rate dependent on the organic matter content of the soil. Tests using known numbers of seeds showed that the smaller seeded species such as Hypericum pulchrum and Digitalis purpurea were trapped by the sieve and were successfully recovered by the cold greenhouse germination treatment.
ii) Germination from within the soil sample.

During the three sampling seasons over one thousand samples were assayed for their density of viable propagules. The large volumes of soil involved in the majority of the experiments made use of the washing technique for all samples impossible. The greater proportion of the samples to be assayed were therefore placed in seed trays in an unheated polythene tunnel and seed density measured by counting the number of germinating seedlings.

The cores were passed through a 0.75 cm sieve in order to remove stones and large organic matter. The remaining soil was then spread to a depth of 1 cm on a 1 cm layer of sterile horticultural sand in plastic seed trays (35 x 24 x 5 cm). Each 10 cm deep sample occupied two trays at this soil depth. The trays were placed on 24 cm wide strips of capillary matting which ran the length of a thirty metre polythene tunnel. The slope of the ground in the tunnel allowed the capillary matting to siphon water from reservoir barrels, providing a constant supply of water to the seed trays. The water was carried by the capillary action of the sand grains from the matting to the soil, the sand also acting as a reservoir for the seedling roots. During the final growing season a water pipe was laid to the tunnel allowing a sprinkler system to be used in conjunction with a drip feed supply.

Mesh curtains used in place of tunnel doors allowed a free circulation of the air and restricted the passage of contaminants to the trays. However as a precaution trays of sterile sand were laid at random throughout the tunnel to test for immigrants. In
three seasons the only species to germinate in the trays was *Senecio vulgaris* and all records of this species were therefore discarded.

1.4.4 Seedling identification.

Each week seedlings of sufficient size to be identified were removed from the seed trays, recorded and discarded. Those seedlings which could not be identified were transplanted to pots containing potting compost until of sufficient size to be identified. The seed trays were stirred after each flush of seedlings to ensure complete germination. Tests with soil washed after two stirrings showed that 93% of the viable seeds were recorded at that time. All seed trays were subjected to three stirrings.

During the course of the study the temporal development of the seed banks of several species were followed in detail. This involved numerous germinations and identifications, and for these species seedlings were regularly removed, grown on and identified to ensure that a single species was being examined and not a mixture of similar seedling forms. This was particularly important for *Hypericum*, where it was felt possible that more than one species may have been present.
1.5 Floristic Composition.

Table 1 illustrates the site characteristics, number of samples and floristic composition of all seedlings germinating from the soil samples removed during the woodland studies. Each species in the seed bank flora is placed into a vegetation group based on those described by Nakagoshi & Suzuki (1977). In this grouping system the species are divided into seed bank categories according to the method of arrival of the seeds at the sampled site.

Group 1: Seeds deposited by vegetation established in the ground flora of the sampled site.

Group 2: Seeds deposited by species absent from the vegetation at the time of sampling, excluded by closure of the woodland canopy.

Group 3: Seeds deposited each year from the air currents.

It is also possible to distinguish the groupings of Brown & Oosterhuis (1981), which separate the seed bank species into categories of shade tolerance. In their system the group 2 seeds described above would be split into species intolerant of shade and those tolerant of some shade, whilst the species present in group 1 would be shade tolerants. The dividing lines for these groups are fine, and without physiological measurements of tolerance, the grouping technique is subjective.
Table 1a The site characteristics of the columns of Table 1b.

<table>
<thead>
<tr>
<th>Column</th>
<th>Woodland area</th>
<th>Type</th>
<th>No Samples per Area</th>
<th>No Areas</th>
<th>Age (yrs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Warleigh Point</td>
<td>O coppice</td>
<td>10</td>
<td>2</td>
<td>5 &amp; 20</td>
</tr>
<tr>
<td>II</td>
<td>Wareham wood</td>
<td>O coppice</td>
<td>50</td>
<td>9</td>
<td>70-220</td>
</tr>
<tr>
<td>III</td>
<td>Wareham wood</td>
<td>DF plant.</td>
<td>10</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>IV</td>
<td>Wareham wood</td>
<td>DF plant.</td>
<td>10</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>V</td>
<td>Gun Oak Wood</td>
<td>NS/DF plant.</td>
<td>10</td>
<td>2</td>
<td>28 &amp; 48</td>
</tr>
<tr>
<td>VI</td>
<td>Carthmartha</td>
<td>SP plant.</td>
<td>30</td>
<td>1</td>
<td>77</td>
</tr>
<tr>
<td>VII</td>
<td>Morewellham</td>
<td>JL plant.</td>
<td>47</td>
<td>1</td>
<td>26</td>
</tr>
<tr>
<td>VIII</td>
<td>Blanchdown</td>
<td>B plant.</td>
<td>31</td>
<td>1</td>
<td>52</td>
</tr>
</tbody>
</table>

O - Oak (*Quercus* spp.)

DF - Douglas fir (*Pseudotsuga menziesii*)

NS - Norway spruce (*Picea abies*)

SP - Scots pine (*Pinus sylvestris*)

JL - Japanese larch (*Larix leptolepis*)

B - Beech (*Fagus Sylvatica*)

-24-
Table 1b The species composition of seed banks of the sampled woodlands.

<table>
<thead>
<tr>
<th>Species</th>
<th>Coppice</th>
<th>Plantations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Betula pubescens</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>H. non-scripta</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Teucrium scorodonia</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Viola riviniana</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Rubus spp.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Agrostis spp.</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Anagallis arvensis</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Cardamine hirsuta</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Carex spp.</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>2</td>
<td>2/1</td>
</tr>
<tr>
<td>Juncus spp.</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Lotus corniculatus</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Plantago major</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Potentilla sterilis</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ranunculus repens</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Rumex obtusifolius</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Sagina procumbens</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Sarothamnus scoparius</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Trifolium repens</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ulex europaeus</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Veronica officinalis</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Cirsium arvense</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Epilobium spp.</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

H. non-scripta = Hyacinthoides non-scripta

All references to Juncus spp. = J. acutiflorus, J. conglomeratus, J. effusus
Cirsium spp. = C. piluliferum
Agrostis spp. = A. capillaris, A. stolonifera

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The studies of Roberts & Dawkins (1967) and Rampton & Ching (1970) have shown species specific decay rates in buried seeds. It would therefore be expected that after closure of the woodland canopy, each species would disappear from the seed bank at a specific rate which might vary according to depth of burial, soil moisture content etc. As the woodland canopies increase in age the changing configuration of their seed bank floras will reflect the species specific decay rates.

1.5.1 Development of the coppice stand seed bank flora.

The coppice wood seed flora is presented in Table 1 in columns I and II.

Two areas of coppice wood were sampled in order to examine the development of the seed bank flora. Warleigh Point consists primarily of two stands of coppice cleared 5 and 20 years ago. Wareham Wood coppice is composed of a series of adjoining stands of age range 70-220 years. 'Age' here refers to the time that has elapsed since the last canopy clearance by coppicing.

A comparison of the floras indicates that Plantago major, Sarothamnus scoparius and Veronica officinalis, if present at the older site originally, all have seed bank life spans which do not extend to 70 years. In contrast Hypericum pulchrum and Digitalis purpurea were both found in low densities in the older woodlands. Juncus spp. were found within the soils of the majority of coppice woodlands studied, but showed a patchy distribution.
Moore and Burr (1948) quote a 50-90 year life span for Juncus spp. in moorlands. The patchy distribution of the seeds of these species through the time sequence may reflect the ability of this genus to survive in the rides of woodlands, occasionally producing seed which is distributed beneath the canopy.

Data of this type from seed bank surveys can be used to establish only that seeds of a particular species are long lived, not short lived. This is due to two sources of errors; firstly the absence of a species from the soil of a woodland may be due to its inability to colonise the site before canopy closure, and not to death of all the propagules. Secondly, given a constant species decay rate and provided that the total seed bank life span of the sampled species is not exceeded, two areas whose initial density of seeds differ at canopy closure, will exhibit apparently different seed bank survival times. The area with the lower initial seed density will fall below a detectable level before the area of high density. For this reason maximum seed bank life spans can only be quoted as the longest measured to date. When measuring the decay of a seed bank by use of a series of stands of increasing age, this latter source of error can be reduced by measuring mean densities for a group of stands of equivalent age. The varying time periods required for the removal of seed banks of differing starting densities may account for the temporally discontinuous distribution of Juncus spp.
Toole (1946), in discussing the results of the Duvel buried seed experiment, describes how the larger seeded species decay at faster rates than the small. The coppice study results follow this pattern with Plantago major (0.24 mg **), Sarothamnus scoparius (0.55mg), and Veronica officinalis (0.11mg) absent from the older woodlands. Hypericum pulchrum (0.08mg), Digitalis purpurea (0.07mg), and Juncus spp. (Juncus effusus 0.01mg) all have small seeds.

Leavitt (1963) has speculated that small seeds are more easily incorporated into the seed bank, being washed down by the rain, or buried by the influence of soil disturbing animals. He states that this may result in greater dormancy and less predation producing slower apparent decay rates. In addition to this the experiments of Beal (Toole 1946) have shown that the larger seeded species appear to have physiologically shorter life spans.

Large seeds are not absent from the seed bank flora of woodlands. The requirement for a seedling of sufficient size to allow litter penetration and growth beneath the shade of a tree canopy results in the majority of shade tolerant ground flora species having large seeds (Thompson pers comm.). Examples are provided by Hyacinthoides non-scripta (6.17mg) and Teucrium scorodonia (0.87mg), both found within the coppice wood seed banks. Shade tolerant species also have short life spans and form part of the transient seed bank group of Thompson & Grime (1979).

** (All seed weights taken from Grime et al. (1981))
Other species noted for their absence from the seed banks of woodland soils are the dominant tree species (Kellman 1974, Whipple 1978). All samples removed from the woodlands were sieved to extract stones and roots and during this process no viable seeds of *Quercus* spp were recovered. The seeds of *Betula pubescens*, an infrequent canopy species, were present. Hill & Stevens (1981) quote a life span of 2-3 years for this species. Kellman (1978) has discussed the possibility of large seeded species suffering greater rates of predation due to their inability to penetrate the soil surface. Earlier Watt (1919) demonstrated that the seeds of *Quercus* spp are subject to heavy predation from *Microtus* spp. Predation may therefore be a major factor in removing the seeds of *Quercus* spp before the sampling dates in winter.

*Agrostis* and *Carex* species are found in the soils of the older coppice stands whilst absent from the young. Brown and Oosterhuis (1981) record germination of these genera in five areas of neglected coppice (age 30-40 yrs) in North Essex and South Suffolk. It is therefore highly probable that both are apparently absent from the younger stand areas due to sample error and would be revealed by a more intensive survey. Hill and Stevens (1981) noted that after 45 years within the soil the seeds of *Agrostis* spp. were found in low numbers and all were nonviable. The low density of randomly distributed seed found within the soils of the older areas of coppice may therefore be present due to animal dispersal or the occasional wind carried seed.
The work of Brown & Oosterhuis (1981) has also shown that *Sarothamnus scoparius*, *Veronica officinalis* and *Plantago major* are all present in the soil of the 30-40 year old derelict coppice woods they studied. The results of the present study would place the seed bank life span of these species in the 40-70 year range.

Rackham (1975) concluded that *Juncus spp.* and possibly *Centaurium erythraea* can survive the shade phase of the coppice cycle as seeds in the soil. The results of the study of Brown & Oosterhuis (1981) and this survey have shown that many other species associated with coppice woods can also pass through this phase in the seed bank. The data also show that as the length of time between canopy clearances increases, fewer species will appear from the woodland soil, becoming "marginal species" (Salisbury 1924), confined to rides and woodland margins.

1.5.2 Development of the plantation seed bank flora.

The influence of vegetation history on the seed bank of a woodland can be assessed from the remaining six sample sites in Table 1b (columns III to VIII).

Columns III through VI are examples of plantations on sites previously occupied by ancient coppice woodlands. The Wareham Wood data (column II) provide a measure of the woodland seed bank flora that was present before clearfell. After felling the plants which are found at the site are derived from four sources.
The majority germinate from the previous woodland seed bank (Kellman 1974). Others arrive at the site from the airborne seed rain, by spreading from the rides (Salisbury 1924), or by animal dispersal. Growth of the canopy restricts the colonisation time to 10-15 years.

When an area within a mature coppice stand is felled to plant softwood, any colonisation of the newly opened habitat is restricted by its degree of isolation. The surrounding mature woodland limits the availability of new species to the regenerating vegetation. Consequently any species arriving at the site must either be carried in across the surrounding canopy by wind or bird dispersal, or penetrate by animal dispersal and vegetative growth beneath the canopy. This results in newly formed seed banks of low species diversity, similar to those of the original coppice but at higher densities due to reinforcement. A comparison of the original coppice seed flora (column II), and that of a young plantation on a site previously occupied by old coppice (column III) reveals the similarities.

Hypericum pulchrum and Juncus spp. are classified as 1/2 within the youngest plantation flora. The canopy has not completely excluded all light from the ground vegetation and these species survive as mature plants in the gaps between trees (group 1); beneath the trees they are found only in the seed bank (group 2). The exclusion of shade intolerant plants in extending zones from the base of newly planted conifers or regenerating coppice stools may result in a mosaic of seed density distribution with the highest densities at the centre of the area between the trunks.
Canopy closure ensures that only *Rubus fruticosus* is found beneath the plantation canopy as a mature plant; the shade is such that even *Rubus* is reduced to low densities. All other species are banished to the seed bank (columns III & IV). With increasing age and tree size, thinning management alters the light levels at the soil surface. The disturbance caused by the opening of the canopy during this process allows shade intolerant plants to germinate and produce seed until the canopy recloses. *Hypericum pulchrum*, in column IV, is therefore placed in the 2/1 category since it is a species able to exploit this situation. *Luzula sylvatica* reappears in the ground vegetation (group 1) of thinned stands owing to its ability to germinate in the light gaps and survive vegetatively in the increased light environment.

Hill & Stevens (1981) studied plantations in North Wales which had been established on sites previously occupied by derelict woodland. Their results show a similar flora to that found on the Tavistock Woodland Estate areas, with *Digitalis purpurea*, *Betula pubescens*, *Rubus fruticosus* and *Hypericum pulchrum* the main seed bank components. The colonising ability of *Betula pubescens* and seed bank life span of the other species enable them to appear in the ground vegetation after fifty five years of complete canopy.

It would appear that given sufficient time to replenish the seed bank between clearfell and canopy closure, these species may, with invaders from rides such as *Agrostis spp*, or wind borne species (eg. *Epilobium spp*, *Cirsium spp*), form the ground vegetation and seed bank of future plantations.
Columns VII and VIII present examples of plantations whose past vegetation has had a major influence on the seed bank flora present at the time of sampling.

Morewellham wood is planted on an area previously used for the production of market garden produce, mainly strawberries. The seed bank flora can be used as an indicator of the historical ecology of the woodland, the majority of seed bank species being either common weed species associated with horticultural management eg. *Anagallis arvensis*, *Rumex spp.* and *Sagina procumbens*; or they are species associated with abandoned field succession to woodland vegetation eg. *Agrostis spp.*, *Digitalis purpurea*, *Hypericum pulchrum*, *Potentilla erecta*, *Rubus fruticosus* and *Luzula sylvatica*. The composition of the seed bank flora reflects the succession following abandonment.

As with the previous columns, it would be anticipated that with increasing canopy age, the seed bank density and diversity would decrease until only long lived seed bank species remain.

Blanchdown wood Beech plantation presents a similar seed bank-past management relationship, with a flora representing a pastural vegetation history eg. *Holcus lanatus*, *Juncus spp.*, *Ranunculus repens* and *Lotus corniculatus*. This confirms the known history of the site which was rough pasture before afforestation.
1.6 The depth distribution of buried seeds.

1.6.1 Methods.

In order to assess the depth distribution of seeds within the woodland soils, two sites were selected which it was assumed would show significantly different seed bank composition and spatial distribution. Nine cores were removed in a 3 x 3 contiguous grid from both a Japanese larch (Larix leptolepis), plantation (26yrs old) at Morewellham, and an undisturbed area of oak coppice (Quercus spp) (120-130 yrs old), in Wareham wood.

With increasing knowledge of the Morewellham site, it became apparent that the samples removed could produce a misrepresentation of the Larch (Larix spp.) plantation seed flora. The site was situated on a slope and four metres beneath a ride. It is possible that this position suffered disturbance in the form of deposition of loose soil on creation of the ride. In order to test this possibility a second set of nine cores were removed as part of a Morewellham seed bank transect survey, and treated as depth samples. These were taken 20 metres above the ride site. A comparison of the data sets of the two surveys gave an indication of whether disturbance had taken place and a measure of its effects on the seed bank.

Towards the end of the first sampling season an assay of the seed bank of the beech plantation at Blanchdown (52 yrs old) was undertaken. For this survey five randomly positioned cores were removed and each was treated as a depth distribution sample.

All samples were removed using the method described in the coring procedure and were then placed in tight fitting plastic
bags and surrounded by 20cm lengths of half section plastic drain pipe which were taped into position. These prevented damage to the core and mixing of the soil layers.

In the laboratory the samples were divided into a litter layer and successive 2 cm layers. Each soil layer was treated chemically and washed in the seed separator, as described in the methods of sample treatment. The resulting organic matter was then laid in pots on sand (watered from beneath) in an unheated greenhouse. The litter layer was passed through a 0.5 cm sieve to remove the larger constituents and then placed on sand within the greenhouse.

1.6.2 Results and discussion.

The results of the study of seed density distribution by depth are summarised in Tables 2, 3, 4 & 5 and presented in total in Appendix 1.

i) Total seed density results

A preliminary survey shows an approximate correlation between seed density and canopy age. The older areas of woodland, Wareham wood (120 - 130 yrs) and Blanchdown (52 yrs) had lower densities than Morewellham (26 yrs). There are however complications arising from the differences in canopy species and past management histories of each area of woodland. In addition the small number of samples and the restricted area from which they
Table 2 The mean seed depth distribution of the species germinating from the soil of the Morewellham samples (Number / m$^2$).

Woodland age 26 yrs

<table>
<thead>
<tr>
<th>Species</th>
<th>L</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>12</th>
<th>14</th>
<th>16</th>
<th>Tot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis spp</td>
<td>95</td>
<td>875</td>
<td>485</td>
<td>318</td>
<td>271</td>
<td>151</td>
<td>72</td>
<td>32</td>
<td>32</td>
<td>2331</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>64</td>
<td>111</td>
<td>103</td>
<td>183</td>
<td>199</td>
<td>239</td>
<td>175</td>
<td>127</td>
<td>56</td>
<td>1257</td>
</tr>
<tr>
<td>Rubus spp.</td>
<td>334</td>
<td>406</td>
<td>32</td>
<td>0</td>
<td>8</td>
<td>8</td>
<td>16</td>
<td>8</td>
<td>8</td>
<td>812</td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>0</td>
<td>24</td>
<td>64</td>
<td>119</td>
<td>72</td>
<td>119</td>
<td>24</td>
<td>32</td>
<td>0</td>
<td>454</td>
</tr>
<tr>
<td>Carex spp.</td>
<td>111</td>
<td>95</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>214</td>
</tr>
<tr>
<td>Juncus spp.</td>
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<td>16</td>
<td>16</td>
<td>80</td>
<td>48</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>8</td>
<td>184</td>
</tr>
<tr>
<td>Betula pubescens</td>
<td>48</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Luzula sylvatica</td>
<td>8</td>
<td>8</td>
<td>16</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>32</td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Teucrium scorodonia</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>668</td>
<td>1551</td>
<td>724</td>
<td>700</td>
<td>598</td>
<td>525</td>
<td>287</td>
<td>207</td>
<td>104</td>
<td>5364</td>
</tr>
</tbody>
</table>

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Table 3: The mean seed depth distribution of the species germinating from the soil of the Morewellham samples (Number / m$^2$).

Woodland age 26 yrs

<table>
<thead>
<tr>
<th>Species</th>
<th>0</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>12</th>
<th>Tot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis spp.</td>
<td>35</td>
<td>297</td>
<td>191</td>
<td>177</td>
<td>99</td>
<td>71</td>
<td>57</td>
<td>927</td>
</tr>
<tr>
<td>Juncus spp.</td>
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<td>92</td>
<td>64</td>
<td>71</td>
<td>92</td>
<td>106</td>
<td>71</td>
<td>496</td>
</tr>
<tr>
<td>Cardamine hirsuta</td>
<td>0</td>
<td>99</td>
<td>127</td>
<td>85</td>
<td>78</td>
<td>57</td>
<td>42</td>
<td>488</td>
</tr>
<tr>
<td>Epilobium spp.</td>
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<td>120</td>
<td>71</td>
<td>28</td>
<td>7</td>
<td>7</td>
<td>0</td>
<td>353</td>
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<tr>
<td>Digitalis purpurea</td>
<td>7</td>
<td>0</td>
<td>28</td>
<td>57</td>
<td>28</td>
<td>28</td>
<td>21</td>
<td>169</td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>28</td>
<td>50</td>
<td>78</td>
<td>7</td>
<td>163</td>
</tr>
<tr>
<td>Ranunculus repens</td>
<td>7</td>
<td>0</td>
<td>21</td>
<td>50</td>
<td>7</td>
<td>57</td>
<td>14</td>
<td>156</td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>0</td>
<td>7</td>
<td>28</td>
<td>0</td>
<td>35</td>
<td>0</td>
<td>42</td>
<td>112</td>
</tr>
<tr>
<td>Cirsium arvense</td>
<td>64</td>
<td>35</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>106</td>
</tr>
<tr>
<td>Rubus spp.</td>
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<td>85</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>106</td>
</tr>
<tr>
<td>Trifolium repens</td>
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<td>14</td>
<td>14</td>
<td>7</td>
<td>28</td>
<td>21</td>
<td>21</td>
<td>105</td>
</tr>
<tr>
<td>Sagina procumbens</td>
<td>0</td>
<td>21</td>
<td>35</td>
<td>28</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>84</td>
</tr>
<tr>
<td>Anagallis arvensis</td>
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<td>42</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>63</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>7</td>
<td>28</td>
<td>21</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>63</td>
</tr>
<tr>
<td>Viola riviniana</td>
<td>0</td>
<td>28</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>49</td>
</tr>
<tr>
<td>Rumex obtusifolius</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>H. non-scripta</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Vicia hirsuta</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>254</td>
<td>889</td>
<td>649</td>
<td>545</td>
<td>431</td>
<td>432</td>
<td>275</td>
<td>3475</td>
</tr>
</tbody>
</table>

H. non-scripta = Hyacinthoides non-scripta
Table 4 The mean seed depth distribution of the species germinating from the soil of the Wareham wood samples (Number / m²).

Woodland age 120 yrs

<table>
<thead>
<tr>
<th>Species</th>
<th>L</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>Tot</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Betula pubescens</em></td>
<td>297</td>
<td>85</td>
<td>42</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>424</td>
</tr>
<tr>
<td><em>Rubus fruticosus</em></td>
<td>71</td>
<td>28</td>
<td>28</td>
<td>14</td>
<td>7</td>
<td>7</td>
<td>155</td>
</tr>
<tr>
<td><em>Hypericum pulchrum</em></td>
<td>21</td>
<td>7</td>
<td>21</td>
<td>21</td>
<td>14</td>
<td>0</td>
<td>84</td>
</tr>
<tr>
<td><em>Juncus spp.</em></td>
<td>14</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td><em>Carex spp.</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td><em>Digitalis purpurea</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td><em>Epilobium spp.</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>403</td>
<td>127</td>
<td>91</td>
<td>35</td>
<td>49</td>
<td>14</td>
<td>719</td>
</tr>
</tbody>
</table>
Table 5 The mean seed depth distribution of the species germinating from the soil of the Blanchdown beech wood samples (Number / m²)

Woodland age 52 yrs

<table>
<thead>
<tr>
<th>Species</th>
<th>L</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>Tot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juncus spp.</td>
<td>344</td>
<td>891</td>
<td>1057</td>
<td>1248</td>
<td>1604</td>
<td>955</td>
<td>6027</td>
</tr>
<tr>
<td>Agrostis spp.</td>
<td>13</td>
<td>115</td>
<td>115</td>
<td>127</td>
<td>64</td>
<td>13</td>
<td>447</td>
</tr>
<tr>
<td>Lotus corniculatus</td>
<td>0</td>
<td>127</td>
<td>76</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>216</td>
</tr>
<tr>
<td>Rubus spp.</td>
<td>26</td>
<td>64</td>
<td>89</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>192</td>
</tr>
<tr>
<td>Epilobium spp.</td>
<td>0</td>
<td>64</td>
<td>26</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>90</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>0</td>
<td>26</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>39</td>
</tr>
<tr>
<td>Trifolium repens</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>0</td>
<td>0</td>
<td>26</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>0</td>
<td>13</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Ranunculus repens</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>396</td>
<td>1228</td>
<td>1415</td>
<td>1414</td>
<td>1681</td>
<td>981</td>
<td>7115</td>
</tr>
</tbody>
</table>
were removed, ensures that a comparison of the density is inappropriate at this stage. Density is treated more fully in a later section.

Figure 5 illustrates the depth distribution (in 2 cm layers), of the total seed density of all species in each area of woodland. As described above the general trend is for a decline in total seed density with canopy age. The profiles show that this is brought about by decay at all levels in the soil. The studies of Roberts & Dawkins (1967), Rampton and Ching (1970), and Toole (1946) have shown that individual species decay within the soil at unique rates, although variation may be induced by differing environmental conditions. The decline in total seed density is therefore a combination of individual decay rates and will be altered by the species composition of the seed bank.

The seed distribution throughout the four profiles indicates a concentration of seeds in the uppermost layers of the soil. Leavitt (1963) describes how the profile shape may arise from the ease with which seeds penetrate the litter layer, when compared to the mineral soil. The litter layer, being less compact, allows rainfall to wash seeds to the lower layers where they are slowed by the relative impermeability of the mineral soil. This results in a concentration of seeds at the humus-mineral interface. Below this the seed density shows an exponential decrease with depth (Leavitt 1963, Moore & Wein 1977). This would be the situation expected beneath the ideal undisturbed woodland. The Morewellham surveys show similarities with this distribution, with fewer seeds in the litter compared to the 2 cm depth and a decline.
Figure 5. The distribution of total seed density with depth in the soil of woodlands of increasing age. The figure demonstrates the influence of single species dominance on the profile shape.

(a) Morewellham 1

N^2 seeds / M^2

Depth (cm)

(b) Morewellham 2

(c) Blanchdown wood

(d) Wareham wood

-41-
below this layer. The two profiles have similar shapes and suggest the possibility of profile form being related to soil type. This will however be masked by both floral composition and past management differences and would be difficult to quantify.

The older woodlands exhibit similar profiles to those of Morewellham, although there are important differences. Blanchdown for instance shows an increase from the 1 to 2 cm layer with a decline below, if _Juncus spp._ are excluded from the results. The _Juncus spp._ profile shifts the modal class from the 2cm to the 8 cm depth by virtue of their dominant proportion in the total density of seed. Presumably the small size of _Juncus spp_ seed allows them to penetrate to depths which larger seeds cannot.

The Wareham Wood profile is also dominated by a single species in this case _Betula pubescens_. The short lived seeds of this species occur in large quantities in the litter layer of the sampled area. Their short life span (1-2 years Hill & Stevens 1981) restricts the time available to penetrate to depth within the soil and they are found only at the surface. In contrast the total seed density of the other species has declined to low levels as the woodland canopy ages; their seeds are relatively evenly distributed with depth.

Two factors contribute to the problems of interpreting seed profiles.

First, the time at which seeds were deposited. It is rarely possible to distinguish between seed depositions separated in time. Kellman (1978) associates bimodality in a seed profile with two separate inputs, but most profiles are produced by
intermittent inputs and show no separation in the soil.

Second, the degree to which the original profile has been altered by the disturbance of management regimes. For example Kellman (1978) and Roberts & Stokes (1966) have shown how seed can be incorporated at depth by agricultural management.

The total species profile is therefore the result of a complex of factors unique to the past history a woodland; species composition of the flora before planting and after; the frequency of seed deposits; seed size and longevity; soil type and compaction; and the disturbance regime to which it has been subjected.

Between site comparisons must therefore be treated with caution as within site variation can be great (as demonstrated by Morewellham sites 1 and 2). In attempting to unravel the vegetation history of an area individual rather than total species distributions may be of greater importance.

ii) Individual species profiles.

In the discussion of species composition the seed bank flora was divided into three categories:

1. Shade tolerant species present both in the vegetation and the soil at a site.
2. Shade intolerant species owing their presence in the seed bank to the vegetation at that site before the closing of the canopy.
3. Seeds arriving by deposition from air currents or animal activities.
Is it possible to identify these categories from an examination of their soil seed bank profiles?

A characteristic of the seeds of species in categories 1 (and often 3) is their short life span, in the region of 1-3 years (Thompson & Grime 1979). The seeds of these species should therefore be confined to the surface layers of the soil, owing to the short time available for soil penetration. All seeds of Betula pubescens germinating from the depth profile samples were confined to the upper 4cm of the soil layers, in both the Wareham Wood and Morewellham surveys (Figure 5). Hyacinthoides non-scripta and Teucrium scorodonia show similar profiles. Rubus fruticosus can also be placed at least partly in this category, but as will be discussed later there may be a case for placing Rubus in the 1/2 category.

Epilobium spp. at Morewellham and Blanchdown, and Cirsium arvense at Morewellham 2 (Figure 6a) are category 3 species.

Figure 6b illustrates the profile of Lotus corniculatus, a category 2 species. No seeds are present in the litter layers; the majority are found at the mineral humus interface, numbers decreasing with increasing depth in the soil. As discussed earlier seed size will play a major role in governing the shape of the profile, smaller seeds being able to penetrate to greater depths. A comparison of Figure 6b with Figure 5c, (the distribution of Juncus spp. at Blanchdown) illustrates this. High densities of the small seeds of Juncus spp. occur at depth in the profile. Seed size may not, however, account for all such differences. The length of time for which seed was deposited, and
the period of time between deposition and sampling, may have been
greater for Juncus spp, allowing the seeds to penetrate further
into the soil.

The majority of species found within the seed banks fall
into category 2, examples being provided by Hypericum pulchrum,
Digitalis purpurea, and Rumex acetosella. Symonides (1978) in a
study of Eucalyptus forests, states that the majority of seeds
within the soil were deposited by past vegetation and are found
in the deeper layers of the profile, a result in agreement with
this study.

Following canopy closure the action of the soil fauna and
rainfall will gradually move seeds of category 2 species to lower
layers, the rate of movement being governed by seed size and
shape. At the same time, seeds in the upper layers of soil may be
exposed to greater rates of predation, premature germination and
fungal attack. With increasing age, surviving category 2 seeds will be confined to the deeper soil layers. Figure 7 illustrates the seed profiles of *Digitalis purpurea* in the four woodlands sampled for depth distributions. If it is assumed that due to the disturbance caused by the creation of the ride, the soil of the Morewellham 1 area is relatively younger than that of Morewellham 2, the four woodlands provide a sequence of increasing age. The sequence illustrates a greater loss of seeds from the upper soil layers with preservation only at depth in the older soils.

iii) Morewellham disturbance profiles.

Morewellham sites 1 and 2 show variation in both species composition and densities. A characteristic of this variation is that those species which are able to exploit a disturbed soil by germinating and producing seed in restricted light levels, show an increased density at site 1.

Figure 8 compares the profiles of *Hypericum pulchrum* and *Agrostis spp.*. A third example is provided by *Digitalis purpurea* (Figure 7).

If the disturbed soil of Morewellham 1 has been subjected to a fresh seed input, the increased seed density should also be accompanied by a shift towards the upper layers of the profile. All three species illustrate this increased density in these soil layers.

-46-
Figure 7. *Digitalis purpurea* depth distributions beneath woodland canopies of increasing age since last clearance.

Morewellham 1 ( < 26 yrs )

Morewellham 2 ( 26 yrs )

Blanchdown ( 52 yrs )

Wareham Wood ( ≈ 200 yrs )
Juncus spp. also show an increase in the seed density of the litter layer at site 1 (Figure 9a). This would be anticipated as Juncus spp. are found within the woodland rides, and are able to colonise disturbed areas by distribution of seeds from this site. Figure 9a illustrates that owing to the horizontal heterogeneity of the seed bank, the relatively small sample size of the depth profile study does not allow us to compare seed densities, only their depth distributions.

Species apparently unable to exploit a disturbed habitat in low light levels do not show a density increase when comparing the two areas. Figure 9b illustrates how the profile of Rumex acetosella changes. This could be due to inability to germinate in the gap environment of the disturbed area, or the species may be able to germinate, but seedling survival and/or the growth rate may be insufficient to enable seed production. Certainly many of the highly shade tolerant species associated with the relic strawberry field seed bank, (eg Trifolium repens, Ranunculus repens, Sagina procumbens and Anagallis arvensis) are absent from the soil of area 1.
Figure 8. The depth distribution of two species in an undisturbed (Morewellhan 2) and a disturbed (Morwellhan 1) area of a woodland.

**Agrostis spp.**

Frequency /m²

Morewellham 1  a)

![Graph showing depth distribution of Agrostis spp. in Morewellham 1 and Morewellham 2]

Morewellham 2

**Hypericum pulchrum**

Frequency /m²

Morewellham 1  b)

![Graph showing depth distribution of Hypericum pulchrum in Morewellham 1 and Morewellham 2]
Figure 9. The depth distribution of two species in an undisturbed (Morewellhan 2) and a recently disturbed (Morwellhan 1) area of a woodland.

**Juncus spp.**

Morewellham 1  a)  

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Frequency /m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
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<td>6</td>
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</tr>
<tr>
<td>8</td>
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<td>12</td>
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</tr>
<tr>
<td>14</td>
<td></td>
</tr>
<tr>
<td>16</td>
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</tr>
</tbody>
</table>

Morewellham 2  

<table>
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<th>Frequency /m²</th>
</tr>
</thead>
<tbody>
<tr>
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<td>1</td>
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<tr>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
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</tbody>
</table>

**Rumex acetosella**

Morewellham 1  b)  

<table>
<thead>
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<th>Depth (cm)</th>
<th>Frequency /m²</th>
</tr>
</thead>
<tbody>
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<td>0</td>
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<tr>
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<td></td>
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<tr>
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<tr>
<td>8</td>
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<tr>
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</table>

Morewellham 2  

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Frequency /m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
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<tr>
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<td>4</td>
<td>1</td>
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<tr>
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</tr>
<tr>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>
1.7 Horizontal distribution surveys.

