Modelling forest landscape dynamics in Glen Affric, northern Scotland

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Declaration

I hereby confirm that the work contained in this thesis is my own except where assistance is acknowledged.

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Abstract

Consideration of forest management at the landscape scale is essential if commitments to the conservation of biodiversity are to be upheld.

The ecosystem management approach, developed largely in North America, has made use of various landscape modelling tools to assist in planning for biodiversity maintenance and ecological restoration. The roles of habitat suitability models, metapopulation models, spatially explicit population models (SEPMs) and forest landscape dynamics models (FLDMs) in the planning process are discussed and a review of forest dynamics models is presented. Potential is identified for developing landscape models in the UK for both landscape restoration projects and semi-natural woodland management.

Glen Affric, in northern Scotland contains a large area of native pine and birch woodland and is the subject of a long-term restoration project. A new model, GALDR (Glen Affric Landscape Dynamics Reconstruction) is introduced and is believed to be the first FLDM developed for British woodland. The theory behind the model is described in detail and preliminary results and sensitivity analyses are presented. Furthermore, GALAM (Glen Affric Lichen Abundance Model), a new SEPM for the rare epiphytic lichen *Bryoria furcellata* is also described.

Results of simulations from the linked GALDR and GALAM models are presented which shed light on the role of landscape heterogeneity in determining the dynamics of lichen habitats and populations. It is concluded that, whilst much work will be required to develop a management-oriented decision support system from the GALDR model, the modelling process may aid researchers in the identification of knowledge gaps in ecological theory relevant to management and restoration.

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1 Introduction

The forester deals not in years and decades but in centuries, and it is true to say that he is interested not only in what was done two centuries ago but also in what happened in the forest a thousand or more years ago.

Mark Louden Anderson (1967; vol. 2, p.556)
in 'A history of Scottish forestry'.

I fear that, in recent years, too many ecologists have yielded to the temptation of finding a problem that can be studied on a conveniently small spatial and temporal scale, rather than striving first to identify the important problems, and then to ask what is the appropriate spatial scale on which to study them (and how to do this if the scale is large).

Robert May (1993; p. 2)
in 'The effects of spatial scale on ecological questions and answers'.

Woodland nature conservation in Britain has been shaped by assumptions about both the character of natural woodland and the effects of man on the woodland we see today. Latterly, much has been done to build up a realistic appreciation of the historical elements in British woods. Now, we need to reassess the natural elements and to consider their implications.

George Peterken (1996; p.9)
in 'Natural woodland'.

1.1 Themes, problems and tools

The three quotes at the head of this chapter serve to illustrate some of the major themes of this thesis. The first theme relates to timescales. Anderson's quote is of interest principally for its corollary: that the forester of one thousand years hence will be interested in what is done *now* and in the immediate future. Furthermore, if the interests of future generations are believed to be worth consideration, it clearly behoves today's foresters to consider the consequences of their actions into the next millennium.

The second theme is of spatial scale, and particularly of spatial scales large enough to encompass the concept of 'landscape'. Consideration of large spatial scales is equally as vital as consideration of long timescales. Furthermore, the two concepts are intrinsically linked (Urban *et al*., 1987); the scale at which a system is observed will tend to be inversely related to the apparent rate of change of the system. Conversely, the longer a supposedly self-contained system is observed, the more likely it is that the assumption of self-containment will be seen to be insufficient to explain the behaviour of the system.

The third theme concerns consideration of natural processes as a means of reconstructing a Scottish natural woodland that was lost long ago, and hence informing woodland management and habitat restoration. Until recently, concepts of natural woodland were based exclusively on what Peterken (1996) called the *original-natural* woodland: i.e. the pre-anthropogenic woodland pattern. This may be exemplified by the many references made to the woodland distribution map of McVean and Ratcliffe (1962). Consideration of the natural processes rather than the original-natural woodland allows reconstruction of *present-natural* (what might have developed from original-natural woodland in the absence of people) or *potential-natural* woodland (that which might develop from current woodland, disregarding long term trends other than succession).

A fourth theme concerns the differences in approach taken by the two disciplines of forestry and ecology. Traditionally, these disciplines operated in rather different conceptual spheres, even if their practitioners worked in the same physical locations; foresters dealt with the practicalities of producing timber from woodlands whilst ecologists wrestled with theories of ecosystem function or population dynamics. More recently however, the remit of forestry has widened to accept responsibility for societal values as well as, notably, maintenance of biological diversity. Concurrently, ecology as a discipline has expanded. Thus, today, the problems facing foresters may be the same as those facing woodland ecologists, restoration ecologists, landscape ecologists and many other applied ecologists.

The central problem addressed in this work is how to secure conservation of biodiversity in woodlands over large spatial scales and long timescales. Clearly, conservation over long timescales is desirable from an ethical point of view, as well as necessary in slowly changing ecosystems such as woodlands. Therefore, the adoption of large spatial scales is also necessary to allow consideration of natural processes over the entirety of the timescale. The practical problems of conservation become more immediate when the object is habitat restoration since the default option of minimal intervention no longer exists. Newton *et al.*, (2001) criticize the approach of past and current ecological restoration projects in Scotland for the lack of ecological theory underpinning practice.

With reference to Peterken's quote, two questions may be identified which may be crucial to solving the above problems:

- what will the consequences of management actions be in particular ecosystems?
- which patterns and processes might be expected in present-natural and/or potential-natural woodland?

As indicated by May (1993), the difficulties inherent in dealing with large spatial scales and long timescales are considerable. Traditional methods of field experimentation and plot-based sampling fail to address adequately the issues involved at larger scales.

Thus, it is clear that a requirement exists for tools that may allow ecological research to be brought to bear on the problems outlined above. Such tools may be broad in application like the ecosystem management approaches currently being developed in North America (see Section 1.2.2). However, the tools referred to in this work are generally decision support systems or forest models of one kind or another.

Writing on the use of models in ecological restoration in Scotland, Newton *et al.* (2001) state 'predictive tools [would enable] the impacts of management decisions on the composition, structure and functioning of woodland systems to be evaluated. Such tools would be invaluable to the restoration planning process. For example, it would be of value to be able to predict where natural regeneration would be likely to occur, how the composition of the forest might change with time in response to disturbance and successional processes, and how the landscape context of the woodland might influence which species are able to colonize the newly available habitat.' (p.189)

The above discussion highlights the requirement for predictive, landscape level tools for woodland management and ecological restoration. The next three sections of this chapter serve to analyse the problems in greater depth as well as review the various types of tool which may be pertinent. From this perspective, the project aims will be set out in section 1.5. A description of the study area, Glen Affric, concludes the chapter.

1.2 Biodiversity

Global commitment to biodiversity was first realized at the 1992 United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro. This was followed by a European commitment to sustainable management of forests, developed at the Second Ministerial Conference on the Protection of Forests in Europe (Helsinki Declaration) in 1993. Article 2 of Resolution 2 of the Helsinki Guidelines states:

> *'The conservation and appropriate enhancement in forests should be based both on specific, practical, cost-effective and efficient biodiversity appraisal systems, and on methods for evaluating the impact on biodiversity of chosen forest development and management techniques'.*

In turn the UK responded to the commitments to forestry practice made at Rio and Helsinki with the publication of *Sustainable Forestry: the UK Programme* (Anon., 1994), and subsequently *The UK Forestry Standard* (Forestry Commission, 1998).

The UK Forestry Standard emphasizes the importance of conservation of biodiversity in forests, in particular those species and habitats subject to EU directives and UK Biodiversity Action Plans. Compliance with the UK Forestry Standard, as well as certification under the UK Woodland Assurance Scheme (UKWAS Steering Group, 2000), requires that managers produce long term plans to ensure maintenance of important species and habitats. The UKWAS certification standard also requires that 'the impacts of woodland/forest plans [are] considered at a landscape level, taking due account of the interaction with adjoining land and other nearby habitats'.

1.2.1 Planning and management for biodiversity

Planning for biodiversity is an exacting task. Quite apart from the philosophical difficulties of deciding which components of biodiversity *should* be present on a site, practical difficulties arise from the complexity and unpredictability of species responses to management action. As stated by Ferris *et al*. (2000), our understanding of biodiversity response to stand level factors such as age structure and species composition is improving, but the significance of differing spatial patterns of habitat to biodiversity is currently very hard to quantify. Theories of landscape ecology suggest that it is not just *which* habitats are present that is important to species survival, but also the spatial arrangement of habitats in the landscape. However, the effects of pattern will vary; different species *see* the landscape in different ways. For large, mobile species, the limiting factor may be simply the quantity of suitable habitat. Species occupying patches of fragmented habitat within an inhospitable matrix may exist in a system of sub-populations known as a metapopulation (Levins, 1969; 1970), where individuals may occasionally move between patches and sub-populations may at times become extinct and recolonize. In this case, because dispersal between populations is governed by the inter-patch distance and the nature of the intervening ground, the spatial structure of the patch network influences the viability of the entire super-population. Spatial scales of metapopulations vary enormously according to the dispersive ability of the species; the concept has been applied to caribou (*Rangifer tarandus caribou*) in forest in Saskatchewan (Rettie and Messier, 1998), as well as marsh fritillaries (*Eurodryas aurinia*) on heaths in the UK (Warren, 1994).

The metapopulation concept also emphasizes the importance of landscape dynamics as well as landscape structure to species survival (and hence to maintenance of biodiversity). This is illustrated by Valverde and Silvertown's (1997) study of the common primrose (*Primula vulgaris*) in woodland. Primroses are light demanding, so they do not survive under a closed canopy and local populations are associated with treefall gaps. The metapopulation structure is therefore determined by the pattern of canopy gaps but, crucially, this structure is also changing as new gaps are created and old ones close; the metapopulation dynamics of the primrose are closely coupled with the gap-phase dynamics of its habitat.

Although it is difficult to determine which species behave as true metapopulations (and many may not; Harrison, 1994), the above example demonstrates how species viability may be dependent on the particular interplay between spatial and temporal patterns of disturbance. This may be particularly so for species of old growth woodland, many of which are specialists and poor colonizers (Peterken *et al.*, 1995), in areas where the pattern of small-scale (gap-phase) dynamics is replaced by or augmented with a larger-scale disturbance regime.

Clearly then, for biodiversity planning to be effective, consideration must be given to the entire landscape and its associated dynamics. The spatial scale at which one considers the landscape should probably be dictated by the largest scale at which any organism uses the landscape. For instance Craighead (1979) reported that the Yellowstone population of grizzly bear (*Ursos arctos*) required at least 5,000,000 acres (~ 20,000 km^2) of habitat to remain viable. Appropriate timescales are more difficult to define. According to principles of sustainability, management actions should not compromise potential for species to maintain populations in perpetuity, but clearly planning on infinite timescales is not a practical option. Although operational planning will be, by necessity, relatively short term, it would be desirable at least to gain a broad view of consequences in the very long term. Just as today's landscapes are a product of many centuries of past management, current management practices will leave their mark on the landscape as a legacy for as many years to come.

1.2.2 Ecosystem management

In Canada and the USA, consideration of a holistic approach to sustainable forest management, prompted by increasing concern over biodiversity decline, has led to the concept of ecosystem management (e.g. see Franklin, 1997; Grumbine 1994). Rather than any particular technique or system, ecosystem management is perhaps best described as a set of guiding principles. Themes include:

- consideration of wide spatial and temporal scales;
- adaptive management;
- acknowledgement of the human role as part of the ecosystem;
- synthesis of knowledge across disciplines;
- maintenance of ecological integrity.

The last theme consists of three strands:

- maintenance of viable populations of native species;
- representation of habitats;
- maintenance of ecological processes (e.g. natural disturbance, nutrient cycling).

The complexity involved with keeping track of so many aspects of the ecosystem over large spatial scales and long timescales has led Larsen *et al.* (1997) to argue that computer modelling is a necessary component of the ecosystem management approach. Modelling allows researchers and managers to assess the likely effects and relative benefits of varying landscape management scenarios by performing experiments that would be unfeasible in the 'real world'. The creation of an 'end-product' will be the primary aim of many modelling projects, but the discipline of model development itself may also be a useful way to encourage collaboration between researchers, synthesize knowledge, and identify research priorities.

1.3 Landscape modelling approaches

A variety of modelling approaches has been developed to address the issue of maintenance of ecological integrity or biodiversity at the landscape scale. Models have generally focused on one or more of species, habitats, natural disturbance and management. A drawback of the species approach is that by focusing on one or a few species, one effectively ignores the rest of the species present in the ecosystem. In some instances this may be justified where management of a site is explicitly directed at conservation of particular (usually endangered) species. Often this is not the case, in which case the approach may be generalized by focusing on species guilds or keystone, umbrella, or biodiversity indicator species (Simberloff, 1998; Ferris and Humphrey, 1999).

1.3.1 Habitat suitability models

Although earlier habitat suitability models were non-spatial (Schamberger and Krohn, 1982), the method lends itself well to implementation on GIS and has been used widely in this way (Donovan *et al.*, 1987). A number of habitat variables (e.g. canopy cover, elevation) are used to produce a habitat suitability index (HSI) for a particular species. The HSI is intended to be roughly correlated with the carrying capacity of the habitat for the target species or probability of occurrence of the species within its habitat. Habitat suitability models can be categorized according to whether they are deductive or inductive (Stoms *et al.*, 1992). Deductive models are constructed according to theoretical knowledge of the habitat requirements of the target species, and the HSI is usually derived from the habitat variables according to some rule-base. Inductive models are constructed from observations of species presence; the HSI is constructed according to correlation with habitat variables using a method such as logistic regression.

At the most basic level of application, the technique can be used to simply calculate the total quantity of suitable habitat in a landscape. A more sophisticated approach is to critically examine the spatial arrangement of the resulting habitat. The most usual way to do this is by calculation of landscape indices or metrics (Diaz, 1996; O’Neill *et al.*, 1988) – quantifications of landscape pattern such as patch size distribution, fragmentation and contagion. Tools such as HABSCAPES (Mellen *et al.*, 1995) use landscape metrics to assess suitability of entire landscapes for species. A third approach to the use of GIS-based habitat suitability modelling is to incorporate the HSI as a base layer in some form of population model.

1.3.2 Metapopulation models

Since its original conception, metapopulation theory has been expressed in terms of models (Levins, 1969; 1970). Early models were analytical in nature and landscape applications were strategic in approach. Recent developments linking metapopulation models with GIS have allowed a tactical approach to landscape-level biodiversity research. Practical applications of metapopulation modelling often use Population Viability Analysis (PVA) to determine the impact of differing management scenarios on likelihood of extinction. For example, Akçakaya and Atwood (1997) used a commercial metapopulation modelling package, RAMAS GIS (Akçakaya, 1994), to model the metapopulation dynamics and risk of extinction for the California gnatcatcher.

1.3.3 Spatially explicit population models

An alternative method of relating species population dynamics to spatial pattern in landscapes is provided by spatially explicit population models (SEPMs; Dunning *et al.,* 1995). The advantage over metapopulation models is that no assumptions need to be made about the population structure of the species in question (Rushton *et al.*, 1997). Generally, SEPMs model population dynamics directly on a spatially explicit representation of the landscape (usually raster grid or hexagonal tessellation) whereas GIS-linked metapopulation models derive a connected graph (a set of vertices connected by edges) structure from a HSI map, then model population dynamics according to the graph structure. Additionally, SEPMs may be individual-based rather than population-based models – i.e. the location of each individual of the target species is explicitly modelled.

OWL (McKelvey *et al.*, 1992), a SEPM for northern spotted owl (*Strix occidentalis*) was used by the Bureau of Land Management to aid decision-making in relation to a range of management scenarios in western Oregon over a period of one hundred years (Turner *et al.*, 1995). Over timescales as long as this, representing the landscape as a static entity would be a dubious assumption in most circumstances.

The OWL model used a dynamic landscape in which habitat age was increased over each timestep of the population dynamics model. In landscapes with more complex vegetation dynamics, particularly those where natural disturbance has a major effect on structure, it may be desirable to simulate landscape dynamics with more sophistication. Holt *et al.* (1995) made the case for linking SEPMs to another class of model – vegetation dynamics models – at a time when landscape-scale models of vegetation dynamics were in their infancy.

1.3.4 Forest landscape dynamics models

Vegetation dynamics models take a variety of forms; of particular interest is the newly emerging class of forest landscape dynamics models (FLDMs). FLDMs may be defined as spatially and temporally explicit simulation models of forest vegetation change operating at landscape scales. As well as providing a mechanism for generating dynamic landscape representations for population dynamics and habitat models, FLDMs may also be useful as stand-alone models of tree species and forest habitats. This may be particularly so if some of these species or habitats may be perceived as keystone species or ecosystems (DeMaynadier and Hunter, 1997). A major factor in the recent burgeoning of FLDMs has been the rapid progress made in computing technology over the last decade. Simulation of large landscapes at high resolution places heavy demands on processing speed and memory usage. (By way of an example, a 10 km × 10 km landscape represented by a 50 metre resolution raster grid possesses 40,000 cells in which stand dynamics must be simulated.)

Mladenoff and Baker (1999b) place FLDMs in the domain of landscape ecology, although generally their antecedents have been non-spatial stand-scale models of community dynamics, used to explore concepts of succession, ecosystem dynamics, and natural disturbance. Many FLDMs owe their development either to transition models (such as Cattelino *et al.*, 1979), or gap models of the type first produced by Botkin *et al.* (1972). A review of forest dynamics models, including FLDMs is presented in Chapter 2.

1.3.5 Integrated approaches to landscape modelling

Despite the case made by Holt *et al.* (1995) for linking spatially explicit population models with vegetation dynamics models, published examples of linked models are still rare. One example is Westervelt and Hopkins' (1999) model of desert tortoise

(*Gopherus agassizii*) in the Mojave Desert. More recently, Akçakaya (2001) demonstrated a linkage between the forest landscape dynamics model LANDIS and the metapopulation modelling package RAMAS. An example of a linked FLDM and SEPM is presented in Chapter 6 of this thesis.

It seems highly likely that linked models will become more common, given the limitations that the assumption of a static landscape place on modelling long term spatial dynamics of populations. The potential exists for integrated modelling frameworks (see Figure 1.1), where one landscape dynamics model provides a basis for population models for a range of target species. In sophisticated examples, population models for habitat-modifying species such as large ungulates would provide a feedback loop to the landscape dynamics model by influencing vegetation dynamics. Such a system would not have to rely entirely on natural vegetation dynamics; forestry-oriented models of timber growth and yield (e.g. Teck *et al.*, 1996) can deliver variables of relevance to habitat models, despite their primary purpose being non-ecological (Holt *et al.*, 1995). Many landscapes contain mixtures of diverse vegetation types ranging from the intensively managed to nearly natural with wild species using both types. In such cases, combining yield models with FLDMs may provide a mechanism for assessing potential ecological integrity of the whole landscape.

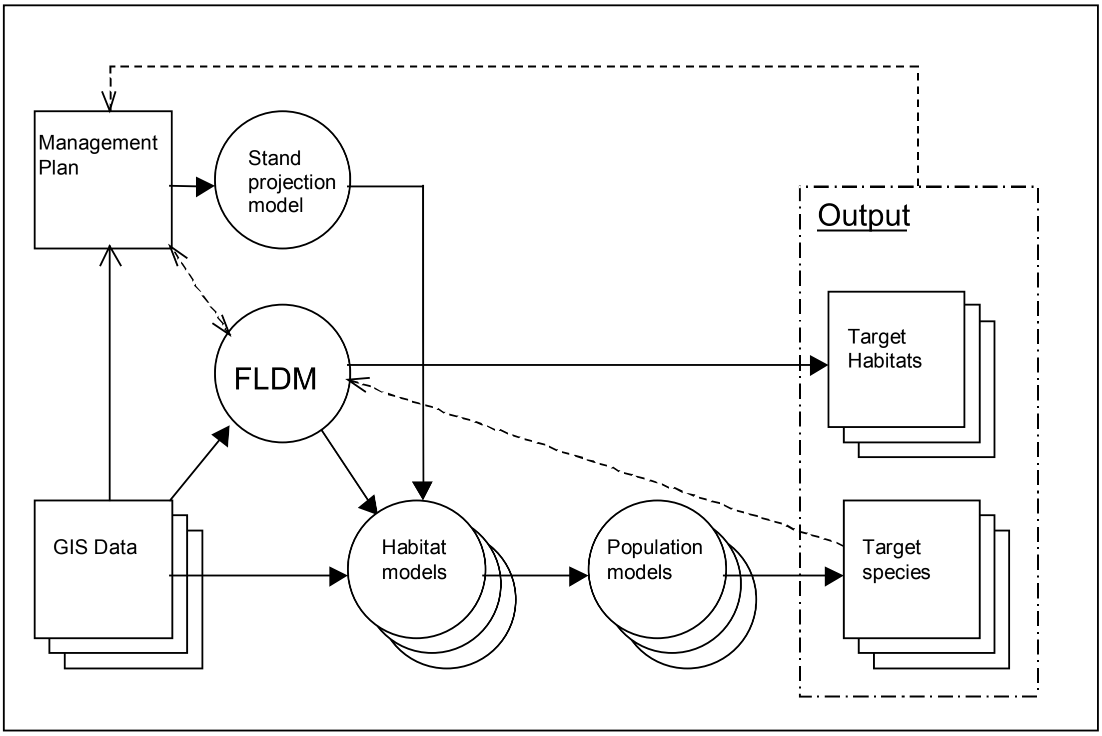


Figure 1.1 A diagrammatic representation of an integrated modelling solution. Solid arrows represent data flow; dotted arrows represent influence.