1.7.1 Methods.

Four woodlands were selected for assessment of the horizontal distribution of the seed bank. Two were known to have been planted on previously unforested land.

a) In Morewellham Wood

A plantation of Japanese larch (*Larix leptolepis*), planted in 1957 on a site previously used for the cultivation of strawberries.

b) In Blanchdown Wood

A plantation of beech (*Fagus sylvatica*), planted in 1913 on a site previously used for both copper mining and later sheep pasture.

Two additional sites were also selected, both of which had a long history as woodland.

c) In Carthamartha Wood

A plantation of a mixture of Scots pine (*Pinus sylvestris*), and Douglas fir (*Pseudotsuga menziesii*), dating from 1906, which had been subjected to the normal thinning regimes. Previously the site was occupied by an oak (*Quercus spp.*) coppice wood.
d) In Wareham Wood

A derelict Oak coppice (Quercus spp.), stand undergoing self thinning. Using the techniques described later the stand was dated to approximately 1860, ie the approximate date of last coppicing.

Soil samples were removed from each of the four woodlands in a contiguous transect of cores (Morewellham 39 cores, Blanchdown 31 cores, Carthmartha 44 cores, Wareham wood 60 cores). A greater number were taken from the woodlands with the oldest canopies, where it was assumed the lowest density of seeds would be found.

Cores from the Morewellham and Blanchdown soils were divided into 0-5 and 6-10 cm samples, sieved and placed in separate seed trays. Each core from the other woodlands was sieved as a single unit, divided into two equal portions and placed in separate seed trays in the polythene tunnel.

Owing to the use of the first nine cores of the Morewellham transect in the repeated depth profile survey (see page 34), they were placed in an unheated greenhouse after treatment in the soil washing apparatus. Tests of this apparatus showed no significant difference between the samples treated in this way when compared to those laid in the polythene tunnel without treatment.
1.7.2 Results & Discussion.

i) The distribution of total seed densities.

Figures 10 and 11 illustrate the results of the horizontal distribution surveys.

All four of the woodland areas studied reveal contagion (variance to mean ratio of greater than unity) at the sample size used in this survey programme. As would be expected, considering the different histories and compositions of the stand canopies, there is no correlation between either depth of burial of the seeds or stand age, and the degree of contagion measured. Cores with high seed densities tend to occur together, perhaps indicating that contagion is caused by factors such as local topography (depressions etc.), which influence the collection or incorporation of seeds. In those woodlands where the samples were divided into two depths (figure 10), there is no correlation between the densities at the two depths.
Figure 10. The horizontal distribution of total species density measured at 0-5 and 5-10cm depth ranges in two seed bank transects.

a) Morewellham Wood

b) Blanchdown Wood
Figure 11. The horizontal distribution of total species density measured in two seed bank transects.

a) Carthamartha Wood

b) Wareham Wood
Kellman (1978) examined the horizontal and vertical distribution of seeds in the seed banks of a tropical crop field and pasture. By comparing the relationship of total density in the 0-5 and 5-10 cm layers along a transect, he found that the seeds in the upper layer of soil exhibited greater contagion. In order to explain this result he stated that

"decreasing depletion rate (of individual species seed density) with depth should produce seed populations whose modal age increases with depth. Under constant depletion rates absolute spatial heterogeneities in the seed distribution will decrease in older populations".

The results of the present study are not consistent with those of Kellman (1978). Although Blanchdown exhibits less contagion in the lower soil layers, the difference in variance to mean ratios is slight (0-5cm 4.35, 5-10cm 3.64). The data for Morewellham reveal the opposite result with variance to mean ratio greatest in the lower soil layers (0-5cm 7.41, 5-10cm 9.3).

The development of contagion at depth in a seed bank is not dependent only on the rate of decay of its constituents. It will also be affected by the ability of individual species seeds to penetrate the soil layers (dependent on seed size and shape), and on the maximum longevity of the seed; short lived seeds may not have sufficient time to penetrate to depth and will be confined to the upper layers.
The period of time between the establishment of the seed bank and the removal of samples is also critical. Kellman's samples were removed from vegetation which had been subjected to consistent management for a minimum of eight years. The seed bank input and decay rate can perhaps therefore be assumed to have been in a relatively stable equilibrium. In contrast the seed bank of the Morewellham woodland studied has undergone major changes, since it has no seed input at present, but is derived from the succession which took place after abandonment. The majority of species have therefore not yet penetrated to any great depth and are found only in the 0-5cm layers. With time seeds will gradually move down the profile and alter the contagion measured in the profile distributions, the rate of change being dependent on the soil structure in the transect area. Kellman (1978) has revealed that contagion may differ with depth of burial, but the situation is more complex than the explanation he presents.

In agreement with the depth profile results, the youngest woodland (Morewellham) had the greatest seed density, with a decline as the woodlands increase in age. This is a development previously noted by Oosting & Humphries (1940), Livingstone & Allessio (1968), and Hill & Stevens (1981). The complications arising from the thinning regime to which Carthamartha has been subjected will be discussed later.
Assays of distributions of total seed densities are of limited value in the study of a seed bank, although they can provide indications of trends within the soil distribution. For instance the seed bank density of the first twelve cores of the Morewellham transect is significantly greater than the remaining twenty seven. This seems to indicate recent disturbance, at or near to this end of the transect. However, in order to investigate these trends, and the reasons for them, the distributions of individual species must be examined.

ii) The distribution of individual species seed densities.

Appendices 2 - 5 contain the density of individual species germinating from each core removed in the woodland transect sampling programme.

a) The Morewellham Wood transect.

The results of the total seed density transect revealed an apparent difference between the density of the initial twelve cores and the rest of the samples. Earlier it was noted that cores 1-9 were treated in a cold greenhouse after extracting the organic matter and seeds from the soil. Tests have shown no significant effect of this treatment on seed recovery, so the possibility of the difference being caused by the sample treatment can be excluded; the increased density is also seen to extend beyond the ninth core into cores treated in the polythene tunnel.
Examination of individual species distributions for the same area, reveals that certain species (eg *Cardamine hirsuta*, *Juncus spp.*, and *Epilobium spp.* Figures 12(i) a, b & c) exhibit increases in seed density at this end of the transect, while others do not (eg *Agrostis spp.*, *Ranunculus repens* and *Trifolium repens* Figures 12(i) d and 12(ii) a & b).

Species which reveal an increased seed density at the start of the transect seem to be those which can exploit disturbance which has created a gap in the woodland canopy, eg thinning. These include four species which were apparently able to exploit the disturbance of Morewellham area 1, described in the depth profile survey ie. *Juncus spp.*, *Epilobium spp.*, *Digitalis purpurea* and *Hypericum pulchrum*, with the addition of *Cardamine hirsuta*. The species showing no response are perhaps restricted by the light environment of small gaps in the canopy.

An examination of the site at this end of the transect, after the sample results were known, revealed disturbance caused by an extraction rack situated several metres from the first coring position. This management technique involves the removal of a line of trees to enable the withdrawal of timber cut during thinning of the stand. The line, now overgrown by *Rubus fruticosus*, runs at right angles to the transect and two metres from the beginning. This would provide sufficient disturbance to explain the changes in seed bank density found in the transect. The distance between the rack and first coring position may account for the decline from the first coring position. The seed produced would be distributed from the disturbed area and decrease in density in the direction of the transect.

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Figure 12 (i) The frequency distribution of individual species seed densities for the Morewellham Wood transect.

a) Cardamine hirsuta

b) Juncus spp.

c) Epilobium spp.

d) Agrostis spp.
Figure 12 (ii) The frequency distribution of individual species seed densities for the Morewellham Wood transect.

a) *Ranunculus repens*

b) *Trifolium repens*

c) *Anagallis arvensis*

d) *Sagina procumbens*

Distance (M)
Figure 12 (iii) The frequency distribution of individual species seed densities for the Morewellham Wood transect.

a) *Hypericum pulchrum*

b) *Digitalis purpurea*

c) *Rubus fruticosus*

Distance (M)
b) The Blanchdown transect results.

Figure 13 illustrates the distribution patterns of the five most abundant species in the transects. Appendix 3 lists all the germinations.

A comparison of these results with those of the depth survey (page 39) reveals one of the problems associated with seed bank sampling. Two species, Digitalis purpurea and Rumex acetosella, occur within the depth samples but are absent from the transect results. Similarly Lotus corniculatus shows a highly contagious distribution in the random depth sampling but not in the transect, whilst Juncus spp. exhibit less contagion in the results from the transect survey. These are the inevitable consequences of sampling an apparently highly heterogeneous seed bank with a relatively small number of soil cores.

Blanchdown was a pasture before planting of the trees and the seed concentrations may therefore be due to collection in animal droppings (Dore & Raymond 1942). This would produce clumping of the seeds of a variety of species in a small area, as seems to be the case near the beginning of the transect.
Figure 13  The frequency distribution of individual species seed densities for the Blanchdown Wood transect.

a) Agrostis spp.

b) Trifolium repens

c) Juncus spp.

d) Ranunculus repens

e) Rubus fruticosus

Distance (M)
c) The Carthamartha transect results

The five most abundant species found in the soil of the Carthamartha transect are illustrated in Figure 14. A result which stands out from this survey is the fact that *Hypericum pulchrum* is present in higher densities than would be expected in the soil of coppice woodlands of similar age. The density of 965 seeds/m² compares with a measure of 157 seeds/m² for a stand of coppice of equivalent age in the same area. Both woodlands have had management histories which consist of regular coppice cycles up until the date of planting or abandonment. It would therefore be expected that under a closed canopy, with similar soil types, the seed banks decay rates would be comparable.

An explanation of the differences may lie in the younger plantations surrounding the sampled stand, which were thinned in the previous year. The removal of the cut trees disturbs the soil and provides a suitable light gap for *Hypericum pulchrum* to germinate and produce seed, thus reinforcing the seed bank of the plantations managed in this way. In many younger plantations *Hypericum pulchrum* can be found surviving until the canopy has regrown to close the gap.

*Agrostis spp.*, *Carex spp.*, *Rubus fruticosus* and *Luzula sylvatica* also show increases in seed density when the soil of this stand is compared to that of younger plantations. This may also be due to the effect of thinning which allows colonisation of the stand by partially shade tolerant species from the reservoirs created by rides. These species can then survive in the increased light environment of the older thinned stands. (Hill & Stevens 1981).
Figure 14  The frequency distribution of individual species seed densities for the Carthamartha Wood transect.

a) Hypericum pulchrum

b) Rubus fruticosus

c) Agrostis spp.

d) Luzula sylvatica

e) Carex spp.

Distance (M)
d) Wareham Wood transect results.

Appendix 5 presents the results for the transect of soil cores removed from an area of the derelict coppice in Wareham Wood. The two most abundant species, Hypericum pulchrum and Rubus fruticosus, are illustrated in Figure 15.

As with the depth distribution samples for old coppice woods, the number of species in the soil is low. With a canopy closed for 120 years and little significant disturbance of the transect soil there are few seeds remaining. Hypericum pulchrum, the most abundant of the species, shows a contagious distribution at low density, while Betula pubescens and Epilobium spp. both occur at random along the transect, as would be expected from wind dispersed species which are absent from the vegetation. Agrostis spp. does show concentration in a single core, but whether this is a remnant from past vegetation or deposition in an animal dropping (possibly a bird) is impossible to detect.
Figure 15. The horizontal distribution of individual species density measured in the Wareham Wood seed bank transect.

a) *Hypericum pulchrum*

b) *Rubus fruticosus*
iii) Extrapolation to additional surveys.

The majority of individual species distributions reveal contagion (variance to mean ratio of greater than unity) which must be taken into consideration when devising a sampling regime to investigate any particular species.

The number of sampling units which are required to derive an estimate of the mean seed density to within a standard error of 20% of the population mean for a sampled species is calculated from

\[ N = \frac{25s^2}{\bar{x}} \]

\[ \text{Elliot (1977)} \]

Where

- \( N \) - sample number to produce a result to within the given accuracy.
- \( s^2 \) - the variance derived for that species from any previous sampling regime.
- \( \bar{x} \) - the mean of the previous survey results.

For the four woodlands sampled Table 6 lists the canopy age and the calculated number of samples, of equal size to those of the initial surveys, required to produce an accurate measure of seed density for each species. Comparisons of these sample frequencies reveal that, as would be anticipated from the structure of Elliot's formula, the species with lowest density
Table 6 The number of 78.5 cm$^2$ samples cores which would be required to produce an estimate of mean seed density with a standard error of 20% of the population mean for all species germinating in four woodlands.

<table>
<thead>
<tr>
<th>Woodland</th>
<th>Morewellham</th>
<th>Blanchdown</th>
<th>Carthamartha</th>
<th>Wareham</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial Core No</td>
<td>39</td>
<td>31</td>
<td>44</td>
<td>60</td>
</tr>
<tr>
<td>Canopy Age</td>
<td>26</td>
<td>70</td>
<td>77</td>
<td>120</td>
</tr>
<tr>
<td>Species</td>
<td>Sample frequency</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agrostis spp.</td>
<td>13</td>
<td>32</td>
<td>35</td>
<td>708</td>
</tr>
<tr>
<td>Ranunculus repens</td>
<td>21</td>
<td>170</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trifolium repens</td>
<td>38</td>
<td>77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juncus spp.</td>
<td>45</td>
<td>71</td>
<td>259</td>
<td></td>
</tr>
<tr>
<td>Rubus fruticosus</td>
<td>52</td>
<td>16</td>
<td>47</td>
<td>43</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>53</td>
<td>175</td>
<td>69</td>
<td>404</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>72</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epilobium spp.</td>
<td>79</td>
<td>282</td>
<td>281</td>
<td></td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>99</td>
<td>24</td>
<td>81</td>
<td></td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>115</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cirsium arvense</td>
<td>146</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anagallis arvensis</td>
<td>166</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cardamine hirsuta</td>
<td>176</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sagina procumbens</td>
<td>192</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>307</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Betula pubescens</td>
<td></td>
<td></td>
<td></td>
<td>281</td>
</tr>
</tbody>
</table>
and the greatest degree of contagion in the seed bank (measured by the variance to mean ratio), require the greatest number of samples to be taken. The highest (and clearly quite unrealistic) number is that for *Agrostis spp*, which requires 708 cores to be removed from Wareham Wood.

Whipple (1978) has discussed the problems associated with estimating the seed bank densities of a complete woodland from small sample areas. He states that as a result of these difficulties the reliability of comparisons of measured density between separate areas or differing ages is doubtful. As Roberts (1981) has pointed out this can be overcome by use of error analysis, demonstrated by Champness (1949) and Elliot (1977). Moore and Wein (1977) state that comparisons of woodland seed bank densities are hampered by a lack of published data which include individual core variance and would allow error analysis.
1.8 Changes in seed bank density with time.

1.8.1 Introduction and Methods.

Measurement of the decline of seed density with age, within the soils of a single woodland, requires the regular removal of samples during a set time period. Clearly this is impossible for the study of a seed bank over the two hundred year period which is represented by the stands of the Tavistock Woodland Estate. The closest approximation that can be achieved is the sampling of a series of woodland areas of varying age. Oosting & Humphries (1940) and Livingstone & Allessio (1968) have used this method in attempting to follow the development of seed bank floras during woodland succession.

When using this technique it is necessary to select areas which, apart from their canopy closure date, have similar vegetation histories. This ensures, to the limited extent that it can be ensured, that the initial seed banks were of similar composition and density. If it is further assumed that the environmental conditions before the closing of the canopy of each woodland were similar, then the sample series will provide an estimate of the changes taking place beneath a single area of ageing canopy.

Moore & Wein (1977) have demonstrated that the species composition of the canopy will influence woodland ground vegetation and therefore seed bank composition and density. They cite Oosting & Humphries (1940) and Livingstone & Allessio (1968) as examples of studies which cannot be used to quantify seed bank
development owing to differences in the canopy species of the sampled areas. The stands of a woodland selected for study must therefore be of species which create similar conditions beneath the canopy. This constraint restricted the number of plantations within the Tavistock Woodland Estate which could be used in a quantitative survey of seed bank development.

In an exploratory survey 10 randomly sited soil cores were removed from five plantations, all established on sites previously occupied by ancient coppice (>100 yrs). The age range of these plantations extended from 9 to 77 years and all were located in the upper Tamar woodlands.

Seven coppice areas whose approximate ages had been calculated using the calibration regression of section 2.5.1(ix) were also sampled. To these were added both the depth and transect survey results from the coppice areas. Owing to the absence of younger coppice stands (<30 years) in the upper Tamar woodlands, samples were also removed from two areas of 5 and 20 yr coppice in the Warleigh Point nature reserve, a regularly cleared oak coppice (Quercus spp.) woodland situated at the confluence of the Tavy and Tamar (see site descriptions).
1.8.2 Development of total seed density

Tables 7 and 8 list the measured densities of buried seeds of both individual species and totals from the sampled coppice and plantation woodlands. Within the limits of the assumptions described in the methodology, the series can be used as an approximation of the developments taking place in a single area of woodland as the canopy increases in age. Figure 16 illustrates the development of total seed density measured in the coppice woods over a 5 to 200 year range of stand ages.

It has been demonstrated earlier in both the floristic composition and depth distribution studies, that as the woodland soil ages, the removal by decay of the short lived seeds produces a change in the species composition of the seed bank. This results in a gradual increase in the percentage composition of the remaining long lived species, and a consequent reduction in the overall decay rate.

Roberts & Dawkins (1967) and Rampton & Ching (1970) have demonstrated how each constituent species in the seed bank shows an exponential decrease in seed density with time. Their results, which were established by burial of seeds at specific depths in cultivated soil, can be applied to a field situation if treated with caution. A simple simulation program can be constructed to show that a seed bank composed of several species, each of which exhibits a unique average exponential decay rate will, when total seed bank density is plotted on a log scale against time, demonstrate a curvilinear decline. The rate of decay is
Table 7 The seed densities recorded in Oak (Quercus spp.) coppice stands of increasing age.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average ( # ) seeds / m²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>10237</td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>7856</td>
</tr>
<tr>
<td>Rubus fruticosus</td>
<td>993</td>
</tr>
<tr>
<td>Viola riviniana</td>
<td>13</td>
</tr>
<tr>
<td>Juncus spp.</td>
<td>13</td>
</tr>
<tr>
<td>Ulex europaeus</td>
<td>26</td>
</tr>
<tr>
<td>Teucrium scorodonia</td>
<td>13</td>
</tr>
<tr>
<td>H.non-scripta</td>
<td>13</td>
</tr>
<tr>
<td>Veronica officinalis</td>
<td>13</td>
</tr>
<tr>
<td>Plantago major</td>
<td>547</td>
</tr>
<tr>
<td>Betula pubescens</td>
<td>11</td>
</tr>
<tr>
<td>Agrostis spp.</td>
<td>11</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>13</td>
</tr>
<tr>
<td>Carex spp.</td>
<td>2</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>19177</strong></td>
</tr>
</tbody>
</table>

H.non-scripta = Hyacinthoides non-scripta

<table>
<thead>
<tr>
<th>Column</th>
<th>Woodland</th>
<th>Area</th>
<th>Estimated Age (yrs)</th>
<th>Number of Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Warleigh point</td>
<td>1</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>II</td>
<td>Warleigh point</td>
<td>2</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>III</td>
<td>Gun Oak</td>
<td>E3a</td>
<td>74</td>
<td>10</td>
</tr>
<tr>
<td>IV</td>
<td>Wareham</td>
<td>D1a</td>
<td>120</td>
<td>60</td>
</tr>
<tr>
<td>V</td>
<td>Wareham</td>
<td>D1e</td>
<td>126</td>
<td>9</td>
</tr>
<tr>
<td>VI</td>
<td>Wareham</td>
<td>D2b</td>
<td>161</td>
<td>20</td>
</tr>
<tr>
<td>VII</td>
<td>Wareham</td>
<td>D2b</td>
<td>161</td>
<td>8</td>
</tr>
<tr>
<td>VIII</td>
<td>Wareham</td>
<td>D2b</td>
<td>200</td>
<td>15</td>
</tr>
</tbody>
</table>
Table 8 The seed densities recorded in plantations of increasing age.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average N(^2) seeds / m(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>13878</td>
</tr>
<tr>
<td>Hypericum pulchrum</td>
<td>2101</td>
</tr>
<tr>
<td>Rubus spp.</td>
<td>293</td>
</tr>
<tr>
<td>Juncus spp.</td>
<td>13</td>
</tr>
<tr>
<td>Luzula sylvatica</td>
<td>0</td>
</tr>
<tr>
<td>Cirsiurn arvense</td>
<td>0</td>
</tr>
<tr>
<td>Cardamine hirsuta</td>
<td>0</td>
</tr>
<tr>
<td>Cyperus spp.</td>
<td>0</td>
</tr>
<tr>
<td>Ulex europaeus</td>
<td>0</td>
</tr>
<tr>
<td>Agrostis spp.</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>16285</td>
</tr>
</tbody>
</table>

Column | Woodland | Area | Estimated Age(yrs) | Number of Samples | Tree Species
---|----------|------|--------------------|--------------------|-------------------
I | Wareham | D1c | 9 | 10 | DF
II | Wareham | D2a | 15 | 10 | DF
III | Gun Oak | E3f | 28 | 10 | NS
IV | Gun Oak | E3a | 48 | 10 | JL/DF
V | Carthamartha | B3f | 77 | 39 | SP/DF

DF - Douglas fir _(Pseudotsuga menziesii)_
SP - Scots pine _(Pinus sylvestris)_
NS - Norway spruce _(Picea abies)_
JL - Japanese larch _(Larix leptolepis)_

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Figure 16. The decline of total seed density in the soils of coppice stands of increasing age.

The curve is fitted by eye

× Measured densities / m²
+ Data from Brown & Oosterhuis (1981)
controlled by the ratio of the individual species decay rates.

Additional variation will also be introduced by the seed input of the shade tolerant ground vegetation and wind carried seed. A species which appears in both of these categories is *Betula pubescens*. In Wareham Wood, where it is an occasional canopy species, the seeds of this species comprised 51% of the total seed bank at one sampling position. The seeds are short lived and the time at which the seed bank is sampled in each year of the survey will be critical to the measured total decay rates. If total species seed density is to be used for comparative purposes it may therefore be advisable to omit the shade tolerant species from the results.

A further complication affecting only the plantation data is that woodlands of several differing canopy species were sampled, a factor which can influence both past and present ground flora composition (Moore & Wein 1977), and consequently affect the seed bank decay rates. An example is provided by the Japanese larch (*Larix leptolepis*) plantations of Morewellham, which allow a secondary canopy of *Rubus fruticosus* to be formed beneath them. In comparison Douglas fir (*Pseudotsuga menziesii*) and Norway spruce (*Picea abies*) exclude all ground flora at similar canopy ages.

Seed bank composition differences can be reduced by sampling plantations with similar histories, (eg plantation on old coppice) but the canopy species restrictions, in terms of both the environmental conditions beneath the canopy and the management to which each is subjected (eg thinning regimes), reduce the number of potential sites available in the survey.
area. These limitations when applied to the plantation study ensure that there are insufficient comparable data for quantification of seed bank development in the separate stand types.

As with both the depth and spatial distribution studies, the use of total seed bank density is of limited value. The conditions which must be satisfied by each woodland restrict the number of areas available and consequently the accuracy of the results. Changes in density of individual species are of much more interest.

1.8.3 Individual species developments.

i) Coppice woodlands.

The change in density of each species in a soil seed bank over time would be expected to follow an exponential decay function. This will be an average value dependent on the depth at which the seeds are buried (Rampton & Ching 1970), and environmental conditions characteristic of the area. Each species will disappear from the seed bank at an age governed either by the decay rate and the initial density of propagules, or in the case of short lived seeds, the maximum seed life span of the species.
The development of the seed banks of the shade intolerant species (category II) throughout the woodland sequence follows the expected pattern. Relatively short lived species ( <50 yrs, including Ulex europaeus, Veronica officinalis, and Plantago major), are absent beyond the two youngest woodland soils sampled.

Four genera continue to survive in the soil after 50 years beneath a canopy of trees. Juncus spp. (J. acutiflorus, J. conglomeratus & J. effusus) are present in low densities throughout the coppice woodland sequence but show a patchy temporal distribution after 70 years. Whether this is due to survival from the open canopy period or to infrequent input of wind carried seed from the surrounding areas cannot be determined from these results. The appearance of Juncus spp. in the surface layers of the Wareham wood depth survey would seem to indicate a wind carried seed input. In comparison with this study Moore & Burr (1948) quote a 50-90 yr life span for Juncus spp.

Digitalis purpurea is absent from the soils of greater than 130 years age, although its absence from one area (Dla) suggests a patchy distribution at low density before this canopy age. As stated previously this may be due to differences in the seed bank densities present at canopy closure.

Hypericum pulchrum remains throughout the sequence of sampled coppice stands. This indicates a greater seed bank life span for this species than for Digitalis purpurea, since the densities are similar when measured in the young coppice stands. When the mean density of Hypericum seeds in the coppice stand soils is plotted on a logarithmic scale against stand age, the resulting decline
is not linear (Figure 17), as would be expected from the results of Roberts & Dawkins (1967) and Rampton & Ching (1970). The reasons for the apparently curvilinear decline will be examined later in section 1.9.

Rubus fruticosus is found in similar densities to Hypericum pulchrum throughout the older stands. Marks (1974) quotes Rubus spp. as having a 50 year seed bank life span and since they do not normally flower beneath a complete canopy, another explanation must be found for the presence of their seed in old woodlands. Jordano (1982) has demonstrated that the seeds of Rubus spp. are bird dispersed in Europe, and the seeds may therefore derive from a combination of animal dispersal and flowering and seed production in the canopy gaps created by treefall (Watt 1947). Certainly Rubus fruticosus is able to survive vegetatively beneath a closed woodland canopy which allows it to exploit the occasional canopy gaps created by windthrown trees.

With increasing size of the trees in a stand, self thinning brings about a reduction in tree density and consequently an increase in the amount of light reaching the soil surface (Salisbury 1924). The raised light levels allow invasion from the rides or woodland edges of species able to withstand some shading. This may account for the increase in Luzula sylvatica and Carex spp. which, although absent from the ground flora, do occasionally appear in the gaps created by windthrown trees.
ii) Plantation woodlands.

It will be recalled that the plantations sampled were all planted on the site of ancient coppice. The results obtained from the two youngest plantations are consistent with Kellman's (1974) observations that the seed bank is the major source of ground flora species in recently felled woodland. Most species present in the seed bank of these areas are also in the vegetation observed to germinate after clearfella of ancient coppice.

Observations within the Tavistock Woodland Estate have shown that few species germinate after clearance of ancient coppice. The predominant species germinating are *Hypericum pulchrum*, *Rubus fruticosus*, *Luzula sylvatica*, *Carex spp* and occasionally *Digitalis purpurea*, the new seedling flora being dependent on the age of the cleared coppice stand. These germinating species are present in the seed bank of the older coppice stands, (recorded in Table 7) and also in the samples removed from the plantations laid down after clearance of coppice (Table 8). Indeed the seeds of old coppice and young plantations are remarkably similar.

*Agrostis spp* are characteristic of the successional vegetation of newly cleared areas of old coppice, spreading by dispersal from the rides to form a thick carpet within 2-3 years after cutting and remaining until the new canopy closes. It is therefore surprising that the seeds of these species do not appear in the seed bank of the young plantations. Hill and Stevens (1981) quote a 45 year seed bank life span for *Agrostis spp*. The absence of the seeds may be due to the low numbers of
samples removed in the preliminary survey. However in all twenty samples removed from these young plantations no *Agrostis spp* seedlings were recorded.

The Gun Oak woodland results differ from those of the other plantations. *Digitalis purpurea* is found as a single seed and *Hypericum pulchrum* is absent. There is also an abundance of *Ulex europaeus* in the soil which would not be expected in a sample removed from an area planted on what was old coppice.

A possible explanation may be that the sampled sites are surrounded not by coppice areas but by older plantations. *Ulex europaeus* is dominant in the rides between these plantations and has been seen to spread quickly after clearfell, forming a dense canopy. This canopy would exclude both *Digitalis purpurea* and *Hypericum pulchrum* from the recolonising vegetation, preventing refurbishment of the seed bank.

Several problems prevent the use of these plantation results in establishing a sequence of seed density changes with age. First there are the differing degrees of isolation to which the sites are subjected, second the influence of the management. In order to maximise yield the forester will regularly remove selected lines of trees with the aim of reducing inter-tree competition. The removal of the thinning lines disturbs the soil and also increases light levels at the soil surface. It has been noted that in the plantations of the Tavistock Woodland Estate the altered environment beneath these lines allows *Hypericum pulchrum* to germinate from the seed bank and produce seed.
Rubus fruticosus surviving vegetatively beneath the canopy is also able to produce seed and Agrostis spp. can exploit the situation by spreading from the rides.

The resulting seed input raises the seed bank level in the thinning lines above that found in unthinned coppice of similar canopy age. With variation in growth rates of the canopy species, and consequently differing management practices, the aggregation of the sample survey results into a single age sequence is not advisable.

1.8.4 Comparisons with other woodland surveys.

Brown and Oosterhuis (1981) have studied the seed banks of five lowland coppice areas on the Essex / Suffolk border, removing samples from the 0-5 and 5-15 cm soil layers. The similarities in floristic composition between the two studies have been described earlier in Section 1.5.1. The total seed bank densities for their 0-10 cm soil layer can be estimated, and have been plotted on Figure 16 with the results from this survey. The results are clearly comparable with those from woodlands of similar age in the Tamar valley. The variation in species composition and the unknown history of the Essex / Suffolk woodlands limit the use of these comparisons. Brown and Oosterhuis (1981) have published no estimates of individual species densities so that there can be no comparisons at this level.
The only study of plantation seed banks which can be related to the Tavistock Woodland survey is that of Hill and Stevens (1981). They examined the seed bank of a Douglas fir (Pseudotsuga menziesii) plantation which had been felled at 55 years of age. The plantation had been sited on a derelict mixed conifer (Larix decidua, Picea abies) and hardwood (Acer pseudoplanatus, Castanea sativa, Fagus sylvatica, Quercus spp) plantation, felled 9-13 years before planting with softwoods. The period between felling and planting differs significantly from the Tavistock Woodland Estate stands, but the seed bank of age 55 years compares with those in the Tavistock woodlands. Digitalis purpurea (4300 seeds / m²), Ulex gallii (273 seeds / m²), Rubus fruticosus (137 seeds / m²), and Hypericum pulchrum (126 seeds / m²) were the common species, with Agrostis spp, Juncus spp, and Carex spp. also present.

The density of Digitalis purpurea in the study of Hill and Stevens (1981) is greater than that of woodlands of similar age in the Tavisock study. This is most probably due to the longer period of abandonment after clearfell of the original woodlands.

The density of seeds of Ulex gallii in the work of Hill and Stevens (1981) compares with that for Ulex europaeus in the Gun Oak woods. Ulex spp. may be able to colonise the plantations after thinning of the trees, though whether from surviving seed or by invasion is unknown.

Hypericum pulchrum seeds in the Hill and Stevens (1981) study may, as is the case with Carthamartha, be derived partly from reinforcement during management.
1.9 The Hypericum pulchrum and Digitalis purpurea surveys.

1.9.1 Introduction and Methods

The results of the preliminary survey of coppice woods showed that the mean densities of Digitalis purpurea and Hypericum pulchrum, when plotted on a log scale against the age of the canopy, indicated a curvilinear decline, not the expected linear relationship. In order to investigate this in more detail a further sampling programme was initiated, concentrated on the decline of the seed bank of these two species in the soils of coppice stands. Fifty samples were removed from eight areas of the Tavistock Woodland Estate coppice. Two additional woodlands, Greystone wood and Lifton wood, situated to the north of the upper Tamar woodlands, were also sampled. These areas provided two coppice stands in the 30-40 year age range which were not available in the upper Tamar woodlands.

The results allow an assessment of the seed bank development of Digitalis purpurea and Hypericum pulchrum beneath coppice stands in the age range 5 - 220 years.

1.9.2 Hypericum pulchrum

Figure 17 illustrates the results of the survey of the seed bank density of Hypericum pulchrum for the coppice woodlands studied. The seed bank decay does not follow a linear function with time on a log scale. After an initial rapid decline to
Figure 17. Log(seed density / m²) plotted against stand age for Hypericum pulchrum in the soils of coppice woodlands.
approximately 80-100 years the decay slows and is followed by an apparent slight increase in seed density.

Several hypotheses can be put forward to explain this apparent increase in the seed density of older woodlands. Firstly, the assumption made when measuring the decay rate by use of stands of differing age is that, within relatively narrow limits, the initial densities of the seed banks of each of the areas of woodland were identical at canopy closure. If this was not the case then differing seed bank starting densities for each woodland could result in the observed decay curve (Figure 18).

Figure 18 A family of linear decay results produced by a single decay rate with differing starting densities.

- Sample result based on a series of parallel decay rates in the soil.
- Points that would be anticipated if this were the situation.
- Measured decay curve

Log (Density) 

Time
During the sampling survey it was noted that in stands aged over 80 yrs, *Hypericum pulchrum* was able to germinate, flower and shed seed on the disturbances caused by treefalls (Section 1.9.2 ii). Consequently the mean density values for stands over this age cannot be used in the calculation of a regression of density against stand age. The decay rate of *Hypericum pulchrum* seeds within coppice stands was therefore calculated from the initial five stand seed densities which appear to lie on a straight line. The starting densities required to be present at canopy closure in order to produce the mean densities measured in the older stands can then be calculated. This calculation reveals that the starting densities would have to be in the region of 10 million seeds / m² or 1000 seeds / cm². Clearly these densities are 100 X those recorded in the seed banks of the young coppice stands. It is unlikely that the seed density of any species in the soil would reach this level and this possibility can therefore safely be rejected.

The remaining hypotheses that can be put forward to explain the development of the *Hypericum pulchrum* seed bank fall into two categories. Either i) differing decay rates between or within stands; or ii) seed input to the soil from natural disturbance or management of the woodland. These hypotheses are not exclusive.
i) Variability in decay rates.

Between stands.

It is possible that the decay rate of the seeds in the seed bank could vary according to environmental conditions. If each of the woodland areas has a different mean exponential decay rate for *Hypericum pulchrum*, then a family of decay curves would be exhibited (Figure 19).

Figure 19 A series of decay functions initiated from a single seed density.

- Sample results which may be detected.
- Sample results that would also be anticipated.

--- Measured decay curve.
In order to derive the measured decay pattern for *Hypericum pulchrum* the decay curves would have to be biased, the older stands having slower rates of decay throughout their existence, an unlikely event. Selection of adjoining woodland areas of similar topographical form and exhibiting no significant differences in either vegetation or canopy species reduces the likelihood of major variations. If regions of distinctly differing seed bank preservation exist within woodlands, stands of similar age would be expected to show greater variation in seed density (Figure 19).

Within stands.

The causes of death of a buried seed within the soil seed bank can be split into three broad categories: predation or fungal decay; premature germination placing the seedling in an environment in which it is unable to survive; and physiological death of the propagule due to "old age".

It is generally accepted that predation of seeds is greatest at the soil surface and decreases with depth (Leavitt 1963, Thompson 1987). Large seeds suffer greater rates of loss than small due to higher rates of predation and also the faster burial rates of the small seeds removing them from the soil surface.

Germination of seeds within the soil has been shown to be stimulated by light flash (Wesson & Waring 1967), temperature fluctuations (Thompson et al 1977), leaching of inhibitors and scarification (Ballard 1973). With increasing depth of burial the amount of light and also the fluctuations in soil temperature
will decrease. The environmental conditions to which the seed is exposed will be more stable (Harper 1977), and premature germination will therefore be less likely.

As a result of the decreasing influence of both predation and environmental triggers, physiological death may be the largest factor in loss from the seed bank in the lower profiles (Roberts 1981). This can result from several possible causes the majority of which produce the death of the embryo and therefore influence seed bank longevity, e.g. depletion of the stored energy reserves, or a build up of waste products.

Rampton and Ching (1970) have shown that the decay rate of seeds in the soil is related to depth of burial. Each species that they examined illustrated a unique exponential decay rate which declined with depth. As was discussed in Section 1.8.2 a simulation model can be used to illustrate that if a seed bank is made up of a range of species each of which exhibits an independent exponential decay rate, then the overall decline in the total seed density when plotted on a log scale will be curvilinear. This can also be applied to the seed bank of a single species with differing decay rates induced by depth of burial. If a series of seed bank samples are removed which include a range of soil depths then the result of plotting seed density against canopy (seed bank) age on a log scale will also be a curvilinear decline similar to that illustrated in Figure 17.
ii) Seed input to the soil.

Management of the woodlands

Canopy clearance allows *Hypericum pulchrum* and, in a gap of sufficient size, *Digitalis purpurea* to germinate and produce seed. This has previously been shown to affect the seed bank of Carthamartha wood.

Each area of woodland was examined before sampling in order to establish whether it had been disturbed. None showed evidence of management by felling of single trees or thinning. Girth of all canopy species were measured in each area; none exhibited signs of disturbance i.e. areas of significantly differing girth in plotted distribution curves; a bimodal girth distribution would be anticipated in stands which had been managed as coppice with standards. As was discussed earlier (Section 1.2), it was apparent from the presence of decaying stumps that some timber trees had been removed at around the time of abandonment of the coppice. The disturbance caused by this felling would have had an effect similar to the thinning described for the Carthmartha woodlands (Section 1.7). However, the number of such stumps in the stands is very low (one tree in every two or three stands) and seed input from these disturbances cannot account for the raised seed banks throughout the stand area. As far as possible management has been excluded as a possible source of major variations in seed density.
Windthrow and recruitment to the seed bank.

While surveying the older Wareham Wood coppice areas it was noted that those treefalls which create both a canopy gap and soil disturbance by uprooting allow germination and growth of Hypericum pulchrum seeds present in the turned soil. Root disturbance is necessary to remove the covering litter layer which the seedlings of Hypericum pulchrum cannot penetrate. The mature plants resulting from this disturbance produce a new seed input to the seed bank surrounding the fallen tree. This seed input is finally halted by closure of the canopy gap through extension growth by branches of the surrounding trees. Similar processes have been described in N.American temperate woodland (Marks 1974) and in tropical forests (Putz 1983).

During the development of a coppice stand, if sufficient trees fall to create conditions which allow reinforcement of the surrounding seed bank, this input may provide a mechanism by which the decline in density of a seed bank can be halted.

In order to examine the effect of a single treefall on the seed bank of Hypericum pulchrum, a series of transects were removed from the soil surrounding the root disturbance of wind thrown trees on which reinforcement had occurred.

The first series of transects were removed from a windfall which had occurred two years previously. A single Hypericum pulchrum plant had established at the apex of the disturbed mound and had distributed one year's seed input to the surrounding
soil. A transect of cores was removed in a line starting beneath the plant and extending into the surrounding canopy. The results provide an estimate of a single year's seed input to the seed bank of this species.

A second series of cores were removed radiating out from a treefall on which several Hypericum pulchrum plants had established and produced seed throughout the period for which the canopy was open. The data from this second survey allowed measurement of the distribution of seed input to the seed bank by a completed windthrown tree disturbance.

Figure 20 illustrates the pattern of seed density in the first transect. It can be seen that reinforcement of the seed bank has taken place up to 90 cm beyond the soil disturbance. The seed distribution pattern revealed by the transect is one of increasing density up to 50 cm from the base of the plant, with a decline from this maximum across the rest of the measured distance. The results show similarities in dispersal pattern with those measured by Salisbury (1942) for Verbascum thapsus.

Additional plants which germinate from seed produced by established plants will further reinforce the seed bank. During this period rainfall and frost erosion erode the disturbed mound, and this erosion of surface soil which is relatively rich in seeds, results in a concentration of seeds at the periphery of the disturbed area (Figure 21).

Plants which germinate on the edge of the disturbance mound distribute seeds to a greater distance than a plant in the centre of the mound, which may be why the area of reinforced seed bank
Figure 20. The seed dispersal of *Hypericum pulchrum* from a single plant on a 2 year old treefall disturbance.

Extent of the soil disturbance.

--- Mean background density level

Distance (m) from the plant
Figure 21. The seed distribution of Hypericum pulchrum along three transects of soil cores removed radiating away from the centre of a disturbance mound.
in Figure 21 extends to 4.5 metres from the centre of the disturbance.

The transects of cores taken from around the fallen trees demonstrate that the resulting seed input can have a significant effect on the seed bank of *Hypericum pulchrum*. Is this disturbance sufficient to arrest the expected decline in density of the seed bank? This question will be considered in greater detail in the second part of this thesis.

1.9.3 *Digitalis purpurea*

The developments in the seed bank of *Digitalis purpurea* (Figure 22) are similar to those in *Hypericum pulchrum*, but the results are confused by several zero seed densities. The decline in seed bank density is rapid up to a canopy age of approximately 100 years, but by this age the seed density is low (cf. Figure 17) and the variation caused by sampling of differing stands is sufficient to mask any clear trends in the data. It is not therefore possible to distinguish clearly between the following 3 possibilities:–

1) The seeds of *Digitalis purpurea* reach their physiological age limit and the density rapidly drops.

2) The decay follows a linear decline.

3) The decay form is curvilinear.
Figure 22. Log seed density/ m$^2$ plotted against stand age for *Digitalis purpurea* in coppice woodlands.
A comparison of the two species decay curves reveals that *Hypericum pulchrum*, which is able to exploit windthrown tree disturbance, clearly illustrates an apparent decrease in its decay rate with time. *Digitalis purpurea* is also long-lived but appears to have a requirement for larger gaps in the canopy in order to germinate, flower and set seed (personal obs.). Treefall seed input to the soil may therefore be a significant factor only in the dynamics of the *Hypericum pulchrum* seed bank. The absence of a clear curvilinear decline in *Digitalis purpurea* is circumstantial evidence that seed input from fallen trees may play a part in arresting the decline of the *Hypericum pulchrum* seed bank.
1.10 Development of the seed bank spatial distribution with time.

1.10.1 Introduction and Methods

On closure of a newly formed woodland canopy the pattern of seeds in the seed bank, and future developments in this pattern, will be dependent on factors related to both the historical ecology of the stand and the environmental attributes of the area. Among these factors influencing the pattern of the seed bank are:

1) The seed bank pattern present before opening of the canopy or planting of the trees.
2) Patterns of seedling survivorship, plant distribution and seed dispersal during the open canopy phase.
3) Seed survivorship within the soil beneath the canopy.

It might be anticipated that owing to individual species differences in seed dispersal, the seed bank pattern may be species specific. If species specific decay rates are then superimposed on this pattern, development of any subsequent pattern might also be anticipated to be species specific. In order to test this hypothesis the pattern of seed bank development was examined by use of Taylor's power index (Taylor 1961).
The index relates the variance of a spatial distribution to its mean and is expressed as

\[ b \quad V = a \quad u \]

or

\[ \log V = \log a + b \log u \]

Where \( V \) is the variance of the sample set
\( u \) is the mean of the sample set
\( a, b \) are species specific constants derived from a regression of log variance against log mean.

The value of \( a \) is a sampling parameter of little biological significance, while \( b \) is an indicator of the degree of aggregation ( \( b > 1 \) indicates aggregation).

Taylor and Woiwood (1980) have demonstrated that data sets with a variance of less than 4 and a mean of less than 2 introduce errors to the regression data. These data sets were therefore excluded from the results. Linear least squares regression can provide values for \( a \) and \( b \), but these must be treated with caution as this method requires the axes to be independent of each other. Clearly the mean and variance of a data set are interlinked and therefore significance tests of differences of slope and intercept can only be used as guides to trends in the data.

Three species were found at sufficient sites, after removal of sites with a mean seed density of less than 2 and variance 4, to enable evaluation of \( a \) and \( b \) for Taylor's index. These were Hypericum pulchrum, Digitalis purpurea and Rubus fruticosus.
1.10.2 Results and Discussion.

The Taylor's power regressions calculated for the three species are illustrated in Figures 23, 24, and 25. Table 9 presents the results of the significance tests carried out on the data sets.

Table 9. The significance levels of t tests performed on three species seed bank distributions in two woodland environments.

<table>
<thead>
<tr>
<th>Data comparisons</th>
<th>Significance tests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between species</td>
<td>b</td>
</tr>
<tr>
<td>H. pulchrum vs D. purpurea</td>
<td>ns</td>
</tr>
<tr>
<td>H. pulchrum vs R. fruticosus</td>
<td>ns</td>
</tr>
<tr>
<td>D. purpurea vs R. fruticosus</td>
<td>ns</td>
</tr>
<tr>
<td>Between management regimes</td>
<td></td>
</tr>
<tr>
<td>Rubus</td>
<td>plt vs coppice</td>
</tr>
<tr>
<td>Hypericum</td>
<td>plt vs coppice</td>
</tr>
<tr>
<td>Digitalis</td>
<td>plt vs coppice</td>
</tr>
</tbody>
</table>

As stated previously these significance tests can only be used as indicators since the two data axes are not independent. All $b$ values calculated for the data sets fall within the range of 1.5 - 2.0, indicating that there is aggregation within the soil and confirming the conclusions drawn from the investigations of distribution by transects of cores.
Figure 23. The Hypericum pulchrum Taylor's power relationships for coppice and plantation data.

\[ \log S^2 = 0.362 + 1.616 \log \bar{X} \]

- Plantation Data
- Coppice Data

\( \bar{X} = 2 \)

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Figure 24. The Digitalis purpurea Taylor's power relationships for coppice and plantation data.

\[ \log S^2 = 0.362 + 1.616 \log \bar{X} \]
Figure 25. The *Rubus fruticosus* Taylors power relationships for coppice and plantation data.

\[ \log S^2 = 0.009 + 1.976 \log \bar{X} \]
The results of the t tests performed on the data indicate that there are no significant differences between the Taylor's indices calculated for the three species; the relationships are not species specific. As illustrated by Figures 23, 24 & 25 the variance of the data points about the regression is considerable and any small differences in parameters would only be detected by larger data sets drawn from a larger number of sampled woodlands.

The result is surprising given that *Rubus fruticosus* is bird dispersed and *Hypericum pulchrum* and *Digitalis purpurea* are both wind dispersed. Management technique (plantation or coppice) also appears to have no significant effect on the distribution form (Table 9). The distribution patterns of all three species show a basic similarity, but the cause of this common pattern remains hidden.
Woodland rides as seed reservoirs.

1.11.1 Introduction and methods.

Salisbury (1924) described the appearance of the plant species associated with the open canopy phase of the coppice cycle as a process of ebb and flow. He envisaged that plant species excluded by the shade of a complete canopy survive within the increased light environment of the rides and are then able to recolonise a cleared area after coppicing.

Rackham (1975) described two species which he thought were able to survive in the soil of the coppice area as dormant propagules, reappearing in the vegetation after each clearance. These were *Juncus spp* and *Centaurium erythraea*. After sampling of the soil beneath coppice canopies of approximately 40 yrs of age, Brown and Oosterhuis (1981) have established that the seed bank life span of many other species also enables them to persist in the flora appearing after canopy clearance. They have described how this is the main method by which species establish after cutting, and that Salisbury's ebb and flow method of recurrent invasion is of little consequence in regular clearance cycles.

The studies described earlier have illustrated that with increasing canopy age, many species are no longer found within the seed bank flora, and the importance of areas of relatively light canopy such as rides between stands, will increase. On clearance of the canopy these areas may act as seed sources in the way described by Salisbury (1924).
In order to investigate the diversity and density of species in the ride areas in comparison with those beneath an adjacent canopy, a transect of soil cores was removed from across a derelict ride in Wareham Wood. The ride canopy was complete and the ground flora was comparable to that beneath adjacent coppice, consisting of occasional *Lonicera periclymenum*, *Rubus fruticosus*, and *Luzula sylvatica*.

1.11.2 Results and Discussion.

The seed density of species germinating in the cores removed from across the derelict ride are presented in Appendix 6. Table 10 compares the mean densities with those of the Wareham Wood transect, removed from beneath a 160 yr old coppice canopy.

Figure 26 illustrates the species distributions measured across the ride. Peaks in seed density appear to coincide with the ride area for some species e.g. *Juncus spp*, *Oxalis acetosella* and *Luzula sylvatica*, although it should be noted that these results are derived from a single transect and that associations of the peaks with the ride area environment could only be established conclusively by further samples.
Figure 26  The frequency distribution of individual species seed densities measured in a transect of soil cores taken across a ride.

Extent of the ride disturbance

a) Juncus spp.

b) Rubus spp.

c) Hypericum pulchrum

d) Luzula sylvatica

e) Oxalis acetosella

Distance (M)
Table 10  A comparison of the seed densities of a 160 yr old
coppice stand and an adjacent ride.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean seed density/core</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ride</td>
</tr>
<tr>
<td>Juncus spp</td>
<td>5.6</td>
</tr>
<tr>
<td>R. fruticosus</td>
<td>4.8</td>
</tr>
<tr>
<td>H. pulchrum</td>
<td>3.6</td>
</tr>
<tr>
<td>L. sylvatica</td>
<td>1.2</td>
</tr>
<tr>
<td>O. acetosella</td>
<td>0.3</td>
</tr>
<tr>
<td>Carex spp</td>
<td>0.1</td>
</tr>
<tr>
<td>Agrostis spp</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Two shade intolerant species are found in the seed bank of
the ride, Juncus spp inside the ride area, Hypericum pulchrum at
the edges. An examination of the rides that are in use throughout
the woodlands reveals that this may be caused by differences in
the ability of the adult plants to withstand the disturbance of
forestry vehicles. Juncus spp seem able to survive in the centre
of the rides between the wheel tracks, while Hypericum is able to
set seed only at the ride edges.

The three shade tolerant species also reveal differences in
their seed bank distributions. Luzula sylvatica, the least shade
tolerant of the three, is found in both the ground flora and in
the seed bank of the ride area. In this species seed production is apparently confined to the ride and does not extend into the more heavily shaded regions on either side.

**Oxalis acetosella**, a species found in the ground flora throughout the coppice stands, germinated only in the ride samples. This may indicate that although shade tolerant, *Oxalis* can only flower and produce seed in the higher light levels of the ride environment.

**Rubus fruticosus** reveals an increased seed density throughout the ride area with a decline towards the stand interior. The open canopy may be preferred by bird species for perching etc. and the seed bank would therefore display raised levels in this area. *Rubus* may also flower only within the ride area but observations suggest that this is not the case in the Tavistock Woodlands.

Table 10 illustrates the raised seed bank density levels of the ride in comparison with the soil beneath the canopy. The data indicate that the rides become increasingly important as sources of seed for recolonisation with the decline of the seed bank beneath the main canopy. *Juncus* spp especially would benefit from this reservoir as it is absent from the seed bank beneath the canopy. Brown & Oosterhuis (1981) have illustrated that the 'ebb and flow' of species to and from a ride area does not occur in sufficient densities to form a significant percentage of the flora after clearfell of young coppice woods, when compared to that germinating from the seed bank. However as the seed bank density is reduced beneath the canopy, the reserve provided in the soil of the rides becomes of greater value to recolonisation after clearance.
1.12 Conclusions drawn from the survey of the woodland seed banks.

The results of the seed bank survey of the Tavistock Woodland Estate, when combined with those drawn from other studies, allow a simple description of seed bank dynamics to be developed.

Immediately after closure of a woodland canopy and exclusion of the shade intolerant species, the floristic composition, density and spatial distribution of the seed bank will depend on the history of the site. In this survey the past management practices that have been detected include arable, horticultural and woodland.

Exclusion of the shade intolerant plants results in a gradual decrease in the seed density within the soil. As the studies of Roberts & Dawkins (1967) and Rampton & Ching (1970) have established, the rates of decay will be species specific. They may also be related to the depth of burial. Smaller seeded species will, through the action of rainfall and soil animals, penetrate to greater depths at faster rates than large seed. As depth increases the effects of predation, fungal attack and environmental fluctuations are reduced (Kellman 1978, Harper 1977). Conditions therefore favour increased survivorship of deeply buried seeds. Subjected to the higher surface decay rates, the majority of shade intolerant species will be found at depth, with a constantly changing layer of short lived seeds above them deposited by the shade tolerant vegetation surviving in the woodland.
With the passing of the seed bank life span of each species, or the decay rate within the soil reducing the density of seeds below a detectable level, species disappear from the seed bank. They will become the "marginal species" described by Salisbury (1924), existing only in rides and clearings, and must reinvade by seed dispersal if the canopy is removed. It might be anticipated that with the passage of time even the long stay species would be removed and the persistent seed bank (Thompson & Grime 1979) would disappear.

After the first 80 yrs of rapid decay, the decline of the seed bank of Hypericum pulchrum slows to almost zero. Two main theories have been put forward to explain this phenomenon. The first concerns the decrease in decay of the seed bank with increasing depth of burial. The seeds of the seed bank remaining after 80 yrs of canopy have been shown, by the Wareham Wood depth survey, to be concentrated mainly in the lower soil layers. At this depth decay may occur at a rate which is too slow to measure accurately. The second possibility (which may occur in conjunction with the first) is that the input of seed from disturbance caused by wind thrown trees is sufficient to halt the decline in density of the seed bank. If this is the case the seed bank of shade intolerant species may perhaps be maintained indefinitely beneath a closed canopy. This mechanism has been discussed previously by Grubb (1977).

The possibility that Hypericum pulchrum may be able to maintain a seed bank beneath a closed tree canopy is of particular interest. Marks (1983) considered the question of where early "old field" species were found in America when the
continent was completely covered by woodlands, before the advent of European man. Marks (1983) concluded that the majority of species must have existed in areas of continual disturbance such as valley sides, river banks etc, spreading from these sites as the tree canopy was cleared. He also lists three species which were able to occupy woodland clearings created by windthrow etc, by virtue of a relatively long seed bank life span and animal dispersal. The species are Phytolacca americana, Prunus pennsylvanica and Rubus strigosus. If it can be shown that Hypericum pulchrum can survive within woodland soils by existing on a diet of treefall disturbance, then other species may also show similar habits and can be added to Mark's (1983) list of the species of open habitats which can exist within apparently "closed" woodlands.
SECTION 2.

A windthrown tree disturbance simulation model.

2.1 Introduction

The fall of a forest tree creates a gap in the canopy which is closed either by extension of the surrounding branches, or by growth of a new tree or group of trees. This has become known as "gap replacement" (Watt 1947) which has been studied in both temperate (Watt 1947, Bray 1956, Auclair & Cottam 1971, Marks 1974, Whittaker & Levin 1977, Barden 1981, Runkle 1982, White, Mackenzie & Bushing 1985) and tropical forests (Hartshorn 1978, Brokaw 1982, Putz 1983, Hubbell & Foster 1986) and is considered to be one of the main mechanisms by which species diversity is maintained within climax forests (Whitmore 1982). The coarseness of the mosaic produced by this process is dependent upon the gap generator. Fire and storm damage create large expanses of disturbance resulting in a coarse grained environment whilst individual treefalls, through disease or windthrow, produce less dramatic changes and a fine grained mosaic.

Watt (1947) and Ehrenfeld (1980) have demonstrated that removal of the canopy causes changes in the production and reproductive efficiency of the shrub layer and ground flora beneath the gap. Watt (1947), in a study of the Chiltern beech woods, established that the ground flora passes through phases
similar to the canopy trees. On opening of a gap, the increased light levels produce a rise in the growth rate of those plants which were able to survive vegetatively beneath the canopy. The new environment may also allow establishment, growth and reproduction of shade intolerant species previously excluded by the complete canopy; Watt (1947) used the term building phase to describe these changes. On reaching the gap carrying capacity, the vegetation of the ground flora enters a mature phase. Finally, closure of the canopy results in a decrease in photosynthetic production by the vegetation (degenerate phase), bringing about a reduction in abundance of shade intolerants until only shade tolerant species survive.

Accompanying the vegetative development of the shrub layer and ground flora is a successional colonisation of the "regeneration niche" created by windthrow (Grubb 1977). Thompson (1980) has demonstrated that plants of the ground flora establish on the fallen trunk and branches. Hypericum perforatum (Salisbury 1942), Juncus spp, Verbascum spp (Grubb 1977) and several pioneer tropical tree species (Putz 1983) all germinate from seed in soil which is disturbed by uprooting.

Soil disturbance mounds are not produced by every fall within the forest. In temperate forests Runkle (1982) measured a rate of 20% of windthrows resulting in mounds, while Putz (1983) measured 22% for tropical forests. The work of Stephens (1956), which demonstrated the importance of wind thrown soil disturbance in the topography of the forest floor, has led to many subsequent studies. Brewer & Merritt (1978) examined the rates of mound formation within temperate forests and used this to produce
estimates for the turnover time for the complete forest floor soil. Putz (1983) has carried out a similar study on the Barro Colorado Island tropical forests which also demonstrates the ability of pioneer tree species to germinate on the soil mounds. He believes that this may be a method by which these species are maintained within the tree canopy of tropical forests.

This dynamic system had been described previously by Marks (1974) after a study of the pin cherry (*Prunus pennsylvanica*) in the Hubbard Brook research forests. He demonstrated the ability of this species to persist within the community by germination from the seed bank within gaps caused by fallen trees. He then put forward a simple verbal model of the life history of pin cherry in relation to regular minor disturbances created by the removal of single canopy trees and also irregular major clearances.

The development of the topography of the mound of soil created by a windthrown root disturbance and its physical and chemical characteristics have been investigated by Lutz (1940). Hutnik (1952) has shown how these characteristics may be a controlling factor in the position at which various species establish on the mound.

In a theoretical study Grubb (1977) has given a summary of the major processes involved in the invasion of a canopy gap by seed. He also lists the characteristics of a gap that may be critical to establishment and survival of a seedling and which exert an influence in selection of the species that will be successful in claiming the opening. The lists are presented in Table 11.
Table 11. The processes involved in colonisation of a gap and the characteristics of the gap that may influence establishment (Grubb 1977).

<table>
<thead>
<tr>
<th>Processes</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germination</td>
<td>Time of formation</td>
</tr>
<tr>
<td>Establishment</td>
<td>Size and shape</td>
</tr>
<tr>
<td>Onward Growth</td>
<td>Orientation</td>
</tr>
<tr>
<td>Production of viable seed</td>
<td>Nature of the soil surface</td>
</tr>
<tr>
<td>1) flowering</td>
<td>Litter present</td>
</tr>
<tr>
<td>2) pollination</td>
<td>Other plants present</td>
</tr>
<tr>
<td>3) setting of seed</td>
<td>Animals present</td>
</tr>
<tr>
<td>Dispersal of seed</td>
<td>Fungi, bacteria, viruses</td>
</tr>
<tr>
<td>1) Through space</td>
<td></td>
</tr>
<tr>
<td>2) Through time</td>
<td></td>
</tr>
</tbody>
</table>

Grubb (1977) also described a theoretical system, based on differences in regeneration niche, which allows coexistence of two species, even if one excludes the other by competition when of equivalent physiological age. This includes the possibility of one species surviving as a seed bank and appearing within gaps created by removal of the dominant species, a situation similar to that described by Marks (1974). The seed bank species will only survive within the community if the rates of gap formation, seed production and dispersal within areas of disturbance are in a balanced equilibrium with rate of decay of the seed bank. If seed decay is greater than the level of input, or seed dispersal
results in a restricted distribution which does not reach the surrounding trees and is therefore unable to exploit the possibility of further gaps, then the seed bank species will be removed from the community at a rate controlled by the decay and input parameters.

The system described by Marks (1974) and the list of characters given by Grubb (1977) are verbal models of seed input to forest soils by treefall disturbances. *Hypericum pulchrum* windthrow germination found within the Tamar valley coppice woodlands can be described in similar terms. It does not, however, allow prediction of future seed density within the soil, and for this a demographic study must be carried out. The remaining part of this thesis describes the construction of a series of computer programs designed to simulate the dynamics of the *Hypericum pulchrum* seed bank beneath woodlands, together with the experiments necessary to estimate the values of the parameters used in the model. The model can be used to investigate the effects of alterations of individual parameters on future plant and propagule densities.

The model simulates changes in the coppice wood stand by following the growth and mortality of individual trees. It also reproduces the development of the seed bank beneath the canopy, taking account of both decay rates and windthrown seed input to the soil. Section 2.2 reviews the literature and briefly describes the structure of the programs, while subsequent sections describe those programs in greater detail.
2.2 Literature Review.

2.2.1 Models simulating woodland stand growth.

Simulation of woodland stands using mathematical models has followed five main methods: yield tables, differential and difference equations, stochastic processes, distributional methods and individual tree simulations. A comprehensive review is provided by Monserud (1975).

The first four methods all involve the use of equations which simulate mean stand parameters. They model development by producing girth class changes, distribution alterations and yields for the stand as a single unit. There is no consideration of individual trees within the stand and the models therefore lack the sensitivity which this provides.

In considering windthrown tree mortality within woodland stands an individual tree growth model is required. This type of simulation considers each tree as a separate unit. The models fall into two categories dependent on whether intertree distances are used within the simulation.

i) Distance dependent individual tree simulations.

In this category of model, intertree distances are assessed within the stand and used in calculation of a competition index for each tree which relates the growth of a tree to the amount of competition which it experiences from all surrounding trees. In the simulations of Newnham (1964) and Monserud (1975), growth of
a tree is a function of its potential growth and its competition index. Potential growth is established by measuring the growth of a tree of equivalent girth in a competition free environment. This is then reduced by the amount of competition received from the neighbours within the stand, by use of the index.

The results of this form model can be used to assess various management regimes by alteration of the controlling parameters. It would provide the ideal model for the simulation of the Hypericum pulchrum seed bank dynamics beneath a tree stand. Unfortunately when using this model format there is a penalty in the large amounts of data that must be collected over a number of years and from various habitats in order to obtain any degree of accuracy. The models are also computationally complex, especially when edge effects are considered, requiring large amounts of computer space and time. For the limited requirements of the Hypericum survey a less complex simulation method is adequate.

ii) Distance independent individual tree growth models.

As with the previous models this simulation method considers each tree as an individual unit. However trees are grown according to their relationship with mean stand parameters rather than intertree distances. This method lacks the sensitivity of distance dependent models but is computationally faster due to a reduction in complexity; this is particularly the case when hardwood species dynamics are simulated. Softwood species are usually considered to have circular canopies and are modelled with conic shapes or circular areas of influence.
This simplification when applied to the irregular canopy structure of a hardwood tree is difficult to justify. The tree should ideally be considered on the basis of independent sectors of canopy each subject to a separate competition index. This would then reproduce the form of tree often found in the Tamar woodland coppice stands, in which a vertical line from the canopy centre to the forest floor falls several metres from the base of the tree owing to substantially greater extension growth on one side. Programs which produce canopy growth in independent sectors are complex and therefore the TREFAL simulation used a simple circular canopy.

2.2.2 The simulation of seed bank dynamics.

The measurement of the density of viable seeds in the soil has been a recognised procedure since the studies of Brenchley and Warington (1930). Part of this research has involved studies of the seed bank densities of soils beneath natural temperate woodlands (Johnson 1975, Whipple 1978, Petrov 1977); of managed woodlands (Brown and Oosterhuis 1981, Hill and Stevens 1981); and tropical forests (Guervara and Gomez Pompa 1972, Putz 1983).

The majority of studies have established only the identity, density and degree of contagion of the species present in the seed bank. However, with increased knowledge of the importance of seed banks within communities, recent work has involved the recognition of budgets of seed input and loss from the soil (Kellman 1974, Sarukhan 1974, Van Baalen 1982).
Sagar and Mortimer (1976) used data from several demographic studies of plant populations to produce a model in the form of a flow diagram of life history stages. This has been used to identify the parameters which should be measured for the demographic study of a plant species and was used by Van Baalen (1982) in a study of *Digitalis purpurea*. The flow diagram model allows comparison of the life histories of a range of species in differing environments (Sagar and Mortimer 1976).

Theoretical mathematical models of the influence of a seed bank on life history have been constructed by Cohen (1966), MacDonald & Watkinson (1981) and Levin (1977). They have been used to investigate the selective factors acting on annual plants in terms of dispersal, germination percentage and survivorship probabilities.

The advent of the computer, with its ability to perform large numbers of calculations in a short period of time, now allows construction of simulation programs which follow the form of Sagar and Mortimer's (1976) flow diagrams. Parameters surveyed in the natural environment can be modelled to reproduce measured rates of development with controlled degrees of stochastic variation. Alterations of simulation parameters, in conjunction with use of the Monte Carlo technique of establishing the probability of the various outcomes, can then be used to assess the stability of the modelled system.
2.2.3 Structure of the selected model format.

After evaluation of the various methods available for the simulation of the growth and development of a woodland stand, it was apparent that due to the restricted time available for the production of a distance dependent model, a distance independent model should be used.

The seed bank model chosen for the study is a simplification of that of Cohen (1966).

\[
S_{(t+1)} = S_{(t)} - D_{(t)} + I_{(t)}
\]

where

- \( S \) - seed bank density at any position within the stand soil area.
- \( D \) - annual decay of the seed bank
- \( I \) - input in any year from windthrown trees
- \( t \) - time in years.

The seed bank model is a modification of many previous studies, in that it is designed as an area of soil over which the tree stand is superimposed. This allows an assessment of the development of the spatial distribution patterns of the seeds in the soil with respect to decay and fall input. This is an area which has not previously been considered in seed bank dynamics, but which is of considerable importance to the continued existence of a seed bank of *Hypericum pulchrum* beneath the coppice canopy.
The woodland windthrow - seed bank simulation system was produced in the form of three separate programs, each written in Fortran 77. These are responsible for

1) construction of the woodland coppice stand
2) construction of the stand seed bank
3) simulation of the growth and development of the woodland stand and the decay and input to the soil seed bank.

An illustration of the three main programs and the interface files is presented in Figure 27.

1) WOODLAND:

This program simulates the woodland stand to be used in the model TREFAL. An area of soil of 51 x 51 m is produced within the computer memory, designed in the form of a 170 x 170 array grid, each square representing a 30 x 30cm area of soil. These values were used to employ the largest number of grid squares that could be held in the computer's virtual memory, and consequently the greatest possible degree of accuracy in the simulation. Using data supplied by the operator the trees are scaled to fit within the area of the stand, ensuring no overlap of canopies; the condition found within natural coppice stands. Trees of the required size are positioned at random on the array grid squares.

The model creates a file TREES which stores the tree grid positions and girth measurements for use in the simulation of stand-seed bank interactions.
Figure 27. A description of the relationships between the programs and files of the complete simulation model.

(a) \texttt{t.data}

(b) \texttt{density parameters}

(c) \texttt{WOODLAND}

(d) \texttt{CONBANK}

(e) \texttt{trees}

(f) \texttt{c.bank1}, \texttt{c.bank2}

(g) \texttt{rate parameters}

(h) \texttt{TREFAL}

(i) \texttt{windthrow girths and positions TREP}

(j) \texttt{OUTPUT}

(k) \texttt{final seed bank files FBANK1, FBANK2, FBANK3, FBANK4, FBANK5, FBANK6}

--- control files

--- simulation programs

--- output files
2) CONBANK:

By use of the seed dispersal pattern of *Hypericum pulchrum*, measured in a natural coppice stand, CONBANK creates a simulated seed bank. This is carried out by superimposing the dispersal pattern repeatedly on the 170 x 170 array grid, until the density required for that stand's soil is reached. Adjustment to the CONBANK parameters allows regulation of the density and variance of the seed bank created by this program.

The files C.BANK1 and C.BANK2 contain the simulated seed bank comparable to that of natural woodland stands of similar age. Two files hold the seed bank since a 170 x 170 matrix grid of the size required by the model is too big for the input and output operations of the computer system.

3) TREFAL:

TREFAL uses the files created by WOODLAND and CONBANK to create a simulation which combines both canopy trees and the seed bank. It models the woodland development in the form of growth, self thinning and random windthrow, according to parameters measured by the operator in the surveyed coppice woods. Treefall reinforcement of the seed bank is reproduced within the simulation in association with the annual loss by decay of seeds from the soil.