1.4 UK perspectives on landscape modelling

Neither ecosystem management nor landscape modelling have yet been applied seriously in the UK. To some extent, this may be a product of differing scientific and management cultures, but a more significant factor is probably the contrasting nature of the landscapes. North America possesses large publicly owned forest areas under non-intensive management and subject to natural disturbance regimes. These areas (e.g. Yellowstone) have tended to serve as the testing grounds for ecosystem management and associated modelling projects. In contrast, natural forests and disturbance regimes in the UK now exist only as a subject for academic speculation (Peterken, 1996). The fragmentation of our remaining semi-natural woodland has led to management having taken place at the individual woodland scale – i.e. in terms of tens of hectares rather than thousands or millions. This has been compounded by the pattern of ownership. Generally, areas large enough to be considered landscape units in an ecological sense will consist of various ownerships with a diversity of management aims and objectives.

1.4.1 Forest landscape restoration

In recent years, however, there has been a growing interest in the restoration of entire forest landscapes in the UK (Humphrey *et al.*, 2003). Although many projects involve only a single landowner, some have crossed ownership boundaries to include multiple owners (e.g. Life '97 Atlantic Oakwoods Project, Sunart). Generally, the objectives of such schemes will be to restore ecological integrity (see earlier section) and an ecosystem management approach, or components thereof, may be appropriate. Certainly there will be need to consider management at a wider scale than has been traditional (Ferris *et al.*, 2000). The scale of UK restoration projects is unlikely to match those of North American ecosystem management projects. However, where the landscape consists of a diverse range of habitat types and physical features, the principles will be similar.

Could landscape modelling in the context of ecosystem management be useful for planning forest landscape restoration in the UK? One school of thought argues that active management is unnecessary for restoration at the landscape scale beyond the removal of threats and negative pressures; allowing landscape processes to occur at the entire landscape level will ensure that populations of species persist, as they must have done in pre-settlement landscapes. However, this approach is problematic for several reasons.

1. The resulting future-natural (*sensu* Peterken, 1993) vegetation would not resemble pre-settlement (i.e. original-natural) pattern. Indeed, a legacy of artificiality may persist for many generations of forest change.

2. The scale of the project may not be large enough to support viable populations even if an original- or present-natural state could be attained.

3. A *laissez faire* approach to restoration may not be fast enough to support viable populations. Tilman *et al.* (1994) have predicted that species that persist in fragmented habitat may appear to be surviving, but in fact may only be able to do so for a limited number of generations before becoming extinct. Therefore, some species that currently exist in fragmented habitats may in fact be on the edge of

extinction. Effective restoration strategies for the conservation of such species would be aimed at reversing habitat fragmentation in the shortest time possible.

On the other hand, striving to rapidly achieve an original or present-natural pattern will necessitate intensive management effort, and there will be a period of quite high artificiality in the transition period. Establishing an appropriate level of intervention that will maintain populations of key species is likely to be critical for those planning for restoration.

1.4.2 Models for forest landscape restoration

A modelling approach might be able to assist the restoration planning process in two ways.

1. If some form of present-natural woodland is the objective of restoration, there will be a broad spectrum of possible states as well of possible trajectories towards those states. Application of an FLDM could indicate a range of states for present-natural woodland.

2. An integrated modelling approach could be used to assess different goals (e.g. minimal intervention versus continuing conservation management) and methods of achieving restoration (e.g. planting versus natural regeneration) in terms of the likely effects on particular habitats and species (including potential reintroductions). It may be possible to gauge whether the scale of the restoration is large enough to allow natural processes to progress untrammelled or whether some control must be retained.

Planning tools such as the Native Woodland Model (NWM) (Hester *et al.,* 2003) and Ecological Site Classification (ESC) (Pyatt *et al.*, 2001) can be used to indicate patterns of present-natural vegetation in the landscape. However, while these models may be useful in making predictions on the species composition of natural woodland, they convey nothing of the structure of the woodland, and essentially portray it as a static entity. Such models are of great utility in current forest planning, but it is possible that they could be even more useful if integrated into a dynamic modelling framework.

1.4.3 Developing modelling solutions in the UK

An integrated landscape modelling approach, such as that presented earlier in this chapter, for UK forests and woodland would be a long-term goal. Certainly, the amount of development needed to even approach such a system for a single landscape project or forest type would be daunting. Nonetheless, progress is being made on the types of models that could form the elements of a system similar to that which has been described. In addition to the work presented in this thesis, work is ongoing in Woodland Ecology Branch, Forest Research on development of habitat suitability models for a range of species including red squirrel (*Sciurus vulgaris*), adder (*Vipera berus*) and capercaillie (*Tetrao urogallus*) (for the latter, see Stewart, 2000). Rushton (1997) also describes SEPMs that have been developed for the red squirrel.

1.5 Project aims

The strategic aim of the project is to develop modelling techniques that will allow better understanding of landscape processes over long timescales and thus be of direct benefit to managers of semi-natural woodlands, landscape planners and restoration ecologists. Realization of these benefits in full will require models that are flexible, robust and adequately tested. To achieve this will require not only significant amounts of work on model development, but also consultation exercises with various experts and stakeholders (Fall *et al*., 2001). Thus, the full development process in the wide sense is beyond the scope of the current project and therefore a narrower aim has been set for the project, which is

to develop a forest landscape dynamics model for Glen Affric that will predict change in habitat characteristics relevant to a range of key species, and hence allow further predictions of population dynamics of key species.

The project outputs will thus consist of:

- a FLDM that will predict change in tree species composition and forest structure over large spatial extents and long timescales.
- an example of a linked SEPM based on habitat characteristics determined by the FLDM.

The first step in the realization of the above objectives is to examine approaches that have been made to similar or related problems in the past. Thus, a literature review of published forest dynamics models (FDMs) is presented in Chapter 2. The review is not restricted to FLDMs because this type of model is relatively recent and examples are often derived from non-spatial models or spatial models operating at scales smaller than the entire landscape.

The challenge presented above is just that which has been addressed by the development of the model described in Chapters 3-5. The question of species colonization and survival in a dynamic landscape has also been addressed by the development of a lichen abundance model presented in Chapter 6.

1.6 Study area – Glen Affric

1.6.1 Situation

Glen Affric is situated in the northern highlands of Scotland, at a latitude of roughly 57° 17’ N and longitude 5° W. The location of Glen Affric is illustrated in Figure 1.2. The lowest part of the glen, at the confluence of the rivers Affric and Glass, lies at 80 metres above sea level, whilst the surrounding mountains at the west of the Glen rise to over 1000 metres, the highest being Carn Eige at 1183m. The Glen contains two major lochs, Loch Affric to the west and Loch Beinn a’ Mheadhoin to the east. Numerous smaller lochs and lochans are scattered over the glen. The study area is entirely contained within a 20 km by 10km rectangle corresponding to the Ordnance Survey grid-squares NH12 and NH22. A map of the study area showing place-names and topographic features is presented in Figure 1.3.

Figure 1.2 Location of Glen Affric in Scotland.

1.6.2 Geology

The solid geology of the area consists of metamorphic sedimentary rocks of the Moine succession, chiefly quartz-feldspar granulites, mica-schists and quartz-mica-schists (Peacock *et al*., 1992). Thin bands or lenses of calcsilicate rocks may occur locally as subordinate associates of the more quartzose rocks. On the lower slopes, the bedrock is overlaid with thick deposits of till and loose morainic drift, forming an undulating hummocky topography. Above the level of the lateral moraine there may be thin drift or bare rock. The superficial deposits also include large areas of deep peat; mapped units occur mainly in the northern corries and subsidiary glens but extensive areas also exist in the west of Glen Affric.

1.6.3 Soils

The soils are of the Arkaig association, derived from Moinian lithologies. Soils below 225 m elevation are mainly podzols and peaty podzols, although significant areas of brown earth (sometimes slightly pozolized) may be found on south facing aspects, particularly at the eastern end of the Glen (Pyatt, 1995). Surface water gleys, peaty gleys and deep peats may also occur, but at lower elevations are restricted to small areas in concavities or shelves. Base-rich flushes also occur at lower elevations but are local and uncommon. Above 225 m, the major soil types are peaty podzols, peaty ironpan soils, peaty gleys, deep peats and rankers, with alpine and subalpine gleys occurring at higher elevations. Soils are rarely homogeneous over large areas; a common pattern is of topographically defined mosaics of two or three soil types.

1.6.4 Climate

According to the ESC climatic classification (Pyatt *et al*., 2001) Glen Affric falls into the Cool Moist, Cool Wet, Sub-Alpine and Alpine zones (Pyatt, 1995). A steep rainfall gradient occurs from east to west: annual rainfall figures are 1600 mm at the eastern end of Loch Beinn a' Mheadhoin, 1800 mm at the eastern end of Loch Affric and 2800 mm at Athnamulloch (Forest Enterprise, 1997). Rainfall is also strongly correlated with elevation, rising to about 3800 mm in the mountains at the western end of the glen. Steven and Carlisle (1959) report a mean annual temperature of 6.1°C with a January mean of 1.7°C and a July mean of 12.2°C.

1.6.5 Vegetation

The vegetation of Glen Affric was described by Steven and Carlisle (1959) and has been more recently surveyed by Averis (1994) using the National Vegetation Classification (NVC; see Rodwell 1991a,b).

Tree species

The most conspicuous feature of the vegetation is the extensive woodland of Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *Betula pubescens*). The majority of birch in the west of Glen Affric is likely to be downy birch while silver birch appears to be more common on well-drained slopes in the east. Rowan (*Sorbus aucuparia*) is widespread thought the glen, but tends to be scattered and does not from a woodland canopy as pine and birch do. Holly (*Ilex aquifolium*) is also widespread, but is distinctly more scarce than rowan.

The distribution of most other tree species tend to be restricted in some way, with the greatest tree species diversity being found in the east. Goat willow (*Salix caprea*) and alder (*Alnus glutinosa*) are mainly found along streamsides, a habitat also favoured by aspen (*Populus tremula*), which is also found on south facing crags. Hazel (*Corylus avellana*) may be found as an understorey species beneath some of the birch stands on richer soils. Oak (*Quercus petraea*), wych elm (*Ulmus glabra*), ash (*Fraxinus excelsior*), gean (*Prunus avium*) and juniper (*Juniperus communis*) are all present in the eastern end of the glen but are distinctly rare.

Of the native tree species only Scots pine are likely to have been planted, but various non-native conifer species (e.g.: lodgepole pine, *Pinus contorta*; Sitka spruce, *Picea sitchensis*) have been planted for timber in the past. Large areas of productive plantation remain in Guisachan and Cougie forests, but in Glen Affric most of the exotic conifers have been removed, whilst the pine plantations are now being managed for conservation objectives. A map of the semi-natural and planted woodland is presented in Figure 1.4.

Communities

The native pinewoods are ascribable to NVC community W18 with variation in subcommunities generally dependent on aspect and moisture. The heathy W18b tends to show a preference for drier ground on south facing slopes whilst W18d favours wetter ground often found on the north facing slopes. Small areas of W18e can be found on steep rocky slopes. The birchwoods fall into NVC types W4, W11 and W17 with differences marked out by variation in soil moisture and nutrient status. The W17 woodland is generally heathy and mossy. It may be floristically similar to the W18 pinewood where the two communities form mosaics. The W11 woodland is more grassy and herb-rich than W17 and is associated with richer, well-drained soils in the eastern part of the glen. In places, the W17 and W11 communities may intergrade. W4 woodland is characteristic of wet ground; depressions or level ground amongst hummocky moraine or water collecting areas on steeper ground. Small areas of W4 may form along soakways in pinewood or W17 woodland. At the very eastern end of the study area, where the River Affric passes through a steep gorge, there is one very small stand of W9 upland ashwood. The open ground vegetation consists of semi-natural heath and mire communities such as H21 heath, M25 wet heath and M17 blanket mire.

Age structure of the woodlands

Steven and Carlisle describe the age structure of the Affric pinewoods as ‘uneven-aged by groups’ (p.181) with the majority of pine trees having established from 1820-1880, albeit with many trees established before 1880 and a few from 1920-1950. A later study of age structure of pinewoods on the South side of Loch Beinn a’ Mheadhoin (Arkle and Edwards, 1996) produced a broadly similar picture from cores taken from 182 pine trees. The results differed from Steven and Carlisle’s in that a complete absence of trees establishing from 1920-1960 was noted and trees from 1700-1820 were just as numerous as those from 1820-1880.

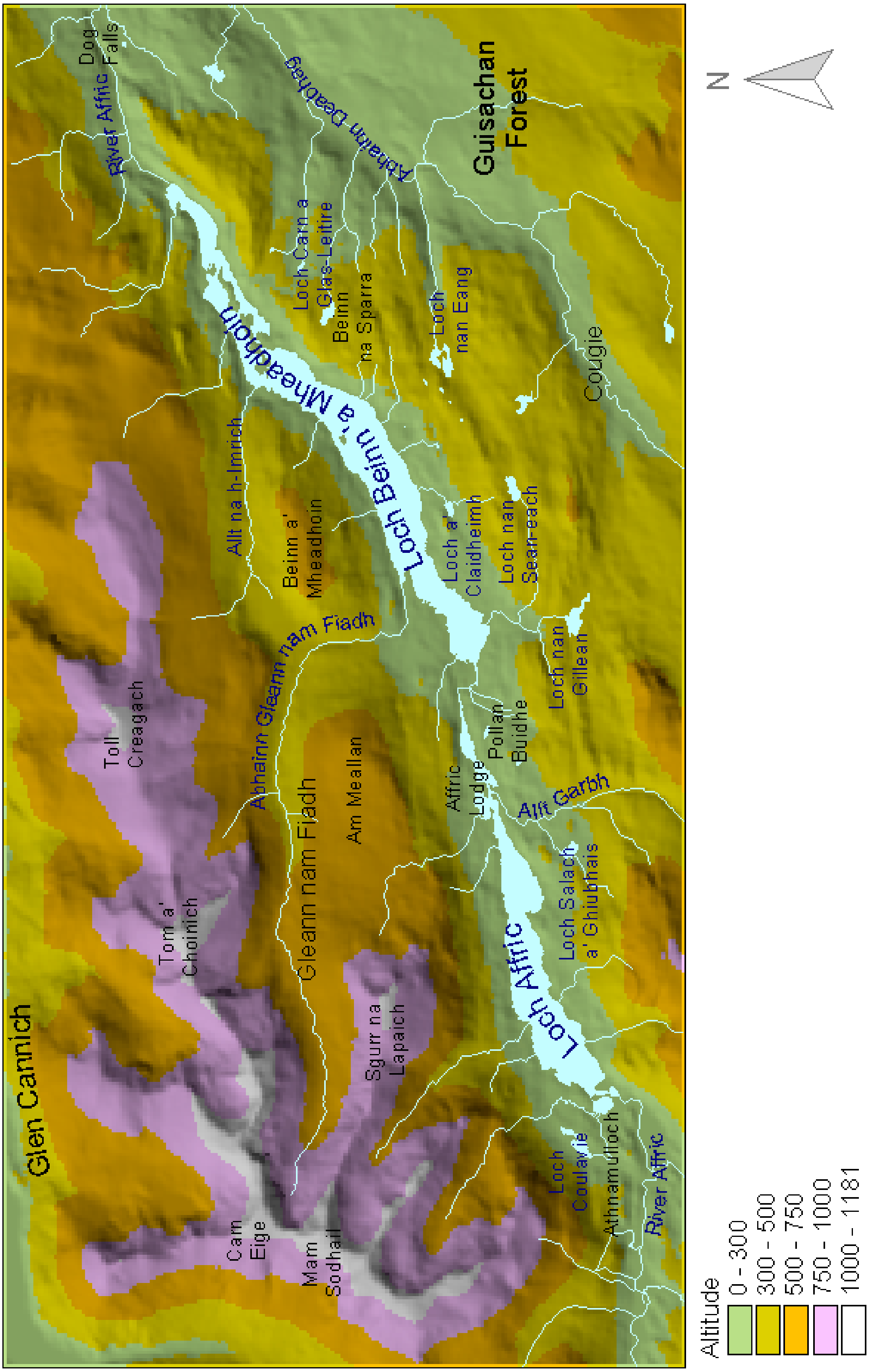


Figure 1.3 Place names and topographical features in the Glen Affric study area. The legend shows altitude according to the digital terrain model (DTM). The map extent is 20×10 km – subsequent maps of the study area show the same extent.

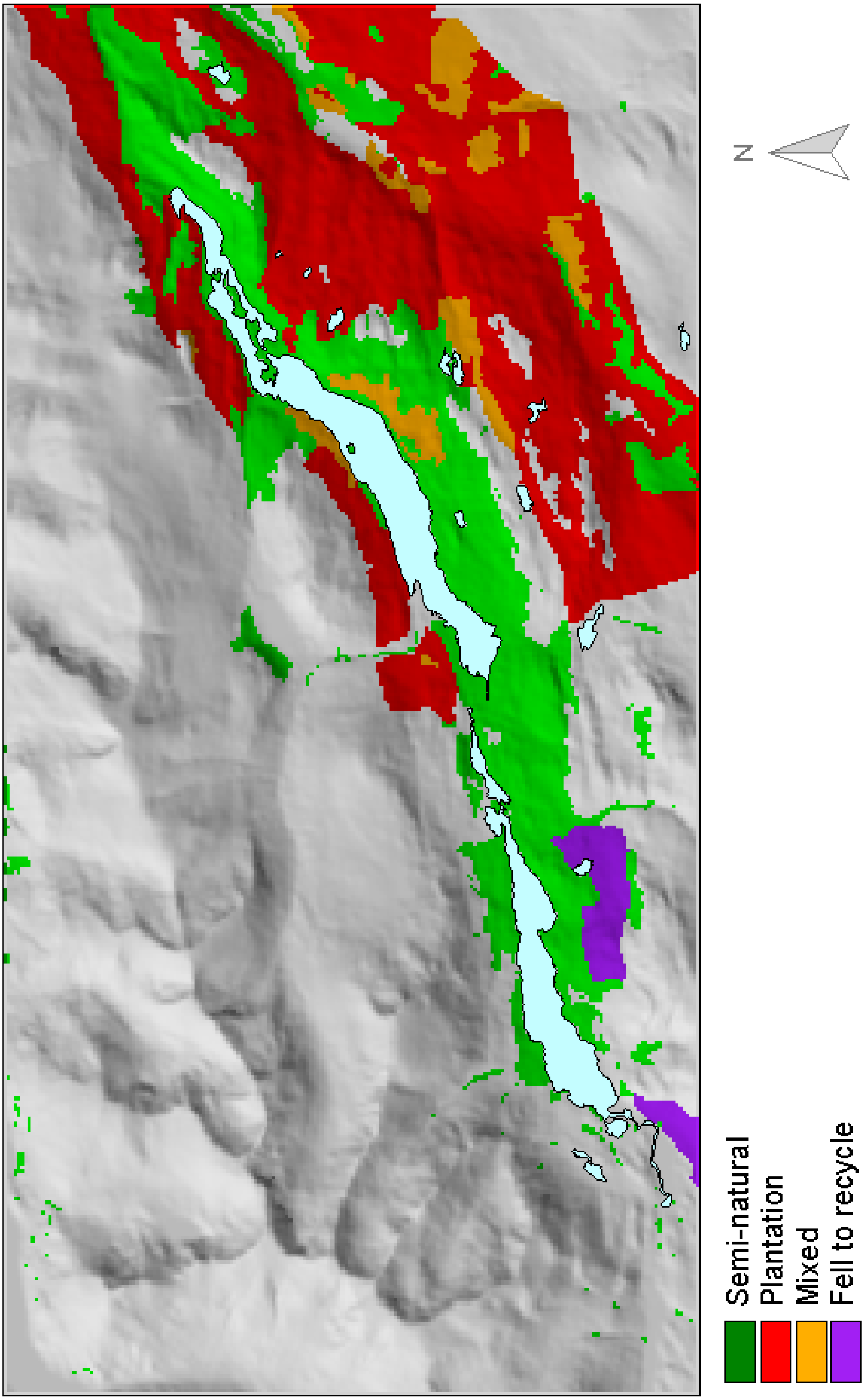


Figure 1.4 Plantation and semi-natural woodland in Glen Affric. The 'fell to recycle' category covers plantations of lodgepole pine felled in the late 1990s.