The final output is a series of files containing the final seed bank spatial pattern, the remaining tree positions and the developments through which the simulation has passed in reaching the final state.
2.3 WOODLAND - the coppice stand simulator

The program WOODLAND is designed to create a file (TREES) containing the parameters describing a simulated coppice stand.

2.3.1 WOODLAND theory

Through wind damage, created by movement of adjacent branches, the canopies of the trees within a naturally self thinning coppice stand are not overlapping; WOODLAND allows for this. TREFAL, the program in which the woodland stand is to be used, is a distance independent model; it does not use canopy shape or size in the calculation of stand development rates. This allows the removal of many computational complexities by the use of circular canopy shapes for each tree. This simplification leads to a difficulty in scaling of the sum of the canopy areas of the trees to match the total area of the model stand. The requirement for no overlap and the use of circular canopies ensures that there will be wastage between the trees areas (Figure 28). This must be taken into consideration in the scaling calculations.

WOODLAND makes the assumption that canopy area of any tree in a stand is proportional to its girth.

ie. Canopy area = \( \pi C G^2 \)

Where C is a constant and G the tree girth.
The model uses this relationship in the calculation of the scalar required to enable any distribution of trees to be arranged within the simulated stand area.

Within a self-thinning coppice stand the dominant factor limiting growth is the energy derived from the available canopy area. Those trees which capture greater areas of canopy space will grow faster. The use of a scalar relating canopy area (in grid units) to girth, makes allowance for this fact by producing the greatest canopy areas for the largest tree girths.

Figure 28. An example of the wastage between circular canopies when fitting them to a stand area
2.3.2 Parameter derivation

Coppice stands were surveyed using a 51 x 51 m quadrat size matching that of the simulation. Each quadrat was laid out within the area of the stand to be studied in a position which removed the edge effects of rides and clearfelled land. The girths of all canopy trees within the quadrat were then measured at 1.3 m above ground level and the data, after separation into 10cm girth classes used, to create the WOODLAND control file TDATA.

TDATA allows the operator to use WOODLAND to create, in simulated form, any surveyed coppice stand. The file contains the parameters required by the model to produce a known distribution of girth classes. These are

1. the number of girth classes.
2. the smallest class size (cm).
3. the class interval (cm).
4. the frequency of trees in each class.

2.3.3 WOODLAND Model procedures

A flow diagram presenting the essential features of WOODLAND is illustrated in Figure 30. A listing of WOODLAND is provided in Appendix 7.
i) Scaling of the canopy areas.

The size of the largest two dimensional, square array available on the Plymouth Polytechnic PRIME 9950 computer is 170 x 170 units. In order to utilise this area each unit is set to correspond to a 30 x 30 cm area of soil. This therefore produces a 51 x 51 m simulation area within the models WOODLAND, CON_BANK and TREFAL. Each square within the array is referred to by Cartesian coordinates with an inverted Y axis (Figure 29).

Figure 29 The Cartesian coordinates used in identifying the seed bank grid squares.
Figure 30. A flow diagram of the main processes used to create the trees by WOODLAND.

File TDATA.
- Number of girth classes = c
- Smallest class size = sm
- Class increment = i
- Frequency of classes = Fc

Calculate class sizes using sm, i and c

Call Scale
- Class = sm
- Fr = Fc x Class X
- CF = 1

Calculate canopy radius

Select random grid coordinates

Check new grid coordinates and the canopy with all previously sited trees.

If CF = CF + 1 then:
- no overlap
- Store tree position, girth and canopy radius.

If X = X + 1 then:
- Yes
- CF = Fr

If X = Largest class then:
- No
- File all stored trees

STOP
In order to position all the trees of the given stand distribution within the simulated area, a scalar \( K \), is enumerated by SUBROUTINE SCALE.

If it is assumed that for a single tree

\[
\text{Canopy area} = \pi C G^2
\]

then the total stand canopy area is given by

\[
\text{Total canopy area} = \pi C \sum_{i=1}^{N} G_i^2
\]

where \( N \) is the number of trees in the stand. The simulated stand area is 170 x 170 grid units or 28900 x 900 cm\(^2\), and the scalar relating the total canopy area to that of the soil area is given by

\[
k = \sqrt{\frac{28900 \times 900}{\pi C \sum G_i^2}}
\]

if

\[
K = \frac{k}{\sqrt{\frac{900}{C}}}
\]

then

\[
K = \sqrt{\frac{28900}{\pi \sum G_i^2}}
\]

where \( k \) and \( C \) are constants and \( K \) the required scalar also a constant.
This is the ideal case in which tree canopies are a perfect fit to the soil area. In the simulation model the use of circular canopies results in waste between trees. This must be allowed for by a reduction in the stand area within the scaling equation. A reduction to 70% of the original area is found to be adequate.

\[
K = \sqrt{\frac{28900 \times 0.7}{i = N}} \\
\sqrt{\pi \sum_{i = 1}^{G^2}}
\]

ii) Tree simulation.

Stand trees are positioned on the 170 x 170 array grid at random, the only condition being that there is no overlap of canopies. Coordinates are selected at random from the array grid x and y axes (1-170) for each tree. The position chosen is then checked by SUBROUTINE CHECK, to ensure that placement of the tree at that point does not produce an overlap of canopies with any previously set tree. Overlap is found by calculation of the distance between trees, using their array grid positions.

\[
D = \sqrt{(X_i - X_j)^2 + (Y_i - Y_j)^2}
\]

D is the distance in array units between trees, Xi and Yi are the Cartesian coordinates of tree i on the grid
If the distance between trees is greater than the sum of their canopy radii

\[ D > (K \cdot G_i + K \cdot G_j) \]

where \( G_i, G_j \) are the girths of trees \( i \) and \( j \), then there is no overlap and the tree position and girth are recorded.

If \( D < (K \cdot G_i + K \cdot G_j) \)

the position is rejected and a new set of grid coordinates calculated.

To ensure that there is sufficient room to position the largest of the canopies within the stand, trees are positioned in order of size classes with the largest classes first and the smallest set around them.

Occasionally it is found that after a number of attempts at placing a tree on the grid no position has been found to set it. In this instance SUBROUTINE SCAN is called. This routine checks all positions on the grid in an attempt to fit the tree. If a position where there is no overlap is found the tree is placed there. If however due to the pattern of trees already present there is no space to place the required size of tree the program stops. If this occurs during a run two options are available: Rerun the program to produce a new set of data points or, if the problem recurs, then adjust the reduction percentage to increase the allowance for waste around the circular canopies.
iii) WOODLAND Output.

After completion of a run the program produces the file TREES. For each simulated stand this contains

1. the x coordinate of each tree
2. the y coordinate of each tree
3. the girth of each tree
4. the adjusted canopy radius for each tree.

the final parameter is used in checking the program results.
2.4 CONBANK the contagious seed bank simulator.

In order to simulate the changes taking place in the Hypericum pulchrum seed populations beneath self thinning coppice woods, TREFAL requires a model seed bank of known density and spatial variance. This is provided by the computer simulation CONBANK. The model uses a Hypericum pulchrum seed dispersal pattern, derived from the woodlands of the Tamar Valley, to reproduce the desired distribution within the simulated seed bank matrix.

2.4.1 Theory.

Disturbance of the soil by coppicing allows Hypericum pulchrum seeds to germinate, flower and disperse fresh seed to the surrounding soil. This 'new' component of the seed bank can be assumed to be the result of the overlapping seed shadows of an approximately random distribution of Hypericum plants. As a result of differing seed production for each plant, the reinforced seed bank will be a complex pattern of varying densities.

Obviously this is extremely difficult to simulate. A simplification must be arrived at which produces the required seed bank mean and variance. In order to achieve this, the seed distribution pattern for Hypericum pulchrum was measured in the coppice stands of the Tavistock Woodland Estate. These data were then used to produce a model seed bank by repeatedly
superimposing the measured distribution at random on the seed bank array to be used by TREFAL. Adjustment of the density of seed input by use of a scalar allows the mean and variance generated by the model to be altered.

2.4.2 Parameter derivation

i) Mean and variance of the initial seed bank

The results illustrated in Figure 17 show that there is a considerable variation in the estimates of seed bank density in the younger stands. This is due to both variation within the woodland soil and the sample errors of the survey technique.

In order to derive a value for the seed bank density of a younger coppice stand of given age, a regression of the first five data points was calculated. The derived regression equation (see also Figure 47) can be used to determine the seed bank density of Hypericum beneath (for example) a 35yr old canopy.

\[
\log (\text{Density}) = 3.99 - 0.0283 \times (\text{Age})
\]

for Age = 35 yrs Density = 999 seeds / m\(^2\)

The spatial variation, described by the variance, can then be calculated by substitution into the Taylor's power relationship derived in Section 1.10
Log (V) = 1.618 Log (Mean) + 0.367

Variance = 166070 for 999 seeds / m²

These values must be simulated by the CONBANK model for a 35 year old coppice woodland seed bank.

ii) The seed dispersal pattern for Hypericum pulchrum

Theory

Measurement of the pattern of seeds deposited on to the soil by Hypericum pulchrum requires lines of sticky traps positioned at set distances from the base of a series of plants. To conform to the conditions under which the young coppice seed banks are formed, this should be carried out in a newly cleared coppice stand in which regeneration of the stools is taking place. In reality the number of Hypericum pulchrum plants releasing seeds into this environment is sufficient to mask the dispersal pattern for any single plant.

To remove this background seed production, three seed bearing Hypericum pulchrum plants were transferred to large treefall gaps within the Wareham Wood coppice stands. There were no other Hypericum plants in these gaps.

In freshly cleared coppice the regenerating stools and remaining standards will cause wind speeds to differ from those of clearfelled areas. This difference will be increased as the stools put on the rapid regrowth characteristic of the coppice
shoots (Rackham 1980). The use of large canopy gaps created by treefalls will therefore produce a better estimation of the wind environment of newly cleared coppice areas, when compared to that derived from the adjacent clear felled stands.

Methods

Three Hypericum pulchrum plants bearing seed were extracted with sufficient soil to ensure continued survival from clear felled areas of Wareham Wood. The plants were placed individually in flower pots and each positioned at the centre of the largest area of a treefall gap free of the fallen tree.

Traps made from 10 x 20 cm and 30 x 20 cm sheet hardboard, coated in aluminium foil, were placed in a circular pattern around each plant (Figure 31), each held in place by a six inch nail through the centre. Using a paint brush tree grease was applied to each board after which 1 cm bird net, cut into 5 x 1 m lengths was supported on wire hoops over the trap lines. This cover allowed access to the traps by seeds but prevented leaves from reducing the effective trapping area.

Traps were laid in June 1984 and collected after complete seed dispersal in December of the same year.

During the first two weeks of trapping, the seed bearing stems were shed from all the plants in the clearfelled area and two of those transported to tree fall gaps. This resulted in restricted dispersal of the seeds, confining them to the
Figure 31. The configuration of traps used to measure the seed dispersal pattern of *Hypericum pulchrum*.  

- □ 20x10 cm traps
- △ 30x20 cm traps
immediate vicinity (10 - 20 cm) of the Hypericum plants. This phenomenon did not occur for the remaining experimental plant, nor those plants producing seed on the treefalls within the coppice stands. Such shedding of capsules has not been observed in previous years or subsequently. It is possible that the severe drought in the South West in 1984 made the stems of plants in the clear felled areas brittle and resulted in this shedding. Trapping of seeds was therefore abandoned for all but the plant on which the capsules were retained.

After lifting the traps were returned to the laboratory. The foil was removed from the boards and the larger pieces of debris (leaves and twigs etc) removed. Each individual trap was treated by cutting of the tree grease covered foil into 4cm wide strips, which were then placed in a bath containing 50 cm³ of xylene and left to soak for 20 minutes. The xylene dissolves the tree grease and removes the trapped seeds from the foil. The resulting mixture was then passed through a filter paper to collect the organic matter which was washed in alcohol and finally water. The residue, separated from the filter paper by hand, was placed in the soil washing apparatus described in Section 1.4.3 ii, and washed on to the collecting sieve. This removed all particles finer than 1mm in diameter. The remaining debris were placed in a petri dish and hand sorted using a binocular microscope to extract all the Hypericum pulchrum seeds.
Results and discussion.

The numbers of seeds per trap measured at various distances from the Hypericum plant are presented in Figure 32.

The measured distribution is biased towards the south of the plant, which may be a reflection of either the predominant turbulence patterns in the gap or the prevailing winds. The density is at a maximum beneath the plant, dropping quickly with increased distance from the centre, to a maximum range of 2 m. Figure 33 presents the data for all traps, converted to the density of seeds per cm$^2$, plotted against distance from the plant. This measured seed input pattern provides the basis for the CONBANK simulation program.

The results of the seed trapping are comparable with those of the soil transect data for treefalls measured in Section 1.9.2 b (Figures 20 & 21), although dispersal from treefalls extends to greater distances from the plant owing to the height of the disturbance mound. With increasing girth of the fallen tree and therefore size of the soil mound, plants which germinate and establish at height will shed seeds which disperse to greater distances. This is due to both the increased time taken for seeds to reach the soil during dispersal and faster wind speeds which are related to height above the soil surface.
Figure 32. The frequency of seeds trapped at distances of up to 2 m from a *Hypericum pulchrum* plant.
Figure 33. The density of *Hypericum pulchrum* seeds falling per cm² of trap area at increasing distances from the source plant.
2.4.3 Simulation of the *Hypericum pulchrum* seed bank.

In order to produce a seed bank of given seed density CONBANK first establishes the 170 x 170 matrix of 30 x 30 cm simulated soil units which will be used by TREFAL. A simulation of the measured *Hypericum pulchrum* seed dispersal pattern is then repeatedly superimposed on to the stand matrix at random until the required density is reached.

The simulated seed dispersal pattern is illustrated in Figure 34. It consists of a square recruitment matrix over which the seed density decreases with distance from the centre. The density of seeds at each position is derived from a transformation of the measured *Hypericum* seed input pattern (Figure 33). The trapping data were first adjusted to produce the density of seeds falling on a 30 x 30 cm square at each distance from the plant. A Log(y+1) transformation was then used to produce a straight line relationship (Figure 35).

The relationship derived is

\[ \log \left( \frac{\text{Density}}{900 \text{ cm}^2 + 1} \right) = 2.84 - 0.0144 \text{ (Distance)} \]

This was then used to calculate the density of seeds falling at the centre of each square on the seed recruitment matrix (Figure 34).
Figure 34. The simulated seed bank recruitment pattern for *Hypericum pulchrum* used in CONBANK.

\[ 180cm \]
\[ 150cm \]
\[ 120cm \]
\[ 90cm \]
\[ 60cm \]
\[ 30cm \]
\[ 30cm \times 30cm \]

\[ \text{INT}(630i) \]
\[ \text{INT}(232i) \]
\[ \text{INT}(85i) \]
\[ \text{INT}(31i) \]
\[ \text{INT}(11i) \]
\[ \text{INT}(3i) \]
\[ \text{INT}(1i) \]

\[ i \] - The scaling factor for the simulation
\[ \text{Int}(x) \] - rounded to nearest integer value.
Figure 35. The Hypericum pulchrum seed dispersal pattern measured in the Tamar valley woodlands, transformed to establish the number of seeds falling on a 900cm² area.
In order to allow adjustment of the seed input in the dispersal pattern a scale factor \( i \) is used at each of the matrix positions. Alterations to \( i \) can be used to reduce or increase the seed input in order to control the final seed bank variance. Values of \( i \) below 1.0 reduce the input density of the recruitment matrix. It therefore requires a greater number of random dispersal pattern inputs to achieve a given density, with a consequent reduction in variance. Values of \( i \) greater than 1.0 increase the variance.

2.4.4 Simulation results

The simulated seed bank required by TREFAL in order to model a 35 year old woodland has a density of 999 seeds/\( m^2 \) and a variance of 166070. In order to produce these values, \( i \) was initially set to 1 and a run of CONBANK carried out.

The means and variance of 50 samples removed by the TREFAL simulation from the generated seed bank were

\[
\text{Mean} = 1031 \text{ seeds/} m^2 \\
\text{Variance} = 597105
\]

A t test can be used to examine the significance of the difference between this variance and that used in calculation of the regression for the Taylor's power relationship. It must be noted that this procedure has limitations due to the inevitable relationship between the mean and variance of the data used in
calculating the regression. The test revealed that the variance of the 50 samples was significantly greater than that of the regression data. The scalar was therefore reduced to a value of 0.9 and a new seed bank simulation run performed.

The result was a seed bank sample mean of 990 seeds / m$^2$ and variance 154416, values which did not differ significantly from the seed bank required for the TREFAL simulation run.

Table 12 shows the results of five simulation runs of TREFAL with the means and variances of 50 samples removed at the start of each run. The third column of the table presents the results of t tests performed on each data set. Each reveals that there is no significant difference ($p < 0.05$) between the generated values and those used to derive the Taylor's power relationship within the limits of the t test under the given conditions. A value of $i = 0.9$ is therefore suitable for the generation of the required seed bank.

The table also reveals that the variation exhibited by the simulated seed bank data can differ from the Taylor's power calculated values by a considerable margin before becoming significantly different. This may be caused by the relationship of the mean and variance influencing the t test.
Table 12 The mean density and sample variance of fifty 30 x 30 grid squares sampled from the seed bank simulation, with t tests of their values against those derived from the coppice stands.

<table>
<thead>
<tr>
<th>Density</th>
<th>Variance</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>990</td>
<td>154416</td>
<td>NS</td>
</tr>
<tr>
<td>726</td>
<td>109888</td>
<td>NS</td>
</tr>
<tr>
<td>1013</td>
<td>405499</td>
<td>NS</td>
</tr>
<tr>
<td>614</td>
<td>82928</td>
<td>NS</td>
</tr>
<tr>
<td>866</td>
<td>251710</td>
<td>NS</td>
</tr>
</tbody>
</table>
2.5 TREFAL-a model simulating the influence of woodland disturbance processes on a seed bank.

The model TREFAL is designed to simulate the development over a number of years of both a self thinning coppice stand and the seed bank of the soil beneath. The simulation can be divided into three main areas.

a) Woodland processes.

b) Seed bank processes.

c) Treefall-seed bank interactions.

Each section simulates a different part of the woodland and seed bank development.

a) Woodland processes

With increasing age of the stand individual trees increase in girth. Each increases at a rate proportional to the amount of competition to which it is subjected by its immediate neighbours. The increase in size of stand trees results in greater competition between them and hence self thinning. This self thinning is not uniform in its effect; smaller suppressed trees are removed at greater rates (Harper 1977).

In addition to self thinning, trees are also removed by windthrow. Those which have diseased roots, or are growing in poor soil conditions are felled by the wind, apparently at random.
TREFAL must simulate all of these changes in one form or another, in order to produce a comparable development within the model.

b) Seed bank processes

Roberts & Dawkins (1967) have shown that the decay of seeds in a soil seed bank may be exponential. The model TREFAL must account for this by reducing the density of seeds throughout the soil using a set probability function each year. Each seed must be treated as an individual unit in the population dynamics of the seed bank.

c) Treefall-seed bank interactions

This section of the model uses parameters derived from both the woodland stands and the seed banks of the Tamar valley.

The size of disturbance and consequently the number of seeds exposed by a treefall is proportional to the girth of the falling tree. Tree girth is also relevant to the size of the canopy gap created and consequently the length of time for which fresh seed is distributed to the seed bank around the fall. Given a mean seedling mortality rate a minimum number of seeds need to be disturbed before the fall is colonised by a single mature plant. i.e. There will therefore be a threshold density of seed in the soil exposed by a fallen tree, below which reinforcement of the seed bank no longer occurs.
The interaction section must also account for the distribution of seeds at various distances from the fall, and how the density of input is altered by changes in tree girth.

A flow diagram of the main components of TREFAL is presented in Figure 36. The model is initiated with a simulation time of INY years starting at a woodland age of ISA years. The treefall (IFFR), thinning (IFTH) and seed bank decay rates (DECR) are set by the operator to the required values. The files TREES and C.BANK 1 & C.BANK2 are created by previous runs of the WOODLAND and CONBANK models described earlier.

After completion of the simulation a set of files is produced containing the parameters describing the details of the run and the final tree positions. These can be used to examine the effects of the falls created on the spatial pattern of the final seed bank contained in BAN.RES1 and BAN.RES2.
Figure 36. A flow diagram illustrating the interactions between the subroutines of TREFAF.

START
Read TREES
Read C.BANK1
C.BANK2
Operator controlled data
INY, ISA, IFPR, IFTH, IFPR
DECR, TH
C = ISA

QFALL = 1? —Yes
No

QTHIN = 1? —Yes
No

GROWTH
DECAY
AUGMENT
At 10yr intervals store the girth distribution
At 5yr intervals store the run data
C = ISA + INY
Yes
File all results

STOP

THROW
REPPAC
SHUFFLE
THROW
FIND
SHUFFLE
2.5.1 Woodland processes.

The section of the TREFAL simulation model which is responsible for the development of the stand of trees is split into three subsections.

1. Windthrow (Subroutine QTHROW)
2. Thinning (Subroutine QTHIN)
3. Growth (Subroutine GROWTH)

The relationship between the three subsections and their subroutines is illustrated in Figure 37.

i) Changes in stand density

The decrease in density of a stand of trees is the result of several factors, the main cause of mortality being self-thinning. Individual trees compete for available space as they grow. Those which cannot maintain a place in the canopy are overgrown, shaded and unable to capture sufficient energy to survive. They die and fall without creating a gap in the canopy. Disease and windthrow will also cause tree mortality although to a lesser extent. The TREFAL stand simulation separates mortality into two forms

a) Windthrow: all trees which fall to create both a canopy gap and soil root disturbance.

b) Thinning: all other forms of mortality, including loss of branches, snapping of the trunk, disease and removal by competition with neighbours.
Figure 37. A flow diagram of the subroutines responsible for woodland development in the TREFAL model.
During the time available for this survey of the Tamar woodlands, two forms of density change could be measured.

1) the rate of windthrow

2) the total density of stands of differing age, from which the rate of loss can be calculated.

The relationship between these factors is given by

\[ \text{Total density change} = \text{Windthrow} + \text{thinning loss}. \]

Measurement of the rate of windthrow for the stands of the Tamar valley, when subtracted from the rate of total density change, allows the rate of thinning by other causes to be calculated.

\[ \text{ii) Derivation of the windthrow rate.} \]

Two methods were combined to measure the rate of windthrow in the woodland stands.

The first involved the counting of all trees falling within the area of the coppice wood stands over the period of study. This rate can then be extrapolated to the time period for which the simulation is to be performed. This method has been used previously by Skeen (1976), Falinski (1978), and Brewer and Merritt (1978) for temperate woodlands, and by Putz (1983) and Brokaw (1982) for tropical forests. The short time span over which
this survey was carried out ensured that the errors associated with this method were large when applied to a 200 yr period of simulation. The first method was therefore combined with a second to increase the accuracy of the predictions.

The second method involved establishing the year of fall of trees which had fallen before the study period. A method was developed to estimate the year of fall of trees windthrown up to 45 years previously.

iii) A technique for assessment of the year of fall of windthrows

The investigation of the year in which a tree fell from the canopy involves tree ring cores removed from the trees surrounding any gap created by windthrow. Several studies of forest disturbance history have shown that a rapid increase of stem ring increment occurs after removal of the canopy by disease (Auclair and Cottam 1971), storms (Packham and Harding 1982), or death of individual trees (White, MacKenzie and Bushing 1985). The merits and difficulties of using cores for forest studies are discussed by Lorimer (1984).

In the crowded environment of a self thinning coppice stand the rate of growth of canopy trees is limited by competition for space. After removal of a tree by windthrow there is a rapid increase in growth of the branches occupying a position adjacent to the gap, ie. larger annual growth increments when compared to those formed previously in the suppressed years.

-160-
Figure 38 presents an illustration of this response. Position 1 corresponds to the release year of the tree and is followed by increased ring widths due to canopy expansion into the gap. Subsequent closure of the canopy produces a decrease of the increment widths to a level supported by the new canopy area of the tree. Position 2 of Figure 38 corresponds to the time of canopy closure.

Figure 38 An illustration of the changes in ring width of a tree released from competition by an adjacent fall. (Hypothetical)

Ring width (cm)

Time (yrs)

1 - Year in which the canopy opened
2 - Year in which the canopy closed
Ring core surveys can therefore be used to identify three parameters for the TREFAL model, for a treefall of given girth:

1) whether the tree produced a canopy gap
2) the year of fall
3) the duration of the canopy gap.

In any year growth will be controlled by both climatic effects and competition between neighbouring trees. In order to examine the degree to which these two controlling factors influence tree growth, ring widths were measured in cores from trees within adjacent undisturbed stands. The results established that occasionally climatic effects have an influence on all the trees of a stand, however the greatest influence on the growth rate of any tree was competition with neighbours. All significant, rapid increases in girth increment were therefore assumed to be due to changes in the competitive status of the tree and were used for detection of fall dates and canopy gap duration.

Methods

The face of the tree from which the ring core is taken may affect the result. Oak (*Quercus* spp) shoots exhibit asymmetrical growth of stem rings during regrowth of the canopy after coppicing (Rackham 1980). The removal of competition from one quadrant of the tree canopy may therefore result in increased growth of the face of the trunk positioned towards the gap in
comparison with those facing away from it. To remove the possibility of errors caused by differing coring positions, all cores were removed at 1.3 m above ground level on the face adjacent to the canopy gap or treefall. Three cores were removed from each tree to a depth of 10 cm. This provided sufficient rings for an examination of the past 45 years of tree growth. It was estimated that trees which had fallen before this time period may be difficult to detect due to decay of the trunk.

In the laboratory cores were examined beneath a binocular microscope and the width of each growth ring measured using a graticule eye piece. Comparisons of all trees surrounding the windthrow gaps provided mean estimates of the time of fall and the number of years for which the canopy gap remained open.

A map of Wareham Wood, illustrating the positions of those trees which fell creating canopy openings sufficient for *Hypericum pulchrum* to germinate, is presented in Figure 39. Of the 28 trees illustrated, 1-25 fell before the study commenced and 26-28 fell during the study. Trees 9,12,14,18 & 21 fell adjacent to rides and no attempt was made at assessing their ring width distributions. However, examination of the state of decay of these trees revealed that they had a high probability of having fallen after the oldest falls within the stands. They were therefore included in the survey densities.
Figure 39. A map of Wareham Wood illustrating the distribution of windthrown trees within each of the coppice stands.

- Coppice stands
- Softwood Plantations
- Clearfelled coppice.
- Coppice inaccessible due to *Rhododendron ponticum*
- Areas inaccessible due to topography
- Treefall disturbances on which *Hypericum pulchrum* was established
Results.

Figures 40 a and b illustrate ring increments of two cores removed from trees adjacent to windthrows T20 and T23, and demonstrates the difficulties involved in obtaining the year of fall and duration of canopy gap.

Ring widths of cores from different windthrows show little if any correlation, suggesting there is rather little influence of climate on ring width. This may be an indication of the overriding effect of competition on growth of individual trees. The cores clearly show the release from competition of the two trees, indicated by the increased width of the ring increments. Table 13 presents the complete data set for all windthrows assayed by coring.

Two smaller windthrown trees (17 and 19) revealed no distinct change in the annual growth increment of the surrounding trees. Both disturbances had single *Hypericum pulchrum* seedlings, both of which died within one year of discovery. This suggests that *Hypericum pulchrum* seeds may germinate on the root disturbance caused by fallen trees during early spring before leaf expansion, but fail to survive in the relatively deep shade. It therefore appears that fallen trees which were too small to have a detectable effect on neighbouring trees (below about 76cm girth) did not produce a canopy gap of sufficient size to allow *Hypericum pulchrum* to survive beneath the opening. TREFAL allows for this in its simulation of the disturbance processes.
Figure 40. Tree ring increments for two trees adjacent to windthrows within the Tamar coppice stands.

T20

No. yrs before coring

T23

No. yrs before coring.
Table 13. Parameters derived from ring cores of trees surrounding windfalls. The tree numbers refer to those in Figure 39.

<table>
<thead>
<tr>
<th>Windthrown Tree</th>
<th>Girth (cm)</th>
<th>No Yrs since fall</th>
<th>Canopy Gap time span</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>226</td>
<td>4</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>154</td>
<td>4</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>100</td>
<td>8</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>78</td>
<td>23</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>146</td>
<td>19</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>85</td>
<td>9</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>137</td>
<td>12</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>170</td>
<td>31</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>9</td>
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<td></td>
<td>EE</td>
</tr>
<tr>
<td>10</td>
<td>130</td>
<td>18</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>90</td>
<td>22</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td>EE</td>
</tr>
<tr>
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<td>175</td>
<td>25</td>
<td>25</td>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>100</td>
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<td>23</td>
<td>NSG</td>
</tr>
<tr>
<td>17</td>
<td>62</td>
<td></td>
<td></td>
<td>EE</td>
</tr>
<tr>
<td>18</td>
<td></td>
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<td>NSG</td>
</tr>
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<tr>
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<td>13</td>
<td>EE</td>
</tr>
<tr>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>150</td>
<td>30</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>160</td>
<td>28</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>240</td>
<td>25</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>150</td>
<td>32</td>
<td>32</td>
<td></td>
</tr>
</tbody>
</table>

EE - Edge effects prevented accuracy in core estimates

NSG - No significant change in growth pattern
In a 32 year period before this study 23 trees fell to produce a soil disturbance and a canopy gap (ie excluding trees 17 & 19), 3 fell during the study. The maps used in management of the Tavistock Woodland estate were used to estimate the area over which these falls occurred (24.72 acres, 9.99 hectares Figure 39). During the 32 year period the rate of fall was therefore 0.0813 trees/hectare/yr. This rate does not include the double treefall that occurred during the study, tree 1 felling tree 2. The simulation of double falls would introduce additional complexities to the model and so trees 1 and 2 were treated as two separate falls.

iv) Duration of the canopy gap.

The data from the survey of treefalls can be used to determine a relationship between the girth of a falling tree and the length of time the canopy gap remains open (Figure 41). The regression equation of gap duration against girth of the falling tree is:

\[ \text{Gap duration} = 0.1016 \text{ (Girth)} + 7.547. \]

This regression formula is used by TREFAL to calculate the length of time for which seeds are distributed from each treefall to the surrounding soil. The simulation assumes that the seed input ceases in the year of canopy closure.
Figure 41 The relationship between the duration of the canopy gap created by a falling tree and the girth of the tree.

\[ \text{Gap duration} = 0.1016 \times (\text{Girth}) + 7.547 \]
v) Windthrow simulation in TREFAL

Using the fall rate measured in the previous section, the rate of treefall to be found within a 51 x 51 m area of stand was calculated.

Rate per hectare = 0.0813 trees/yr.
Rate per 2601 m² = 0.0211 trees/yr.

For use in the program TREFAL this value is converted to an integer by multiplication by 10,000 and assigned to a label IFFR, the model fall rate.

In order to calculate whether a tree falls in any year, subroutine QFALL generates a random integer from an even distribution range (1-10,000). If the integer generated falls below the set value IFFR (in this case 211) then a flag is set for a tree to fall. The use of the even distribution of integers in QFALL corresponds to a probability of fall of IFFR/10,000, the fall rate measured for the 51 x 51 m stand area.

On receiving a flag indicating that a fall is to take place subroutine THROW selects a tree at random. The position and girth of this tree are passed to subroutine REPFAC for calculation of the seed bank input data. The tree is then removed from the storage array by subroutine SHUFFLE.
vi) Thinning of the stand trees

Subroutine THIN is the section of TREFAL simulating the removal of trees from the stand by all other means. This includes disease and structural failure of both branches and stems, but is predominantly due to competition between neighbouring trees. The nature of this process results in the removal of a greater proportion of the smallest trees of the stand, the suppressed weaklings. This bias towards death of small trees brings about a transformation of class distribution shape, from the positively skewed self thinning form (Harper 1977) towards normality (Monserud 1975). Subroutine THIN must preferentially select trees for removal from those in the lowest size classes in order to mimic this transformation.

Parameter derivation.

As shown previously the relationship between treefall rate, thinning rate and change of stand density can be expressed as

\[
\text{Thinning} = \text{Decline of stand} - \text{Windthrow.} \\
\text{rate} \quad \text{density} \quad \text{rate} \quad \ldots \ldots (1).
\]

Data collected from the 51 x 51 m quadrats placed within the coppice stands of the Tamar valley can be used to derive the rate of decline of density (Figure 42). The regression equation is:

\[
\text{Stand density} / 2601 \text{ m}^2 = 132.3 - 0.432(\text{Age}) \ldots \ldots (2)
\]
Substitution of the rate of decline \( (2) \) into \( (1) \) allows calculation of the rate of thinning for the woodland stands as they age.

Thinning rate = \(-0.432 - (-0.0211) = -0.41 \) trees/2601 m²/yr.

vii) Thinning simulation in TREFAL

The parameter used for the rate of decline by thinning in the model TREFAL is IFTH. This is an integer value derived from \( \text{IFTH} = \text{thinning rate} \times 100 \). For the above example \( \text{IFTH} = 41 \).

In order to simulate thinning of the model coppice stand at the rate chosen by the operator, the subroutine QTHIN uses the random number function LN. LN calculates an integer value in the range 1-100 and if less than \( \text{IFTH} \), QTHIN returns a flag value indicating a tree is to be removed from the stand. This removes trees from the stand with a probability of \( \text{IFTH}/100 \) or the thinning rate measured previously.

Subroutine THIN is responsible for removal of the trees from the stand. In order to achieve the transformation of class distribution described earlier, this must be carried out by a procedure which is biased towards removal of trees in the lowest girth classes. Subroutine THIN achieves this by calculation of a random integer with range 1-100, equivalent to a percentage range. Trees are then removed from the four smallest girth classes of the distribution in the probability ratio 50:25:15:10,
ie. a random value of 48 would remove a tree from the smallest class of the stand, 80 from the third smallest. This simulation results in a class distribution transformation equivalent to that of the measured woodlands, from positive skew towards normality.

viii) Simulation results for the changes in stand density.

The change in girth class distribution of the woodland stand is discussed in the next section after inclusion of the tree growth parameters.

The combined effect of thinning and windthrow mortalities on the density of trees within the simulation is shown in Figure 42. The figure illustrates the density changes taking place in two simulations for stands growing from 35 to 235 yrs of age. It can be seen that TREFAL provides an adequate representation of the real density changes.

ix) Individual tree growth.

To investigate the result of windthrown tree disturbance on the seed bank of a self thinning woodland, a model is required which reproduces a close approximation to the stand growth patterns. This is the function of subroutine GROWTH.

As discussed previously TREFAL is a distance independent growth simulator. The competitive interactions between neighbouring trees are removed in order to reduce the
Figure 42. The density of trees contained within a 2601 M² area of self thinning coppice stand and the TREFAL simulated decline in the model stand density plotted against stand age.

- --- Regression derived from the stand data
- -/- Development simulated by TREFAL

Number of trees / 2601 M²

Estimated stand age (yrs)
computational complexity of the model. Trees within the woodland grow at rates determined by their position within the stand girth range. This ensures that the largest trees grow at the fastest rates, a situation corresponding to that within naturally thinning woodlands (Harper 1977). A minor problem caused by this simplification is that a tree surrounded by smaller neighbours grows at a rate equal to one surrounded by trees of greater girth. In both a real stand and a distance dependent model the growth rates of such trees would differ. The advantages of a reduction in complexity are the removal of both the edge effects associated with forest growth simulators and the problems associated with irregular canopy shapes.

Derivation of individual tree growth rates.

Throughout the coppice woods of the Tavistock Woodland Estate, the girth of trees which had fallen or snapped at the base, within the past 3 years, were measured at a position equivalent to 1.3 m above ground level. These trees were then sectioned at a point as near to the base as possible using a chain saw. The sections were removed to the laboratory where ring counts were used to produce age estimates for each tree.

The data collected by this method were then used to produce a girth - age relationship for individual trees growing within Oak coppice woodlands (Figure 43). Mohler et al. (1978) have demonstrated that the exterior dimensions of a tree develop in a sigmoid form. The trees of the coppice stands sampled in this
Figure 43. Girth (measured at 1.3 m) plotted against stand age for trees felled in selected self thinning stands.

\[ \text{Girth} = 0.751 \times \text{Age} + 28.8 \]
survey are neither young nor mature in respect of the Oak life span. Thus the mid-range of the sigmoid growth form can be approximated to a linear function and a least squares regression used to derive the equation of this relationship.

\[
\text{Girth} = 0.751 \times \text{(Age)} + 28.89
\]

This function can then be used for derivation of the mean age of measured woodland stands.

Derivation of stand growth rate.

In a plant stand undergoing self thinning the majority of individuals are suppressed weaklings and the size class distribution is positively skewed (Harper 1977). Selfthinning removes the smaller weaker trees and results in a shift of distribution shape from positive skew towards normality (Monserud 1975). Both modal frequency class and mean girth are initially positively skewed and with thinning move towards the centre of the distribution range.

Ideally the modal class should be used for determination of stand age. However, with the errors associated with measurement at 1.3 metres above the ground level due to non-uniform trunk growth and sample error, the mean girth of the stand provides a parameter exhibiting less variance. The errors associated with the use of the mean girth decrease as the stand distribution shifts towards normality with increasing age.
The individual tree growth regression equation has been used to establish the ages of those plots measured in the Tavistock Woodland coppice survey (Figure 44). The use of this regression equation in calculation of stand age produces a straight line relationship when mean girth is plotted against age. This is the development of mean stand girth which TREFAL has to simulate.

It should be noted that the relationship of mean girth to stand age is only as accurate as the girth / age relationship derived in Figure 43. Increased accuracy could only be obtained by extensive felling.

x) Simulation of individual tree growth

The growth of individual trees within the simulation TREFAL is controlled by subroutine GROWTH. The essential characteristics of which are:

1) A tree which survives in the stand must increase in girth annually.

2) The annual growth increment of any tree is proportional to its position in the stand distribution.
Subroutine GROWTH reproduces this effect by the use of the equation

\[ G = M + (P \times W) \]

G is the increase in growth for the year of calculation.

M is the minimum growth requirement of a tree, which is inversely proportional to the girth of the tree. A suitable value was found to be \( M = \frac{4.5}{\text{GIRTH}} \).

P is the position of the tree within the girth range of the stand and is found by subtracting the smallest stand tree girth from that being assessed.

W is the increment determining the rate at which a tree of position P+1 increases when compared to a tree of position P. If a tree at a position P increases at a rate \( \Delta r \) then the tree at P+1 increases at \( \Delta r + w \).

W is a representation of the competitive superiority of the larger trees of the stand ensuring that those of greatest girth increase at the fastest rates.

After several trials the formulation of W which has given the closest approximation to the measured stand growth rate is

\[ W = \frac{41.0}{(\text{LG} - \text{GMEAN})^2} \]

where LG is the largest girth of the stand and GMEAN the mean girth.
xi) Discussion of simulation results

Figure 44 presents a comparison of the increase of mean stand girth for two simulation runs of TREFAL using the data obtained from the natural coppice stands of the Tamar woodlands. The figure illustrates that TREFAL produces a curvilinear relationship and adjustments of the parameter W allow this to be fitted to the natural stand data.

Use of a different formula for calculation of the growth of individual trees may produce a linear growth for the mean stand girth in the simulation. However, given that the data from the Tamar woodlands are only assumed to be linear, further measurements would have to be obtained from the coppice stands before refinements of the model could be justified. Considered in the context of the assumptions made in the rest of the simulation, the curvilinear form of the growth function used by TREFAL provides an adequate approximation of the growth rates over the measured range of sizes. Extrapolation beyond 235 years would, however, have to be treated with caution.

Figure 45 illustrates the development of the coppice wood girth class distribution in comparison with the results of a TREFAL simulation. The figure shows that the changing girth class distributions of the simulated stand are apparently a sufficiently good fit for the analysis of seed bank dynamics. However, attempts at testing the goodness of fit using a chi squared test suffer from the dominant influence of one or two class differences. The natural distributions were all derived in any case from single quadrats and are therefore subject to sample errors.
Figure 44. The regression line of mean stand girth plotted against canopy age with two of the growth curves for the same parameter derived from the TREFAL simulation model.

Mean Girth = 0.751 (Age) + 28.8
Faster growth rates of the larger trees produces an increase in the distribution range for the stand. Figure 45 illustrates that the parameters chosen for both weighting and minimum growth for each class, produce a changing distribution range comparable to that of the sampled stands. The sample data from the coppice woodlands, as would be expected, show greater variation than the simulation results. This is due both to sample error and also differences between the environments in which each stand is growing, i.e. variation associated with sampling stands of differing age rather than following a single stand throughout its history.

The use of a two parameter function for individual tree growth induces problems associated with the stand distribution. If the minimum growth of each class is set too low then the trees of the smallest class where \( W = 0 \) can be 'left behind' by the remainder of the distribution. A relatively large frequency class of small trees may therefore become detached from the main distribution. An illustration of this is provided by the 61 - 70cm girth class of the 110 and 120 year distributions in Figures 45 a & b, in which a single class is gradually isolated from the stand. Adjusting both the minimum growth for individual classes and \( W \) is required to minimise this effect.

In conclusion the woodland growth and frequency distribution change provided by the TREFAL simulation are adequate for an initial investigation of the seed bank dynamics of *Hypericum pulchrum*. The assumptions made and errors involved in determining the rest of the model parameters ensure that the small differences in distribution generated during growth will be of little significance in the results of seed bank dynamics.

-182-
Figure 45 (a). The frequency distribution of trees within natural coppice stands compared to the TREFAL stand simulation results.

**35 yr Coppice and Model**

![Graph showing frequency distribution for 35 yr Coppice and Model]

**70 yr Coppice**

![Graph showing frequency distribution for 70 yr Coppice]

**70 yr Simulation**

![Graph showing frequency distribution for 70 yr Simulation]

10 cm Girth classes
Figure 45 (b). The frequency distribution of trees within natural coppice stands compared to the TREFAL stand simulation results.

101 yr Coppice

100 yr Simulation

110 yr Coppice

110 yr Simulation

10 cm Girth classes

-184-
Figure 45 (c). The frequency distribution of trees within natural coppice stands compared to the TREFAL stand simulation results.

124 yr Coppice

120 yr Simulation

160 yr Coppice

160 yr Simulation

10 cm Girth classes
Figure 45 (d). The frequency distribution of trees within natural coppice stands compared to the TREFAL stand simulation results.

195 yr Coppice

190 yr Simulation

220 yr Coppice

220 yr Simulation

10 cm Girth classes

-186-
Figure 45 (e). The frequency distribution of trees within natural coppice stands compared to the TREPAL stand simulation results.

226 yr Coppice

230 yr Simulation

10 cm Girth classes
2.5.2 Seed bank processes.

i) Seed bank decay rate.

With closure of the woodland canopy and exclusion of *Hypericum pulchrum* the density of the seed bank begins to decrease. Roberts & Dawkins (1967) and Rampton & Ching (1970) have demonstrated that the expected rate of decay is exponential, i.e. a constant rate of mortality for each seed. The measurements of *Hypericum pulchrum* seed density in the woodlands of the Tamar valley suggest that windthrow allows a reintroduction of seeds to the soil within stands of age greater than about 80 years. In order to remove the influence of this seed input, the *Hypericum pulchrum* seed bank decay rate was therefore derived from woodlands aged less than 80 years. The data used in calculation of the *Hypericum pulchrum* seed bank decay rate are presented in Figure 47. The slope of the regression equation calculated for these data was transformed to give the annual survivorship rate for individual seeds (0.937 seeds/yr).

ii) Simulation of seed bank decay in TREFAL.

Each grid unit of the seed bank array is subjected to an annual decay. This is carried out by two functions IDECYM and IDECYR, illustrated in the flow diagram (Figure 46).

In order to reduce computational time all array units with a seed density of greater than 8 seeds are subject to a decay of
Figure 46. A flow diagram of the subroutines responsible for decay of the seed bank.

\[ I_8 = 1 \]
\[ I_9 = 1 \]

\[ DENSITY = BANK(I_8, I_9) \]

\[ DENSITY < 8? ]

Yes \[ DENSITY = IDECR(DENSITY) \]

No \[ DENSITY = IDECYM(DENSITY) \]

\[ I_9 = I_9 + 1 \]

\[ I_8 = I_8 + 1 \]

\[ I_9 = 170? \]

No \[ I_8 = 170? \]

Yes

\[ I_8 = 170? \]

No

Yes
(Density x 0.937). This is carried out by IDECYM. The result is returned as an integer value.

With seed densities of less than 8 the rounding errors of conversion to an integer become important. A unit density of 7 will be returned to 7 after decay by 0.937. To overcome this the function IDECYR calculates a random number from 1-1000 and if greater than 937 a seed is removed from the array unit. This probability of removal should be correct in theory. In practice the value of 0.937 used in IDECYR produces a decay rate lower than that required. There is almost always an inherent bias in random number generators, either towards the centre or extremities of the required distribution range, and this may account for the difference between anticipated and actual simulated decay results. It was found that an adjustment to \((937 - 12)\) was necessary before the required decay was achieved for unit densities of less than 8 seeds.

iii) Simulation results.

Figure 47 presents the result of a simulation run without treefalls and illustrates the correspondence of the simulated and measured decay rates for *Hypericum pulchrum*.

Figure 48 illustrates the development of the relationship between seed bank log mean and log variance during a run of the model. The program samples 50 seed bank units each 5 years and prints the mean density and variance of the data.
Figure 47. Results of the seed bank simulation, illustrating the change of density taking place without a seed input.

- Natural coppice stand results
- Mean stand density simulation results
- Simulation results measured by sampling 50 random grid squares
- Derived regression

\[
\text{Log (Density)} = -0.0283 \times (\text{Age}) + 3.99
\]
Figure 48. A comparison of the Hypericum pulchrum Taylors power relationships for natural coppice stands and the results of the simulation model TREFAL.

- - - Natural stand regression $\log(v) = 1.616 \log \bar{X} + 0.362$
- - - Model regression $\log(v) = 1.729 \log \bar{X} + 0.0095$
The regression derived from the results is:

\[ \log(V) = 1.729 \log(D) + 0.0095 \]

The relationship for the natural coppice stands of the Tamar woodlands derived in Section 1.10 is:

\[ \log(V) = 1.616 \log(D) + 0.362 \]

The results are not significantly different (\( p < 0.01 \))
2.5.3 Windthrow - seed bank interactions.

In Section 1.9.2 (b) the Hypericum pulchrum seed input to the soil surrounding a windthrown tree was measured using a transect of soil cores. In order to examine the effect of repeated seed recruitment to the decaying seed bank by windthrow, a relationship between the girth of the fallen tree and the annual seed production during the open canopy period, must be established. There are two methods by which this can be achieved.

The first, illustrated by Figure 49, follows the demographic development of the seed population germinating on a treefall mound. Disturbance by windthrow removes both the litter layer and the canopy shade from the seeds stored within the soil. Exposure to the new light environment results in germination and growth of the seedlings. The initial population of germinating plants is then subjected to mortality through lack of establishment, predation & fungal attack, competition, erosion and frost damage, each of which reduces the population size.

Self pollination (a characteristic of the Hypericaceae) removes any need for other plants to be present within the gap or for external pollen. After seed production and dispersal, the fraction of the seed rain incorporated into the seed bank must be measured in order to produce a simulation model.

Demographic simulations of this form have been produced (Sagar and Mortimer 1976) but require lengthy periods of study if the errors associated with the measurement of so many variables are to be reduced to an acceptable level.
Figure 49. The processes involved in recruitment to the *Hypericum pulchrum* seed bank of a woodland soil as a consequence of tree windthrow, during the period when the canopy is open.

Windthrow

\[ \downarrow \]

Disturbance of the soil + canopy gap

\[ \downarrow \]

Seeds at the soil surface

\[ \downarrow \]

Germination

\[ \downarrow \]

Seedlings

\[ \downarrow \]

Adult plants

\[ \downarrow \]

Pollination

\[ \downarrow \]

Seed production

\[ \downarrow \]

Dispersal

\[ \downarrow \]

Dormancy

\[ \downarrow \]

Mortality of all plants

\[ \downarrow \]

Population extinction

-195-
A second method of deriving the yearly rate of seed input to the soil at set distances from the fall was therefore required. The method chosen was to attempt to estimate the yearly seed deposition rate from the final seed densities achieved at the time of canopy closure. These annual inputs were then plotted against the girth of the falling tree in order to derive a recruitment relationship which can be used in a simulation model.

Parameter derivation and simulation of interactions are divided into two sections, each associated with a separate subroutine.

Subroutine REPFAC is used to calculate the required parameters for each falling tree. These relate the girth of the fallen tree to the time taken for the canopy to close, area of soil disturbance and seed input at set distances from the fall. The derived dimensions are stored in two arrays which are used annually within the simulation by subroutine AUGMENT.

Subroutine AUGMENT calculates the seed input to the soil around the fall, using a random number generator with limits set by the parameters stored in the array EQNS, produced by REPFAC. The seed density is increased annually for each treefall until regrowth closes the canopy.
i) Parameters relating to subroutine REPFAC.

The simulation of fall girth and array grid coordinates has been described in Section 2.5.1 (v), as has the method of calculating the length of time for which the canopy is open.

ii) Windthrow-soil disturbance interaction.

Putz (1983) measured the windthrown trees of Barro Colorado Island tropical forests and demonstrated a relationship between the girth of a falling tree and the area of soil disturbed. Following disturbance of the seed bank, plants can colonise potential sites which extend to the edges of the mound area. The distribution of seeds from a windthrown tree mound will therefore be related to the size of the soil disturbance area and consequently the girth of the fallen tree.

A secondary effect which was revealed in Section 1.9.2 (ii) is that seeds deposited on the disturbance mound are carried by erosion to the edges. There is therefore a concentration of Hypericum seeds at this position which must be taken into consideration.

Methods

The girths of trees which had fallen within the self thinning coppice and disturbed the soil were measured at 1.3 metres above ground level. Each treefall mound was then surveyed to derive the dimensions illustrated in Figure 50.
Figure 50. The dimensions measured for windthrown trees in the areas of coppice woods.

![Diagram of tree trunk showing dimensions H and W with labels for Soil Mound and Soil pit.]

Results.

The data derived from these measurements were used to calculate regressions of the relationship between girth and the dimensions H and W. Figures 51 and 52 illustrate these relationships. They demonstrate that over the range of girths of falls within the Tamar woodlands, the relationship can be approximated to a linear function and regression equations calculated.

The derived equations

\[ H = 0.5925 \times G + 20.98 \]
\[ W = 1.308 \times G + 12.47 \]

are used by TREFAL in calculation of the disturbance dimensions of falls within the model stand.
Figure 51. Height of disturbance measured against girth for treefalls within the coppice stands.

\[ H = 0.5925(G) + 20.88 \]
Figure 52. Width of disturbance measured against girth for treefalls within the coppice stands.

\[ W = 1.308(G) + 12.47 \]
iii) The girth - seed bank recruitment relationship for windthrow.

In Section 1.9.2(ii) it was established that windthrown trees can add *Hypericum pulchrum* seeds to the soil seed bank and that the input was greatest at the periphery of the disturbance area.

With increasing girth of the falling tree the areas of soil disturbance and canopy gap are greater. This exposes more *Hypericum* seeds and allows a longer period of time for seed input to the seed bank. It would therefore be anticipated that there may be an approximate relationship between the seed input at a fixed distance from the fall and the girth of the falling tree.

In measuring this relationship it should be noted that trees with larger girths may be of greater age and fall above seed banks of lesser density, partially offsetting the effects described above. Unfortunately no account can be taken of the seed density of the disturbed soil at the time of the fall, due to the extreme spatial variability of the seed bank density (Section 1.9.2). However an estimate of the mean stand seed bank density at the time of fall may be made by use of the densities measured in the Tamar coppice survey, the time taken for the canopy to close and the measured *Hypericum pulchrum* seed bank decay rate.

There are *a priori* grounds for believing that initial seed bank density and the size of the fallen tree may both play a part in determining the final input to the seed bank. If it is assumed that following the first seed production ( in the second year after the fall ), the density of plants established on the fall
is determined by the availability of suitable sites, erosion
rates and seedling competition with mosses etc, then the initial
seed bank density may not be a critical factor in the final seed
input to the soil. On the other hand, if the number of suitable
colonisation sites on the fall remains greater than the number of
arriving seeds, then the initial density may be critical.

In order to examine the relationship of initial seed bank
density at the time of fall to the final seed input to the soil
from the disturbance, it would be necessary to measure a series
of falls of equal girth within areas of differing seed bank
density. There were not sufficient treefalls to do this and so,
for the purposes of TREFAL, it was assumed that disturbance area
is the critical factor and that seed bank density at the time of
fall has no influence.

Bearing in mind these limitations, an experiment was
conducted in order to determine the relationship between the
girth of falling trees and the completed seed input to the soil
at the time of canopy gap closure.

Methods

The girths of eight fallen trees, all of which were known to
have reinforced the *Hypericum pulchrum* seed bank, were measured
at a point that was equivalent to 1.3 m above ground level when
standing. The trees covered a range of girths from 85 - 240 cm,
and each disturbance revealed evidence of recent closure by the
presence on the disturbed soil of etiolated *Hypericum pulchrum*
plants which produced few seeds after flowering.
Using the tree ring methods described in Section 2.5.1 (iii) the year of fall and time taken for the canopy to close over each disturbance were calculated. The area of soil surrounding each fall was then sampled using the soil corer in the pattern described in Figure 53.

Figure 53. The core sampling patterns for treefall disturbance.

Section 1.9.2 (ii) demonstrated that the majority of seeds within the soil of the reinforced area are present at the edge of the disturbance. They arrive at this position both through dispersal from the plants and erosion of the disturbance mound. The coring positions must allow for this concentration as well as the increase in size of the disturbed area with larger tree girths. To achieve this cores were removed from the disturbance itself, from the edge of the disturbance, and at 30cm intervals extending out from the disturbed area. The 30cm interval was to
enable a direct correlation with the seed bank array of the TREFAL simulation.

Data from the transect of cores removed when examining the distribution of Hypericum seed from tree 16 (Section 1.9.2 (ii)), were also used in the final analysis.

Interpretation and analysis of measured core densities in relation to the requirements of TREFAL.

The densities of seed recorded at the various sampling positions on the eight treefalls are recorded in Table 14. TREFAL requires an estimate of the seed input per year at a given distance from a treefall of specific girth. In order to calculate this input several assumptions concerning the input must be made. Seed input to the soil during the period when the canopy is open will rise, as the plants colonise the fall disturbance and then decline as the canopy closes and the other species (especially Rubus and mosses) colonise the disturbance (Figure 54).

Figure 54. The time course of Hypericum pulchrum seed input on a single treefall.
Table 14 The N2 seeds / core removed at five positions on and adjacent to windthrows which had complete canopy above them.

<table>
<thead>
<tr>
<th>Fall No</th>
<th>Girth (cm)</th>
<th>Gap Length (yrs)</th>
<th>Background density (per core)</th>
<th>Measured core density A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
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<tr>
<td>6</td>
<td>85</td>
<td>8</td>
<td>2.5</td>
<td>6 15 10 6 1</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9 10 3 2 2</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
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<tr>
<td>7</td>
<td>137</td>
<td>12</td>
<td>1.5</td>
<td>0 10 3 6 3</td>
<td>18</td>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1 0 1 4 2</td>
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<td>6</td>
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<tr>
<td>8</td>
<td>170</td>
<td>32</td>
<td>1.5</td>
<td>0 14 3 7 0</td>
<td>10</td>
<td>8</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0 15 5 25 16</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
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<td>11</td>
<td>90</td>
<td>19</td>
<td>1.5</td>
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<td>19</td>
<td>41</td>
<td>6</td>
<td>0</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>0 31 4 2 0</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
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<td>13</td>
<td>175</td>
<td>25</td>
<td>1.5</td>
<td>0 1 1 8 0</td>
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<td>26</td>
<td>9</td>
<td>0</td>
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<td></td>
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<td>0 5 10 4 0</td>
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<td>6</td>
<td>7</td>
<td>2</td>
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<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
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<td>0 0 6 4 2</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>2</td>
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<tr>
<td>16</td>
<td>100</td>
<td>23</td>
<td>1.5</td>
<td>0 4 34 14 7</td>
<td>2</td>
<td>26</td>
<td>9</td>
<td>0</td>
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<td>0 0 1 2 29</td>
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<td>0</td>
<td>0 0 4</td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td>0</td>
<td>0</td>
<td>0 0 4</td>
<td></td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>0 2 8 1 4</td>
<td>0</td>
<td>0</td>
<td>0 0 4</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>160</td>
<td>34</td>
<td>1.5</td>
<td>0 0 2 3 5</td>
<td>15</td>
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<td></td>
<td></td>
<td>10 13 40 12 7</td>
<td>0</td>
<td>0</td>
<td>0 0 4</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>240</td>
<td>25</td>
<td>1.5</td>
<td>0 4 8 7 8</td>
<td>0</td>
<td>0</td>
<td>0 0 4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0 0 0 12 6</td>
<td>0</td>
<td>0</td>
<td>0 0 4</td>
<td></td>
</tr>
</tbody>
</table>

A - On the disturbance
B - Edge of the disturbance
C - 30 cm from the edge
D - 60 cm from the edge
E - 90 cm from the edge

-205-
Clearly the exact shape of the seed recruitment curve, whose general form is shown in Figure 54, cannot be determined other than by direct observation and also will probably be different for each tree.

In order to overcome this problem TREFAL assumes that the final seed bank is produced by a uniform input throughout the reinforcement period (Figure 55).

Figure 55. The average uniform seed density input to the soil used by TREFAL.

Seed input per unit area

Time(yrs)

The assumed rate will be the average of that from the fall date to canopy closure. For a constant seed bank decay rate, the total seed input to any point is given by

\[ T_r = a d^i + a d^{i-1} + a d^{i-2} + \ldots + a d^2 + a d \]

where \( T_r \) is the seed density at the end of a period of \( i \) years; \( a \) is the seed input at that position in year \( i \) and \( d \) the average annual seed bank decay rate for that species.
The average seed input $\bar{a}$ is given by

$$\bar{a} = \frac{a_1 + a_2 + \ldots + a_i}{i}$$

and $n = i$

and

$$\tilde{T} = \bar{a} \sum_{n=1}^{d}$$

Where $\tilde{T}$ is an estimate of $Tr$ at any given coring position.

At the time of sampling the number of seeds present in the soil core $T_c$ is given by

$$T_c = Tr + Tb$$

Where $Tb$ is the background level of seed bank density. By subtracting the average background level at the time of sampling the number of seeds deposited during reinforcement can be established.

Therefore $\tilde{T} = T_c - Tb$

and

$$\bar{a} = \frac{T_c - Tb}{x=i}$$

$$\sum_{x=1}^{d} \quad \ldots \ldots \quad (1)$$

-207-
The average seed input per year at a given point on or around the treefall disturbance is derived from the measured core density $T_c$ by use of equation (1). The values of $d$ derived from the young coppice woodlands and of $T_c$ from the treefall soil can be used to calculate the average seed inputs at various coring positions from the data in Table 14, and these derived values are presented in Table 15.

Table 15 The derived average annual seed input, $\bar{a}$

(\text{N}^2 \text{ seeds} / \text{m}^2 / \text{year})$, at positions on and adjacent to windthrows which had complete canopy above them.

<table>
<thead>
<tr>
<th>Fall No</th>
<th>Position</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Average seed input</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>78.0</td>
<td>183.3</td>
<td>97.5</td>
<td>27.9</td>
<td>3.9</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>92.0</td>
<td>122.8</td>
<td>8.3</td>
<td>39.0</td>
<td>11.2</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>27.9</td>
<td>107.0</td>
<td>16.5</td>
<td>135.3</td>
<td>141.5</td>
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<tr>
<td>11</td>
<td></td>
<td>93.1</td>
<td>272.9</td>
<td>57.4</td>
<td>40.3</td>
<td>4.7</td>
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<tr>
<td>13</td>
<td></td>
<td>0</td>
<td>9.5</td>
<td>36.6</td>
<td>39.3</td>
<td>33.8</td>
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<tr>
<td>16</td>
<td></td>
<td>49.0</td>
<td>46.6</td>
<td>226.6</td>
<td>36.2</td>
<td>110.1</td>
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<td></td>
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<td>126.0</td>
<td>43.6</td>
<td>29.0</td>
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<tr>
<td>24</td>
<td></td>
<td>0</td>
<td>9.0</td>
<td>57.8</td>
<td>84.8</td>
<td>39.7</td>
</tr>
</tbody>
</table>

A - On the disturbance
B - Edge of the disturbance
C - 30 cm from the edge
D - 60 cm from the edge
E - 90 cm from the edge
Discussion of results.

Figures 56, 57, 58, 59, and 60 show the calculated inputs plotted against the girth of the falling tree for each cored position. In the absence of evidence of curvilinear relationships, linear regressions have been performed on each data set and the equations are presented with the figures.

The variation about the regression is very large and appears to change with girth. It can be seen that for the first three coring positions, (on and at the edge of the disturbed area and 30cm from the disturbance), there is an apparent decrease in seed input with increasing girth. The 60cm sample position illustrates increased input with increasing girth, although the variance of the data is considerable. Finally the input at 90cm seems unrelated to girth.

Before discussing these results, it might be useful briefly to summarise those characteristics of a windthrown soil disturbance which may have an influence on the yearly introduction of *Hypericum pulchrum* seed to the soil.

First, disturbance area, which affects:

a) the number of seeds exposed at the soil surface
b) the number of sites suitable for exploitation by

*Hypericum pulchrum*
Second, canopy gap size, which affects:

c) the light environment of the soil area
d) the time required for the trees surrounding the gap to grow and close it.

In initiating the seed bank reinforcement survey it was postulated that with increased girth of the falling tree all four of these characteristics would increase, with a corresponding increase in the number of seeds added to the seed bank. The results of the survey indicate that this may not be the case. Several characteristics of the treefall which alter with girth need to be reconsidered in an attempt to explain the results.

The first possibility concerns the time span of seed bank reinforcement. It is assumed that seeds were distributed to the soil over the period of time for which the canopy was open. The gap time span can then be used as described previously to establish the yearly seed input. If for any reason (seedling competition with mosses, erosion, etc) the reinforcement period were restricted to a shorter time than that for which the canopy was open then errors would occur. However, examination of treefalls throughout the woodlands shows that seed is produced throughout the open phase, although competition with mosses does restrict colonisation of the mound by seedlings. The time factor can therefore be considered as not having a significant effect.

A second possible explanation for a decrease in the yearly input of seeds with increasing tree girth, is the effect of increased area and volume of disturbance on the environment of
the seeds and seedlings which establish on the soil. As the disturbance area increases it has been assumed that the additional soil contains approximately the mean seed bank density of *Hypericum pulchrum*. The number of sites available for colonisation has also been assumed to increase in direct proportion to the disturbance area and hence tree girth. In reality an increase in the girth of the falling tree results in larger, higher soil mounds and deeper pits. The seeds of *Hypericum pulchrum* are concentrated in the upper 10cm of the soil (Section 1.6.2 (ii)) and the soil of the pit and the base of the root ball therefore contain very low seed densities. In these areas colonisation does not take place until erosion has released the soil and uncovered seeds of the upper layers, unless seed is deposited from plants elsewhere on the disturbance. The increased height of the soil mound and steeper slopes lead to greater rates of erosion than on smaller falls. A greater period of time is therefore required for the soil to stabilise, making establishment by seedlings difficult.

Personal observations suggest that two additional environmental variables which have a substantial effect on the larger treefall mounds are drought and freezing of the soil. As a consequence of increased gap size, greater wind speeds and faster drainage due to the raised aspect of the mound sides, the larger falls are subject to drought during the summer. The soil crumbles and erodes to the lower slopes, removing established seedlings. In winter treefall mounds beneath gaps in the canopy freeze to a depth of up to 10 cm, subjecting the seedlings to heavy
mortality. Each of these environmental effects may act to reduce the number of plants and restrict the increase in density with increased mound size.

If \( L \) is taken to be a linear dimension of the soil mound (e.g., the average radius of disturbance), the volume of soil disturbed increases as a cube of \( L \). If with increased size of the fall, the number of seeds resulting from germination etc., does not follow an equivalent increase, then there will be a reduction in average soil seed density with increasing fall girth. This situation will arise if, as seems likely, the seed production increases in proportion to surface area of the mound.

The recruitment relationships derived for the seed bank input follow two forms. Those measured on the disturbance, at the edge of the mound and 30 cm from the mound illustrate decreases in seed density with increased girth. For the reasons described this may be caused by a failure of the seed production to increase proportionately with the changes in disturbance volume. Away from the mound at 60 and 90 cm the density increases or remains constant in relation to girth. At these positions soil does not dilute the falling seed and any increase reflects the total increase in production on the larger mound.

Clearly these results are based on assumptions made from a restricted data set and any inferences can only be used as guides to further analysis of the pattern of seed deposition around the fallen tree mounds. The regression equations calculated from the data are used in subroutine REPFAC to model the seed input from a fall with the degree of caution that the above restrictions place on the results.
Figure 56. The annual *Hypericum pulchrum* seed input to the fall mound plotted against the girth of the falling tree.

Density = 121 - 0.512 (Girth)
Variance = 6767
Figure 57. The annual *Hypericum pulchrum* seed input to the seed bank at the edge of the soil disturbance mound.

\[ \text{Density} = 248 - 1.12 \text{ (Girth)} \]
\[ \text{Variance} = 13271 \]
Figure 58. The annual *Hypericum pulchrum* seed input to the soil at 30cm from the edge of the disturbance mound.

Density = $203 - 0.775 \times \text{Girth}$

Variance = 39920
Figure 59. The annual Hypericum pulchrum seed input to the soil at 60cm from the edge of the disturbance mound.

Density = 0.0 - 0.377 (Girth)
Variance = 2891
Figure 60. The annual *Hypericum pulchrum* seed input to the soil at 90cm from the edge of the disturbance mound.

Density = 49.3 + 0.029 (Girth)
Variance = 7100

Seed input No. / m² / yr

Girth (cm)
iv) Simulation of the windthrown seed input matrix

Each tree which falls within the simulation model TREFAL initiates a series of calculations which determine the annual reinforcement of the surrounding seed bank. The data from these calculations, performed by subroutine REPFAC, are stored in the two dimensional arrays IRFAC, an integer array of 9 parameters and EQNS, a real array with 10. A new fall brings about an extension of these arrays by addition of the new data set.

v) IRFAC parameters

The counter IFC is used to refer to the number of the treefall within the simulation model.

IRFAC (IFC,1): This value is the length of time taken for the canopy to close over the fallen tree. It is derived from the equation measured in Section 2.5.1(iv.)

\[ \text{Time to close (yrs)} = \text{INT} \left( 10 \cdot (2.708 \times 10^{-3} \times d + 0.924) \right) \]

This value determines the length of time for which seed bank reinforcement takes place for any treefall.

IRFAC (IFC,2): This array value, initially set to zero, determines the number of years for which seed has been reintroduced to the soil from the fall. The parameter is used by the seed dispersal subroutine AUGMENT, and is increased by a unit value with each input of seed. If IRFAC(IFC,2) = IRFAC(IFC,1) seed input has finished.
IRFAC(IFC,3): This is the X value of the treefall coordinates on the stand seed bank array grid.

IRFAC(IFC,4): This is the Y coordinate on the stand seed bank array grid.

IRFAC(IFC,5-8): These are the array positions recording the dimensions of the area of soil disturbance. The use of a grid of array squares in simulating the stand seed bank ensures that a simplification of the disturbance area shape must be used. The area is reduced to a rectangle of base \( W \) and a height \( 2H \), where \( W \) and \( H \) are the dimensions measured in section 2.5.3(i)

\[
W = 1.308 G + 12.47 \\
H = 0.5925 G + 20.98.
\]

Figure 61 presents the disturbance for a treefall as it is simulated on the array grid in relation to the fall X, Y coordinates. The values of a — d correspond to IRFAC (IFC, 5-8).