1.6.6 History

Paleoecological investigations reported by Tipping *et al*., (1999), mainly from pollen analysis, have revealed that the now very sparsely wooded West Affric estate (west of the present study area) was once well wooded with a diverse range of tree species. The decline of this woodland has been attributed to a combination of climatic deterioration and anthropogenic influences including stock grazing and muirburn. Palynological work in the currently wooded part of Glen Affric is in progress, but preliminary evidence is available from Pollan Buidhe (see Figure 1.3). This work indicates woodland has been continuous in the landscape since colonization in the early Holocene but that locally, cyclical dynamics with open ground may take place (Wolff and Tipping, 1999).

It is thought that the inclement climate and infertility of the soil prevented the area from becoming heavily settled by humans (Wield, 2001). The earliest record of ownership is that of the Chisholm clan who owned Glen Affric and surrounding lands from the fifteenth to nineteenth centuries (with a brief hiatus due to the seizure of their lands following the Jacobite uprisings) (Steven and Carlisle, 1959). The earliest records of timber extraction date from 1560 when material from Glen Affric was used to repair a bridge in Inverness (Anderson, 1967). A sawmill was set up near Loch Beinn a' Mheadhoin around 1750 and shortly afterwards a contract was set up with the English Iron Company to supply 1000 trees per year for 30 years (Forest Enterprise, 1997). The Old Statistical Accounts of Scotland of 1792 refer to the floating of logs cut from Chisholm lands down the river Glass. In the early part of the nineteenth century, the landowner, William Chisholm, evicted the tenants from much of his land in Strathglass and Glen Affric so that the crofters' cattle might be replaced by sheep (Steven and Carlisle, 1959). It is recorded that by 1858 the Chisholm lands were inhabited by just six tenants and 30,000 sheep (Forest Enterprise, 1997). The nineteenth century saw the rise of romanticism and the celebration of wilderness; thus, the New Statistical Accounts of Scotland of 1841 refer to the grandeur of the 'relics of the old Caledonian forest' in Glen Affric (p. 491). This aesthetic shift may be linked with the emergence of the hunting estate in the highlands of Scotland. The Affric Lodge was built in 1864 by the first Lord Tweedmouth and by the latter part of the nineteenth century the hunting of deer for sport was the major land use in Glen Affric (Forest Enterprise, 1997).

The Forestry Commission acquired the adjacent estates of Fasnakyle and Affric in 1951 for the purposes of timber production. Also at this time, a dam was built which raised the water level of Loch Beinn a' Mheadhoin by about six metres and extended its length by three kilometres. At first, the Forestry Commission followed their timber production objectives in the normal manner by felling mature trees and planting with exotic conifers. However, following the publication of Steven and Carlisle's (1959) book, interest in native pinewoods grew and, worried by seemingly very poor natural regeneration, the Forestry Commission began to encourage the regeneration of the woodlands by fencing and deer control. By the 1970's, regeneration success was seen over significant areas. In 1994, Glen Affric was designated a 'Caledonian Forest Reserve' by Forest Enterprise and the management objectives were revised to emphasize habitat restoration as the main objective (Wield, 2001).

1.6.7 Designations and Conservation Status

Most of the semi-natural woodland in Glen Affric has been designated a Site of Scientific Interest (SSSI) and in April 2002 it was designated as a National Nature Reserve (NNR) reflecting the national importance of the habitat as well as the species assemblages found there. Parts of the glen are also designated as a Special Area of Conservation (SAC) under the EU habitats directive and a Special Protection Area (SPA) under the EU birds directive.

Glen Affric contains the largest area of native pinewood outside Speyside and rare or scarce species from a range of taxonomic groups are found there. The fungus flora of native pinewoods is particularly distinctive (Orton, 1986) and Glen Affric shows a good range of typical species including rarities such as the stipitate hydnoid *Hydnellum ferrugineum* (Newton *et al*., 2002). The lichen flora of Glen Affric is especially rich and is of national importance for its pinewood species (see Section 6.1). As is generally the case with native pinewoods, the vascular plant flora is not particularly diverse, but Glen Affric contains distinctive plants including twinflower (*Linnaea borealis*), one-flowered wintergreen (*Moneses uniflora*) and creeping ladies tresses (*Goodyera repens*).

The reserve houses two Biodiversity Action Plan (BAP) ant species: the Scottish wood ant (*Formica aquilonia*) and the hairy wood ant (*Formica lugubris*). Fourteen species of dragonfly may be found including the Brilliant emerald (*Somatochlora metallica*), one of the rarest in Britain (Forest Enterprise, 1997). A rare BAP spider, *Clubiona subsultans*, previously only found in semi-natural pinewood stands has recently been discovered in plantation Scots pine in the Glen (Usher and Humphrey, in press).

The Affric pinewoods are important for many birds including capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), crested tit (*Parus cristatus*) and Scottish crossbill (*Loxia scotica*); eagles (*Aquila chrysaetos*) and ospreys (*Pandion haliaetus*) are also resident. Many species of mammal are found including celebrity species of conservation interest such as otter (*Lutra lutra*), pine marten (*Martes martes*), red squirrel (*Sciurus vulgaris*) and wild cat (*Felis silvestris*).

1.6.8 Current management

Most of the study area is currently under the ownership of Forest Enterprise, but some parts of separate estates are also included; West Affric estate, west of Athnamulloch, is owned by the National Trust for Scotland, while the North Affric estate is in private ownership. The current management for the Forest Enterprise estate is outlined in the management plan (Forest Enterprise, 1997), although this document is currently undergoing revision. The principal management objective is restoration, including the following actions:

- removal of non-native species;
- *naturalization* of planted Scots pine of local origin, by thinning at varying intensities to diversify structure;
- tree planting, only in areas where natural regeneration is unlikely due to lack of seed source;
- control of deer numbers by culling;
- core woodland area to be perimeter fenced to allow tighter control on deer numbers;
- informal recreation by the general public is provided for by the provision of maintained footpaths and parking facilities.

2 Literature review of forest dynamics models

2.1 Introduction

In this chapter, the literature on forest dynamics models is reviewed with a view to identifying useful techniques for the purposes of the project. In this respect, the review is selective and biased; more attention is given to modelling approaches likely to be relevant to the project and its objectives. Whilst the overall subject of the thesis is forest landscape modelling, this review also covers models at the stand scale. This is because many forest landscape models have originated as scaled-up stand-level models and the modelling concepts employed in stand models may be applicable as components of landscape models.

2.1.1 Types of forest dynamics models

A forest dynamics model may be defined as a predictive model that depicts the change of some forest attribute (or attributes) over time. Although the emphasis here is clearly on forests, a few vegetation models of wider application have been included where these may be pertinent to forest modelling.

No model can simulate all attributes of a system; thus the choice of simulation variables will closely reflect the objectives of the modelling exercise. Forest dynamics models may be loosely organized into types according to their intended application as well as methods of construction. Various methods of classification are possible; some important distinctions are outlined below which have been informed by reviews by Munro (1974), Shugart and West (1980), Shugart (1984), Dale *et al.*, (1985), Vanclay (1994), Liu and Ashton (1995), Waring and Running (1998) and Mladenoff and Baker (1999a).

Application objectives

Models are commonly classified according to the objectives of the application. By far the most fundamental division of objectives in forest models is between those originating from the disciplines of forestry and ecology. Forestry models have tended to concentrate on the production of timber whilst ecological models have focused on ecosystem function and succession.

Organizational resolution

Models are also frequently classified according to level of organizational resolution; commonly a division between *individual-based* models and *stand-based* models is employed (Munro, 1974; Liu and Ashton, 1995; Liu and Ashton, 1998). In the former type each tree is modelled as an individual entity whilst in the latter type tree attributes are aggregated over the whole stand. Vanclay (1994) considers that such a division is really a simplification of a spectrum of resolutions. Thus, models that aggregate individuals according to size class or age class are considered intermediate in the spectrum.

Operating scale

The operating scale of a model is more or less independent of the organizational resolution, except that the organizational resolution must be finer than the operating scale. Thus, both individual-based and stand-based models may operate at either stand or landscape level. The distinction between stand and landscape scales relies on heterogeneity; thus a landscape is large enough to be heterogeneous in terms of climate, soil type and vegetation cover whilst stands are generally considered homogeneous in relation to these factors. Typically, stand scale is expressed in the order of no more than a few hectares whilst landscape scales range from hundreds to million of hectares.

Spatiality

There is a loose connection between spatial models and landscape models. Whilst many landscape models are also spatial models there are examples of non-spatial landscape models (e.g. Shugart *et al.*, 1973) as well as stand-scale spatial models (e.g. Busing, 1991; Pacala *et al.*, 1996). Although many models are completely non-spatial in design, spatially explicit models vary in the degree to which processes are modelled spatially. Typically, a spatial model is composed of non-spatial sub-models linked by spatial processes. Alternatively (or additionally), it may be parameterized by spatial data. The nature of the 'space' may also vary: a topological space is defined by the connectivity of its elements; a metric space includes a definition of distance; elements in Cartesian spaces can be described by x-y co-ordinates. Occasionally three-dimensional spaces may be explicitly modelled (e.g. Pacala *et al.*, 1996). There has been a tendency for models to become more spatially explicit as information technology has developed.

Planning objectives

Where models are aimed at informing management decisions, a distinction may be made between *strategic* and *tactical* decision making processes (and the models supporting these). Strategic planning involves developing broad strategies for dealing with problems rather than prescribing for individual cases. Tactical planning focuses on particular management actions at the site level.

Stochasticity

The division between deterministic and stochastic is absolute for individual processes within models but many models are composed of a mixture of deterministic and stochastic submodels. Generally models are described as stochastic if they contain any stochastic elements (e.g. Liu and Ashton, 1998; He and Mladenoff, 1999). In contrast, the distinction between mechanistic and empirical models is a relative one even for individual processes. Whilst some models may be absolutely empirical, mechanistic models must consist of empirical elements at some level.

As a convenience for discussion, the forest dynamics models are classified according to the diagram in Figure 2.1. Not all forest dynamic models fit neatly into this scheme so this classification is not intended as a general systemization of forest dynamics models; rather it is an aid to the description and analysis of the subject in the present context.

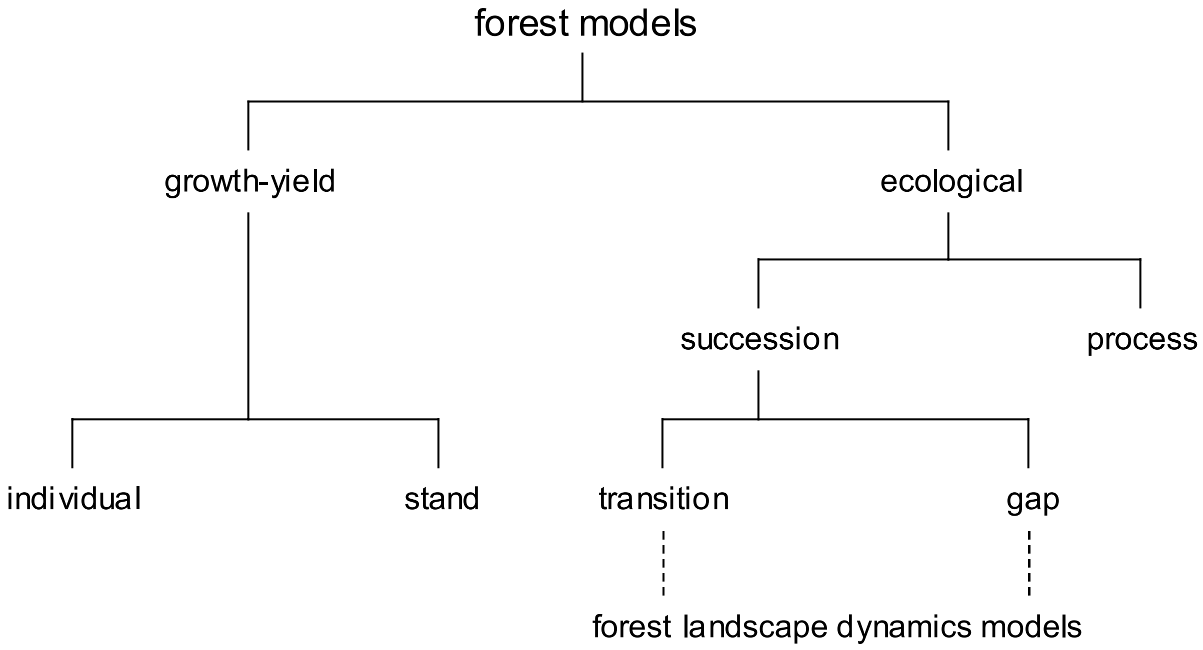


Figure 2.1 A hierarchical classification of forest dynamics models.

2.2 Growth-yield models

The term *growth-yield models* is used here to describe any forest dynamics model where the forecasting of timber quantity (generally in volume terms) is a principal objective. Usage in this case follows Liu and Ashton (1995). Munro (1974), Dale *et al*. (1985) and Vanclay and Skovsgaard (1997) use the term *forest growth models* for the same meaning but this usage was felt to be ambiguous.

Growth-yield models probably represent the first known cases of forest modelling of any form. The 17th century Chinese *Lung Ch'uan codes* are the first recorded instances of predictive models of forest growth (Vanclay, 1994). However, the roots of modern growth-yield models lie in the yield tables designed for German forests in the late 18th century.

Yield tables are produced by the establishment and continual re-measurement of a large number of plots on a variety of sites to give estimates of the changes in stand variables (e.g. height, basal area and volume) with age.

Stand growth is heavily dependent on site conditions, so models are produced for a range of *quality classes* or *yield classes*. Determination of site class will generally be based on assessment of previous growth.

The first yield tables for Britain were drawn up for Scots pine (*Pinus sylvestris*), European larch (*Larix decidua*) and Norway spruce (*Picea abies*) in 1920 (Forestry Commission, 1920). Currently, the UK forestry profession uses yield tables derived from the growth models of Edwards and Christie (1981).

Growth-yield models are generally divided into individual-based models and stand-based models. Ek and Monserud (1979) have compared results using both methods and found that individual-based models held the advantage over stand based models in applications where conditions differed to those used to calibrate the models. Yield tables and many stand-based models are generally restricted to even-aged stands of a single species. However, matrix methods based on methods used to model animal populations (Leslie, 1945 and 1948) have been used to model uneven-aged stands (Buongiorno and Michie, 1980).

The first individual-based growth-yield model was famously described by Newnham (1964) for Douglas fir. Many models have followed with varying degrees of complexity. Two useful reviews that compare individual based growth-yield models with gap models are given by Dale *et al*. (1985) and Liu and Ashton (1995).

Whilst growth-yield models are diverse in construction methods (Liu and Ashton, 1995) some features are general. Because the accuracy of timber quality is at a premium there is a heavy trade-off with generality. Most growth-yield models are designed for a certain forest type or region and generally use a single measure of site quality (such as yield class). Data requirements for growth-yield models are usually heavy further inhibiting portability. The range of species considered is usually restricted to a few that are commercially important. Regeneration is often not considered since most models are based on plantation forestry. These limitations severely restrict the applicability of growth-yield models to habitat modelling.

However, the breakdown of barriers between traditional forestry and conservation leading to growing awareness of non-market benefits in managed forests may be inducing change in forestry sector modelling. The Forest Vegetation Simulator (FVS; also known as Prognosis) is a growth-yield model designed by the United States Forest Service (USFS) which forecasts various environmental indicators as well as timber attributes (Teck *et al*., 1996). FVS simulates non-timber attributes such as coarse woody debris (CWD) levels, water quality in streams and cover of shrubs, bryophytes and lichens. It can also be used to predict habitat quality indicators for various keystone and specialist species. FVS is designed so that it can be used to project changes at the watershed (landscape) scale and includes mechanisms to link with GIS. However, spatial processes within the landscape are not simulated: each of the landscape subdivisions acts independently of the others.

Although distance-dependent individual based models (Munro, 1974) consider spatial interactions between trees to modify growth, spatial interaction at larger scales have not been a feature of growth-yield models. GIS is rapidly becoming standard technology in forest management and growth-yield models may easily be incorporated into such systems, yet the need for spatial interaction at the stand or landscape scales is limited because of the compartmentalized nature of forestry operations.

2.3 Ecological models

The term *ecological models* is something of a catch-all used to describe all forest dynamics models originating from an ecological perspective or simulating ecological processes or characteristics of forests. A convenient division can be made between *process models*, which attempt to model processes according to first principles of plant physiology, and *succession models,* which model changes in species composition or structural characteristics of the vegetation as a result of succession and disturbance.

2.3.1 Process models

Vanclay (1994) defined *process models* as those that 'attempt to model the processes of growth taking as input the light, temperature and soil nutrient levels and modelling photosynthesis, respiration and allocation of photosynthates to roots, stems and leaves' (p.70). (Models of this type have also been termed *ecosystem process models*, *biogeochemical models* and *physiological models*.) The output of process models is generally in terms of biomass accumulation, carbon and water balances and nutrient levels (Waring and Running, 1998). Process models generally do not depict changes in species composition or stand structure. In view of this, process models generally have even less direct relevance to the modelling of biodiversity or habitat attributes than do growth-yield models. This said, process models might find a role in improving the realism of succession models. Bossel (1991) emphasized the need to link process models with succession models and steps in this direction have been made by Pastor and Post (1986) and Friend *et al*. (1993).

2.4 Succession models

Succession models offer a more promising route to modelling aimed at predicting habitats, since they generally model change in species composition at some resolution. Whilst at its most coarse this might be nothing more than a description of dominant species, even this information is of more use than measures of timber volume or biomass as a basis for inferring habitat conditions.

Succession models can effectively be divided into transition models and gap models. This division is in practice similar to a division of stand-based and individual-based models. However, while most transition models are stand-based and gap models are generally individual-based there is no logical reason why this should be so and indeed, there are exceptions to this rule (e.g. Horn, 1975a,b; Fulton, 1991).

2.4.1 Transition models

A transition model can be defined as one in which the described vegetation can exist in one of a finite number of discrete classes (cover states). This distinguishes them from models where descriptions of vegetation occur along continua (of species abundance for example). The discrete classes may commonly be community types or successional stages of stands. Less usually, they may be species on plots. Transition models are dynamic models: for change to occur the modelled units must undergo *transitions* from one cover state to another.

The possible transitions in such models can be represented by *replacement sequences* (Moore and Noble, 1990). A replacement sequence may be defined as a directed graph in which the vertices represent the cover states and the edges represent the transitions. The replacement sequence is an abstract concept but can be represented graphically if the transitions are not too numerous (Figure 2.2 is an example). The transitions may occur (a) according to a rule base (deterministic), (b) with defined probabilities (stochastic) or (c) with a combination of the two. Alternatively, some transitions may be left undefined, to be applied according to some imperative exterior to the model.

Markov models

The stationary Markov model is the simplest form of stochastic transition model. The form of the process is as follows.