IRFAC (IFC,9) This array value is reserved for use by subroutine AUGMENT. It is used to test whether seed has been dispersed to the soil in any years leading up to that in the calculation at the time of input. A further explanation will be presented when describing the AUGMENT simulation.
Figure 61 The simulated treefall seed input grid

\[ \begin{align*}
IHT & = \text{INT}(2 \times H) \\
a & = \text{INT} \left( \frac{IHT}{2} \right) \\
b & = IHT - a \\
c & = \text{INT} \left( \frac{IW}{2} \right) \\
d & = IW - c.
\end{align*} \]

vi) EQNS parameters.

Array EQNS stores the parameters for the mean and variance of seed input to the soil at the dispersal distances measured in Section 2.5.2 (iii).

Subroutine REPFAC examines whether the girth of the fallen tree is sufficient to create a canopy gap and allow seed recruitment. If the girth is less than 76cm (Section 2.5.1 (iii)) then the reinforcement parameters are all set to zero. If equal to or greater than 76cm the equations for the measured density of seed input to the fall area, the edge, 30, 60 and 90 cm are used to calculate the mean values of the model seed deposition distribution for that fall. The variance about the distribution mean is given by the variation measured in the regression equations of Section 2.5.2 (iii). The odd values of \( i \) in EQNS(IFC,i) refer to the means calculated from the equations, the even values of \( i \) refer to the variance of the data.
vii) Investigation of the seed density required for recruitment to the seed bank by windthrow.

The fall of a tree which creates the required conditions for germination of *Hypericum pulchrum* will result in a recruitment to the surrounding soil only if sufficient seeds are disturbed. If very few seeds are exposed then no seedlings may survive to maturity and there will be no input.

The rate of decline in seedling density measured on the fall disturbance is the result of a combination of predation, competition, drought, frost damage and erosion. These processes are directly or indirectly related to the size of the canopy gap created by the falling tree. A canopy opening allows increased drought and frost damage, and consequently increased erosion rates. Greater light levels increase seedling growth rates but also allow more rapid invasion of other species eg. *Rubus fruticosus*.

In general a minimum number of seeds must be exposed in order to produce any recruitment to the seed bank. Since the number of seeds exposed is largely a function of seed bank density, there is a threshold of buried seed density for a fall of given size, below which disturbance will not result in seed bank reinforcement. Unfortunately the relatively simple model used here cannot take account of the inevitable spatial and temporal variation in seedling mortality, and therefore a mean constant threshold seed bank density must be used. An example of such temporal variation is that the seedlings of the related *Hypericum perforatum* are particularly susceptible to drought (Tisdale et al. 1959)
and therefore it may be that for Hypericum pulchrum the dry summers of 1976 and 1981 increased the relevant threshold levels for those years.

Two experiments were carried out in order to assess the effects of seed bank density and seedling mortality on the density of mature plants produced after 1 year of growth. The first compared the seedling mortality rates on falls beneath complete canopies and canopy gaps, within two stands of known age. The second used differing known seed bank densities in order to evaluate a threshold level for the TREFAL model.

viii) An investigation of the influence of mortality of Hypericum pulchrum seedlings on the density of first year plants produced on a treefall mound.

With increasing woodland age, tree girth, canopy area and consequently windthrow canopy gap size increase. Tree density decreases and light levels beneath the canopy increase. Does this reduce the mortality of seedlings growing on mounds in older woodland stands, with a consequent reduction in threshold densities for a given fall girth? In an attempt to answer this question, artificial treefall mounds were created in two stands of differing age. Survivorship of the cohorts of seedlings germinating on these disturbances was then followed for a year.
Methods.

Two stands of coppice within the Tavistock Woodland Estate were examined for gaps in the canopy created by treefalls which did not produce soil disturbance. These are the result of snapping of the trunk either through wind damage or disease. Within each such canopy gap an artificial soil disturbance was created by removal of one square metre of soil to a depth of 20cm. The soil extracted was laid in a pile beside the pit, simulating the mound and pit created by a natural windthrow.

An equivalent number of disturbances were then created beneath the tree canopy within each stand area, allowing a comparison with the canopy gap results.

Table 16 shows the areas chosen, their canopy age, the number of disturbances created within them and the Hypericum pulchrum seed bank densities measured in section 1.9.2. This revealed a significantly higher (p < 0.05) density of seeds in the soil of the younger woodland.

Table 16. The statistics derived for the two areas containing the simulated treefalls.

<table>
<thead>
<tr>
<th>Area</th>
<th>Age (yrs)</th>
<th>Number of Falls</th>
<th>Seed bank density/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Open gap</td>
<td>Closed canopy</td>
</tr>
<tr>
<td>D1f</td>
<td>130</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>D2b</td>
<td>160</td>
<td>6</td>
<td>7</td>
</tr>
</tbody>
</table>
The disturbances were created in February of 1984 and examined as often as possible until March 1985. Each seedling was given a plastic label which allowed identification of fresh germinations and mortality at each visit.

Using a MEGATRON LUX METER four readings of light levels were recorded above each artificial treefall disturbance. The measurements were taken beneath a cloud covered sky in July 1984; cloud cover diffuses the incident light and removes inaccuracies caused by sunflecks. A series of readings were also taken in clear felled areas to enable a comparison of canopy, canopy gap and open canopy light levels.

Results

Tables 17 a & b show the light intensities measured above the disturbance created both under the canopy and within the treefall gaps. The values are calculated from a mean of four readings. The mean light level of a clear felled area measured at the same time was 13680 Lux.

The light levels differ significantly between canopy gaps and intact canopy for both areas \( (p<0.025) \), between the two intact canopies \( (p<0.025) \) and also between the canopy gaps for the two areas although the difference in the latter is not statistically significant \( (p<0.1) \). As anticipated the older stand has higher light levels beneath the canopy and, presumably due to the greater size of the falling trees, increased light at ground level within the fall areas.
Table 17(a). The mean intensity of incident light beneath the canopy and canopy gaps for area Dlf.

<table>
<thead>
<tr>
<th>Open gap</th>
<th>Canopy cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fall No</td>
<td>Light Intensity (lux)</td>
</tr>
<tr>
<td>1</td>
<td>1250</td>
</tr>
<tr>
<td>2</td>
<td>2463</td>
</tr>
<tr>
<td>3</td>
<td>975</td>
</tr>
<tr>
<td>4</td>
<td>1425</td>
</tr>
<tr>
<td>5</td>
<td>1550</td>
</tr>
<tr>
<td>6</td>
<td>635</td>
</tr>
<tr>
<td>7</td>
<td>715</td>
</tr>
<tr>
<td>8</td>
<td>605</td>
</tr>
<tr>
<td>9</td>
<td>960</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>1175.3</td>
</tr>
</tbody>
</table>

Table 17 (b) The mean intensity of incident light beneath the canopy and canopy gaps for area D2b.

<table>
<thead>
<tr>
<th>Open gap</th>
<th>Canopy cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fall No</td>
<td>Light Intensity (lux)</td>
</tr>
<tr>
<td>1</td>
<td>1263</td>
</tr>
<tr>
<td>2</td>
<td>1100</td>
</tr>
<tr>
<td>3</td>
<td>2063</td>
</tr>
<tr>
<td>4</td>
<td>1675</td>
</tr>
<tr>
<td>5</td>
<td>1925</td>
</tr>
<tr>
<td>6</td>
<td>1613</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>1606.5</td>
</tr>
</tbody>
</table>

$0.0043 \text{ Watts/sqm} = 1 \text{ lux}$
Recruitment to the artificial disturbance.

Tables 18 a,b,c and d show the numbers of seeds germinating between each sampling date. The first germinations did not occur until late June, throughout both stands in the gaps and beneath the canopy. It is known that Hypericum species require relatively high temperatures in order to germinate. Grime et al (1981) report that Hypericum pulchrum will not germinate at temperatures below 11°C in the field. In the South West the summer of 1984 was late, with a long cool spring, which may account for the timing of germination. During each survey year seeds within soil samples, placed in the polythene tunnels at Rumleigh Experimental Station, germinated several weeks ahead of those in the field. This indicates that external temperature may be the major factor controlling the date of the first germinations of Hypericum.

The importance of the timing of germination is related to the time at which the leaf canopy of the trees is complete. Germination in June ensures that the seedlings grow beneath the complete canopy shade, unless within a fall gap. This may reduce both germination percentage and survivorship of seedlings.

The effect of a canopy on germination can be assessed by comparing the average numbers of seedlings germinated throughout the year on the disturbance beneath the canopy with those within canopy gaps. A t test shows that canopy has no effect on germination and it can be postulated that the seeds received sufficient light through the canopy or before leaf break to stimulate germination. As already stated the date of germination may therefore be mainly affected by the onset of a suitable
Table 18a Artificial Treefall in area Dlf.

Open canopy recruitment

<table>
<thead>
<tr>
<th>FALL №</th>
<th>21.6.84</th>
<th>11.7.84</th>
<th>17.8.84</th>
<th>27.9.84</th>
<th>10.11.84</th>
<th>23.3.85</th>
<th>TOTAL</th>
</tr>
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<tr>
<td>1</td>
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<td>4</td>
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<td>0</td>
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</tr>
<tr>
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<td>0</td>
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</tr>
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<td>2</td>
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<td>1</td>
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<td>0</td>
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</tr>
<tr>
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<td>Σ</td>
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<tr>
<td>S.D</td>
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<td>1.90</td>
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</tbody>
</table>

-227-
Table 18 b  Artificial Treefall in area Dlf.

Closed canopy recruitment.

<table>
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<tr>
<th>FALL No</th>
<th>21.6.84</th>
<th>11.7.84</th>
<th>17.8.84</th>
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<td>0.76</td>
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<tr>
<td>S.D</td>
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<td>0.73</td>
<td>0.53</td>
<td>0</td>
<td>4.83</td>
</tr>
<tr>
<td>% of Tot</td>
<td>69.67</td>
<td>13.45</td>
<td>7.89</td>
<td>5.67</td>
<td>4.45</td>
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<td>100</td>
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Table 18c Artificial Treefall in area D2b.

Open canopy recruitment.

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<tr>
<th>FALL No</th>
<th>21.6.84</th>
<th>11.7.84</th>
<th>17.8.84</th>
<th>27.9.84</th>
<th>10.11.84</th>
<th>23.3.85</th>
<th>TOTAL</th>
</tr>
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<tr>
<td>1</td>
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<td>48</td>
</tr>
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<td>1</td>
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<tr>
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<td>1</td>
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<td>12</td>
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<td>( \bar{X} )</td>
<td>17.67</td>
<td>3.83</td>
<td>5.83</td>
<td>3.17</td>
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<td>S.D</td>
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<td>3.87</td>
<td>3.37</td>
<td>0.44</td>
<td>0</td>
<td>19.67</td>
</tr>
<tr>
<td>% of Tot</td>
<td>57.61</td>
<td>12.49</td>
<td>19.01</td>
<td>10.34</td>
<td>0.55</td>
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</tbody>
</table>

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Table 18.4  Artificial Treefall in area D2b.

Closed canopy recruitment.

<table>
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<tr>
<th>FALL No</th>
<th>21.6.84</th>
<th>11.7.84</th>
<th>17.8.84</th>
<th>27.9.84</th>
<th>10.11.84</th>
<th>23.3.85</th>
<th>TOTAL</th>
</tr>
</thead>
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<td>13</td>
</tr>
<tr>
<td>8</td>
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<td>2</td>
<td>6</td>
<td>4</td>
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<td>16</td>
</tr>
<tr>
<td>X</td>
<td>16.28</td>
<td>6.57</td>
<td>5.29</td>
<td>2.29</td>
<td>0.14</td>
<td>0</td>
<td>30.57</td>
</tr>
<tr>
<td>S.D</td>
<td>8.40</td>
<td>8.38</td>
<td>5.09</td>
<td>2.14</td>
<td>0.38</td>
<td>0</td>
<td>21.90</td>
</tr>
<tr>
<td>% of Tot</td>
<td>53.25</td>
<td>21.49</td>
<td>17.30</td>
<td>7.49</td>
<td>0.56</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
temperature regime and/or exposure by erosion.

An examination of Tables 18 a,b,c and d reveals that in all disturbances, the majority of seedlings appeared in an initial germination flush; responsible for 50-70% of the total seedlings marked throughout the year. Subsequently germination declined and ended in September. Germination throughout the year beneath both canopy and gaps points to sufficient light reaching the seeds through the canopy after exposure by erosion.

Table 19 compares germination for each sampling occasion between the two stand areas. The data for the canopy gaps illustrate significant differences between the sites for 2 of the sampling occasions (the first and third). The complete canopy areas have significant differences for three sampling occasions. In all cases more seeds germinated in area D2b than Dlf and differences within sites were not significant.

As described previously area Dlf is younger and has a significantly greater seed bank density. It would therefore be expected that for a fixed disturbance area a greater number of seeds would be exposed to the light in the younger woodland stand. However D2b has higher light levels than Dlf, which may explain the increased germination, although if this were the case then one might expect increased germination in canopy gaps relative to intact canopy, but this was not found.

It may be that light levels influence survivorship in the initial phase of growth between germination and identification. This could produce apparently higher germination densities from an area of lower seed density.
Tables 19 a & b A comparison of the germination of buried seeds on artificial treefalls at two sites on 5 sampling occasions. Within site differences were not significant.

Table 19 a Open gap areas.

<table>
<thead>
<tr>
<th>Area</th>
<th>SAMPLING DATE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>21.6.84</td>
</tr>
<tr>
<td>D1f</td>
<td>6.22</td>
</tr>
<tr>
<td>D2b</td>
<td>17.67</td>
</tr>
<tr>
<td>Significance</td>
<td>2.5%</td>
</tr>
</tbody>
</table>

Table 19 b Closed canopy areas.

<table>
<thead>
<tr>
<th>Area</th>
<th>SAMPLING DATE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>21.6.84</td>
</tr>
<tr>
<td>D1f</td>
<td>6.89</td>
</tr>
<tr>
<td>D2b</td>
<td>16.28</td>
</tr>
<tr>
<td>Significance</td>
<td>2.5%</td>
</tr>
</tbody>
</table>
Survivorship on the artificial disturbances.

The survivorship tables for the cohorts of seedlings from the initial flush (germinating before 21.6.84) are illustrated in Figure 62.

There is heavy mortality immediately after germination in each cohort. Growth during the summer is accompanied by a gradual reduction in numbers through erosion and drought. This is followed by heavy mortality in autumn due to the covering of seedlings by falling leaves. This is especially severe in the treefall pits. The depressions act as collectors of falling leaves and contain a litter thickness several times that of the woodland floor surrounding them. The litter cover excludes the light from the seedlings, removing all those at the base of the pit.

A second form of mortality to which the Hypericum seedlings are subject throughout winter is frost damage. Clarke (1953) has reported that for Hypericum perforatum only seedlings which have produced more than six leaves can withstand heavy frost. The canopy gap of a treefall area allows the soil temperature to fall to lower levels than those of the areas under complete canopy. This results in the soil freezing to a depth of several centimetres. The greater mortality in the canopy gaps over the winter period may therefore result from frost mortality.

It seems from Figure 62 that seedlings beneath intact canopy suffered greater mortality than those under gaps. The differences are not statistically significant for either area but nevertheless the trend seems clear. Mortality seems to be greater beneath the
Figure 62. The survivorship of four cohorts of Hypericum pulchrum seedlings emerging in the first year germination flush on artificial treefall disturbances beneath full canopy and windthrown canopy gaps within two coppice stands.
intact canopy in the very early stages of establishment, while later any differences are relatively slight.

The dominant factor affecting the population dynamics of Hypericum pulchrum on fall disturbances was assumed to be the light levels, but it now appears that other factors may also play a part, including temperature, erosion, drought or any of the environmental parameters altered by removal of the canopy.

For the purposes of the TREFAL simulation it has been found that no mature plants are present on treefall disturbances which do not create a canopy gap.

ix) Measurement of the threshold seed density required to produce a single mature plant.

The experiments measuring seedling recruitment and mortality of populations on treefall disturbance provide an illustration of the dynamics involved in establishment of mature plants on treefalls. The system is clearly complex and a simplification must be arrived at for use in TREFAL. It was therefore decided to attempt an estimation of the minimum density of seeds within the soil necessary for the production of at least one mature plant. This involved the establishment of artificial seed banks of specific densities within fall areas and the measurement of the final number of first year plants produced from them.
Methods.

Hypericum pulchrum seeds which had been hand picked and sorted were mixed in a series of densities in 250 cm³ volumes of soil. The soil had been extracted from an agricultural field and was known to contain no Hypericum seeds.

Each volume of soil containing the Hypericum seeds was then spread to a uniform depth of 2 cm in plastic seed trays. The significance of a depth of 2 cm is that this was found in laboratory experiments to be the maximum depth from which Hypericum pulchrum could germinate in disturbed soil. The trays were laid in a canopy gap, created by treefall, within the Wareham Wood coppice stands in March of 1984 and collected a year later in March 1985. The density of Hypericum plants was recorded in each tray in March 1985.

Results.

Figure 63 shows the relationship between the number of plants growing in the trays and the original soil seed density. There is clearly a correlation, and a straight line regression ( in the absence of an indication of curvature ) provides the regression equation.

\[ \text{Number of first year plants} = 0.0513 \times \text{(seed density)} + 0.387. \]

This equation was then used to calculate the number of seeds required to produce a single plant, a density of 12 seeds.
Figure 63. The relationship between the number of seeds germinating in a 250 cm$^3$ volume of soil and the density of 1st year *Hypericum pulchrum* plants

Density = 0.0513 (Seed Density) + 0.387 of plants
Discussion.

In relating the results of this experiment to the TREFAL simulation model, the differing conditions between the experiment and those on a fall mound must be taken into consideration.

The seed trays hold areas of soil which are not subject to the erosion from which natural disturbances suffer. Seedlings are therefore far less likely to be dislodged. In addition the lack of erosion will not reveal seeds buried just beneath the level to which the light can penetrate. The seeds trays will therefore tend to exhibit greater survivorship but lower repeated germination compared to natural treefalls.

The seed trays also contain a shallow layer of soil which cannot draw water from beneath. They are therefore subject to more severe drought than a treefall disturbance.

This experimental result can therefore only be used as a rough guide to the probable order of magnitude of the true threshold levels. The threshold density is one factor which could profitably be varied in order to test its effect on the outcome of TREFAL.

x) Simulation of the windthrown seed input to the soil.

Subroutine AUGMENT is the section of TREFAL which is responsible for the annual increment of the seed bank surrounding the simulated windthrows. It uses the data provided by subroutine REPFAC in the form of the arrays IRFAC and EQNS.
For each tree that has fallen since the start of the simulation run the subroutine calculates whether the canopy above it is still open. This is carried out by subtracting the length of time for which the canopy has been open from the length of time for which the gap is to be open, derived from the girth of the fallen tree. If the difference is greater than zero the canopy gap is open and the subroutine will add seeds to the surrounding soil, if the threshold seed bank density is exceeded. After each year the length of time for which the gap has been open is increased by one.

The subroutine checks whether the seed bank threshold has been exceeded on a previous occasion. If so IRFAC (IFC,9) will be set to 1. In any year if IRFAC (IFC,9) = 1 then seed will be dispersed to the model seed bank. If not, as in the case of a freshly fallen tree, the subroutine calculates the effective seed density of the fall disturbance and compares this with the threshold value measured in the previous section.

Using the parameters given by IRFAC (IFC,3-8) the subroutine calculates the density of seeds within the soil covered by the disturbance area. Clearly not all of the seeds will be brought to the surface, so that from this total density the subroutine must calculate an effective seed bank density.

The lifting of the soil by the tree roots creates a mound in which the majority of seeds are found. The pit surface contains few if any seeds. Mortality caused by litter cover will also reduce this density after germination.

It can be assumed that the mound of disturbance is a half spheroid. Germination experiments in the laboratory have shown
that *Hypericum pulchrum* seeds emerge from a maximum soil depth of 2 cm. This allows, for a given radius of spheroid, the calculation of the proportion of the soil from which *Hypericum pulchrum* can be expected to emerge i.e. the outer 2 cm layer. Using the extremes of the parameter $W$ measured in order to calculate soil disturbance area, (Minimum radius = 55 cm, maximum = 157) the range of proportions of the spheroid volume in the outer 2 cm can be calculated for the disturbances in the Tamar valley woodlands.

- Radius = 55 cm  ratio = 0.11.
- Radius = 157 cm  ratio = 0.04.

A median of 0.075

If the median ratio is multiplied by the total seed bank density within the mound, the result is the number of seeds in the outer 2 cm of soil. However the mound will be continually eroding with time, exposing a greater number of seeds than those stored in the surface 2 cm. If 25% of the radius is removed to expose all the seeds contained within it the median ratio increases to 0.58.

Clearly the enumeration of a threshold and also its subsequent incorporation into the model is very difficult. It was therefore decided initially to use a ratio of 0.2, a value equidistant between those of the median 2 cm and 25% ratios. Variation of the parameter within the model, as with the threshold value, will enable an evaluation of its effect on the model seed bank.

After calculation of the total seed density for the area of disturbance the value is multiplied by 0.2 to produce the
effective density, and this is then compared with the threshold value. If the relative density is greater than the threshold value seeds are dispersed to the soil and the value of IRFAC (IFC,9) is set to 1. This is equivalent to saying that a mature plant has been produced and that the threshold does not have to be checked again for that fall.

If the value is less than the threshold there is no seed input for that year. The threshold value of treefalls which have not resulted in an input are rechecked every year. This is to establish if the seed density of the disturbance has had an input from outside ie another fall, which has raised the density sufficiently to enable seed production. In assuming an even distribution of seeds within the mound, the model makes no allowance for contagion.

After establishing that seed is to be added to the seed bank, subroutine AUGMENT uses the mean seed input parameters for each distance from the disturbance, stored in EQNS. The mean input and standard deviation for each distance from the disturbance are used by the function RN to calculate a random seed input to each square surrounding the fall. These values are calculated and added annually until the canopy gap closes.
2.5.4 Additional TREFAL subroutines.

Two subroutine not described previously are used by TREFAL to output data.

Subroutine TDISTN calculates the distribution of girth classes in 10cm increments at 10yr intervals. The results are stored until the final year and then placed within the file GCLASS.

Subroutine SAMPLE selects 50 of the stand seed bank array units at 5 yearly intervals. The mean and variance of the units are then calculated, converted to values for metre squares, and stored for output at the end of the run.

2.5.5 TREFAL output.

At the end of a run TREFAL produces seven output files.

RUN.RES - the developments through which the tree stand density, stand mean girth, treefall density, seed bank density and sample density and variance have passed during the run. All values are produced at 5 yearly intervals.

GCLASS - the 10 yearly change in tree girth distribution.

FALL DATA - the arrays IRFAC and EQNS which are used to ensure the correct operation of the program during the run.
BAN.RES1/BAN.RES2. - the final seed bank densities of each stand array unit.

TREP - the x,y array grid coordinates, girths and year of fall of each windthrow created by the model.

F.TREES - the final positions of the remaining stand trees, with their girths.

Examples RUN.RES and GCLASS are provided in APPENDIX 9 with a complete listing of TREFAL.

2.5.6 Random number generation and side effects within the model.

When analysing a simulation model with the aim of establishing how variations in each of the constituent parameters influence the final results, two forms of random number set are required. Both forms are generated by accessing a larger set of random numbers which can be envisaged as being stored within the generating system in a table.

Non-repeatable random number sets differ with each run of the model. These are generated by accessing the data table at a new position at the start of each run. The required random numbers are then read in sequence from the table starting at this position. In order to provide a new starting position for each
run the table is usually accessed at a point which is calculated by making use of the time. Two runs will be initiated at differing times and therefore will have a high probability of having differing sets of random numbers. The data sets generated using this method allow an analysis of the range of possible outcomes resulting from a fixed parameter set.

If the results of changes made to a single parameter are to be investigated by this method, a series of runs must be performed and the probability of each of the various outcomes calculated. These probabilities are then compared with those generated by different values of the parameter after repeated simulations for each of its states. Clearly this method is impractical in terms of computer user time when investigating numerous parameters each with a wide range of values.

To overcome this problem the N.A.G. subroutines allow calculation of repeatable random numbers. In this instance the random number table is accessed in a set position for each run, the model reads the same list during each simulation. Variations in model output using the repeatable random number generator will therefore be produced only by changes made to the model parameter set. If required the N.A.G. subroutines allow generation of differing repeatable random numbers by alterations of the position of the initial table entry.

A problem with use of a repeatable random number generator is that side effects of model parameter changes may influence the output. An example is provided by alterations to the parameter TH, the threshold of seed density required before reintroduction of seed takes place. If in one run TH is set to a low value and a
reintroduction occurs on a specific fall, then the subroutines which carry out the procedure will use a fixed number of random values \((x)\). They will read these from a position \(n\) and after completion, the next random number value accessed in the table will be \(n+x\). If \(TH\) is now raised such that the threshold density is greater than that in the disturbed soil then no reintroduction takes place and the subroutines are not called. The next subroutine to call a random number accesses the table at position \(n\) rather than \(n+x\). The variation in the results of the model are therefore not only due to change in \(TH\) but also to the accessing of differing random values. To overcome this problem with \(TH\), subroutine RRAND is built into the model. It reads in the \(x\) values required by a fall input for all falls which do not reintroduce seed. This ensures that all succeeding subroutines access the \(n+x\) th value. All variations in model output are therefore solely due to changes in \(TH\).

A similar side effect occurs when changing \(DECR\), the seed bank decay rate. Lowering the rate results in fewer calculations of the probability of death for seed densities per unit of lower than 8. Consequently fewer random numbers are used as \(DECR\) is raised to reduce decay rates. This results in the removal of the repeatable characteristics of the model and the side effect of alterations to the seed bank decay rate producing differing numbers of windthrows.

The opposite effect results when \(IFFR\), the rate of fall of trees producing disturbance, is altered. Here a greater number of falls will require a larger input of random numbers. This produces changes in the times at which trees fall and the
positions and girths selected for falling.

Unfortunately through lack of time in the model building phase of the study these faults were not corrected. They must therefore be taken into consideration when analysing the results from changes in these two parameters.
2.6 Simulation results

TREFAL was used to examine the influence of the seed input generated by windthrown soil disturbance on the modelled *Hypericum pulchrum* seed bank. Each of the parameters was set to a value derived from the surveys of the Tavistock Woodland Estate coppice stands, and a series of simulation runs performed. In each case the predicted seed bank development was compared with the seed densities measured in the natural stands.

The results of three runs with all parameters set at their measured values are illustrated in Figures 64, 65 and 66. Figure 64 illustrates the decline in simulated stand soil mean seed density in comparison with the values obtained from natural woodlands. Owing to the fact that the natural stand densities were obtained from a random sampling programme and are therefore subject to sample errors, Figures 65 and 66 illustrate, for the same runs of the model, the mean seed density calculated at five year intervals from 50 random samples of the simulated soil area and the 95% confidence limits for some of these values.

The figures show that the model seed bank density falls faster than the real one. There is a slight reduction in the rate of decline when a windthrown seed reinforcement occurs, but as would be anticipated when sampling a contagiously distributed population, this is less apparent in the random sample results. In both cases the seed banks disappear from the soil before 200 years of complete canopy. It would appear that the input of seed from single falls cannot compensate for the loss of seed from the
Figure 64. The average seed bank density for the total soil area of the TREFAL simulation, plotted against stand age.

Model parameter values
DECR = 0.937
TH = 12
IFFR = 211
IFTH = 41

- No falls during the run
- 5 falls 2 of which produced a seed reinforcement at 59 & 103 yrs
- 7 falls 2 of which produced a seed reinforcement at 52 & 75 yrs
- 7 falls 3 of which produced a seed reinforcement at 69, 105 & 113 yrs
- Seed density development of the natural stands
Figure 65. The changes in seed bank density, measured from 50 random samples of the TREFAL simulation soil area, plotted against stand age.

Parameter values
- DECR = 0.937
- TH = 12
- IFPR = 211
- IFTH = 41

- No falls during the run
- 5 falls 2 of which produced a seed reinforcement at 191 & 217 yrs
- Seed density development of the natural stands

95% C.L.

Zero values

Stand age (yrs)
Figure 66. The changes in seed bank density, measured from 50 random samples of the TREFAL simulation soil area, plotted against stand age.

Parameter values

$\text{DECR} = 0.937$

$\text{TH} = 12$

$\text{IFFR} = 211$

$\text{IFTH} = 41$

- No falls during the run
- 7 falls 2 of which produced a seed reinforcement at 52 & 75 yrs
- Seed density development of the natural stands

- 95% C.L

Zero values

Stand age (yrs)
soil throughout the stand area. The model therefore reveals that given the values derived for the simulation parameters from the natural coppice stands, the rate of input of seed from treefall disturbance is insufficient to maintain a *Hypericum pulchrum* seed bank in the soil. The input is sufficient to retard the rate of loss, but only for short periods.

In order to assess the potential of treefall disturbances in reducing the rate of loss of the *Hypericum* seed bank, the parameters of the model were modified and their influence on the pattern of decay examined. As previously described this was carried out using a repeatable random number data set.

Parameter groups which have a direct influence on the seed bank dynamics are:-

i) TH, the threshold value of seed density at which a treefall disturbance will reintroduce fresh seed to the surrounding soil.

ii) the combined rates of wind-throw (IFFR) and thinning (IFTH) in removal of trees and production of soil disturbance.

iii) the rate of decay of seeds within the soil (DECR).

iv) the number of seeds produced by a fall of specific size and their dispersal range.
The first three can be adjusted within the model and their influence on the simulated seed bank assessed, but the final parameter group of seed production and dispersal cannot realistically be modified without further data. As was discussed in their derivation (Section 2.5.3 (iii)), the seed input equations were obtained from a limited data set and further conjecture as to their form, without additional experimentation, would be of little value. These parameters must therefore be considered in the final discussion but cannot be altered.

In the three remaining parameter groups the component of the simulation which has the greatest influence on seed input to the soil is the threshold value of seed density at which reinforcement occurs (TH). Any reduction in the value of TH allows a greater number of the falls in a simulation run to reintroduce seed to the soil.

Variations in the value of TH resulted in the *Hypericum pulchrum* simulated seed bank development illustrated in Figure 67. As the value of TH is progressively decreased from 20 to 0, a greater number of falls produce a seed input to the soil and the seed bank persists beneath the canopy for longer. The greatest seed bank persistence is found when TH is set to zero. This implies that a fall which creates suitable conditions for the reintroduction of seed to the seed bank, but which has no *Hypericum pulchrum* seeds in the disturbed soil, is colonised by plants arriving as seed either in the air currents or by animal dispersal. In the seed trapping experiment (Section 2.4.2) it was established that seed is not carried to great distances by
Figure 67. The influence on the decline of seed bank density of alterations to the value of TH, the threshold of seed frequency below which reinforcement of the seed bank does not occur.
the air currents, and since no animals have been described as
transporting or feeding on Hypericum pulchrum seeds, the
occurrence of a TH = 0 colonisation and reinforcement may
therefore be extremely rare.

To enable further analysis of the TH = 0 simulation the model
was reset to non-repeatable random number generation and a series
of runs performed. The results are illustrated in Figure 68. It
is apparent that even with every suitable fall producing an input
of seeds, the seed density does not reach that measured in the
natural woodlands, although the seed bank does persist at a lower
density.

When altering the parameters of the model in subsequent
simulations it was decided to hold TH constant at zero. If any
combination of parameters produced seed densities greater than
those measured in the natural stands the value of TH could then
be increased to re-examine its influence on the seed bank decay
pattern.

Figure 69 presents the results of a series of simulation runs
with all parameters constant except IFFR, the rate of fall of
trees producing disturbance, and IFTH, the rate of thinning. The
two parameters are adjusted simultaneously in order to reproduce
the decrease in tree density measured within the coppice stands
of the Tavistock Woodland Estate, i.e. the total decline in tree
density due to all causes was held approximately constant.
Figure 68. The changes in seed bank density during a series of model runs with TH set to zero.

Model parameters

TH = 0
IFFR = 211
IPTH = 41
DECR = 0.937
Figure 69. The influence of thinning and the rate of fall of disturbance creating trees on seed bank decay.

<table>
<thead>
<tr>
<th>IFFR</th>
<th>IPFH</th>
</tr>
</thead>
<tbody>
<tr>
<td>211</td>
<td>41</td>
</tr>
<tr>
<td>300</td>
<td>40</td>
</tr>
<tr>
<td>400</td>
<td>39</td>
</tr>
<tr>
<td>500</td>
<td>38</td>
</tr>
</tbody>
</table>

Log (N seeds / m²)

Stand age (yrs)
As the frequency of falls increases the simulation uses a larger set of random values and the results suffer from the previously discussed side effects, i.e. they become non-repeatable for alterations to model parameters. Seed bank decay with the values of IFFR set at 500 and 400 illustrates this problem. At approximately 200 years canopy age the seed bank of the run with IFFR set to 500 rapidly declines, followed by a recovery at 220 years with the input of seeds from a fresh fall. The seed bank of the IFFR value of 400, in contrast, increases after 200 years of canopy age.

The simulation runs with IFFR set at 400 and 500 show that with sufficiently high rates of fall the mean seed density attains an equilibrium value, the rate of decay being balanced by the input from windthrow. This equilibrium value is approximately 8 seeds/m², well below that of the natural stands. The mean seed bank density is in any case a misleading figure, since the actual seed pattern exhibited by the model consists of large areas devoid of seed with small patches of high concentrations surrounding past falls. Within the natural coppice seed banks there is a relatively even distribution of seeds surrounding the high density patches from windthrows. This is illustrated by the core sample density distributions recorded when measuring the decline of the seed bank of *Hypericum pulchrum* beneath coppice canopies of increasing age (Table 20, with mean and variance illustrated in Figure 17, page 87). Figure 15 (page 68) illustrates the relative abundance of *Hypericum* seed within the soil in a transect of cores.
Table 20. The frequency distributions of soil cores containing increasing densities of *Hypericum pulchrum* seeds, removed from coppice stands of various ages.

<table>
<thead>
<tr>
<th>Coppice Stand</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
<th>VIII</th>
<th>IX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (yrs)</td>
<td>33</td>
<td>36</td>
<td>70</td>
<td>101</td>
<td>110</td>
<td>126</td>
<td>161</td>
<td>131</td>
<td>220</td>
</tr>
<tr>
<td>N of Cores</td>
<td>20</td>
<td>30</td>
<td>50</td>
<td>50</td>
<td>50</td>
<td>50</td>
<td>50</td>
<td>50</td>
<td>50</td>
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</table>

<table>
<thead>
<tr>
<th>Number of seeds</th>
<th>Frequency of cores</th>
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</thead>
<tbody>
<tr>
<td>0</td>
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<tr>
<td>1</td>
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</tbody>
</table>

It must also be recalled that this equilibrium is only achieved with TH set to zero, i.e. an external seed input to the disturbed soil when there are no seeds exposed. Higher values of TH only delay the extinction of the seed bank.