In a system with n cover states C_1 *-* C_n *the probability of a transition over a single timestep from* C_i *to* C_j *is given as* P_{ij}*, where the elements of* P_{ij} *are constant over time and over repeated transitions.*

The condition that the transition probabilities are constant over time defines the process as stationary (Usher, 1979; Binkley, 1980). The condition that the transition probabilities are constant over repeated transitions (i.e. the probability of transition to any other state is dependant upon the current cover state but independent of previous cover states) is sometimes referred to as the Markov property (Van Hulst, 1979, Binkley, 1980). However, it is worth noting that Usher (1979) reports confusion in the ecological literature about the exact nature of the Markov process. The above definition describes a 1st order process, but some authors extend the definition to *n*th order processes – i.e. that the transition probabilities depend upon the last *n* cover states where *n* is a positive integer. Nonetheless, in general it appears that studies of Markov processes in vegetation usually use the term to refer to 1st order systems.

The best known Markov models of forest dynamics are those of Waggoner and Stephens (1970) and Horn (1975a,b). The model of Waggoner and Stephens is based on field measurements taken from 327 plots in a mixed broadleaved forest. Measurements were first taken in 1927 and were repeated at ten-year intervals up to 1967. Plots were assigned to one of five classes depending upon dominant species and transition probabilities calculated for each of the four ten-year transitions. There were insufficient data to provide a rigorous test of the Markov property but the authors considered that the comparison of the four transitions showed the process to be broadly stationary. However, in a re-examination of the same data Binkley (1980) concluded that the observed process was not stationary and that more complex models were required to explain the successional dynamics.

Horn (1975a) presents a Markov model of individual tree by tree replacement. In the absence of long term data focusing on actual tree replacements, Horn made the assumption that one could infer replacements from the presence of advance regeneration (saplings) under mature canopies. Further, he assumes that each sapling present under a canopy tree will have an equal chance of replacing the mature tree in the event of local disturbance: a seemingly dubious assumption given the differing growth rates of species. Nevertheless, the model derived from these data was shown to produce a steady state solution of species composition remarkably similar to the actual species composition of the forest. (Actual species composition was derived from separate data to avoid circularity.)

A spatially explicit Markov-type model (MOSAIC; Frelich *et al.* 1998) is discussed in Section 2.6.

Semi-Markov models

Moore and Noble (1990) consider that stationary Markov models are inadequate for describing vegetation dynamics since successions often occur after reasonably predictable times.

An alternative to the simple Markov model which takes account of this is the semi-Markov model (Moore, 1990; Acevedo *et al.*, 1996a,b). In a semi-Markov replacement sequence the probabilities for transitions are not fixed but instead are conditional on the time that the vegetation unit entered the current state. Thus transitions representing successional change may have *holding times* associated with them whereby the transition cannot occur until the vegetation unit has occupied a successional stage for a fixed time period. Acevedo *et al.* (1996b) present a semi-Markov model based on gap model results (see Section 2.5.3).

A framework for producing transition models based on a semi-Markov process is provided by the Vegetation Dynamics Development Tool (VDDT; ESSA Technologies, unpublished). VDDT is a Windows based application designed as a management tool for exploring the effects of disturbance and management on vegetation structure and composition. Successional pathways take the form of a special case of the semi-Markov process where successional transitions occur deterministically after holding times have elapsed and disturbances occur stochastically with fixed probabilities that are independent of elapsed time. Cover states can be defined by the user in any way they please though example models describe cover states by a combination of dominant species and stand development stage (e.g. of the types described by Oliver and Larson; 1996).

Differential equations models

Consider a Markov process on a mosaic of *n* vegetation units with a fixed timestep *t*. If, simultaneously, the size of the vegetation units is shrunk (thus increasing their number) and the timestep is reduced, then in the limit as *n* tends to infinity and *t* tends to zero, a system of 1^{st} order differential equations is obtained. This system is isomorphic to the Markov process and may even be considered a special case of a general form of Markov model (Bharucha-Reid, 1960; cited in Shugart *et al.*, 1973). The resulting system is purely deterministic rather than stochastic and has rates of flux in place of the transition probabilities. The outputs of such models show smooth changes in cover state proportions, tending to a steady state solution.

Shugart *et al.* (1973) employ such a system of differential equations to simulate succession over large regions. A scale of 10^4 - 10^6 km^2 is quoted, however the structure of the model is not spatially explicit. The figures given probably reflect the smallest area which would act as a ‘quasi-equilibrium’ and the largest area which could be considered as belonging to a common ‘forest type’. The model presented for the western Great Lakes region effectively comprises three separate systems for xeric, mesic and hydric site types – implying that these systems are independent and transitions do not occur between site types.

Similar methods have been applied by Loucks *et al.* (1981) and Johnson and Sharpe (1976).

Summary of Markov-type models

The principal advantage to using Markov-type models (i.e. Markov models, Semi-Markov models and systems of differential equations analogous to Markov models) is that they are mathematically tractable. This implies that future states and steady-state solutions can be arrived at by analytical means which do not require large quantities of computer processing resources. However, as computational power has become greater and more accessible, this advantage has diminished in importance in building stand models. Nevertheless, it remains an advantage in the development of cell-based spatial models where implementation of stand scale models has to be repeated for each cell or landscape unit (see Frelich *et al.*, 1998). In simulations such as these where higher order processes are to be investigated, simplicity and tractability at the submodel level may be advantageous to the understanding of the system.

On the other hand, the simplicity of such models may also be a limiting factor in some applications. Markov-type models may or may not *describe* succession adequately for any given ecosystem, however they can never hope to *explain* successional processes in any way. In this way these models are analogous to empirical stand models of growth-yield. Similarly, substantial quantities of data are required to parameterize Markov-type models. Robust parameterization requires the monitoring of permanent plots containing replicates of all possible cover states. Where the number of cover states is large and the time-scale of the successional processes is long, this will require a large resource expenditure. A further implication of this is that models will tend to be highly specific to the forest type (possibly even the particular study area) for which they were created.

Whilst Markov-type models may be useful in formulating models for strategic decision-making, their use for tactical decisions is limited by their inability to predict on a site by site basis. In view of this, they may be better used as a heuristic modelling technique than as a predictive tool.

Vital attributes

The theory of vital attributes, first presented in Noble and Slatyer (1977), later described by Noble and Slatyer (1980), forms a basis to many modelling approaches (e.g. Cattelino *et al*. 1979; Kessel and Potter, 1980; Roberts, 1996a,b; Mladenoff *et al*., 1996). Each species is considered to possess a set of three (sometimes four) attributes which are critical in determining the species continuing survival on a site subject to disturbance. These attributes are described below.

- Method of persistence

This denotes the mechanism by which species persist on a site after disturbance. This may be by dispersal from exterior populations (D), persistence of seeds in soil as a seed bank (S), persistence of seeds with protective measures in the canopy (C), or by vegetative regrowth following survival by some part of the individual (V).

- Conditions for establishment

Species are divided into tolerant species (T), which may regenerate at any time irrespective of whether other species already occupy the site; intolerant species (I) which are only able to regenerate after disturbance when competition is low, and species that require the presence of mature individuals of their own species or some other species to regenerate (R).

- Life history

For each species a life history is described, consisting of the timings of four critical events following disturbance. These events are as follows.

p - The point at which propagules are plentiful enough to allow regeneration following disturbance.
m - Maturity: the point at which individuals reach reproductive age.
l - The point at which the species is lost from the stand as reproducing individuals.
e - Local extinction of the species when no viable propagules remain.

If some measure of the relative abundance of species in the stand is called for in the modelling application, a fifth ‘attribute’ (actually a collection of attributes) may be added. This attribute collection consists of maximum size, growth rate and mortality.

Multiple pathways of succession

The multiple pathways model of Cattelino *et al.* (1979) was developed out of a desire to model differing successional pathways arising from varying disturbance regimes: ‘many communities follow a single regeneration pathway under ‘normal’ fire periodicities, yet widely depart from it when subjected to very short or very long inter-fire periods’ (p. 41).

The model describes species presence on a site according to cover classes of combinations of species with succession and disturbance being represented as transitions between classes. The compositional changes brought about by transition events are defined by rules inferred from Noble and Slatyer's (1977) vital attributes theory. As such the model is a completely deterministic simulation of the species composition of a single stand of vegetation. Since multiple instances are not considered, disturbance is effectively a user-defined event. It may occur at any point in the succession and the consequences will depend upon when it does occur, but the timing of disturbance occurrence is not simulated.

Because of the relative simplicity of the model structure and since multiple instances are not considered, applications of the model can be represented completely as transition diagrams (See Figure 2.2). Thus, the use of a computer to run simulations is completely obviated.

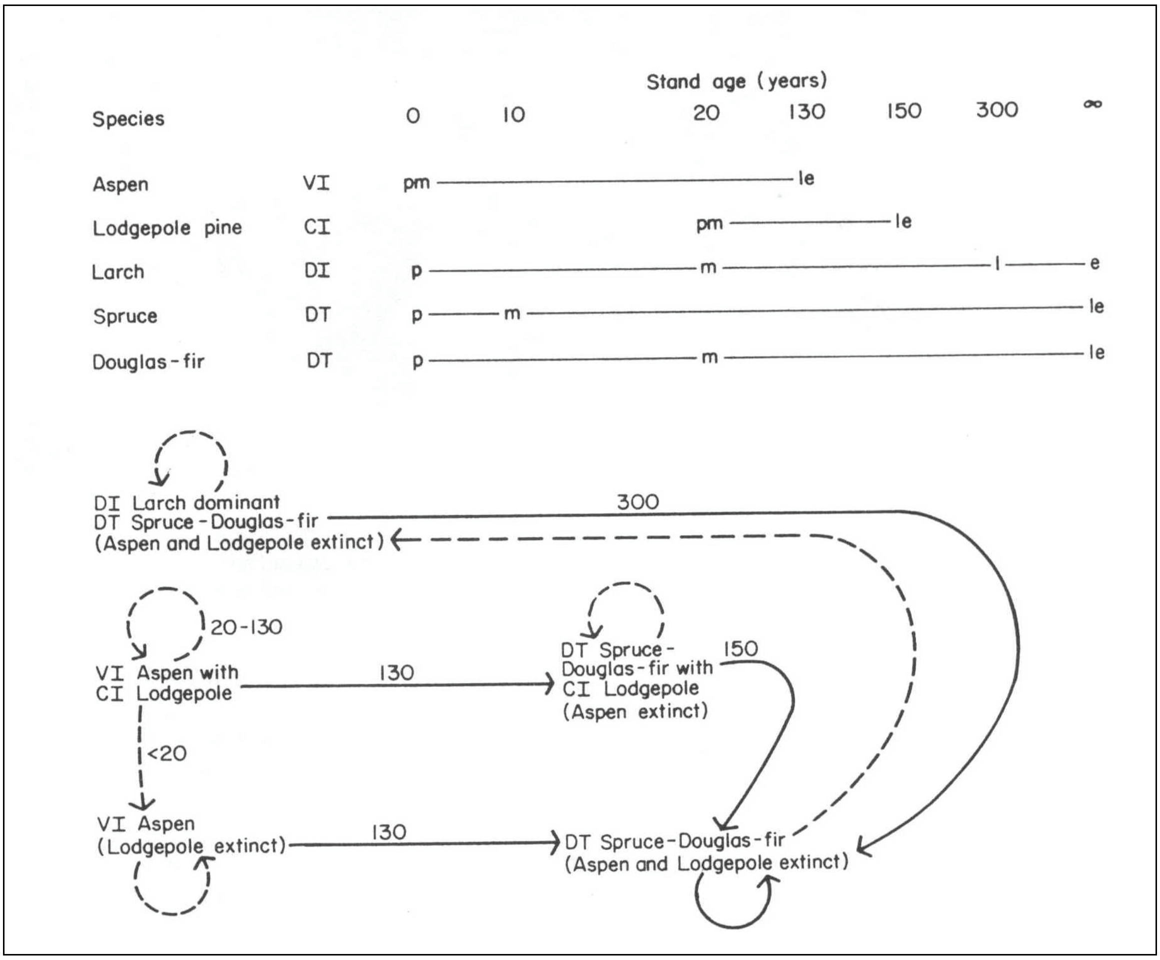


Figure 2.2 Vital attributes and multiple pathways replacement sequence diagram for northwestern Montana aspen community types. From Cattelino et al. *(1979).*

The vital attributes for each species are shown at the top of the figure (persistence and establishment followed by life history). The resulting pathways diagram shows successional transitions as solid arrows and disturbances as broken arrows. The values shown alongside transitions indicate the stand age at which the transition takes place.

Kessell and Potter (1980) identified four areas that they considered deficient in the Cattelino model and set about producing a refined version of the model for a set of Montana forest communities. These deficiencies were as follows.

1. Change in relative species abundance was not simulated.
2. Disturbances were assumed to have the same effects whatever the intensity.
3. Succession was modelled only for overstorey species.
4. The stochastic nature of seed arrival from nearby stands was not considered.

The refined model addressed the first three of these problems but the fourth was considered too difficult to handle at that time.

The first problem is resolved by adding additional community cover types to the pathway diagrams. For example: a transition previously modelled as a succession from Douglas fir/lodgepole pine/subalpine fir forest to Douglas fir/subalpine fir forest over a stand development of 220 years can be redescribed as a sequence of five transitions, with additional cover classes containing incrementally less Douglas fir.

The second problem was dealt with by defining critical values of scorch height for each disturbance transition. Field measurements had shown that fire scorch heights greater than the critical value would generally cause a major change in overstorey composition, whereas lesser fires would be more liable to leave the overstorey composition unchanged.

Whereas the original intention had been to use a similar vital attributes type method to model understorey development, it was discovered that insufficient data were available for understorey species. As a workaround, a slightly modified version of the overstorey model was used with the understorey composition being modelled empirically.

One of the objectives for the multiple pathways modelling effort was to include the models as modules in FORPLAN, a forest management decision support system (DSS) (Potter *et al*. 1979). (Although the term 'decision support system' had not been coined at this time, FORPLAN is clearly such.) FORPLAN incorporates succession models with fire risk modelling and effects of disturbance and management on animal populations.

FATE

The FATE (Functional Attributes in Terrestrial Ecosystems; Moore and Noble, 1990) modelling system operates from a similar starting point to the vital attributes/multiple pathways models in that rules of species abundance are derived from a set of attributes for each species. In the case of FATE these are called *functional attributes*. The objective of the authors in producing FATE was to produce a predictive model that provided more resolution of species abundance than the vital attributes/multiple pathways approach but with less computing resource usage than a gap model. In addition, the model was designed to be mathematically tractable and easily applicable to wide ranges of terrestrial ecosystems.

The authors point out the gulf between the individual and population (stand) based modelling approaches and so present a model based on cohorts of vegetation. The model operates at a *discrete quantitative* resolution, i.e. variables for plant attributes and abundance are ordinal categories (such as high, medium, low) and runs on incremental time steps (generally annual). Species are grouped into functional groups or guilds.

Example model runs are presented as single successional sequences and the results compared with equivalent paths of multiple pathways type models (but not with gap models with which general comparisons are also made). The logical framework used to project the dynamic sequence of succession from functional attributes is rather difficult to extricate from the text.

Spatial pattern in beech forest

The forest succession model described by Wissel (1992) is something of an oddity. It is a partially stochastic model to describe the spatial patterning and dynamics of a middle-European beech (*Fagus sylvatica*) forest. Although modelling objectives are broadly similar to previous modelling efforts (e.g. Smith and Urban, 1988; Busing, 1991) no reference is made to this work or indeed any of the usual approaches to forest succession modelling (such as gap models or transition models).

The model simulates the forest as a grid of plots that may contain a single mature beech tree, several smaller broadleaved trees or a gap. A cyclical succession mechanism is assumed to take place. The cycle starts off with a canopy gap, proceeds to colonization by birch, mixed broadleaves, and finally beech. Chronological progression through the cycle is purely deterministic except for the completion of the cycle – from beech to canopy gap – which is a stochastic event. The spatial interaction is based on the assumption that mature beech trees are intolerant of full sunlight on their trunks. On this basis, the probability of any beech tree dying is increased if canopy gaps exist to the south. This simple rule generates clustered patterns in the model output.

2.5 Gap models

The group of forest dynamics models known as gap models has dominated the literature on ecological models of forest dynamics since the inception of the first model, JABOWA, in 1972 (Botkin *et al*. 1972). Many variants of the JABOWA and its direct descendant FORET (Shugart and West, 1977) have been produced by a variety of authors. These models simulate the dynamics of individual trees on a small plot over long time periods (usually tens or hundreds of years). Individuals interact by altering the environment in the plot so that the size of the plot is usually taken to be similar in size to the gap left by the removal of a mature canopy tree. Gap models are built from both deterministic and stochastic submodels, so must be run multiple times in order to yield meaningful results. As a bare minimum the model output describes changes in species composition, age structure, size distribution and vertical stratification. In addition, individual models may simulate dynamics of other components of the forest (e.g. ground vegetation; Kellomäki and Väisänen, 1991).

2.5.1 Structure of gap models

The structure described is that of a typical basic gap model such as JABOWA though variations of later models may be noted. The description given is a digest taken mainly from Shugart (1984) and Botkin (1993). An illustration showing the components of a gap model is shown in Figure 2.3.

Gap models generally have six components:

1. Site variables
2. Species variables
3. Growth submodel (deterministic)
4. Resource submodel (deterministic)
5. Recruitment submodel (stochastic)
6. Mortality submodel (stochastic)

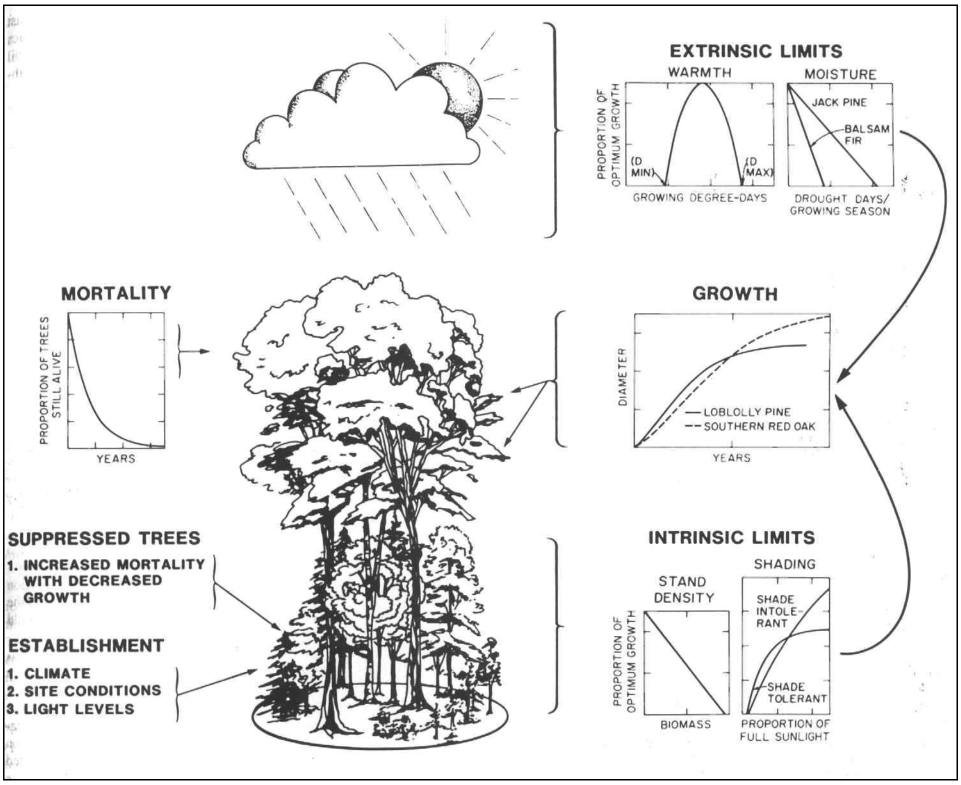


Figure 2.3 Stylized representation of the major components of a typical gap model (FORENA). Taken from Solomon and Bartlein (1992).

Site variables

The following variables are generally recorded for each site. These are included so that the effect of site type on forest dynamics can be investigated.

- Gap size – commonly 10 x 10 m.
- Accumulated temperature – some approximation of the integral of temperatures greater than some minimum temperature for growth (usually around 5°C).
- Soil fertility (nitrogen levels) - measured as some quantity of available N per unit area.

- Soil moisture – often measured as minimum distance to the water table.

Species variables

The species variables determine the manner in which individuals interact in the model simulation. The following variables are the basic variables recorded for species in most gap models. Individual models may record many more variables pertinent to their particular application.

- Continuous variables
    - Maximum age
    - Maximum diameter
    - Maximum height
    - A_1, A_2, A_3 form factor variables
    - R, growth rate parameter
    - Minimum and maximum accumulated temperatures found within geographical range of species.