Alterations to the rate of fall and thinning do not, therefore, appear to result in changes in the stand density which mimic those of the natural stands.
The final parameter of TREFAL which can be adjusted within the model in order to assess its influence on the seed bank decline is the decay rate of seeds within the soil (DECR).

Figure 70 illustrates the results generated after varying DECR through the range 0.937 to 0.970. A reduction in the decay rate (i.e. an increase in DECR), produces a corresponding decrease in the rate of decline of total seed bank density and an extended period of survival for the Hypericum seed bank beneath the canopy. As discussed in section 2.6 the simulated seed bank decay is afflicted by the side effects of random number selection. As the frequency of use of random numbers declines with increased survivorship of seeds, the time of fall, location and girth of falling trees are altered. The varying times at which seed input from the falls causes an upturn in the mean seed bank density illustrates this problem (Figure 70).

Extrapolation of the results produced by alterations to DECR reveals that by holding all parameters constant apart from DECR, it would require a seed survivorship in the range of 0.99-0.999 to reproduce the seed densities measured in the 100 - 240 year old coppice. This very low decay rate would not, however, reproduce the rapid decline in density followed by stabilisation found in the natural coppice stands (Figure 17). The decline would be approximately linear (on a log scale) and the values simulated beneath 70 - 100 year canopies would therefore be too high.
Figure 70. The influence on the decline of seed bank density of alterations to the value of the seed mortality rate DECR.

Parameter values

- \( TH = 12 \)
- \( IFFR = 211 \)
- \( IFTH = 41 \)

<table>
<thead>
<tr>
<th>DECR</th>
<th>0.937</th>
<th>0.945</th>
<th>0.960</th>
<th>0.970</th>
</tr>
</thead>
</table>

Stand age (yrs)
Two parameters could not be adjusted during the examination of the sensitivity of the simulation model, owing to the degree of variability in the results used to derive them. These were the number of seeds produced on a fall and their dispersal from the soil mound.

The distance over which seeds were dispersed was set at 1.2 m within the model. Figure 71 illustrates the results of a simulation run in which seven trees fell and the parameters were set at the values measured in the coppice stands. The areas of reinforced seed bank (the unshaded square) and of soil disturbance (shaded) are superimposed on the positions of all trees present at the start of a run. Even before thinning has taken place all trees are situated outside the areas of reinforcement. It is clear from Figure 71 that overlap of the seed shadow of a disturbance mound onto the soil disturbed by a subsequent tree fall is likely to be an extremely rare event. Thus the rate of fall of trees, in combination with the area over which the seeds are dispersed, is insufficient to allow an extension of the reinforced areas, given the spacing of the trees in the simulated stand, no matter how great the seed production on any individual disturbance.
Figure 71. The distribution of trees and windthrows within a stand simulation, illustrating the dispersal range of seeds from the mounds.

- Tree positions
- Area of soil disturbance
- Maximum simulated seed dispersal range

170 x 170 M
2.7 Discussion of the simulation results.

2.7.1 Implications for Hypericum pulchrum in the Wareham Wood coppice.

The results of simulation runs using the TREFAL program have shown that for the values of the model parameters measured within the Wareham Wood coppice stands, the seed input to the soil by windthrown trees is insufficient to produce the seed bank densities recorded in the older coppice stands. The fall of a tree from the canopy which also creates soil disturbance results in the production of seed in quantities which slow the decline of Hypericum pulchrum, but restricted distribution from the mound confines these seeds to a small area surrounding the disturbance. The result is large areas devoid of seed punctuated by high density patches.

Alterations to the parameters of the model have shown that with the seed input to the soil from falls set at the maximum possible values, the rate of windthrow required to maintain a seed bank of this species, even at a relatively low density, is far greater than that measured in the survey.

The major factor responsible for the failure of windthrow to maintain the seed bank of Hypericum, appears to be limited dispersal. This ensures that seed inputs from separate treefalls never interact to cause a "chain reaction", a condition that must be satisfied before a seed bank of Hypericum pulchrum could be maintained throughout the stand soil by windthrow. Although
treefall disturbance ensures that sites suitable for *Hypericum* continue to be created, the species cannot exploit the situation indefinitely through insufficient dispersal of its propagules and lack of an input from external sources.

Nevertheless the decline of the *Hypericum* seed bank does slow dramatically in older woodlands, and this may be brought about by a differential rate of decay with depth of burial, augmented by occasional seed input from windthrow. The future of the seed bank beneath the Tavistock Woodland Estates would therefore appear to be a gradual disappearance of the *Hypericum* seeds and a reversion to a seed bank typical of natural forests, composed only of the seeds produced by shade tolerant species and the airborne input (Johnson 1975, Whipple 1978).

How long the seed bank of *Hypericum pulchrum* will persist beneath the Tavistock Woodlands cannot be estimated. The seed bank present beneath the 200 year old stand is of similar size to that beneath the 100 year stand, the rate of decay illustrated by Figure 17 being extremely slow. Even after the removal of the seeds from the majority of the stand area, the reinforced patches surrounding falls will be present, possibly for another 200 years. If the canopy is removed before this period then recolonisation of the disturbed soil can take place from these seed bank reservoirs.

An unknown factor in the development of a seed bank is the life expectancy of the constituent seeds. Will the seeds of *Digitalis* and *Hypericum* reach a maximum age limit beyond which survival is not possible, or will they continue depth related decay until extinction? If there is a maximum life expectancy is
this also related to depth of burial?

Rampton and Ching (1970) have measured decreases in the rate of loss of seeds with increasing depth of burial. However, it is not clear why there is a difference in the rates of decay of *Hypericum* and *Digitalis*, species which have similar distributions in the measured profiles and comparable seed size and morphology. Studies of the mechanisms of dormancy in long term seed bank species such as *Hypericum pulchrum* and *Digitalis purpurea* in comparison with shorter lived seeds are required to clarify the situation, especially in relation to the effect of depth of burial.

Grubb (1977) stated that:

"It is probably extremely important for many subsidiary species that they can regenerate from seed that has been in the soil for decades whenever and wherever a gap arises. Examples are species of *Agrostis*, *Holcus* and *Poa* in grasslands of Western Europe and species of *Hypericum*, *Juncus* and *Verbascum* in forests in the same area, able to benefit from gaps made by treefalls."

The results of this study have established that certainly for *Hypericum pulchrum* the ability to exploit disturbance created by treefalls is a function of the length of time for which the canopy has remained closed above the seed bank. Exploitation of treefall disturbance allows *Hypericum pulchrum* to double its seed.
bank life span beneath a "closed" canopy, enabling survival for approximately 300-400 years, perhaps until the next major canopy disturbance. The life span of the *Juncus* spp. seed banks are insufficient to allow them to exploit this situation in the Tavistock woodlands.

The exactness of the TREFAL simulation has already been mentioned in the sections describing the derivation of parameters. Some of the assumptions made concerning competition effects or the simplification of seedling establishment, plant mortality and the levels of seed production from a windthrow disturbance, can be overcome with confidence considering the degree of accuracy expected of the simulation. However, other factors provide opportunities for the improvement of the model by further work, including the lack of a relationship between the seed production on a fall and the size of the seed bank at the time of fall; the absence of a relationship between the rate of windthrow or thinning and the girth of tree or age of the stand; and the seed input and dispersal equations being based on arbitrary relationships that may have differing solutions. This is especially true for the dispersal parameters which have proved critical to the simulated seed bank developments. Sensitivity analysis of the system has revealed the possible outcome of several parameter combinations none of which were able to mimic the results measured in the field. The model has therefore proved useful in assessing the dynamics of the windthrow - coppice seed bank interactions but there is room for modification.
Additional possibilities that could realistically be achieved are:

i) The addition of a three dimensional simulation for the seed bank, allowing the effect of differing rates of decay according to depth of burial to be assessed.

ii) An extension to include recruitment to the tree population, such that as the canopy gaps become too large to be closed by extension growth, the falls are replaced by tree seedlings. The model might then be altered along similar lines to that of Botkin, Janak and Wallis (1972), who developed a multispecies stand model. This would allow extrapolation to greater woodland ages and also enable an examination of the seed bank dynamics in natural forests.

iii) Further detailed investigations of all the generating functions made in this preliminary model, especially the relationship of seed input and dispersal to fall size.
2.7.2 Implications for other temperate woodlands.

The unique feature of coppice stand seed banks is the high density of seeds present as a result of repeated clearing of the canopy, which allows growth and seed production by shade intolerant plants. It is these high densities which ensure that sufficient seeds of *Hypericum pulchrum* are present to allow colonisation of disturbances when windthrows are of sufficient size to create a suitable canopy gap.

In natural temperate woodland stands such as those studied by Falinski (1978), Brewer & Merritt (1978), Runkle (1982) and White et al (1985), the seed bank would be formed after clearance by fire or storms, which would perhaps only allow the formation of a seed bank of lower density than that found beneath newly closed coppice stands. Given the likelihood of a lower seed bank density (compare, for instance, the newly closed plantation canopies to those of the 5 and 20 year coppice in Tables 7 & 8), then virtually all seeds might decay before the trees grew to sufficient size to fall and create the conditions necessary for colonisation of the soil mound. Low densities of seeds in the soils of old-growth forests of Colorado have been demonstrated by Whipple (1978).

Comparisons of the windthrow disturbance rate measured in the coppice stands with other temperate forests are hampered by a lack of published data. The majority of studies have either compared the causes of tree mortality by examining past falls without attempting to measure the time period over which they occurred, or have measured the rate of canopy gap formation...
without giving the cause (Runkle 1981, White et al 1985).

Falinski (1978) established that for the forests of Baloweiza, Poland, the rate of windthrow was 0.96 - 2.16 trees/hectare/year; Brewer & Merritt (1978) measured a rate of 0.205 trees/hectare/year and quote Webster and Gough (1959) as measuring a rate of 0.1 - 0.2 trees/hectare/year in a secondary woodland (the Tavistock coppice survey measured a rate of 0.08 trees/hectare/year). Converted for use in the TREFAL simulation model, the rates measured by Falinski (1978) and Brewer & Merritt (1978) are above those which produce a stable seed density for Hypericum pulchrum, but at substantially lower than measured densities; only the upper value of Webster & Gough (1959) will result in an equilibrium density. The seed pattern throughout the soil at this equilibrium was composed of areas of high density surrounding the falls and zero density between them.

This equilibrium could only be achieved with the threshold for the number of seeds required in the disturbed soil (TH) set to zero. The biological implication of a zero threshold is that there is a wind or animal dispersed seed input to all fall disturbances, a situation previously found for some species in forests (Falinski 1978, Marks 1983), but not for Hypericum.

In contrast to these rates Harcombe & Marks (1983) found no uprooted trees in a five year study of a Fagus - Magnolia forest in Texas, U.S.A.
Putz et al (1983) compared the various modes of mortality of canopy trees within studies of forest dynamics. They found that the range of the percentage of uprooted trees was considerable as is shown by their list of temperate and tropical studies with the addition of the Tavistock data:

<table>
<thead>
<tr>
<th>Author</th>
<th>Snapped</th>
<th>Uprooted</th>
<th>Died Standing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperate forests.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Runkle (1982)</td>
<td>67</td>
<td>19</td>
<td>10</td>
</tr>
<tr>
<td>Harcombe and Marks (1983)</td>
<td>21</td>
<td>0</td>
<td>77</td>
</tr>
<tr>
<td>Gordon (1973)</td>
<td></td>
<td>12 - 72</td>
<td></td>
</tr>
<tr>
<td>Falinski (1978)</td>
<td>7</td>
<td>48</td>
<td>45</td>
</tr>
<tr>
<td>Boe (1965)</td>
<td></td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>Tavistock data</td>
<td></td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Author</th>
<th>Snapped</th>
<th>Uprooted</th>
<th>Died Standing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Putz et al (1983)</td>
<td>70</td>
<td>25</td>
<td>10</td>
</tr>
<tr>
<td>Wood (1970)</td>
<td></td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Jones (1956)</td>
<td></td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>P.D.Coley (Putz et al 1983)</td>
<td></td>
<td>37 &amp; 34</td>
<td></td>
</tr>
</tbody>
</table>
Variation in the rate of uprooting as a percentage of total mortality does not necessarily imply differences in the actual rate of soil disturbance because total mortality rates will also differ between forests. However the various rates measured by Falinski (1978), Brewer & Merritt (1978) and Harcombe & Marks (1983) seem to indicate that there is variation in the degree of disturbance throughout temperate forests.

Soil type and exposure to wind may also play a role. Putz et al. (1983) found no correlation of windthrow rate with topography but Brewer & Merritt (1978) found higher rates of uprooting on dense clay.

Brewer & Merritt (1978) and Runkle (1982) have also measured interspecific differences in the rate of fall of canopy trees. Runkle (1982) presents the following table:

<table>
<thead>
<tr>
<th>Species</th>
<th>No. formi ng gaps</th>
<th>% Uprooted</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em></td>
<td>9</td>
<td>22</td>
</tr>
<tr>
<td><em>Acer saccharum</em></td>
<td>64</td>
<td>11</td>
</tr>
<tr>
<td><em>Aesculus octandra</em></td>
<td>17</td>
<td>18</td>
</tr>
<tr>
<td><em>Betula lutea</em></td>
<td>17</td>
<td>5</td>
</tr>
<tr>
<td><em>Castanea dentata</em></td>
<td>7</td>
<td>50</td>
</tr>
<tr>
<td><em>Fagus grandifolia</em></td>
<td>237</td>
<td>19</td>
</tr>
<tr>
<td><em>Fraxinus americana</em></td>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td><em>Halesia carolina</em></td>
<td>71</td>
<td>17</td>
</tr>
<tr>
<td><em>Magnolia fraseri</em></td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td><em>Tilia heterophylla</em></td>
<td>47</td>
<td>6</td>
</tr>
<tr>
<td><em>Tsuga canadensis</em></td>
<td>163</td>
<td>7</td>
</tr>
</tbody>
</table>
Brewer & Merritt (1978) found in a Beech - Maple forest that the percentage of uprooting differed between species, beech having the higher rate, and also that the uprooted size class distribution of each species was in proportion to their size class distribution within the canopy for the majority of classes, but beech of greater than 75 cm DBH were more susceptible to uprooting.

Putz et al (1983) have shown that the mode of mortality will be related to the growth form of the tree, in terms of the structural shape and the wood properties. Clearly the tall, etiolated form of coppice trees will be conducive to snapping rather than uprooting, although in the highly competitive environment of the coppice stands standing death through competitive shading appears to be the main form of mortality.

The above factors ensure that the TREFAL model would have to be individually tailored to each forest to be used for predictive purposes. It should also be noted that the stand structure of a natural forest, unless "recently" disturbed, will be a mosaic of species, girths and canopy areas; not the monospecific even aged stand modelled in this study. There will be gap replacement of falls in addition to extension growth of the surrounding trees. As described previously a more elaborate model is needed to allow predictions of the possibility of a species surviving on windthrows in these environments.
Brewer and Merritt (1978) calculated that within the stands that they studied, the measured rate of soil turnover by windthrow would require 4167 years to completely cover one hectare of soil surface. By extending their average area of fall disturbance to include the radius of dispersal from a soil mound measured in this study for *Hypericum pulchrum* and by using the same rate of disturbance, the time to disperse *Hypericum* seeds over a hectare of natural forest can be calculated. In Section 1.9.2(ii) the average radius of dispersal of seeds measured from the disturbance mounds by transects of cores was 2.5 metres. This corresponds to a time to disperse seeds over a hectare of 785 years. In the seed trapping experiment Section 2.4.2(ii) the seed was dispersed to approximately 1.5 metres corresponding to a time to cover the hectare of 1307 years. Both times are still considerably beyond the length of time for which *Hypericum* has been found to exist in the soil.

Similarly if we assume, starting with the lower densities likely to be found beneath natural forests, that *Hypericum pulchrum* can exist in the soil for 100 years, then it can be calculated that the seeds would have to be dispersed at least 12.5 m from a fall to enable windthrow to provide a complete coverage of a hectare within 100 years, and thus allow continued existence of the species in the seed bank. The higher rates of disturbance measured by Falinski (1978) reduce the distance of dispersal to 3.9 - 5.8 metres. Bird or animal dispersal over greater distances would reduce the time the seeds would need to remain viable within the soil, but this will reduce the probability of arrival of seed at any site which may result in an
increase in the time spent in the soil ( see the next section ).
Large dispersal distances are characteristic of the animal
dispersed gap colonising species of the North American forests
discussed by Marks (1983) and the wind dispersed species of the
European forests examined by Falinski (1978).

Marks (1983) studied the forests of Eastern North America in
order to find a solution to the question:

" In the primeval landscape ( when the land was covered
by forest ) where were the plants associated with old
field succession today ?"

He identified four possible answers:

1) The successional old field plants evolved on agricultural
land abandoned by Indians.
2) They migrated eastwards following the opening of railway
tracks and the clearance of the forest.
3) Native field plants were the true pioneer or early
successional species that colonised temporary openings caused
by fire, wind and other types of damage to the original
forest. Populations maintained by moving from one temporary
opening to another.
4) They were originally restricted to marginal habitats where
the physical environment prevented forest development.
The first hypothesis was rejected on the grounds of where were the plants before the Indian clearances? The second by the fact that many old field plants have eastern distributions and were described in the eastern floras before clearance of the forests.

Marks (1983) selected 13 species representative of the old field succession and examined their distribution within present day marginal habitats to which forest cannot extend; their distribution within forest canopy gaps; references to the species in past surveys within forest before the onset of clearance; and also the seed dispersal ability of the species in both time (dormancy within the soil) and space. He found that although the species were occasionally found within forest openings in recent and past studies, the sites examined were close to possible sources of seed; no remote sites contained field species.

Marks (1983) also found that rapid growth of woody species within the forest openings restricted colonisation by field species. Colonisation was restricted, except for extreme cases, to one or two years and it was highly unlikely that an intolerant species could become established with a high probability of setting seed after the second or third germinating season.

(Within the TREFAL model it was assumed that the Hypericum recruitment to the seed bank persisted throughout the period of time for which the canopy was open. Growth of shrubs or tree seedlings on or around the mounds is not a limiting factor to establishment. Hypericum plants, although etiolated,
were established beneath recently closed canopy gaps, so that the assumption of reinforcement throughout the gap phase is justified. These limitations to recruitment would have to be simulated if TREFAL were to be extended to natural forests. 

Marks (1983) also classified the old species into divisions of seed dispersal in relation to space and time. Using this method he established that four species would be suitable for gap colonisation by use of animal dispersal and a relatively long seed bank dormancy period. Of the four only *Rhus typhina* was found within forestry openings in past and present floras. He postulated that the majority of old field species would therefore be found in permanent marginal habitats, free from forest, with occasional distribution to adjacent canopy gaps. Only *Rhus typhina* and three species not considered in the thirteen, but known to exist in forest openings (*Prunus pennsylvanica*, *Rubus strigosus* and *Phytolacca americana*), could exploit canopy gaps by means of good dispersal in space (animal dispersal), and time (seed bank dormancy).

As described by Auclair & Cottam (1971) the species which are able to successfully exploit openings in the canopy of forests have:

1) High reproductive potential, producing large numbers of seeds which are usually bird dispersed, ensuring rapid widespread invasion.

2) Mechanisms delaying germination enabling large numbers of seeds to accumulate through a period of years.
3) Seedlings which are vigorous and show no strong seed bed requirements except freedom from competition.
4) Rapid growth under favourable conditions.
5) Tolerance of regressive influences.

*Hypericum pulchrum* could be placed with the marginal species. It has high reproductive potential and good dispersal in time allowing it, in a favourable environment, to accumulate a large seed reserve which has been shown to last for over 200 years. It only requires exposure to light and the correct temperature regime in order for its seedlings to germinate. However, it lacks sufficient dispersal in space, relying on wind dispersal in a relatively sheltered forest environment and its seedlings are also susceptible to shade, drought and freezing. This life history strategy may allow *Hypericum* to survive in open forest or regularly disturbed scrub, occasionally entering forest after major disturbances, but it will not survive beneath relatively stable canopies.
2.7.2 Implications for tropical forest.

Exploitation of a seed bank and windthrow disturbance has also proved to be a potential mechanism for maintenance of tree species within a tropical canopy. Symington (1933), Guevara and Gomez Pompa (1972), Cheke et al (1979), and Putz (1983) have found seeds of early pioneer tree species within the soil of tropical forests. This reserve of propagules allows them to exploit randomly created gaps in the canopy and is one of the mechanisms by which diversity of canopy species is maintained within tropical forests (Hubbell and Foster 1986).

Putz (1983) has established that 11 tropical tree species which were present in a seed bank appeared on treefall disturbance in the forests of Barro Colorado Island. The ability of these species to coexist in the competitive environment of the tropical canopy is dependent on their rapid growth to fill a canopy gap and produce seed before any competitor excludes them.

The seed bank longevity of pioneer tropical tree seeds has been reviewed by Whitmore (1983), who found that in published studies the modal seed bank life span was one year with few species exceeding this period. As with the short lived seed bank species in the soils of the Tavistock survey, the seeds were confined to the uppermost layers of the soil profile (Whitmore 1983, Enright 1985). Putz (1983) measured densities of 742 seeds/m² to 10 cm and 84 seeds/m² from 10 - 20 cm in the soils of Barro Colorado Island; Cheke et al (1979) also found seed to 20 cm.
Cheke et al (1979) measured the distribution of seeds of pioneer trees within seed banks in Thailand. They found viable seed of four species at up to 175 m from the nearest possible source. With a dispersal range of 175 m the area to which seeds of these species are distributed is approximately 9.6 hectares.

Putz (1983) measured a rate of windthrow in the Barro Colorado Island forests of 3.28 trees / hectare / year. Given similar dispersal ranges in the two forests, pioneer trees could therefore exist within the canopy, even without a seed bank, if their rate of windthrown gap capture is greater than or equal to 1 in 30. Brokaw (1982) also measured the rate of gap formation within the tropical forests of Barro Colorado Island, finding a rate of formation of 0.19 gaps per hectare per year suitable for pioneer species (> 150 square metres). Putz (1983) has established that 17% of the Barro Colorado Island gaps are formed by uprooting, and the actual rate of uprooting gap formation that would be derived from Brokaw (1982) would therefore be less than that measured by Putz (1983). The rate of gap capture by pioneer trees exploiting seed bank disturbance would therefore have to be greater, or seed bank longevity increased, to maintain the species within the canopy.

Short periods of seed bank dormancy of pioneer tropical trees may be a mechanism enabling the species to exploit seasonality of the formation of gaps within the forest canopy (Brokaw 1982). As Whitmore (1983) has stated the demonstration that seeds accumulate within tropical soils may by itself be of limited biological significance. Seeds dispersed late in the rainy season or in the following dry season remain dormant in the soil until the next rainy season (Garwood 1982).
It would be interesting to examine the interaction between seed bank longevity and seed dispersal mechanisms and distances in the life history strategy of pioneer tree species. Evidence of a relationship is found in Whitmore (1983), in which he describes the results of Hall & Swaine (1980) who discovered that few of the seeds in their soil samples were wind dispersed. Whitmore (1983) cites this as possible evidence that wind dispersed seeds arrive in the seed rain and only animal dispersed seeds occur in the seed store. Cheke et al (1979) reported that all the pioneer trees germinating from the Malaysian tropical forest soils that they sampled were bird dispersed. Putz (1983) found 11 species of pioneer trees in the seed bank of the Barro Colorado Island forests. Of the six species he lists, Miconia argentea, Cecropia insignis (which comprise 69% of the total), Zanthoxylum paramense and Trema micrantha are animal dispersed. Two wind dispersed pioneer species are listed, only one of which (Luhea seemannii) was found in low density.

In the temperate forests of North America, Marks (1983) found that the only species that could regularly colonise forest canopy gaps from the seed bank were also all bird dispersed. Within the Tavistock Woodland Estate seed banks Rubus fruticosus, which is bird dispersed, is the only species exhibiting these characteristics.

Using seed traps within a Brazilian subtropical montane rain forest, Jackson (1981) measured an inverse correlation between seed size and the probability of arrival of seed at a site. Larger seeds tended to be animal dispersed and therefore had a reduced probability of reaching a site in comparison with
smaller, more evenly distributed, wind dispersed seeds. A reduction in the probability of reaching a suitable regeneration niche may be counteracted by the development of dispersal in time (seed bank dormancy) enabling animal dispersed pioneer species to exploit canopy gaps.

The small size characteristic of the seed of pioneer trees (Putz 1983) may aid in dispersal into gaps by wind and may also be an advantage in penetrating the litter layer of the forest floor and therefore entry into the seed bank beneath. However, not all suitable canopy gaps are created by uprooting; many result from snapping of the tree trunk (e.g. Putz et al. 1983): 70% snapped, 10% uprooted). It would therefore be of advantage to the seedling to be of sufficient size to be able to penetrate the litter layer (Thompson 1987); the small seeds of wind dispersed species produce small seedlings which may only be suited to colonising areas of bare soil. Seed bank dormancy in animal dispersed species may therefore result from selection pressures for the characteristics of Auclair & Cottam (1971) (vigorous seedlings with no seed bed requirements; rapid seedling growth; tolerance of regressive influences), and also the reduced probability of arrival at a site through exploitation of animal dispersal to distribute the heavier seeds that these characteristics imply.

Evidence of a dichotomy in seed longevity within the soil, in relation to the size and dispersal strategy of pioneer species, is also found in the characteristics of the guilds of tropical forest canopy species (separated by differences in regeneration requirements) described by Hubbell and Foster (1986). Two guilds
exploit gaps within the canopy. Early pioneer species persist as dormant seeds in the soil. They have fast growth rates, with early maturation, and flower while still small; they produce seeds which are generally bat or bird dispersed. Late secondary species are of greater stature than early pioneer species, they also persist for longer within the canopy. Many are emergent species (growing taller than the canopy), and have seeds which are wind dispersed (particularly the emergent species) or are distributed by ground mammals. For wind dispersed tree species with a vast production of seed over many years and a height advantage to seed dispersal (in comparison with Hypericum and Digitalis), the seed bank life span may only need to be relatively short to enable exploitation of soil exposed by seasonal windthrows. Pioneer trees which do have a reserve of seeds in the soil are known to be small in comparison with canopy species which exploit other regeneration mechanisms (T.C. Whitmore, pers. comm.).

The greater diversity of trees in tropical as compared to temperate forests has raised much debate; a review of the main theories is provided by Leigh (1982). Could these theories also be responsible for the greater number of pioneer species able to exploit canopy gaps by use of a seed bank beneath tropical forests? Is the canopy gap environment in the tropics more variable, providing regeneration niches for a greater diversity of species? Are the rates of gap formation higher in the tropics?
Ricklefs (1977) suggested that through greater environmental heterogeneity under gaps in tropical canopies, in comparison with temperate forests, a greater number of species could be adapted to exploit openings. He put this explanation forward for inclusion in the list of factors thought to be responsible for the greater species diversity in tropical vegetation. In contrast, a detailed study of the species germinating within gaps on Barro Colorado Island by Hubbell & Foster (1986) found no evidence for specialisation of regenerative niches, the majority of species showing statistical indifference to microsite differences. Nevertheless Brokaw (1982), Denslow (1980), Hartshorn (1978, 1980) and Whitmore (1974) have all stated that the gap size and the seasonal timing of gap formation and seed germination will all affect establishment within the regeneration niche and therefore the species which colonise it.

The rate of gap formation, measured as the turnover rate of the canopy, has been found by Brokaw (1982) to be similar to that measured by Runkle (1978) in temperate forests. In a further study of old growth mesic forests Runkle (1982) measured rates of canopy turnover which were similar to three other studies in temperate forests (Heinselman 1973, Zarickson 1977 and Abrell & Jackson 1977), and to two studies in tropical forests (Leigh 1975, Hartshorn 1978). The mode of mortality to which the canopy trees are subjected also varies considerably within the two forest environments (page 270), but does not appear to differ systematically between temperate and tropical forest.
However, the rates of windthrow measured in temperate forests (Falinski (1977) 0.96 - 2.16 trees / hectare / year, Brewer & Merritt (1978) 0.205 trees / hectare / year, Webster & Gough (1959) 0.1 - 0.2 trees / hectare / year), do appear to be lower than those of tropical forests measured by Putz (1983) which can be calculated as 3.3 trees / hectare / year, but as previously stated rates derived from Brokaw (1982) may be lower. Hubbell and Foster (1986) state that the rate of canopy gap formation is related to topography (wind exposure) but Putz et al (1983) found no correlation with slope of the forest floor.

It would appear from the literature that there may be no significant differences in the rate of windthrown disturbance between temperate and tropical forests. The greater diversity of species colonising from the seed bank of tropical forests may therefore be related to other factors such as the availability of dispersal agents for the larger seed sizes required for penetration of litter or producing seedlings of sufficient size and reserves to tolerate a degree of shading. It may also be a result of variation in the annual level of fecundity allowing rare species to increase in density (Leigh 1982).
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Appendix 1(a). The distribution of species seeds, by depth, in soil cores removed from a Japanese Larch (Larix leptolepis) plantation in Morewellham Woods.

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-296-
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Appendix 1(b). The distribution of species seeds, by depth, in soil cores removed from a Japanese Larch ( *Larix leptolepis*) plantation in Morewellham Woods.

Samples removed as part of the Morewellham transect.

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Appendix 1(c). The distribution of species seeds, by depth, in soil cores removed from a Beech (*Fagus sylvatica*) plantation in Blanchdown Woods.

**Agrostis spp.**

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Appendix 1(d). The distribution of species seeds, by depth, in soil cores removed from an oak coppice stand (*Quercus*) in Wareham Woods

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Appendix 2(a) The number of seeds per core for species germinating in the seed bank transect in Morewellham Wood.

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s.d 2.05 1.44 3.80 5.2 4.53 2.83

I - *Hypericum pulchrum*
II - *Digitalis purpurea*
III - *Rubus fruticosus*
IV - *Cardamine pratensis*
V - *Juncus sp.*
VI - *Epilobium spp.*
Appendix 2(b) The number of seeds per core for species germinating in the seed bank transect in Morewellham Wood.

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s.d   4.37 11.12 2.91 0.27 1.00 1.63

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VIII - Agrostis spp.
IX - Sagina procumbens
X - Holcus lanatus
XI - Luzula sylvatica
XII - Ranunculus repens
Appendix 2(c) The number of seeds per core for species germinating in the seed bank transect in Morewellham Woods.

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\[ s.d = 0.99 \quad 1.54 \quad 2.40 \quad 13.35 \quad 10.04 \quad 19.74 \]

XIII - Cirsium arvense
XIV - Rumex acetosella
XV - Trifolium repens
Appendix 3(a) The number of seeds per core of species germinating in the Blanchdown Beech (Fagus spp.) plantation transect

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I - *Trifolium repens*
II - *Juncus spp.*
III - *Agrostis spp.*
IV - *Luzula sylvatica*
V - *Rubus fruticosus*
Appendix 3(b) The number of seeds per core of species germinating in the Blanchdown Beech (*Fagus* spp.) plantation transect

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I - *Trifolium repens*
II - *Juncus spp.*
III - *Agrostis spp.*
IV - *Luzula sylvatica*
V - *Rubus fruticosus*
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- Hypericum pulchrum
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- Carex spp.
- Agrostis spp.
- Luzula sylvatica
- Juncus spp.
- Epilobium spp.

-315-
Appendix 5(a). The number of seeds per core germinating in the Wareham Wood seed bank transect.

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continues in 7(b)

I - Rubus fruticosus  
II - Hypericum pulchrum  
III - Betula pubescens  
IV - Epilobium spp.  
V - Luzula sylvatica  
VI - Agrostis spp.
### Appendix 5(b) The number of seeds per core germinating in the Wareham Wood seed bank transect.

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\[ \bar{X} = 0.88 \quad 1.27 \quad 0.08 \quad 0.08 \quad 0.08 \quad 0.15 \quad 2.5 \]

\[ \text{s.d} = 1.56 \quad 1.68 \quad 0.28 \quad 0.28 \quad 0.33 \quad 0.80 \quad 2.8 \]

I - *Rubus fruticosus*
II - *Hypericum pulchrum*
III - *Betula pubescens*
IV - *Epilobium spp.*
V - *Luzula sylvatica*
VI - *Agrostis spp.*
Appendix 6. The number of seeds per core for species germinating in the ride seed bank transect.

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\[ \bar{x} = 5.6 \quad 4.8 \quad 3.6 \quad 1.2 \quad 0.3 \quad 0.1 \quad 0.2 \]

s.d \[ 15.0 \quad 5.0 \quad 5.1 \quad 1.7 \]

I  - Juncus spp.
II - Rubus fruticosus
III - Hypericum pulchrum
IV - Luzula sylvatica
V  - Oxalis acetosella
VI - Carex spp.
VI - Agrostis spp.
Appendix 7. WOODLAND The coppice stand tree simulator.

PROGRAM WOODLND

A MODEL DESIGNED TO PRODUCE A STAND OF COPPICE TREES OF
REQUIRED GIRTH CLASS DISTRIBUTION

This model is designed to produce a stand of coppice trees to be
used by the program TREFAL, in simulating the development of a
self-thinning woodland. The trees are positioned within a 170x170
array ensuring that there is no overlap of adjacent canopies.

INPUT FILES-

TDATA- CONTAINS THE PARAMETERS DESCRIBING THE REQUIRED
WOODLAND STAND DISTRIBUTION

  a) THE NUMBER OF GIRTH CLASSES. (NOC)
  b) THE SMALLEST CLASS SIZE (cm)
  c) THE CLASS INCREMENT (cm).
  d) NOC FREQUENCY CLASSES.