- Categorical variables
    - Shade tolerance
    - Tolerance of low nitrogen levels
    - Tolerance of extreme wet and drought conditions

Growth submodel

Growth of individual trees may commonly be expressed in terms of diameter at breast height (D), height (H), leaf area (L), and stem volume (V). In gap models the latter variables are dependent on the first:

$$H = H_b + A_1D - A_2D^2 \qquad (2.1)$$

$$V = D^2H \qquad (2.2)$$

$$L = A_3D^2 \qquad (2.3)$$

where A_i are empirically derived positive constants, H_b = 1.37 m (breast height).

The premise of the growth modelling algorithm is that the increment in tree volume is initially proportional to leaf area but is reduced as the tree approaches its maximum diameter and height. In addition growth will also modified by the trees environment. Thus,

$$\delta\left(D^2H\right)=RL\left(1-\frac{DH}{D_{\max}H_{\max}}\right)f\left(\text{environment}\right) \tag{2.4}$$

where R, $D_{\max}$ and $H_{\max}$ are constants for each species and *f*(*environment*) is a function of environmental variables and includes limitations to growth due to competition as calculated by the resource submodel.

Equation (2.4) is referred to as the *fundamental growth equation* and can be solved for D via Equations (2.1), (2.2) and (2.3).

Resource submodel

Trees interact with each other by influencing the gap neighbourhood. This is one of the most powerful assumptions of the model since it obviates the need to calculate interactions between every pair of trees on the plot.

Generally, the most important mechanism for competition in gap models is via the light regime. Basic gap models assume that all foliage is retained at the very top of the tree. Botkin (1993) justifies this seemingly drastic simplification by arguing that adding complexity would be out of step with available data on crown structure and would add little. Nevertheless, some authors (e.g. Leemans and Prentice; 1987) have taken the obvious step of modelling the leaves as occurring uniformly from the top of the tree to a point at the base of the crown.) The light regime is modelled by representing available light as a function of height, assuming that each tree layer attenuates light proportionally to its leaf area. Each individual is assumed to receive the available light at its highest point (since all the leaves are at the top). In this way, large trees shade all smaller trees in the plot. Growth is modified by available light according to light regime by the factor

$$f_2(p)=A_4\left(1-e^{A_5(p-A_6)}\right) \tag{2.5}$$

where p is available light and A_i ($i \in \{4,5,6\}$) are empirically derived positive constants allocated according to shade tolerance.

Competition for soil water and nutrients is modelled more simply. An assumption is made that a given site can support basal area up to a specified maximum. Thus in the model, basal area is limited by adding the factor

$$f_3(B) = 1 - (B/B_{\max}) \tag{2.6}$$

where B is basal area and $B_{\max}$ is maximum basal area for the plot.

Growth is also modified in a non-competitive manner according to site variables for accumulated temperature, soil nitrogen levels and soil moisture levels.

Recruitment submodel

Factors that influence the regeneration of particular species on a site are numerous and diverse so that this process is extremely difficult to model in a mechanistic fashion. The usual mechanism for modelling establishment is to draw a small number of individuals from the species list at random. The probabilities for establishing different species may be modified by *filters* according to species life histories. The filters that are applied vary according to particular gap models but may include: presence of leaf litter, fire history, light levels, microtopography and climatic conditions.

Mortality submodel

Gap models generally model mortality as occurring in one of three ways: through generalized autogenic factors, through suppression due to competition and through allogenic factors. Firstly, under the assumption that a survival probability density function for a tree follows a negative exponential, it follows that each tree must have a constant probability of death each year from various autogenic causes. This probability will depend on the maximum age defined for the species. Secondly the model assumes that a tree that has been growing poorly will have an elevated chance of mortality. Generally a threshold minimum increment is defined for each species: where an individual fails to achieve this critical value in a given year its chances of survival are substantially reduced. Basic gap models use a rather arbitrary assumption that the probability of survival for a tree that grows below the threshold for 10 successive years will be only 0.01 – thus giving an annual mortality due to suppression of 0.368. These first two causes of mortality are general to the majority of most gap models, the third cause, allogenic disturbance, is modelled in a manner specific to individual gap models and may be omitted by some. Examples of factors are: fire, wind, disease and harvesting operations. The occurrence of such factors may be modelled stochastically or deterministically.

2.5.2 Development of gap models

Output for JABOWA presented in Botkin *et al*. (1972) show that the model is capable of simulating stand dynamics in a realistic fashion for certain forest types. The model was especially adept at reproducing the variation in stand structure and species composition with altitudinal gradients using only accumulated temperature as a proxy for elevation. In particular the transition point from broadleaved to conifer forest was accurately described. JABOWA used only nine characteristics to describe species and seven to describe site; that it should perform so well was perhaps surprising. As Botkin *et al*. (1972) point out: 'that the general behaviour of an ecosystem so complex as a forest can be reproduced from a few characteristics is in itself an interesting and non-obvious result of the simulation' (p.870).

This success of JABOWA prompted other researchers to embrace the gap model concept, the first of these being Shugart and West (1977) with their model, FORET. Shugart and West made very slight modifications to the basic JABOWA design to produce a simulation of forest dynamics in the southern Appalachians. The most significant modification in the FORET model is the ability of certain species to resprout from stumps rather than needing to regenerate from seed. The model was tested by recreating the effects of the chestnut blight (*Endothia parasitica*) which decimated populations of American chestnut (*Castanea dentata*) in the early portion of the twentieth century. Comparison of model output with composition data from 1908 showed close similarities despite the model having been developed using post-blight data.

A swarm of gap models followed the publication of FORET, many of them variations on the FORET model though some claiming JABOWA as a direct antecedent. Given the similarity of these two models the distinction is fine: the discrimination is perhaps more closely linked to the allegiance of the authors than structural aspects of the models. The bulk of the models follow the mould of the JABOWA/FORET design rather closely, the main differences being minor adaptations created to apply the model to a particular area or forest type. Following Liu and Ashton (1995), models that adhere to this original design will be referred to as *conventional* gap models. A list (not comprehensive) of conventional gap models is given below.

FORMIS	Tharp, 1978, cited in Shugart, 1984
FORAR	Mielke, 1978, cited in Liu and Ashton, 1995
SWAMP	Phipps, 1979
KIAMBRAM	Shugart *et al*., 1980
FORICO	Doyle, 1981
BRIND	Shugart and Noble, 1981
FORTNITE	Aber and Mellilo, 1982
SMAFS	El-Bayoumi *et al*., 1984
SILVA	Kerchel and Axelrod, 1984
FORENA	Solomon, 1986
FORCAT	Waldrop *et al*., 1986
FORSKA	Leemans and Prentice, 1987
FORECE	Kienast and Kuhn, 1989
OUTENIQUA	Van Daalen and Shugart, 1989
OVALIS	Harrison and Shugart, 1990
<unnamed>	Spilsbury, (1991)
FORDACK	Kruse and Porter, 1994
EDEN	Pausas *et al*., 1997

Since the basic structure and functions of these models are very similar little more need be said of them in general. However, four of the models are of note due to the relevance of their application.

FORSKA

FORSKA (Leemans and Prentice, 1987) is of interest since it is one of the few published examples of a gap model designed for northern Europe. The model simulates the stand dynamics of a forest in central Sweden so the species composition is similar to that of Glen Affric. However, a major difference between the two species lists is the presence of Norway spruce (*Picea abies*) in the Swedish flora. Despite being one species amongst many the presence of spruce makes an enormous difference to the stand dynamics of the forest type since Norway spruce is shade tolerant whereas all Scottish upland tree species are shade intolerant (see Peterken *et al*., 1995).

A model of uneven aged broadleaves in the UK

Spilsbury (1991) describes the use of FORET to simulate broadleaved woodland in Cumbria by the Institute of Terrestrial Ecology. Further to this, he presents modifications to the growth equations and mortality submodel that allow better comparisons of diameter distributions to be made with field data. Other than the modified growth equations and inclusion of parameters for British species the model is substantially similar to FORET.

FORDACK

FORDACK (Kruse and Porter, 1994) and EDEN (Pausas *et al*., 1997) are notable because they make an attempt at modelling habitat quality as an output alongside the usual gap model outputs. Kruse and Porter (1994) first scanned the literature on habitat evaluation to generate a list of attributes used to characterize habitat. Field measurements of these variables, along with variables that could be output from a gap model, were then recorded on 404 plots in broadleaved forest in the Adirondacks. Stands varied in age since major disturbance from 4 to 80 years. Regression models between habitat and gap output variables were developed and then incorporated into a gap model adapted for the forest type. Most habitat variables were strongly related to stand age. Values for some modelled habitat variables deviated from observed values by up to 50% of total variation at some point in the stand development. However, patterns of habitat variable change over stand development were generally similar for modelled and observed values. The reliance upon regression techniques to model habitat variables will probably result in a model that is highly site-specific.

EDEN

The model of Pausas *et al*., (1997) simulates forest dynamics and habitat quality for arboreal marsupials in Eucalyptus forests in south-eastern Australia. The model is built from two previous models: BRIND, a conventional gap model (Shugart and Noble, 1981) and a statistical model of habitat quality for arboreal marsupials (Pausas *et al*., 1995). Habitat quality, measured as the probability of occurrence of arboreal marsupials, is modelled as a function of site attributes designed to give an indication of the quantity of food and nest sites. The attributes are: foliage nutrients index, quantity of decorting bark, susceptibility of trees to defects, number of potential nesting sites, topographic position and soil nutrient status. The first three attributes are further modelled as functions of species composition and the number of potential nesting sites may be indicted by the number of trees of greater than 60 cm diameter. In this way the habitat quality index can be generated from gap model output. The model was used to investigate the effects of 3 harvesting regimes in 4 site types (i.e. a total of 12 scenarios).

2.5.3 Simplifying and approximating gap models

Gap derived transition models

One method of simplifying gap models simulating very species rich forest types, and an interesting way of analysing the roles of species in maintaining a gap replacement, is presented by Shugart (1984). Shugart characterizes forest trees according to: (a) whether or not they require a canopy gap to regenerate (related to shade tolerance); and (b) whether or not they create a gap when they die (related to size). Thus species can be split into four groups which Shugart terms *roles* since these properties logically characterize the species behaviour in a gap-phase replacement regime. Acevedo *et al*., (1996b) has used this scheme to define a semi-Markovian transition model based on the results of a conventional gap model (ZELIG, in independent plot mode). The gap model results are analysed in terms of dominance (tallest tree) to give transition probabilities and holding times for transitions between each directed pair of roles. The semi-Markov framework can be further approximated by a chain of first-order differential equations to give an analytical solution that closely mirrors the dynamics portrayed by the gap model.

FLAM

FLAM (Fulton, 1991) was designed as a computationally efficient approximation to a gap model. FLAM attempts to mimic the behaviour of the gap model FORSKA but forsakes the individual based approach in favour of a height-class structured population approach. Two major approximations are made:

1. all trees of a species in a given height class have the same stem volume, leaf area and growth increment; and
2. the distribution of tree heights within a class is uniform.

Results from FLAM showed good correspondence with FORSKA results when the number of height classes was in the range of 4 - 20 and when timestep interval was in the range 1 - 5 years. When FLAM was run with eight height classes it required only 5% of the CPU time of FORSKA.

VAFS/STANDSIM

The model of Roberts (1996a) is particularly interesting in that it marries elements of two previously disparate modelling families. VAFS/STANDSIM (Vital Attributes Fuzzy Systems STAND SIMulator) is based on a gap model structure: modules exist for recruitment, growth and mortality in the manner of a conventional gap model. However, vital attributes (Noble and Slatyer, 1977) are used to determine the behaviour of the establishment and mortality modules and the reaction of the trees to disturbance. The major diversion from conventional gap model structure is that individual trees are not modelled, but instead the basic unit of modelling is the presence or absence of ten-year age class cohorts. The time increment for the model is also ten years so the cohorts effectively graduate by one age-class every time-step. The departure from the individual-based approach combined with the ten-year timestep results in a model that runs much more quickly than a conventional gap model, making it suitable for inclusion in a spatially explicit landscape model (see VAFS/LANDSIM; Section 2.5.4). An indicator of species abundance is taken as the sum of age class values for which the species is present. It is intended as a rough measure of biomass under the assumption that the size of the trees is proportional to their age.

2.5.4 Spatially explicit gap models variants

Shugart and Noble (1981) report that conventional gap models may overestimate species diversity in the early stages of recovery from disturbance. This may be due to unrealistic assumptions of presence of propagules arriving on site. If disturbances are large it may be some time before species that have been lost from the disturbed area can re-establish. The manner in which these species recolonize will be related to their dispersal ability and the spatial arrangement of remaining seed sources.

In view of this it has become widely recognized that adding a spatial component to gap models can enhance their performance as well as widen their application to include spatial problems. Several approaches have been taken which incorporate spatial effects but stop short of operating at landscape scales.

ZELIG

Smith and Urban (1988) created the model ZELIG to investigate spatial scaling of forest structural patterns. This original incarnation of ZELIG was based on FORET but applied to a 30 x 30 grid of 10 x 10 m cells. Unlike previous gap models, replicated plots undergo explicit spatial interactions: in ZELIG this consists of extending the gap neighbourhood (see Section 2.5.1) to include portions of neighbouring grid cells. The *zone of influence* is represented as a 20 x 20 m moving window centred upon successive gridcells. In this way the resource submodel is extended to include neighbouring plots, however this is the limit of the spatial interactions considered in ZELIG. Spatial effects of seed dispersal or disturbances such as fire were originally not considered but were reported as under development in a further paper (Urban *et al*., 1991) detailing subsequent applications of ZELIG. Later developments of ZELIG (Urban *et al*., 1999) have moved the model into the realm of the FLDM (see Section 2.6).

SPACE

Whereas ZELIG is an outward looking spatial extension of the gap model concept, SPACE (Busing, 1991) is an analogous inward looking extension. Again a grid cell based approach is used, but SPACE uses a grid with a resolution of 0.5 m, which may not accommodate more than one individual per cell. As in ZELIG, the structure of the model is essentially the same as that for FORET except that the resource submodel operates using an extended neighbourhood. In this case the neighbourhood comprises cells within a 10 m radius of the target cell. SPACE was used to investigate within-plot scale pattern generation during the course of succession.

SORTIE

The model of Pacala *et al*. (1996), SORTIE, takes the same mechanistic approach of the gap models but completely discards the discrete neighbourhood simplification. It may be classified with gap models because of the similarity of objectives, approach and structure (SORTIE includes the six components outlined in Section 2.5.1).

The main enhancements of the SORTIE model over conventional gap models are as follows.

- Trees are assigned exact x-y co-ordinates in SORTIE rather than merely an inclusion in the gap environment.
- In SORTIE the available light to any tree is calculated geometrically by creating a virtual fish-eye photograph taken from the top of the trees crown. This image consists of 216 pixels relating to paths from the camera to the sky. The model calculates interception of these paths with neighbouring trees to generate a map of brightness for each pixel. Each species of tree has a specific light attenuation co-efficient. The interception pixel map is overlaid with a pixel map of *sky brightness* that accounts for daily and seasonal movement of the sun across the sky to produce a *Global Light Index* (GLI) for each tree.
- Distribution of seedlings is dependent on species specific functions of distance to parent trees. A distribution map for each species is calculated as the sum of distributions for all parent trees.
- Growth-dependant mortality functions are tailored to species in the SORTIE model whereas conventional gap models use the same function for all species.

SORTIE was created out of an integrated program of fieldwork and modelling so that fieldwork objectives were tied in with modelling requirements. Whilst this provides for a model with appropriately identified and accurately determined parameterization, it also results in a modelling framework that requires considerable resources to adapt for differing forest types. In SORTIE, competition is modelled as a function of light only since field observations suggested competition for nutrient or moisture was not important. Because of the detail involved in calculating available light in the SORTIE model, the GLI calculation submodel is extremely computationally demanding, taking up 90% of the processing time for the entire model. Because of this, SORTIE uses a five year timestep in place of the annual timestep more usual in conventional gap models.

2.5.5 Summary of gap models and variants

Since the publication of the first gap model (Botkin *et al.*, 1972), the class has come to take prominence in ecological succession modelling. It is perhaps remarkable that so many instances of gap models have been produced with such similar structures. Nevertheless, this demonstrates that the use of gap models is an established technique. The models have been used in a wide variety of woodland types from boreal forest (Leemans and Prentice, 1987) to subtropical (Shugart and Noble, 1981). Many of these models have been tested to some extent (for examples see Shugart, 1984) and enthusiasts claim that they represent forest successional dynamics mechanistically and realistically in a wide range of applications. One of the reasons for the popularity of gap models may be the relative ease of parameterization required to adapt them to cope with any new range of species. JABOWA was designed to use parameters that may be easily extracted from forest inventory data as exists in many forestry departments around the world. A compilation of such parameters (silvics) for north European species has been published by Prentice and Helisaari (1991).

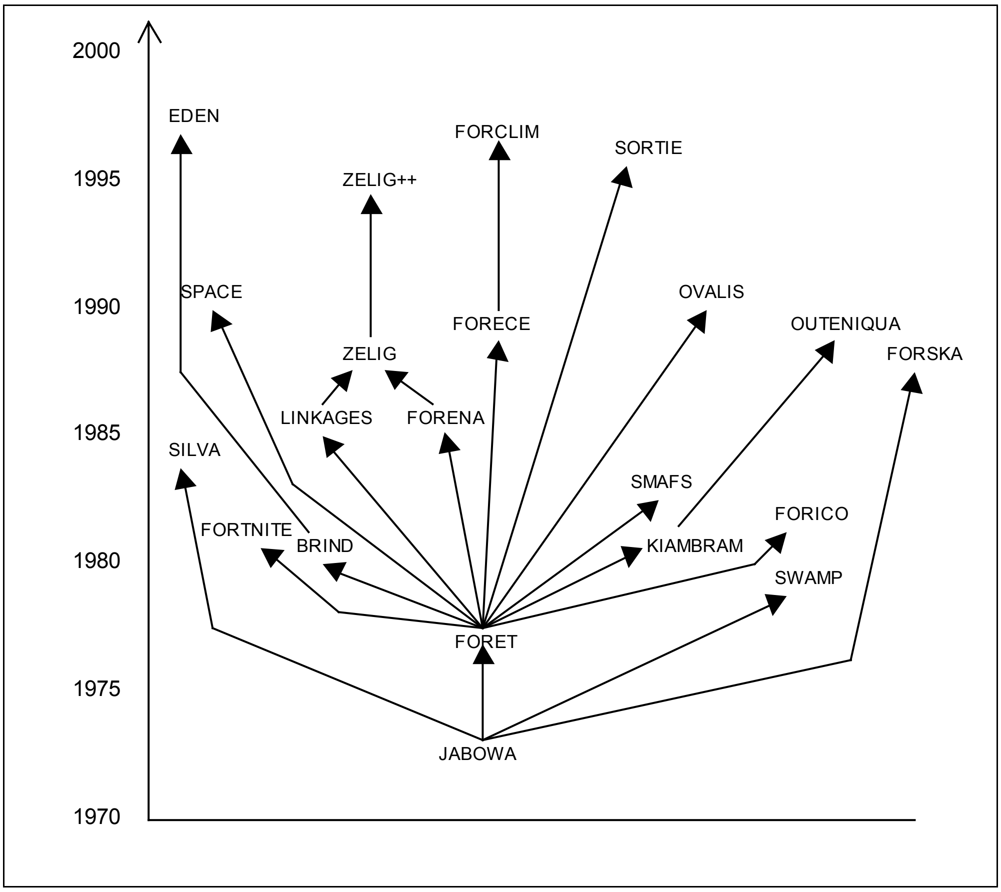


Figure 2.4 Genealogy of gap models. Modified from Liu and Ashton (1995).

A further advantage of gap models is that the output gives detailed representations of species composition and physical structure. This feature has been used to generate models of habitat attributes from gap model output and may provide avenues for biodiversity modelling.

However, the gap approach is not without its drawbacks. The individual-based approach is expensive in processor time and may well be inappropriate for landscape level simulation. Workarounds to this problem as suggested by Fulton (1991), Acevedo *et al*. (1995, 1996a,b) and Roberts (1996a,b) are workable technical solutions but are not so well tested for so many forest types as the conventional gap model type.

Botkin (1993) reported that the principle area in which JABOWA did not perform well was the distribution of diameter classes. Spilsbury (1991) has suggested that the reason why published accounts of gap model adaptations present output in biomass terms is that none produces realistic simulation of diameter distribution. Whilst this is clearly a serious drawback for many forest management applications, for biodiversity assessment precision in diameter output is not at a premium - age class distribution would serve as well or better in this respect. However, problems such as these have brought the realism of the simulation mechanism into question. Some researchers have found that gap models show alarming sensitivity to gap neighbourhood size (D. Golicher, personal communication). Whilst the gap size is intended to broadly reflect the size of a mature canopy tree it is essentially an artificial construct: choice of gap size may be effectively arbitrary where a large range of individual canopy sizes exist. In a more general critique of conventional gap models Pacala *et al*. (1995) express a concern that conventional gap models may *appear* mechanistic, but are in fact largely descriptive and thus may in fact 'reproduce community dynamics for substantially incorrect reasons' (p.39).

Since the principle mode of competition in gap models is that of light it is questionable how well the approach would work when applied to Caledonian forest where all the major tree species are shade intolerant and relative degrees of shade tolerance for species are not well known. Leemans and Prentice's (1987) FORSKA model simulates a forest ecosystem where the gap-phase dynamics are fairly clearly dominated by the role of Norway spruce as a tolerant species that comes to dominate late successional stands. Without the presence of spruce the gap dynamics of this assemblage of species is far more subtle and it remains to be seen whether a gap model could capture such dynamics. Gap models specialize in simulating long successions of tree species, however Scottish upland woodlands may not be subject to successions such as these. Peterken *et al*. (1995) characterize Scottish upland woodland as composed of pioneer species where disturbance is endemic; in the absence of disturbance woods may have to degenerate back to open ground before regenerating once again.

2.6 Forest landscape dynamics models

The term *forest landscape dynamics model* (FLDM) is used here to refer to a spatially explicit forest dynamics model acting at landscape scales. This term is used in preference to Mladenoff and Baker's (1999b) 'forest landscape model' to distinguish such models from static landscape models such as the Macaulay Institute's Native Woodland Model (Hester *et al*., 2003).

The development of FLDMs has stemmed largely from ecological successional models (both gap and transition) although there has also been some influence from GIS and landscape planning (Mladenoff and Baker 1999b). Most of this development has occurred only recently; whilst the gradient fire model of Kessell (1979) may be regarded as an early example of the type, it is only in the last ten years that serious progress has been made in the field. For example, in Baker's (1989) review of landscape models, relatively few were spatially explicit. This recent development of FLDMs has resulted partially from increased awareness of the importance of planning at landscape scales, but advancement of FLDMs has also been closely reliant on GIS and remote sensing technology.

Linkage of dynamic models to GIS varies greatly in the strength of integration. At the loosest level, the GIS may be used to pre-process data for use in an essentially non-spatial model, or to display maps of model output. Such linkages may be referred to as *loose coupling* (Goodchild, 1993). Models may be linked more tightly to GIS if they use the same data structures as the GIS and perhaps use some of the spatial tools of the GIS within the modelling process. The tightest linked models are implemented entirely within a GIS environment and use the GIS scripting language to run the model. The advantage of this approach is that there is no need for linking software to pass data from the modelling program to the GIS. However, GIS programming languages are commonly interpreted and may produce slow models. Additionally such languages may not be as flexible as other modelling environments.

Modelling with GIS is a recent development – Goodchild *et al*. (1996) reported that the concept of using GIS as a tool for spatiotemporal modelling was 'far from being broadly accepted' (p.313). Since then however, GIS technology has been moving apace. Purpose built GIS modelling packages such as PCRASTER at University of Utrecht are being built that attempt to address some of the problems with tightly-linked GIS modelling noted above (Wesseling *et al*., 1996).

In almost all cases, FLDMs subdivide the landscape into parcels that can be treated at the stand-level. These parcels may be either polygons if a vector approach is taken or grid cells if a raster model is used. Often, the FLDM is produced by scaling up from a prior stand-level model (e.g. Acevedo *et al*., 1995; Roberts, 1996b; Urban *et al*., 1999; Kurz *et al*., 2000). Urban *et al*. (1999) present three methods for achieving the scaling up process (see below).

Sampling

A simple method of applying a stand-level model to a landscape is to represent each set of environmental conditions on a case-wise basis and then aggregate the results. This is analogous to the way that field-based studies sample landscapes. The major disadvantage with this method is that spatial processes are not considered so that the resulting landscape-level model is non-spatial (hence not a FLDM).

Brute force

A non-sophisticated method of addressing the problem is simply to replicate stands over the entire landscape. For simple stand-level models and small landscapes this may be a perfectly reasonable approach. However, if the stand model is a complex individual-based model and the landscape large then this method becomes exceptionally unwieldy. To represent every tree in a landscape may become achievable as computing power increases but this places a wide gulf between organizational resolution and operating scale.

Meta-models

A third way of generating landscape models from stand models is to produce an approximation of the stand model that may be replicated at the cell-level of the landscape model. This may be achieved by construction of a transition model that emulates a gap-type model, or by simplifying a gap-type model so that the organizational resolution is coarser than individual-based.

A selection of FLDMs that use a variety of means to represent landscape change is reviewed below. Whilst some of these models are scaled-up versions of earlier stand-level models, some (Mladenoff *et al*., 1996; Frelich *et al*., 1998; Chew, 1997; Liu and Ashton 1998) have been developed specifically to operate at landscape scales.

MOSAIC

Acevedo *et al*., (1995, 1996a) used the approach described by Acevedo *et al*., (1996b) of generating transition models from a gap model (ZELIG) to create a GIS-linked spatial model of forest dynamics (MOSAIC). MOSAIC is further developed from a simple transition model to include the effects of environmental variables. These environmental variables are included as GIS layers. Seed dispersal is modelled by adjusting transition probabilities according to cover states of neighbouring cells. An example of the use of MOSAIC for exploring landscape dynamics is presented for a case study in the Oregon Cascade Mountains. The model is parameterized using a digital elevation model (DEM) with derived variables for slope and aspect and temperature and precipitation modelled as functions of altitude.

The link to GIS is an external one. Environmental variables and baseline information are initially held as GIS raster maps but imported into MOSAIC as ASCII files. Output from the model is exported via ASCII back into GIS format.

VAFS/LANDSIM

Roberts (1996b) extended the VAFS/STANDSIM model (Roberts, 1996a) to operate over entire landscapes to create a landscape model: VAFS/LANDSIM (Vital Attributes Fuzzy Systems LANDscape SIMulator). The model operates on a landscape represented as a tessellation of polygons. The spatial representation is topological rather than Cartesian, meaning that there is a record of polygon adjacency, but no concept of distance between objects. Each polygon is attributed to a habitat type which defines: (a) the probability of regeneration for each species, (b) the mean fire return interval, and (c) a function of fuel accumulation with time. Spatial interactions occur via seed dispersal and fire spread. Regeneration in a polygon is conditional upon the existence of mature age-classes in at least one adjacent polygon. Fire propagation is stochastic but depends on habitat type and fuel accumulation. The example landscapes presented in Roberts (1996b) are synthetic landscapes of 400 hexagonal cells mapped onto tori. (Mapping onto a torus is a standard technique used in spatial modelling when there is a requirement to avoid edge effects. The torus is the topological object created by joining both pairs of the opposite edges of a rectangle.) The model was used to explore the effects of landscape heterogeneity and fire return interval on habitat fragmentation and diversity.

The major limitation of this approach is the vector-based polygon representation. Whilst the vector representation allows efficient use of computer memory it locks the landscape into a pre-ordained structure which cannot be changed. This also affects spatial processes like disturbance and seed-dispersal. Disturbances such as fire and wind often redefine landscape structure but it is very difficult to do this with a vector structure. Simulation of seed dispersal requires a distance metric to calculate seedfall density (Greene and Johnson, 1989). Large and/or extended polygons present difficulties in this respect, yet if all polygons are made small and compact the advantages over a raster representation disappear.

LANDIS

LANDIS (Mladenoff *et al.,* 1996) is a direct descendant of VAFS/LANDSIM (Roberts, 1996a,b) although the authors make 7 distinctions between LANDIS and its ancestor. These are summarized below.

1. Raster approach
2. Spatial interactions are distance rather than neighbourhood based
3. Adaptable to various scales
4. Coded with Object Oriented (OO) C++
5. Includes user interface and spatial analysis capabilities
6. Dynamic link with ERDAS GIS
7. Two interacting disturbance regimes (fire and wind)

The adoption of the raster approach means that LANDIS is based in a Cartesian space rather than a topological space as in VAFS/LANDSIM. This allows more realistic spatial interactions, such as species dependent seed dispersal functions. Patch formation and disintegration can also be modelled. The raster approach also facilitates the use of spatial data as model parameters without the need to calculate parameters for each habitat polygon. Species parameters are shown in Table 2.1.

Table 2.1 List of species life histories that drive LANDIS (from Mladenoff et al.*,1996).*

Long	Species longevity (years)
Mature	Age of sexual maturity (years)
Shade	Shade tolerance class (1-5)
Fire	Fire tolerance class (1-5)
Wind	Windthrow tolerance class (1-5)
Effseed	Effective seed dispersal distance
Maxseed	Maximum seed dispersal distance
Vegprob	Vegetative reproduction probability
Sprout	Maximum sprouting
Estab	Species establishment co-efficient (by land type)

LANDIS appears to be a computationally efficient model; a figure of approximately one hour is quoted for running the model for 500 years on a 500 x 800 grid for 23 species (He and Mladenoff, 1999). However the main drawback to LANDIS is its simplistic representation of cohorts. The binary presence or absence for each age-class may provide acceptably detailed representations of stand structure for forests in which there are many species with a wide amplitude of shade tolerance, giving rise to complex multi-storey stands. However, if applied to a region such as Scotland where there are few shade-tolerant species and stands rarely contain more than a few cohorts, the representation becomes simplistic.

FIN-LANDIS

Pennanen and Kuuluvainen (2002) present a modification of the LANDIS model (see above), designed to allow simulation of fire-prone landscapes in Fennoscandinavia. The principal modification to the original LANDIS model is the replacement of the binary representation of cohorts (present/absent) with a trinary representation, which incorporates two densities of cohorts. This modification allows more complex representation of stand structures and dynamics. At establishment, cohort density depends upon seed density, but later in stand development dense cohorts may be reduced to thin cohorts by fires of intermediate intensity or by senescence.

MOSAIC (2nd instance)

Despite the name, this model described by Frelich *et al*., (1998) is completely unrelated to the MOSAIC mode produced by Acevedo *et al*., (1995) except in that they are both spatial forest dynamics models. The model of Frelich *et al*., (1998) is a spatially explicit Markov model which simulates patterns of tree by tree replacement. In this respect, it is similar to the model of Horn (1975a,b) except for the inclusion of *neighbourhood effects* which are defined as 'any process mediated by canopy trees that affects the replacement probability by the same or other species at the time of canopy mortality' (p.150). Generic neighbourhood effects are simulated without being specified though it is proposed that in general these may include: 'seed rain, stump and root sprouting, alteration of the physical or nutrient status of the forest floor to favour or disfavour germination and establishment of a given species, and the influence of the canopy on local temperature, humidity and light levels' (p.150). As the model is completely non-mechanistic and unrealistic (hypothetical species are employed), it is best seen as an abstract exploration of pattern formation rather than a predictive tool.

Linkage with GIS is basic. Model results are output to ArcInfo, which creates Voronoi tessellations from tree locations. The GIS is then used to calculate landscape metrics from the resulting polygon coverages.

FORMOSAIC

Liu and Ashton (1998) have developed an individual-based landscape model for considering spatial dynamics and forest succession called FORMOSAIC. In the illustrated model scenario the area of forest that is modelled (the focal forest) is a 5 x 5 square grid of cells each 10 x 10 m making up a total area of 0.25 ha. The authors claim that the focal forest may cover areas of 'millions of hectares' (p.181) but since the model is individual-based it is difficult to imagine how this is achievable with contemporary computing equipment and within reasonable timescales.

FORMOSAIC was applied to a tropical forest containing more than 800 tree species. The model was parameterized by inventory data from a permanent study plot. 502 abundant species were individually parameterized, the remaining rarer species being grouped into guilds. Data for recruitment and mortality were sparser so each species was allocated to one of four guilds and parameters were calculated according to guild.

The growth model was dependent on diameter at breast height (dbh), neighbourhood influence (basal area of surrounding trees in plot), slope, elevation and distance to wet areas. Note the simplification of the competition modelling from traditional gap model approach. Each guild has a different dispersal curve so that recruitment is modelled spatially. Seed sources may be within grid cell, in adjacent grid cells or outside the focal forest.

FORMOSAIC records exact locations of individuals within plots. However, initial placing of trees within plots is a random process. This level of approximation seems inconsistent with the aim of assigning individuals to precise locations. Whilst seedfall may approximate a random pattern at the plot scale, recruitment (i.e. to 1 cm dbh) is unlikely to do so. Whilst conventional gap models do not consider horizontal interactions between trees at all, the value of doing so may be undermined if the patterns of trees within plots are purely random.

SIMPPLLE

SIMPPLLE, SIMulating Patterns and Processes at Landscape scaLEs (Chew, 1997) is presented as a 'management tool to facilitate the understanding of landscape dynamics' (p.287). It appears to act as a transition model for polygons on a GIS layer though the structure of the model is difficult to elicit from the description given. The model is not tied to any particular GIS package and works outside the confines of the GIS by interrogating the GIS for the state of the individual polygons and the identity of adjacent polygons. Output from the model can then be brought back to the GIS. The processes of vegetation change appear not to be modelled at all by SIMPPLLE; rather these must be generated from finer scale models, published literature or expert opinion. Processes include fire and insect outbreaks. They may alter the cover state for a polygon and/or alter the transition probabilities from that polygon. Different processes may spread through the landscape in different fashions, but spread must be via adjacent polygons due to the structure of the spatial information. The author notes that to improve the model the modelling procedure may have to be shifted to within a GIS and that a method of changing community boundaries according to process should be included. The most obvious way to achieve the latter would be to use a raster data format, though this is likely to involve heavier processing loads.

TELSA

TELSA, the Tool for Exploratory Landscape Scenario Analysis (Klenner *et al.*, 1997; Kurz *et al.*, 2000) is a spatially explicit extension of the VDDT model (Section 2.4.1). TELSA divides the landscape up into small polygons that result from overlaying management zones with areas of similar forest vegetation and then further subdividing by means of a polygon tessellation. The course of succession in each simulation polygon is deterministic and therefore independent of spatial configuration. Disturbances occur stochastically but may spread across the landscape by means of adjacent polygons. Management activities may then be defined as occurring within certain management units and vegetation cover types. Once simulation has been effected, TELSA may be used to perform spatial analyses on the resulting landscape. TELSA is a tool for strategic planning, designed for operation at scales of 50,000 to 200,000 ha.

2.7 Conclusions

This review has demonstrated that there are a multitude of approaches and techniques available in the modelling of forest dynamics. This perspective is useful because it allows appreciation of the range of possibilities that might be feasible in modelling landscape dynamics in the study area.

To some extent all of the approaches to succession modelling hold some potential for modelling habitat. However, models which present detailed representations of stand composition and structure probably allow more options for biodiversity modelling than simple models. On the other hand, if these representations are too detailed then the scaled up landscape model may become too unwieldy to be of practical use.

Of all the approaches, the spatial transition model is probably the easiest type to actually implement as a computer program. However, the major obstacle to overcome in the production of such models is the definition of the stand replacement sequence.

The empirical method involving remeasuring plots may give statistically valid results at the stand level, but modelling of spatial processes is not particularly feasible since processes are not conceptualized at the stand level. Furthermore, this will necessarily be a long-term project since the interval between plot assessments will need to be long in woodland vegetation.

The semi-mechanistic approach of generalizing a gap model as a transition model is in some ways an improvement in this respect. However, to some extent the problem still exists, since the processes that occur in the gap model cannot be applied to the spatial model and these processes must be somehow generalized into the transition model framework. In addition, this technique involves a two step modelling process and a formalized linking mechanism. In a heterogeneous landscape, the site factors of the gap model will be constantly changing in space so that in fact many transition models will be needed to cover the landscape. If, once the model was complete, changes to the gap model were required, the entire transition model would require re-building.

The third way of defining the replacement sequence is to design it directly on the basis of a conceptual model (e.g. Cattelino *et al*., 1979). This will generally involve more assumptions about the nature of vegetation change than with either of the previous two models. However, it is perhaps a simpler matter to model spatial processes since they can be defined at the same organizational level as the stand dynamics model.

Because spatial transition models tend to represent highly generalized spatial processes they may be best suited to (a) heuristic or exploratory studies of spatial process (such as MOSAIC; Frelich *et al*., 1998) or (b) large scale simulations of vegetation dynamics aimed at driving strategic decision making tools (such as SIMPPLLE; Chew, 1997). Whilst the current modelling project is aimed with decision-support applications in mind, the ability to support planning at the tactical level is also required.

At the other end of the spectrum, the spatial individual-based models tend to be too detailed to apply to the landscape scale. The very fine scale models such as SORTIE and SPACE are clearly not designed for use at the landscape scale; attempting to run

SORTIE for the whole of Glen Affric would probably take months on standard computing facilities.

However, even the extended spatial individual models such as ZELIG are not up to the simulation of tens of thousands of gap sized plots, as would be needed for simulating dynamics in Glen Affric. The closest that individual-based models get to landscape scale modelling is probably the FORMOSAIC model, which is designed to handle large area simulations. However, judging by the fact that the testing reported in Liu and Ashton (1998) used a forest size of 2.5 ha, a total simulated time span of four years and ten replications for each run, it would be reasonable to assume that the technology required to model thousands of hectares for hundreds of years is presently not within reach.

The most suitable type of modelling approach would therefore appear to be of the type exemplified by LANDIS (Mladenoff *et al.*, 1996) where a stand-level model of intermediate complexity is replicated on a raster structure. However, whilst the overall model structure may be suitable, the nature of the representation does not appear to be ideal for a model of woodland dynamics in upland Scotland. Where LANDIS allows many cohorts with little detail for each, a Scottish model might be better served by less cohorts with more detail. The modifications made by Pennanen and Kuuluvainen (2002) go some way to addressing this deficiency, however another difficulty with both LANDIS versions is that they are principally designed for fire-prone landscapes. Whilst natural fires may have occurred in parts of Scotland in the past, it is assumed here that the principle agent of disturbance in the study area would be strong winds (Quine *et al.*, 1999). LANDIS does simulate wind disturbance but this element of the model is rather simplistic since this wind is assumed to be sub-ordinate to fire in importance as an agent of disturbance.

3 Design of the GALDR model

galdragon (*Scott*) *noun* an obsolete Shetland word for a sorceress or witch.
[Old Norse *galdra-kona*, from ***galdr*** crowing, incantation, witchcraft, and *kuna* woman.]

Catherine Schwartz, ed. (1993; p. 680)
in 'The Chambers Dictionary'.

3.1 Introduction

This chapter introduces and gives an outline description of GALDR, the forest landscape dynamics model (FLDM) which forms the core of this work. The model may be described as a stochastic, cohort-based model of natural disturbance and succession. The operational aim of the GALDR model is to depict change in tree species composition and forest structure over large spatial extents and long timescales. This may be achieved by simulating the effects of natural processes such as seed dispersal, regeneration, growth, wind disturbance and herbivory. The first part of this chapter explains the methods used to implement the model and introduces the SELES model development tool. Subsequent sections describe the fundamental design of the model, the data structures employed and the methods of acquiring and adapting input spatial data. More detailed descriptions of individual elements of the model design are provided in Chapter 4.

3.2 Model implementation

3.2.1 Methods of implementing landscape models

The GALDR model is implemented using SELES (Spatially Explicit Landscape Event Simulator), a modelling support tool developed at Simon Fraser University in British Columbia, Canada (Fall and Fall, 2001). In the scoping stages of the GALDR project, various other implementation methods were investigated. These included creating an entirely new model using C++, applying existing models such as LANDIS (Mladenoff *et al.*, 1996) and TELSA (Kurz *et al.*, 2000), developing the model within ArcView GIS, and producing the model with other modelling support environments such as Simile/AME (Muetzelfeldt and Taylor, 1998). Each of these implementation methods was found inappropriate to the project aims in some way. Designing a C++ program to implement the model was found to require a very heavy investment in skills acquisition. Furthermore, a large amount of programming effort is required to create the data structures and functions that would form even a relatively simple model. The main problem with using an existing model is, even when that model has been designed for general application, there is a lack of flexibility. Fall *et al*. (2001) liken the process to forcing a square peg through a round hole, inasmuch as such methods force the research questions to fit the model structure whilst by preference, the opposite influence should prevail. Working within the application framework of a GIS has the advantage of allowing direct access to GIS data and tools. However, experience of using the Avenue language in ArcView demonstrated that using an interpreted scripting language as part of an application can result in very slow simulations. In addition, Avenue lacks tools suitable for cell-oriented raster modelling. The modelling environment Simile offers much better support for modelling at the cell level but, whilst the ability to create multiple entities allows representation of grid-based spatial data, the ability to link with GIS appeared to be limited.