OUTPUT FILES-

TREES- CONTAINS THE TREE ARRAY POSITIONS, GIRTHS
AND CANOPY RADII

INTEGER TREXY(130,2), NOTC(20)
REAL TRERC(130,2), RADC(20)
OPEN(5, FILE='TDATA')
* READ NUMBER OF CLASSES
READ(5,10)NOC
10 FORMAT(12)
* READ SMALLEST GIRTH CLASS
READ(5,30)SC
30 FORMAT(F6.2)
* READ THE CLASS WIDTH
READ(5,30)RINC
30 FORMAT(F6.2)
* READ CLASS FREQUENCIES
DO 100 I=1,NOC
READ(5,30)ITN
100 CONTINUE
CLOSE(5)
* CALCULATE THE GIRTH SIZE FOR EACH CLASS
PROGRAM WOODLND

DO 110 IB=1,NOC
RADC(I3)=(SC*(RINC*IB)-RINC/2.00)
110 CONTINUE

* POSITION OF THE FIRST TREE AGAINST WHICH THE
* SUCCEEDING TREES ARE CHECKED

IX=LN(170)
IY=LN(170)
TREXY(1,1)=IX
TREXY(1,2)=IY
TRERC(1,2)=0 0
TRERC(1,1)=0 0
I3=1

* CALCULATE THE SCALE FACTOR RELATING Girth TO
* CANOPY AREA.

CALL SCALE(RADC,NOC,NOTC,SCA)

* CALCULATE THE POSITIONS OF THE REQUIRED NUMBER OF TREES.
* ENSURING THERE IS NO OVERLAP OF CANOPIES.

DO 130 I1=NOC,1,-1
DO 140 I2=1,NOTC(I1)
120 IX=LN(170)
IY=LN(170)
TCANR=SCA*RADC(I1)
CALL CHECK(IX, IY, TCANR, TREXY, TRERC, I3, IFLAG)
IF(IFLAG.EQ.0)THEN
  ICO=ICO+1
  IF(ICO.EQ.1000)THEN
    ICO=0
    CALL SCAN(TCANR, TREXY, TRERC, I3, IX, IY)
    IF(IX EQ -1)THEN
      PRINT *, 'STUCK'
      STOP
    ENDIF
    GOTO 300
  ENDIF
  GOTO 120
ENDIF
GOTO 130
ENDIF
300 I3=I3+1
TREXY(I3,1)=IX
TREXY(I3,2)=IY
TRERC(I3,1)=RADC(I1)+4-LN(N)
TRERC(I3,2)=TCANR
140 CONTINUE
130 CONTINUE

* FILE THE TREE POSITIONS, Girths, AND CANOPY RADII.

OPEN(6,FILE='TREES')
DO 131 I=1,I3
WRITE(6,135)TREXY(I3,1),TREXY(I3,2),TRERC(I3,1),TRERC(I3,2)
135 FORMAT(2(I4, 5X),2F8.3)
131 CONTINUE
CLOSE(6)
PROGRAM WOODLND

STOP
END

* * * SUBROUTINES

* * CALCULATE A RANDOM NUMBER FROM 1 TO N

INTEGER FUNCTION LN(N)
INTEGER N
LN=INT(((N-1)*RND(0))+1)
RETURN
END

* * SUBROUTINE TO CALCULATE THE SCALE FACTOR RELATING Girth TO CANOPY AREA

SUBROUTINE SCALE(RADC, NOTC, SCA)
REAL RADC(20)
INTEGER NOTC(20)
TAREA=0.0
SAREA=0.0
STAREA=0.0
DO 200 IC=1, NOTC
G=RADC(IC)
TNC=NOTC(IC)
SAREA=G*G*3.142*TNC
TAREA=TAREA+SAREA
200 CONTINUE
SQSCA=30230/TAREA
SCA=SQRT(SQSCA)
RETURN
END

* * CHECK FOR OVERLAP

SUBROUTINE CHECK(I%, IY, TCANR, TREXY, TRERC, I3, IFLAG)
INTEGER TREXY(130,2)
REAL TRERC(130,2)
IFLAG=1
DO 400 I4=1, I3
SQD1=ABS(I4-TREXY(14,1))
SQD2=ABS(IY-TREXY(14,2))
SQD3=SQD1**2+SQD2**2
DIST=SQRT(SQD3)
SEP=TCANR+TRERC(I4,2)
IF(DIST.LE. SEP) THEN
IFLAG=0
ENDIF
400 CONTINUE
RETURN
END

* * CHECK FOR EMPTY SPACES IN THE ARRAY.

SUBROUTINE SCAN(TCANR, TREXY, TRERC, I3, IX, IY)
INTEGER TREXY(130,2)
REAL TRERC(130,2)

-321-
PROGRAM WOODLND

IX=LN(170)
IY=LN(170)
DO 300 I3=IY,170
DO 600 I6=IX,170
   CALL CHECK(I6, I3, TCANR, TREXY, TRERC, I3, IFLAG)
   IF(IFLAG.EQ.1)THEN
      IX=I6
      IY=I3
      GOTO 1000
   ENDIF
300 CONTINUE
600 CONTINUE
DO 700 I7=1, IY
DO 800 I8=1, IX
   CALL CHECK(I8, I7, TCANR, TREXY, TRERC, I3, IFLAG)
   IF(IFLAG.EQ.1)THEN
      IX=I8
      IY=I7
      GOTO 1000
   ENDIF
700 CONTINUE
800 CONTINUE
1000 RETURN
END
Appendix 8. CONBANK The coppice stand seed bank simulator.

PROGRAM CONBANK

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AUTHOR    CHRIS DARBY
PLYMOUTH PLOYTECHNIC
ECOLOGY RESEARCH

DATE        29/1/86

A PROGRAM TO SIMULATE THE HYPERICUM PULCHRUM SEED BANK
BENEATH A STAND OF YOUNG COPPICE TREES.

-----------------------------------------------

This program is designed to build a seed bank of known
seed density, by repeatedly superimposing a measured seed
distribution pattern onto a simulated soil area

OUTPUT FILES-

C.BANK1.C BANK2 - CONTAIN THE 170*170 ARRAY GRID OF
REQUIRED DENSITY OF SEEDS.

INTEGER BANK(170,170), IADD(7)

DENSITY REQUIRED.

D=7035

SCALAR X

X=4

ENSURE THAT EACH ARRAY POSITION HAS AN INITIAL
DENSITY OF ZERO SEEDS

DO 30 J1=1,170
DO 35 J2=1,170
BANK(J1,J2)=0
35 CONTINUE
30 CONTINUE

SET THE DISTRIBUTION PATTERN PARAMETERS

IADD(1)=INT(1*X)
IADD(2)=INT(3*X)
IADD(3)=INT(4*X)
IADD(4)=INT(31*X)
IADD(5)=INT(232*X)
IADD(6)=INT(630*X)

DO 100 I1=1,20000
DENS=0.0
100 CONTINUE

CHECK THE DENSITY REACHED.
DO 600 I10=1, 170
DO 700 I11=1, 170
DENS=DENS+REAL(BANK(I10, I11))
700 CONTINUE
600 CONTINUE
DENS=DENS/(51*51)

* IF THE REQUIRED DENSITY IS EXCEEDED STOP.
IF(DENS GE D)THEN
GOTO 800
ENDIF
I<=LN(170)
IY=LN(170)
DO 200 I2=1, 6
DO 300 I3=IY-(7-I2), IY+(7-I2)
IF(I3 GT 170 OR I3 LT 1)THEN
GOTO 300
ENDIF
DO 400 I4=IX-(7-I2), IX+(7-I2)
IF(I4 GT 170 OR I4 LT 1)THEN
GOTO 400
ENDIF
BANK(I3, I4)=BANK(I3, I4)+IADD(I2)
400 CONTINUE
300 CONTINUE
200 CONTINUE
IF(IY LE 170. AND. IY. GE. 1)THEN
IF(IX LE 170. AND. IX. GE. 1)THEN
BANK(IY, IX)=BANK(IY, IX)+IADD(7)
ENDIF
END IF
100 CONTINUE

* FILE THE FINISHED RESULTS.
800 OPEN(6, FILE='C. BANK3')
WRITE(6, 300)((BANK(13, 16), 16=1-85). 13=1, 170)
CLOSE(6)
OPEN(6, FILE='C. BANK4')
WRITE(6, 300)((BANK(17, 18), 18=86, 170). 17=1, 170)
CLOSE(6)
500 FORMAT(B3I4)
STOP
END

FUNCTION LN(N)
LN=INT(RND(0)*N-1)+1
RETURN
END
Appendix 9(a). TREFAL The coppice stand simulation model.

This simulation is designed to follow the changes taking place in a self-thinning stand of coppice trees. The parameters and rate equations are derived from measurements taken in the Oak (QUERCUS sp) coppice woods of the Tamar Valley, on the Devon - Cornwall county boundary.

MAIN PARAMETERS
ISA- INITIAL WOODLAND AGE
INY- NUMBER OF YEARS THE MODEL IS TO RUN
DECR- SEEDBANK DECAY RATE (FRACTION/YEAR)
IFFR- WINDTHROW RATE (NUMBER/10000 YEARS)
IFTH- SELF THINNING RATE (NUMBER/100 YEARS)
TH- THRESHOLD VALUE FOR THE NUMBER OF SEEDS ON A TREEFALL REQUIRED TO PRODUCE ONE MATURE PLANT.

INPUT FILES-
TREES - CONTAINS THE TREE POSITIONS CREATED BY THE PROGRAM "WOODLAND"
C BANK1.C.BANK2 - CONTAIN THE INITIAL SEED BANK PATTERN GENERATED BY CONBANK.

OUTPUT FILES-
RUN.RES - CONTAINS THE FIVE YEARLY CHANGES IN GROWTH OF THE STAND PARAMETERS, AND THE RESULTS OF THE DENSITY DEVELOPMENT.
GCLASS - THE Girth DISTRIBUTION MEASURED AT TEN YEAR INTERVALS.
* F TREES - THE REMAINING TREE POSITIONS.
* FALL DATA - THE PARAMETERS DESCRIBING THE TREEFALL INPUTS
  TO THE SOIL SEED BANK.
* TREP - THE TREEFALL POSITIONS AND GIRTHS
* BAN. RES1 - THE FINAL SEED BANK.
* BAN. RES2

TREFAL uses the NUMERICAL ALGORITHMS GROUP subroutines
* G05CBF(X) - To produce repeatable stochastic values
* G05CCF(X) - To produce non-repeatable stochastic values
* G05CAF(X) - To generate random numbers with an even distribution of
  range 0 - 1
* G05DDF(A, 3) - To generate random values with a normal distribution
  of mean A and standard deviation 3.

***************
CONTROL SECTION
***************

COMMON /ARRAYS/TREAR(2, 120), GIRTH(120), BAN(170, 170)
INTEGER TH, ITF, TREAR, BAN, TREFP(3, 15), STAND(30, 3), IFFR, ITHIN
INTEGER GTHCL(30, 41), TCLAS(30), ERR, IFTH, IFC, IRFAC(20, 9)
REAL GIRTH, TREFG(13), MDENS(30), MGIR(30), SRES(2, 50), EONS(20, 10)
CHARACTER A*200, B*200, C*130, D*130, E*130, F*20
IOBUFFER=230

INITIALISE G05CAF OR G05CBF

CALL G05C3F(13)

READ THE TREE STAND DISTRIBUTION FROM STORAGE

OPEN(FILE='TREES', UNIT=5)
DO 110 II=1, 300
  READ(5, 300, IOSTAT=ERR, END=200) TREAR(1, II), TREAR(2, II), GIRTH(II), DUM
300 FORMAT (2(F14.3X), 2(FB. 3))
IF(ERR NE 0) THEN
  PRINT*, 'ERROR IN READING TREES FILE'
  CLOSE(5)
  STOP
END IF
110 CONTINUE
200 INDT=II-1
  CLOSE(5)

READ IN THE SEEDBANK DATA

OPEN(3, FILE='C. BANK1')
READ(3, 250, IOSTAT=ERR)((BAN(IR1, IR2), IR2=1, 85), IR1=1, 170)
IF(ERR NE 0) THEN

-326-
PRINT*, 'ERROR IN READING C. 3ANK1'
CLOSE(5)
STOP
ENDIF
CLOSE(5)
OPEN(3, FILE= 'C. 3ANK2')
READ(5, 250, IOSTAT=ERR)((3ANK(IR3, IR4), IR4=96, 170), IR3=1, 170)
IF(ERR NE 0)THEN
PRINT*, 'ERROR IN READING C. 3ANK2'
CLOSE(5)
STOP
ENDIF
CLOSE(5)
250 FORMAT(8SI4)
* OPERATOR CONTROLLED PARAMETERS
* STARTING AGE
* ISA=33
* NUMBER OF YEARS TO RUN
* INY=200
* DECAY RATE
* DECR=0.960
* FALL PROBABILITY (INTEGER<10,000)
* IFFR=203
* THINNING PROBABILITY (INTEGER<100)
* IFTH=41
* THRESHOLD FOR THE NUMBER OF SEEDS NEEDED TO PRODUCE ONE PLANT
* TH=0
* SET THE FALL COUNTERS TO THEIR INITIAL VALUES
* IFC=0
* IN3=0
* ITG=1
* START OF THE ANNUAL LOOP
* RUN FOR INY YEARS STARTING AT ISA YEARS OF AGE
* DO 400 I2=ISA, INY+ISA
-327-
* FOR EACH YEAR CALCULATE IF A TREE FALLS
  CALL QFALL(IFFR, ITF)
  IF SO CALCULATE THE SEED INPUT PARAMETERS
  IF(ITF EQ 1) THEN
    IFC=IFC+1
    CALL THROW(INOT, IRFX, IRFY, G)
    TREFP(1, IFC)=IRFX
    TREFP(2, IFC)=IRFY
    TREFP(3, IFC)=I2
    TREFG(IFC)=G
    CALL REPFACT(IRFX, IRFY, G, IFC, IRFAC, EGNS)
  ENDIF
* FOR EACH YEAR CALCULATE IF A TREE IS TO BE THINNED
  CALL QTHIN(IFTH, ITHIN)
  IF SO REMOVE IT
  IF(ITHIN EQ 1) THEN
    CALL THIN(INOT)
  ENDIF
  SET LOWER LIMIT FOR TREE DENSITY
  IF(INOT. LT. 10) THEN
    GOTO 450
  ENDIF
  INCREASE TREE Girth ANNUALY
  CALL GROWTH(GIRTH, INOT, GMEAN)
  DECAY THE SEEDBANK ANNUALY
  CALL DECAY(DECRA, DENS)
  INCREASE SEED BANK AROUND THE TREEFALLS ANNUALY
  IF(IFC GT 0) THEN
    CALL AUGMNT(IRFAC, EGNS, TH, IFC)
  ENDIF
  EVERY 10 YEARS STORE THE TREE Girth DISTRIBUTIONS
  IDD=INT(I2/10)*10
  IF(IDD EQ 12 OR I2 EQ 15) THEN
    CALL TDISTN(TCLAS, INOT)
    GTHCL(ITG, 1)=I2
    DO 285 J1=2, 40
       GTHCL(ITG, J1)=TCLAS(J1)
    CONTINUE
    ITG=ITG+1
  ENDIF
EVERY 3 YEARS STORE -
AGE, NUMBER OF TREES STANDING, NUMBER OF TREEFALLS.
MEAN Girth of the stand and seedbank density (per m**2)

IC=INT(I2/3)+5
IF(IC.EQ.I2)THEN
IN3=IN3+1
STAND(IN3.1)=I2
STAND(IN3.2)=INOT
STAND(IN3.3)=IFC
MDENS(IN3)=DEN5
MGIR(IN3)=MEAN
CALL SAMPLE(MEAN,SD)
SRES(1,IN3)=MEAN
SRES(2,IN3)=SD
ENDIF

CHECK THE SEED BANK DENSITY TO SEE IF SEEDS REMAIN

IF(DENS.EQ.-1.0E-10)THEN
GOTO 450
ENDIF
400 CONTINUE
END OF ANNUAL LOOP

FILE THE FINAL TREE POSITIONS

OPEN(6,FILE='F.TREES')
D=' X-AXIS Y-AXIS GIRTH'
WRITE(6,410)D
410 FORMAT(A73)
DO 420 J5=1,INOT
WRITE(6,430)TREAR(1,J5),TREAR(2,J5),GIRTH(J5)
430 FORMAT(2X,2(I4,8X),F7 2)
420 CONTINUE
CLOSE(6)

FILE THE FALLEN TREE GIRTHS AND POSITIONS

OPEN(6,FILE='TREP')
DO 800 17=1,IFC
WRITE(6,850)TREP(1,17),TREP(2,17),TREP(3,17),TREFG(17)
850 FORMAT(3(I3.5X),F7 2)
800 CONTINUE
CLOSE(6)

FILE THE FINAL SEEDBANK

OPEN(6,FILE='BAN.RES1')
WRITE(6,1100)((3ANK(I01,I02),I02=1,85),I01=1,170)
CLOSE(6)
OPEN(6,FILE='BAN.RES2')
WRITE(6,1100)((3ANK(I03,I04),I04=86,170),I03=1,170)
CLOSE(6)
1100 FORMAT(B914)

-329-
FILE THE WOODLAND DEVELOPMENT PARAMETERS.

OPEN(6,FILE='RUN.RES3')
WRITE(6,1106)TH
WRITE(6,1107)IFFR
WRITE(6,1108)IFTH
1106 FORMAT('TH=',IB)
1107 FORMAT('IFFR=',IB)
1108 FORMAT('IFTH=',IB)
A=' WOODLAND NO TREES NO FALLS MEAN MEAN BANK SAMPLE
VARIANCE'
B=' AGE PER 30 MSQ PER 30 MSQ GIRTH DENSITY/MSQ MEAN
WRITE(6,1110)A
WRITE(6,1110)B
1110 FORMAT(A100)
DO 1300 I13=1.IN3
WRITE(6,1300)STAND(I13,1),STAND(I13,2),STAND(I13,3),MDENS(I13),SRESC(I13),SRES(2,I13)
1300 FORMAT('X.14.8X.14.8X.14.7X.F6.2X.7X.F7.2X.3X.F9.2)'
CONTINUE
CLOSE(6)

FILE THE DATA TO CHECK THE TREFALL INPUT
OPEN(6,FILE='FALL.DAT')
WRITE(6,1400)(IFAC(I14,I13),I13=1.IFC)
1400 FORMAT(9(4X,14)
WRITE(6,1401)(EQNS(I14.I131),I13=1.IFC)
1401 FORMAT(10(4X.F8.3))'
CLOSE(6)

FILE THE GIRTH CLASS DISTRIBUTION CHANGES
C='AGE 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160
1 170 180 190 200'
E='AGE 210 220 230 240 250 260 270 280 290 300 310 320 330 340 350
I 360 370 380 390 400'
F=' GIRTH CLASSES'
OPEN(6,FILE='GCLASS')
WRITE(6,290)F
290 FORMAT(A20)
WRITE(6,291)C
291 FORMAT(A120)
WRITE(6,292)(GTHCL(J2,J3),J3=1,20),J2=1,ITG)
292 FORMAT(20(I3,1X))
WRITE(6,291)E
DO 293 IC3=1,ITG
WRITE(6,294)GTHCL(IC3,1),GTHCL(IC3,IC4),IC4=21,40)
294 FORMAT(21(I3,1X))
293 CONTINUE
CLOSE(6)
STOP
END
**SU3R0UTINES**

**CALCULATE IF A TREE FALLS IN THE YEAR USING THE FALL RATE (FFR)**

SUBROUTINE QFALL(IFFR. ITF)
  INTEGER IFFR. IW2, ITF
  IU2=LM(i0000)
  IF(IW2 LT IFFR)THEN
    ITF=1
  ELSE
    ITF=0
  END IF
  RETURN
END

**CALCULATE IF A TREE IS TO BE THINNED USING THE THINNING RATE IFTH**

SUBROUTINE QTHIN(IFTH. ITHIN)
  INTEGER IFTH, N4, ITHIN
  N4=LM(100)
  IF(N4. LT. IFTH)THEN
    ITHIN=1
  ELSE
    ITHIN=0
  END IF
  RETURN
END

**CHOOSE THE SIZE AND COORDINATES OF THE TREEFALL AND REMOVE IT FROM STORAGE**

SUBROUTINE THROW(INOT, IRFX, IRFY, G)
  COMMON /ARRAYS/TREAR(2, 120), GIRTH(120), BANK(170, 170)
  INTEGER TREAR, BANK
  REAL GIRTH
  * RANDOM SELECTION
  INTR=LM(INOT)
  IRFX=TREAR(1, INTR)
  IRFY=TREAR(2, INTR)
  G=GIRTH(INTR)
  * REMOVE TREE
  TREAR(1, INTR)=0
  TREAR(2, INTR)=0
  GIRTH(INTR)=0. 0
  CALL SHUFLE(INOT, INTR)
  RETURN
END

**SELECT THE TREE TO BE THINNED FROM THE DISTRIBUTION (PROBABILITIES 30:23:13:10%)**

SUBROUTINE THIN(INOT)
  COMMON /ARRAYS/TREAR(2, 120), GIRTH(120), BANK(170, 170)
INTEGER BANK, TREAT, REAL Girth

* FIND THE SMALLEST TREE CLASS
  GS = Girth(1)
  IFLAG = 0
  DO 600 I4 = 2, INOT
  GSX = Girth(I4)
  IF (GS GT GSX) THEN
    GS = GSX
  END IF
  600 CONTINUE
  ISGC = INT(GS/10.0)

  * CALCULATE THE CLASS FROM WHICH THE TREE IS REMOVED.
  ICI = LIM(100).
  IF (ICI LT 50) THEN
    CALL FIND(ISGC, INOT, IFLAG)
  END IF
  IF (ICI GE 50 AND ICI LT 75) THEN
    ISGC = ISGC + 1
    CALL FIND(ISGC, INOT, IFLAG)
  END IF
  IF (ICI GE 75 AND ICI LT 90) THEN
    ISGC = ISGC + 2
    CALL FIND(ISGC, INOT, IFLAG)
  END IF
  IF (ICI GE 90) THEN
    ISGC = ISGC + 3
    CALL FIND(ISGC, INOT, IFLAG)
  END IF

  IF (IFLAG.EQ.0) THEN
    GOTO 630
  END IF

  * REMOVE CHOSEN TREE
  TREAT(1, IFLAG) = 0
  TREAT(2, IFLAG) = 0
  Girth(IFLAG) = 0.0
  CALL SHUFFLE(INOT, IFLAG)

  RETURN
  END

* LOCATE TREES TO BE THINNED

SUBROUTINE FIND(ISGC, INOT, IFLAG)
COMM = common /ARRAYS/TREAT(2, 120), Girth(120), BANK(170, 170)
INTEGER TREAT, BANK
REAL Girth
  DO 610 ILI = 1, INOT
    IGC = INT(Girth(ILI)/10.0)
    IF (IGC .EQ. ISGC) THEN
      IFLAG = ILI
    END IF
  610 CONTINUE

  RETURN
END

* AFTER THINNING OR TREEFALL REMOVE EMPTY SPACES FROM THE ARRAYS

SUBROUTINE SHUFFLE(IN1, IN2)
COMMON /ARRAYS/TREAR(2, 120), GIRTH(120), BANK(170, 170)
INTEGER TREAR, BANK
REAL GIRTH
DO 700 I3=IN2, IN1-1
   TREAR(1, I3)=TREAR(1, I3+1)
   TREAR(2, I3)=TREAR(2, I3+1)
   GIRTH(I3)=GIRTH(I3+1)
700 CONTINUE
TREAR(1, IN1)=0
TREAR(2, IN1)=0
GIRTH(IN1)=0
IN1=IN1-1
RETURN
END

*       ANNUAL INCREASE OF GIRTH
*      SUBROUTINE GROWTH(GIRTH, INOT, GMEAN)
   REAL GIRTH(120)
   GTOT=0
   SG=GIRTH(1)
   SMG=GIRTH(1)
   DO 300 I3=1, INOT
      GTOT=GTOT+GIRTH(I3)
   300 CONTINUE
   SG=GIRTH(I)
   DO 400 I3=1, INOT
      IF(GG.LT. SMG)THEN
         SMG=GG
      ENDIF
      IF(GG.GT. SG)THEN
         SG=GG
      ENDIF
   400 CONTINUE
   GTOT=GTOT/INOT
   GMEAN=GTOT/INOT
   DIF=BG-GMEAN
   WEIGHT=41.0/DIF**2
   DO 510 IG=1, INOT
      GC=GIRTH(IG)
      D=GC-SMG
      GIRTH(IG)=GIRTH(IG)+((4.5/GIRTH(IG))+(D*WEIGHT)
   510 CONTINUE
RETURN
END

*      SUBROUTINE TO PRODUCE ANNUAL DECAY OF SEEDBANK
*      SUBROUTINE DECAY(DENS, DENS)
   COMMON /ARRAYS/TREAR(2, 120), GIRTH(120), BANK(170, 170)
   INTEGER BANK, TREAR
   REAL GIRTH
   DENS=0
   DO 1001 I32=1, 170
      DENS=DENS+BANK(I32, I33)
   1001 CONTINUE
1001 CONTINUE
* MEAN SEED DENSITY OF THE TOTAL SEEDBANK
DENS=DENS/(31*51)
* DECAY VALUES >8 BY THE MEAN DECAY RATE
* DECAY VALUES <8 BY PROBABILITY OF DECAY
DO 900 IB=1,170
   DO 1010 I9=1,170
      IF(BANK(IB, I9).EQ.0)THEN
         IDUM3=LM(10)
         GOTO 1010
      ELSE IF(BANK(IB, I9) GT 8)THEN
         BANK(IB, I9)=IDECYM(DECR.BANK(IB, I9))
      ELSE
         BANK(IB, I9)=IDECYR(DECR.BANK(IB, I9))
      END IF
1010 CONTINUE
900 CONTINUE
RETURN
END
* MEAN DECAY
* INTEGER FUNCTION IDECYM(DECR,K)
   IDECYM=INT(K*DECR)
   IDUM2=LM(10)
   RETURN
END
* RANDOM DECAY
* INTEGER FUNCTION IDECYR(DECR,L)
   INTEGER PR,N7
   PR=LM(100)
   N7=NINT(DECR*100)
   IF (PR GE N7-12) THEN
      M=L-1
   ELSE
      M=L
   END IF
   IDECYR=M
   RETURN
END
* SUBROUTINE TO PRODUCE THE SEEDBANK INPUT MATRIX
* SUBROUTINE REPFACT(I X, I Y, G, I FC, IRFAC,EQNS)
   REAL EQNS(20,10)
   INTEGER IRFAC(20,9)
   * LENGTH OF TIME FOR WHICH THE GAP IS OPEN
   IRFAC(IFC.1)=INT(10**(2.708E-3*G+0.924))
   IRFAC(IFC.2)=0
   * TREEFALL COORDINATES
   IRFAC(IFC.3)=IX
   IRFAC(IFC.4)=IY
   * DISTURBANCE DIMENSIONS
   H=2*(0.5925*G+20.875)
   W=1.308*G+12.473
   IHT=INT(H/30)
IW = INT(W/30)
IRFAC(IFC.5) = INT(IHT/2)
IRFAC(IFC.6) = INT(IW/2)
IRFAC(IFC.7) = IW - IRFAC(IFC.5) - 1
IRFAC(IFC.8) = IW - IRFAC(IFC.6) - 1

* LOWER LIMIT OF Girth PRODUCING INPUT
IF (G.LT.76) THEN
  IRFAC(IFC.9) = 0
  DO 1111 IX1 = 1, 10
    EQNS(IFC.IX1) = 0.0
1111  CONTINUE
ELSE
* ON THE DISTURBANCE
  EQNS(IFC.1) = (121.0 - 0.512*G)*(9.0/100.0)
  EQNS(IFC.6) = 82.26*9.0/100.0
* INPUT AT EDGE
  EQNS(IFC.2) = (248.0 - 0.775*G)*(9.0/100.0)
  EQNS(IFC.7) = 115.29*9.0/100.0
* 30 CM FROM EDGE
  EQNS(IFC.3) = (203.0 - 0.775*G)*(9.0/100.0)
  EQNS(IFC.8) = 199.89*9.0/100.0
* 60 CM FROM EDGE
  EQNS(IFC.4) = (49.3 + 0.377*G)*(9.0/100.0)
  EQNS(IFC.9) = 53.74*9.0/100.0
* 90 CM FROM EDGE
  EQNS(IFC.5) = (49.3 + 0.029*G)*(9.0/100.0)
  EQNS(IFC.10) = 84.26*9.0/100.0
  IRFAC(IFC.9) = 0
ENDIF
RETURN
END

* FUNCTION TO PRODUCE A RANDOM INTEGER FROM AN EVEN
* DISTRIBUTION OF RANGE 1 - N

INTEGER FUNCTION LM(N)
 INTEGER N
 REAL*8 X,GO5CAF
 X=GO5CAF(K)
 LM=INT(X*(N-1))+1
 RETURN
END

* FUNCTION TO CALCULATE A RANDOM NUMBER FROM A DISTRIBUTION OF
* MEAN A1 AND STANDARD DEVIATION B1 THE FUNCTION RETURNS ALL
* GENERATED VALUES WHICH ARE <0.0 AS 0.0

REAL FUNCTION RN(A1,B1)
 REAL*8 A2, B2, X, GO5DDF
 REAL A1, B1
 A2=DBLE(A1)
 B2=DBLE(B2)
 X=GO5DDF(A2, B2)
 IF (B1 LE 0.0) THEN
   RN=0.0
 ELSE
   IF (A1 LT 0.0) THEN
     RN=0.0
   END IF
   RN=RN+B2
 END IF
RETURN
END
ELSE
  IF(X. LE. 0.0) THEN
    RN=0.0
  ELSE
    RN=REAL(X)
  ENDIF
ENDIF
ENDIF
RETURN
END

*SUBROUTINE TO INCREMENT THE SEED BANK AROUND THE TREEFALLS*

*SUBROUTINE AUGMNT(IRFAC, EONS, TH, IFC)*
COMMON /ARRAYS/TREAR(2,120), GIRTH(120), BANK(170,170)
INTEGER TH, IFC, TREAR(170), BANK, IRFAC(20,9)
REAL GIRTH, EONS(20,10)
*FOR EACH FALLEN TREE*
DO 1500 I16=1, IFC
*CALCULATE IF THE GAP IS CLOSED*
ISEP=IRFAC(I16,1)-IRFAC(I16,2)
IF(ISEP.GT.0) THEN
  IF=IRFAC(I16,3)
  IYF=IRFAC(I16,4)
  IY1=IRFAC(I16,5)
  IX1=IRFAC(I16,6)
  IY2=IRFAC(I16,7)
  IX2=IRFAC(I16,8)
  IF SEED INPUT HAS NOT OCCURED PREVIOUSLY THEN
*CHECK IF THE THRESHOLD IS EXCEEDED*
  IF(IRFAC(I16,9).LT.1) THEN
    SUMTH=0.0
    DO 1510 J4=IYF-IY1, IYF+IY2
      IF(J4.GE.1 AND J4.LE.170) THEN
        DO 1520 J3=IXF-IX1, IXF+IX2
          IF(J3.GE.1 AND J3.LE.170) THEN
            SUMTH=SUMTH+BNK(J4, J3)*0.9
          ENDIF
        1520 CONTINUE
      ENDIF
    1510 CONTINUE
    IF(SUMTH.GE.REAL(TH)) THEN
      IRFAC(I16,9)=1
    ENDIF
  ENDIF
*IF THE THRESHOLD HAS BEEN EXCEEDED THEN INPUT SEEDS*
  IF(IRFAC(I16,9).EQ.1) THEN
  SEED ON DISTURBED AREA
  DO 1600 I17=IYF-IY1, IYF+IY2
    IF(I17.GE.1 AND I17.LE.170) THEN
      DO 1700 I18=IXF-IX1, IXF+IX2
        IF(I18.GE.1 AND I18.LE.170) THEN
          BANK(I17, I18)=3ANK(I17, I18)+NINT(RN*EONS(I16,1)*EONS(I16,6))
        ENDIF
      1700 CONTINUE
    ENDIF
  1600 CONTINUE
END
SUBROUTINE TO PRODUCE TREE GIRTH DISTRIBUTIONS

SUBROUTINE TDISTN(TCLAS, INOT)
COMMON /ARRAYS/TREAR(2,120), GIRTH(120), BANK(170,170)
INTEGER BANK, TREAR, TCLAS(50)
REAL Girth
DO 2300 J=1,50
TCLAS(J)=0
2300 CONTINUE
DO 2400 J7=1,INOT
IETH=INT(Girth(J7)/10)
TCLAS(IETH)=TCLAS(IETH)+1
2400 CONTINUE
RETURN
END

AT 3 YEAR INTERVALS A SAMPLE OF 50 ARRAY UNITS IS SELECTED
TO PRODUCE A SAMPLE MEAN AND STANDARD DEVIATION.

SUBROUTINE SAMPLE(MEAN, SD)
COMMON /ARRAYS/TREAR(2,120), Girth(120), BANK(170,170)
INTEGER BANK, TREAR
REAL GIRTH
TX2=0.0
TDENS=0.0
DO 2500 130=1,30
   IXX=LM(170)
   IYY=LM(170)
   TDENS=REAL(BANK(IXX,IYY))+TDENS
   TX2=TX2+REAL(BANK(IXX,IYY))**2
   2500 CONTINUE
SDENS=TDENS/30.0
MEAN=SDENS*11.1
SD=(TX2-(TDENS**2/30.00))/49.00
SD=SD*11.1
RETURN
END

* SUBROUTINE TO ENABLE THE PROGRAM TO BE REPEATABLE *

SUBROUTINE RRAND(IYF, IY1, IY2, IXF, IX1, IX2)
DO 2600 IC5=IYF-(IY1+4),IYF+(IY2+4)
   IF( IC5 .GE. 1. AND. IC5 LE 170) THEN
      DO 2700 IC6=IXF-(IX1+4),IXF+(IX2+4)
         IF( IC6 GE 1. AND. IC6 LE 170 ) THEN
            DUM=RN(1.0,1.0)
            ENDIF
      2700 CONTINUE
   ENDIF
2600 CONTINUE
RETURN
END
Appendix 9(b). RUN.RES The coppice stand development parameters produced by TREFAL

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Appendix 9(c). GCLASS The development of the coppice stand girth distributions as simulated by TREFAL.