3.2.2 The SELES model development tool

SELES was chosen as the most appropriate development platform because it allows for rapid model prototyping whilst retaining a large degree of flexibility in model design. SELES has proved highly suitable because it has been developed specifically for simulating models of landscape change, and the basic SELES modelling approach agreed well with that of the early GALDR conceptual model. SELES is also very convenient because it is compatible with ArcView GIS and easily available. However, whilst a modelling environment such as SELES allows much greater flexibility than adaptation of an existing model, any implementation will impose limitations and hence influence design.

Raster representation

SELES represents the spatial attributes of the landscape by a collection of raster layers that are held in the computer's Random Access Memory (RAM). These may be exchanged with an external GIS via export files (ArcView, ERDAS or GRASS). The number, extent and resolution of the layers, as well as their interpretation, are all defined by the user (i.e. the model developer). However, all raster layers must be defined at the same spatial resolution and for the same rectangular extent – i.e. a single raster structure underlies all spatial data and processes. Raster layers may be further organized into constructs called *raster vectors*. A raster vector may be defined as a well-ordered set of indexed rasters: $\mathbf{R} = \{\mathsf{R}_1 \ldots \mathsf{R}_n\}$. (A well-ordered set is one for which every non-empty subset has a unique least element – i.e. the elements form a definite sequence.)

Model state

Spatial data is divided into two distinct types by SELES: *static layers* have constant values throughout the simulation run and represent aspects of the landscape that might be regarded as unchanging over the timescale of the model run; *dynamic layers* represent the features of the landscape that change over time. In a typical FLDM the static layers will represent (relatively) permanent landscape aspects such as topography or underlying geology whilst the dynamic layers will represent the forest vegetation and other mutable aspects of the landscape. Together, the static and dynamic layers plus non-spatial global variables describe the model *state* – the complete data representation of the landscape within the model. Although dynamic layers may be initially undefined and only evaluated during simulation, it will generally be desirable for some dynamic layers to contain data at the start of the simulation. Such data compose the *initial state*, and are generally imported from GIS.

Landscape events

A SELES model consists of two principal elements: the model state, and the set of *landscape events*. The landscape events determine the dynamic behaviour of the model – i.e. how the model state changes over time. Typically, each landscape event will represent a well-defined biotic or physical process in the landscape. For example a fire landscape event could simulate the effects of wildfire and make changes to the vegetation layers of the model appropriately. Thus each landscape event may be considered to implement a *sub-model* of the main GALDR model, and subroutines in landscape events may be similarly linked to sub-models of sub-models (which may be termed *modules*).

Landscape events may be defined to occur periodically or episodically. Continuous processes (such as growth) are represented by periodic events occurring every timestep (i.e. at the level of the temporal resolution); such representations of continuous processes may be termed ‘quasi-continuous’ (Fall *et al.*, 2001). Once a landscape event begins, it may initiate on a defined subset of cells from the simulation area, where initiation of some cells may be defined as a stochastic process.

A diagrammatic representation of the structure of a model in SELES is shown in Figure 3.1.

Scripting language

Models are constructed using the domain-specific SELES language. The SELES language is described as *declarative*, meaning that the behaviour of the model is defined by assigning values to a fixed set of *properties*, which interact in a pre-ordained manner. For example, the probability of any landscape event initiating at a particular location is defined by assigning a value to a SELES property called PROBINIT. However, despite the essentially declarative framework, some elements of the language can be considered *imperative*, meaning that the code specifies explicit sequences of steps to be followed. The use of the modelling language in an imperative mode may be exemplified by the use of an IF…THEN construction to control execution of two blocks of code pertaining to different cases.

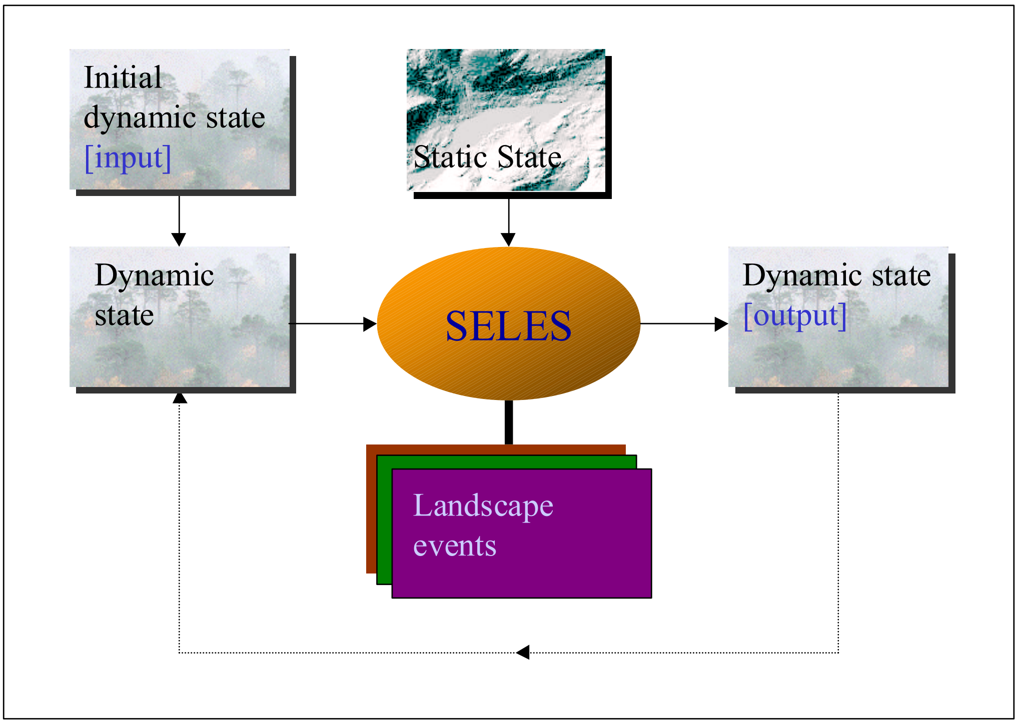


Figure 3.1 A diagrammatic representation of the structure of a SELES model.

3.3 Outline of the GALDR model structure

The following description gives a broad outline of the GALDR model structure.

3.3.1 Extent and spatial resolution

Extent

The focal area of the study is the semi-natural woodland around the lochs in Glen Affric. The study area is bounded by a 20 km by 10 km rectangle corresponding to the Ordnance Survey grid-squares NH12 and NH22 (see Figure 3.2). In strict terms, this defines the extent of the SELES model but since this rectangular area covers ground outwith the focal area of interest, a mask is used to exclude peripheral areas. The use of a mask improves run-time efficiency since it saves evaluating model functions in cells that will not support woodland or are not of interest for any other reason. In fact the GALDR model uses two masks. Because the forest zone in Glen Affric is contiguous with that in other glens (Guisachan Forest to the south, Glen Cannich to the north) the simulation area has been extended to form a buffer zone in which forest dynamics are simulated but not analysed. The two masks define a simulation area and an analysis area. The analysis area is defined as the drainage catchment of the River Affric (i.e. before its confluence with the River Glass), but excluding lochs and high ground over 750 m elevation. The simulation is defined as the analysis area plus a one kilometre buffer, also excluding lochs and high ground. The SELES model area, simulation area and analysis area are shown in Figure 3.2. The model area covers 20,000 ha, the simulation area covers 10,729 ha and the analysis area covers 9,142 ha.

Spatial resolution

The spatial resolution (i.e. the distance between adjacent grid-cells) of the model needs to be carefully balanced. If the resolution is coarse there will be large variation of stand and site variables within each cell. Also, the capability to model some spatial processes may be impaired if the scale at which the process operates is smaller than the model resolution (e.g. seedfall: most seed falls within 50-100 metres of parent trees). If the resolution is very fine, cells may be dominated by individual trees and could not be said to represent a stand. More pragmatically, computation times are much slower for finer resolutions since the number of cells for a given area is inversely proportional to the square of the resolution. The spatial resolution for the

GALDR model has been fixed at 50 metres which seems to be well balanced against the above constraints and agrees with the 50 metre quadrat used for National Vegetation Classification (NVC) in woodland (see Rodwell, 1991).

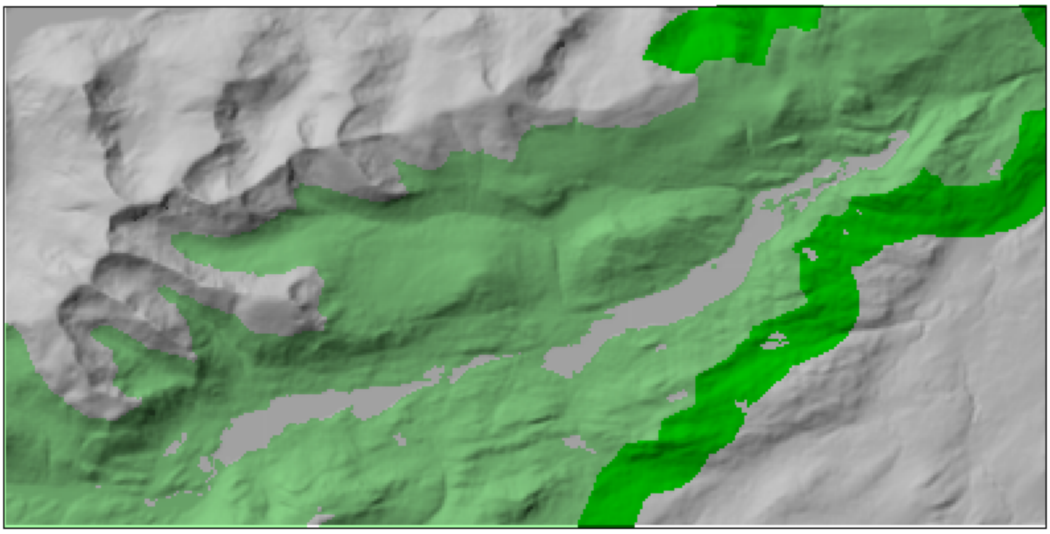


Figure 3.2 Simulation and analysis areas for GALDR. Simulation area - all green areas; analysis area – pale green; buffer zone – dark green.

3.3.2 Timescale and temporal resolution

Temporal resolution

Although the time span covered by the model is not an intrinsic element of the specification, the temporal resolution is integral to model design and must be appropriately matched to the intended duration of simulations. The timestep length, τ, is a model constant in GALDR and thus may be altered with little effort. However, it should be borne in mind that many of the sub-models have been designed to operate at a particular temporal resolution and that modelling assumptions may be less appropriate at changed resolutions. There is an obvious logic to the use of 1-year timesteps in forest dynamics models since many natural processes are periodic annual events (like seed dispersal) or at least vary with annual periodicity (such as tree growth). However, a ten-year timestep has been used for GALDR since this reduces simulation times by a factor of ten. The model is intended to be run for time spans in the order of hundreds of years; thus, it is considered that the coarser temporal resolution will not be significantly detrimental either to the modelling process or to the end product (i.e. time-series outputs). All landscape events in GALDR use a quasi-continuous temporal representation, hence the ten-year timestep will result in much annual variation (e.g. masting in seed production) being averaged out over the time interval.

Time span

A span of 1000 years has been used as the default simulation length. This timescale obviously goes well beyond any management forecast and takes the projection into the realms of potentially changing climates (political and social as well as physical). However, the advantage of taking the very long view is that it allows heed to be given to the opportunities and constraints that may be passed to successive generations.

3.3.3 Represented species

At present, GALDR represents the dynamics of three tree species: Scots pine (*Pinus sylvestris*), downy birch (*Betula pubescens*) and silver birch (*Betula pendula*). However, the two birch species are represented as a single entity (henceforth referred to as simply ‘birch’) since identification to species level can be problematic in some cases and, in practice, the two species are often not distinguished. The GALDR species list has been restricted to these species because pine and birch together form at least 90% of the canopy cover of native woodland in Glen Affric (author’s estimate).

Other tree species present in Glen Affric have been omitted as a simplicity measure; each species added to the model requires significant run-time memory commitment and increases processing time during simulation. Spatial distribution and age-class distribution must also be assessed for each species. It is considered that the restriction of species to pine and birch is an effective simplification that allows the major characteristics of the forest dynamics to be simulated whilst maintaining a level of simplicity appropriate to the relatively early stage of model development. However, this is not to deny the importance of the other tree species in providing for biodiversity. For example, aspen has a rich and distinctive range of species associated with it, including rare species of lichenized and non-lichenized fungi, bryophytes, moths, beetles and flies (Cosgrove and Amphlett, 2002).

Non-native conifer species cover large areas in Guisachan and Cougie forests to the south and east of Glen Affric, but most of the plantations of exotic species in Glen Affric have been removed as part of the restoration programme.

The model has been designed to allow inclusion of additional species without significant changes to the model design or implementation. Thus, the number of represented species is included as a model constant (generally denoted *n*), which has taken a value of two in all simulations completed so far.

3.3.4 Stand structure – dynamic state

The GALDR representation of trees in the landscape is based on a concept of single-species cohorts occurring within discrete stands that correspond to the cells of the underlying raster structure. Mixed-species cohorts are not represented as single entities, but in the context of the whole stand may be represented by separate cohorts of different species but of the same age. There is a data-structure for the representation of cohorts for each species where each cohort may be characterized by three values: age, height, and number of individuals.

Age

Age is defined as time since stand initiation and each cohort is assumed even-aged to the extent that ages of trees in a cohort do not differ by more than the temporal resolution of the model. Age is an important cohort variable in terms of both model function as well as an indicator of habitat conditions. Functionally, age determines the rate and timing of key model processes such as height growth, onset of seed production and cohort death. As a habitat descriptor, age is relevant not only in terms of the age of the trees themselves, but also as an indicator of stand structure (see Oliver and Larson, 1996). In any woodland, the trees themselves provide habitat for a wide range of species and the characteristics of this habitat changes markedly as the trees age. Very old trees may be particularly important because of the wide range of ecological niches they provide.

Height

There are various ways that cohort height may be described. The simplest of these is the average height of all live trees; however this measure is rarely used or measured in forestry because the smallest trees do not usually contribute to the final timber crop. To allow comparison with UK forest measurements and yield models, *top height* has been adopted as the measure of stand height. This is the measure of stand height used in standard UK forestry practice and is defined as 'the average [i.e. mean] height of a number of 'top height trees' in a stand, where a 'top height tree' is the tree of largest breast height diameter in a 0.01 ha sample plot' (Edwards and Christie, 1981; p.18). The concept may be readily applied to cohorts in the same way as it is applied to stands.

Height has been used as the characteristic measure of tree size rather than other measures of size (such as average diameter, basal area, crown size) for two reasons. Firstly, vertical position in a stand indicates competitive ability to a much greater degree than other size measures, and therefore is useful in determining model functioning. Secondly, description of stand structure in terms of cohort heights may define 'vertical stratification', which is thought to be an important habitat characteristic for birds (French *et al*., 1986).

Number of individuals

The GALDR representation assumes that all trees are single stemmed, and thus the number of individuals equals the number of stems. This assumption is well founded for Scots pine, but less so for birch; however the distinction is not crucial for modelling purposes. The number of trees in a cohort, together with the cohort height may define the cohort density. The density of the stand may be determined from the component cohort densities and is a vital characteristic of the type of habitat that the stand provides. Open stands (i.e. of low density) are relatively windy with high light levels, whereas dense stands are darker, more humid and more equable in temperature.

Number of cohorts

The maximum number of cohorts that each species may be allocated in a single stand is a GALDR constant (generally labelled m). Hence, in general, the maximum number of cohorts of all species that may be present in a stand will be the product $n \times m$. The default value of m is three.

In theory, the maximum number of cohorts of any species that might exist in a stand is given by $age_{\max}/\tau$ where $age_{\max}$ is the maximum age attained by any cohort of that species and τ is the temporal resolution. However, including the theoretical maximum number of cohorts would place very heavy demands on machine memory usage as well as increasing simulation times enormously. Furthermore, it may not be necessary to include very large numbers of cohorts to describe vegetation structure in upland woods adequately. The shade-intolerant nature of Scots pine and birch may tend to preclude the development of stands containing very many age-classes. McVean and Ratcliffe (1962) and McVean (1964) state that the most common structures for stands of pine and birch are even-aged or mixtures of two age-classes. Nonetheless, situations may arise in which recurrent sparse regeneration or slow canopy break-up gives rise to a stand of relatively many age-classes. Such circumstances may cause difficulties with representation if cohort numbers are limited; this predicament, termed *cohort-limited understocking*, is discussed in Section 4.4.3.

Cohort data structure

The model represents the cohort structure of the woodland vegetation by a set of three raster vectors for each species. These raster vectors, denoted $\mathbf{A}_i$, $\mathbf{H}_i$ and $\mathbf{N}_i$, for each species i ($1 \leq i \leq n$), contain rasters that, at each wooded cell, give values of cohort age, height, and number of individuals respectively. Furthermore, there exist one-to-one relationships between equivalently indexed raster elements of each of the raster vectors such that all of A_{ij}, H_{ij} and N_{ij} refer to attributes of the same cohort at any particular locus (where R_{ij} denotes the j^{th} element of the raster vector $\mathbf{R}_i$; $1 \leq i \leq n$ $1 \leq j \leq m$). Thus, taken as a whole, the set of cohort raster vectors, $\underline{\mathbf{C}}_i = \{\mathbf{A}_i, \mathbf{H}_i, \mathbf{N}_i\}$, forms a three-dimensional array of rasters and hence a five-dimensional array of individual cohort attributes. The raster elements of each $\mathbf{R}_i$ ($\in \underline{\mathbf{C}}_i$) are indexed at every locus according to the values of $\mathbf{A}_i$. Thus, $\mathsf{A}_{ij} > \mathsf{A}_{i(j+1)}\ \forall j{:}1 \leq j < m$ at every locus and the indexing of H_{ij} and N_{ij} is defined by association with A_{ij}. At a particular locus, $\mathbf{p}$, if the number of cohorts of species i present is k, where $k < m$, then $\mathsf{R}_{ij}(\mathbf{p}) = 0 \Leftrightarrow j > k$, $\forall\ \mathsf{R}_{ij} \in \{\mathsf{A}_i, \mathsf{H}_i, \mathsf{N}_i\}$(i.e. empty cohorts have zeros in all attribute rasters).

The following points relating to the cohort data structure may be noted.

1. For any locus, $\mathbf{p}$, $A_{ij}(\mathbf{p}) = A_{ik}(\mathbf{p})$ if and only if $j = k$, since either equality implies that the two cohorts refer to the same entity (thus the order of the $\mathbf{R}_i$ is well-defined).
2. Since height is a strictly monotonically increasing function of age, the following is true at every locus: $H_{ij} > H_{i(j+1)}\ \forall j{:}1 \le j < m$. However, the same is not necessarily true for N_{ij}.
3. $A_{i1}(\mathbf{p}) = 0 \Leftrightarrow R_{ij}(\mathbf{p}) = 0\ \ \forall j{:}1 \le j \le m,\ \forall R_{ij} \in \{A_i, H_i, N_i\} \Leftrightarrow$ species i is absent at locus $\mathbf{p}$.
4. Individual cohorts of particular stands do not necessarily retain index values as the simulation progresses.

The array of cohort rasters, $\underline{\mathbf{C}}_i$, constitutes what may be termed the *primary* dynamic state. The *secondary* dynamic state consists of layers representing other attributes of the landscape, such as levels of seed abundance, wind speeds and browsing levels. The initialization of the primary dynamic state is described in Section 3.4.1.

3.3.5 Landscape attributes - static state

The static state is loaded into the GALDR model from GIS files and remains unchanged throughout simulation. The GALDR static state comprises the following:

- mask rasters, which define the simulation and analysis areas;
- a digital terrain model (DTM), which represents altitude above sea level;
- a set of topographically-derived rasters, which permit calculation of wind speeds used in the wind disturbance sub-model;
- raster layers of ESC variables, which may determine regeneration suitability, yield class and soil moisture;
- a map of herbivore availability, which may determine grazing and browsing pressure.

In addition, each species is characterized by a set of life history parameters, including values for longevity, growth rate, and seed dispersal distance (See Table 5.1 in Section 5.1).

The DTM used for GALDR is an unmodified copy of the 50m resolution Panorama series produced by Ordnance Survey. The ESC and wind rasters are pre-processed using GIS. The derivation of the ESC rasters is described in Section 3.4.2. Derivation of the wind rasters is described in Section 4.2.2. Construction of the herbivore availability map is described in Section 4.5.6.

3.3.6 Dynamic behaviour

The dynamic behaviour forms the crux of the modelling effort since it allows the model to progress from description to prediction. GALDR dynamic behaviour is governed by five sub-models each implemented by SELES landscape events. These are: stand development, wind disturbance, seed production and dispersal, seedling establishment, and browsing. Bell (2003), writing on landscape change in Glen Affric divides agents of change into those of succession and disturbance. In GALDR, wind disturbance and browsing are disturbance events whilst the rest are succession events, although the stand development model may include some aspects of small-scale (non-spatial) disturbance. Disturbance events that are *not* simulated include fire, avalanche, snow damage (due to snow loading on tree crowns), flooding, landslip, and insect and fungus pathogens (Bell, 2003). Fire is a major disturbance agent in much of the northern temperate forest zone, but it is thought that in Scotland it may have played a minor role except in eastern woodlands (Peterken, 1996; Quine et al., 1999; Quine, 2003). Lightning rarely occurs without associated rainfall, so natural fires are unlikely to occur. Avalanche and landslip damage is small scale and local in occurrence. Snow damage may be widespread but rarely causes significant mortality. Flooding does not cause major damage in Glen Affric because of the topography – there are no large floodplain areas and water drains from the Glen quickly. Insect and fungus pathogens contribute to mortality rather than acting as a single cause (e.g. an already weak suppressed tree may die following insect defoliation). The effects are widespread but of low intensity – such effects are not simulated explicitly but are assumed to be subsumed within general mortality as simulated in the stand development sub-model.

Detailed descriptions of the sub-models are provided in Chapter 4 but an overview is provided below.

Stand development

This sub-model controls the ageing, growth and autogenic mortality of trees within established cohorts. Height growth is calculated according to approximations of the yield models of Edwards and Christie (1981) modified according to yield class as calculated via ESC variables (see Section 3.4.2). Where regeneration has been dense, cohorts in the stem exclusion phase will be subject to mortality according to principles of self-thinning (see Yoda *et al.*, 1963; Zeide, 1987). Cohorts growing beneath a canopy of larger trees suffer higher mortality than those growing in the open. In the old-growth phase, mortality due to old age gradually reduces abundance of trees in the older cohorts as they approach the species maximum longevity.

Wind disturbance

The windthrow sub-model consists of two components: wind speed generation (stochastic), and stand stability (deterministic). The wind speed generation component is a re-engineering of the DAMS model (Quine and White, 1993) designed to simulate individual wind events rather than the overall wind climate. At each timestep, the model generates a raster map of wind speeds corresponding to the most severe wind event over the course of the timestep interval. The stand stability component has been derived from ForestGALES (Gardiner and Quine, 2000), and relates the wind speed required to overturn the trees in each cell to stand height and soil moisture. Windthrow events are initiated where the generated extreme wind speed for a cell exceeds the wind speed required for overturning in the same cell.

Seed production and dispersal

Seedfall is calculated for each species over the entire landscape at each timestep. The abundance of seed falling within a cell is determined by the abundance of cohorts of seed-bearing age. Immigration of seed from nearby cells is dependent upon the abundance and height of seed-bearing cohorts and is determined by a species-specific dispersal function of distance (see Greene and Johnson, 1989). Masting (i.e. year-to-year fluctuation in seed production) is not simulated since it is assumed that any effects would be averaged out over the ten-year timestep.

Seedling establishment

Stand initiation is modelled as a stochastic process where initial seedling abundance is influenced by seed abundance and ESC site suitability for each species. Understorey reinitiation is modelled similarly, but is also subject to light levels at the forest floor (for which stand density is used as a proxy). In reality the occurrence and abundance of regeneration is highly unpredictable, and the underlying reasons for variation are poorly understood at present.

Browsing

The effects of red and roe deer (*Cervus elaphus* and *Capreolus capreolus*) browsing are simulated by reduction in abundance in the seedling stage cohort. Local deer density may depend on a number of factors including shelter provided by topography and mature trees (Palmer and Truscott, 2003), but since knowledge is lacking on the way deer use the entire landscape, consideration of local density has been confined to defining areas where the terrain is too steep to allow deer access. Such areas may provide important refugia for tree populations in times of heavy browsing.

3.4 Acquisition of data for initial and static state

One of the most challenging aspects of any landscape modelling project is acquiring data that accurately describe the current state (or past states) of the landscape. The GALDR model requires input of spatial data representing the current structure and species composition of woodlands in Glen Affric (the initial primary state) as well as data that may be used to predict future development and disturbance (static state). The acquisition and application of such data are described below.

3.4.1 Initial primary state

The subcompartment database

Data from the Forest Enterprise subcompartment database has been used to provide information on species composition and cohort ages for the initial primary state. The subcompartment database is held on a GIS and consists of a spatial representation of the woodland and tabular representation of the vegetation therein. The database is designed as an aid to management of plantation forests and is thus best suited to represent homogenous stands of vegetation. The spatial layer is a vector-based data model depicting forest compartments and subcompartments as polygon entities. Details of vegetation are held in a table of components. There is a one-to-many relationship between subcompartment polygons and components; each subcompartment may house up to nine components. Commonly, each component would relate to a particular timber species, but various categories of open space are also included. Planted crop components would usually contain data in various fields such as planting year, yield class, initial spacing and the area cover as a proportion of the subcompartment area. In Glen Affric, this data representation has also been applied to the semi-natural woodlands. The demarcation of polygon boundaries is more arbitrary than in plantation forests and some component data, such as yield class and spacing are not included. Although there are no planting records for the semi-natural woodlands (they are presumed self-sown, though it is difficult to know whether this is true in all cases), planting figures have been recorded and are presumed to derive from forester's estimates of cohort ages. Being estimates, these figures are expected to include large errors. However, these data still represent the best spatially extended representation of cohort ages that is currently available.

The study area contains substantial areas of planted Scots pine (both of native and non-native origins). In the acquisition of data for GALDR , no distinction was made between planted and semi-natural Scots-pine since the planted Scots pine will be able to provide habitat for many of the same species as the semi-natural pine. The most important differences between planted and semi-natural pinewoods relate to the woodland structure, yet older stands of planted pine may be difficult to distinguish from semi-natural stands.

Extraction of cohort data

To extract data from the subcompartment database to a format that could be applied to the GALDR cohort structure, an Avenue script was written and executed in ArcView. This script produced vector layers which were converted to rasters for cohort age, $\mathbf{A}_i$, and percentage cover, $\mathbf{P}_i$, for each species (examples of cohort age rasters are shown in Figure 3.3). These layers are loaded into SELES to form the basis of the initial primary state; initial state for the raster vector $\mathbf{A}_i$ is thus provided directly, but $\mathbf{H}_i$ and $\mathbf{N}_i$ must be evaluated from $\mathbf{A}_i$ and $\mathbf{P}_i$. This is achieved by setting up initialization landscape events, which occur only at the start of simulations. The height raster vector is evaluated from the age raster vector by use of the general height function used throughout the model (see Section 4.1.3). The evaluation of $\mathbf{N}_i$ relies on the assumption that the values of area proportion contained in $\mathbf{P}_i$ will be approximations of the partial stand density index (pSDI) as defined in Section 4.1.5.

Thus, $\mathbf{N}_i$ may be evaluated according to

$$\mathbf{N}_i = \mathbf{P}_i / (T\,\mathbf{H}_i)^2 \qquad (3.1)$$

where T is a constant defined in Section 4.1.5. The reason for calculating $\mathbf{H}_i$ and $\mathbf{N}_i$ with SELES at the start of the simulation rather than by pre-processing with GIS is that it avoids the need to repeat pre-processing if parameter values are changed.

All of the secondary state in GALDR is generated during simulation and therefore does not require initialization.

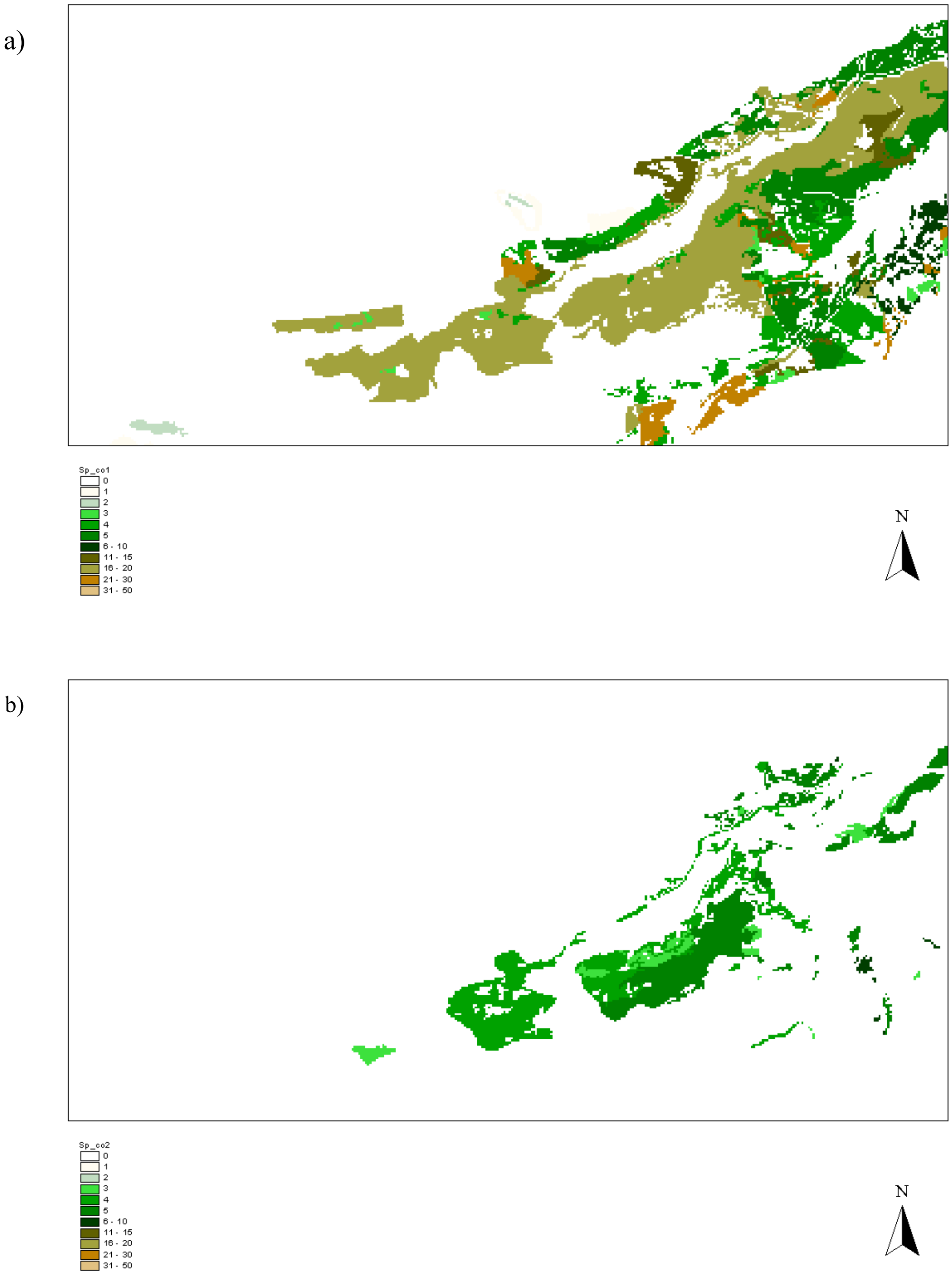


Figure 3.3 GALDR initial primary state: cohort age rasters for Scots pine (species index = 1) a) primary (oldest) cohort, raster element A_{11}, b) secondary cohort, raster element A_{12} (see 3.2.1- Cohort data structure). Legend shows cohort ages in decades.

3.4.2 Static state – ESC variables

Ecological Site Classification (ESC) is a site classification system that allows assessment of site suitability for tree species or woodland communities based on climate and soil characteristics (Pyatt *et al*., 2001). The classification is based on two factors of soil quality and four of climate. The two edaphic factors are soil moisture regime (SMR) and soil nutrient regime (SNR). The four climatic factors included are warmth (accumulated temperature), wetness (moisture deficit), continentality (Conrad index) and windiness (DAMS; see Quine and White, 1993). Detailed definitions of the ESC factors are provided in Pyatt *et al*. (2001). ESC was designed as a forest planning tool to be used at the stand scale but more recently has been applied at the forest landscape scale (Ray *et al*., 2003). ESC may be used to produce suitability indices for tree species or NVC communities as well as yield classes for species.

GALDR requirements

GALDR requires raster maps of habitat suitability indices (HSI) and yield class for Scots pine and birch. A raster representation of SMR is also used to determine stand stability in the wind sub-model. The HSI rasters are used to determine potential for seedling establishment whilst the yield class rasters are used to parameterize height growth models. Use of the ESC species suitability indices to determine potential for natural regeneration is not ideal, since this index is really designed to assess suitability for timber plantations. However, although NVC community suitability assessment is more pertinent to regeneration of semi-natural woodlands, the GALDR approach to woodland dynamics is deliberately species-focused, and thus the species suitability index is more appropriate to the purpose.

Landscape assessment

Landscape-level ESC assessment requires evaluation of ESC factors at the landscape scale. This is relatively straightforward for the climate variables, which may be calculated from multiple regression on geographical co-ordinates and altitude as part of the standard ESC methodology. Evaluation of the soil variables is a more challenging prospect. Best results are obtained when soil maps at an appropriate scale are available for the area. Although many publicly owned forest estates have been mapped at 1:10,000, the best available soil maps for Glen Affric are the 1:50,000 maps drawn up by the Macaulay Institute. These soil maps show very little fine-scale variation in soil quality and the mapping units cover a very broad range of conditions so would not be suitable for ESC assessment if used in isolation. Better results may be possible by combining soil maps with maps of vegetation or land cover.

Native Woodland Model

The approach of combining land cover data and broad-scale soil data to predict woodland development has been used by the Macaulay Institute and Scottish Natural Heritage (SNH) to produce the Native Woodland Model (NWM). The NWM has been described as linking published data and expert knowledge on woodland and scrub development with biophysical digital data to predict potential distribution of native woodland at the landscape scale (Hester *et al.*, 2003).

Determination of ESC variables from NVC

Although the NWM output is in terms of NVC classification rather than ESC variables, estimates of ESC variables may be inferred from NVC type. Each NVC sub-community may be ordinated according to the Hill-Ellenberg scales (see Hill *et al.*, 1999): F (moisture), N (nutrient level) and R (reaction – i.e. pH). An average of the F, N and R values for all species in the floristic list of each sub-community may be calculated, weighted according to frequency (see Pyatt *et al.*, 2001). SMR may be obtained directly from the F value whilst SNR may be obtained from the sum of R and N. Figure 3.4 shows the resulting ordination of NVC sub-communities according to Hill-Ellenberg values. Hill-Ellenberg values are generally aggregated into descriptive classes in ESC assessment; these classes are also shown on the ordination axes of Figure 3.4. From the ordination of sub-communities, minimum and maximum values of F and R+N may be determined.

Topographic mapping of moisture

The NWM may, via NVC class, give broad indication of SMR and SNR, but SMR may also vary considerably with topography. Furthermore, topographic variation occurs on a much finer scale than the polygon representation used by NWM, so it may be used as a fine-tuning of SMR derived from NWM. Burrough and McDonnell (1998) present a method for producing a *wetness index map* (WIM), W, (sometimes referred to as a compound topographic index) from a digital terrain model:

$$W = \ln(U/G) \tag{3.2}$$

where U is the contributing catchment area (the product of cell area and number of upstream cells) and G is the angle of slope. A 50 m resolution WIM raster was produced for the Glen Affric study area. The resulting WIM was characterized by very high values on cells covering streams. These high values were thought to be unrepresentative of the cell as a whole, thus stream values were replaced by a low-pass filter (3x3 kernel) value of the WIM raster. Hence, isolated high WIM values were brought closer to the neighbourhood average, while larger areas of high WIM values were preserved. This modified WIM was then standardized by linear transformation to produce W^*, for which minimum and maximum are zero and one respectively.

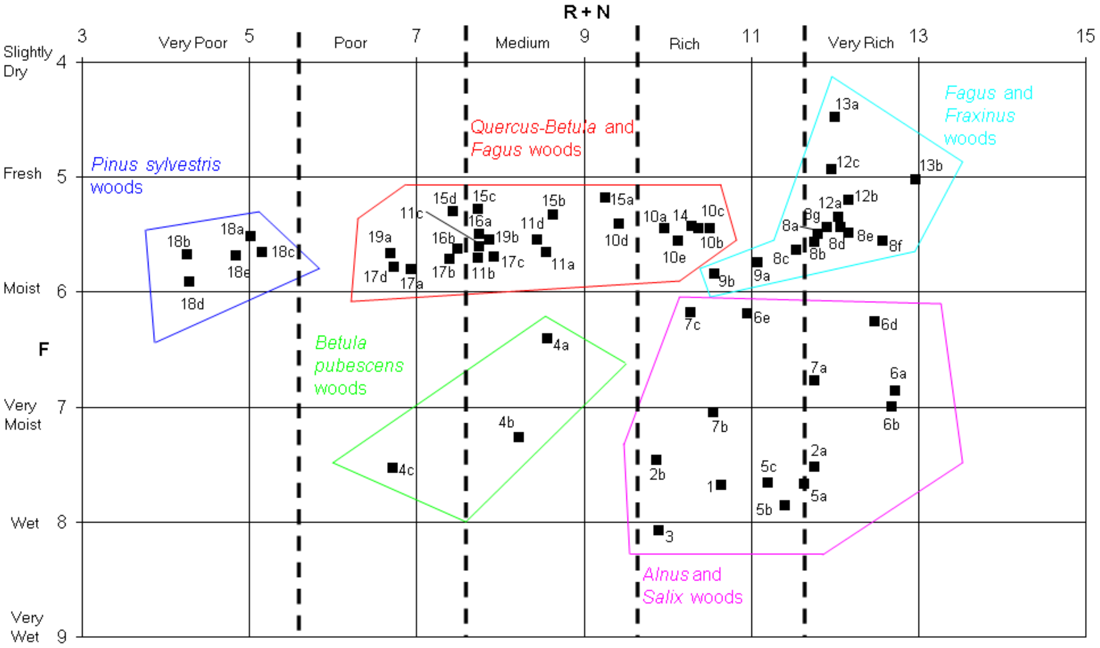


Figure 3.4 Ordination of NVC woodland sub-communities according to Hill-Ellenberg values of F (relating to SMR) and R+N (relating to SNR). The dashed lines show groupings of similar woodland types. Figure from Pyatt et al. *(2001).*

Evaluation of soil quality variables

The method of estimating SMR and SNR from NWM output is as follows. For each polygon of the NWM layer, a list of NVC communities present is drawn up (since polygons may contain more than one NVC community). From the list of NVC communities, minimum and maximum values of F and R+N may be determined by taking minima of minimum NVC values and likewise for maxima. From these, vector GIS layers of NWM polygons with minimum and maximum F and R+N values were created. These were then converted to four 50 m resolution raster layers:

F_{min}, F_{max}, P_{min} and P_{max} (where P rasters contain values of R+N). Then rasters of SMR and SNR were calculated respectively as

$$S_M = F_{min} + W^*(F_{max} - F_{min}) \tag{3.3}$$

$$S_N = P_{min} + Z(P_{max} - P_{min}) \tag{3.4}$$

where Z is a 50 m resolution raster with cell values randomly distributed according to a uniform distribution on (0,1). The rasters S_M and S_N are illustrated in Figure 3.5.

Assessment of yield class and HSI

Calculation of yield class and HSI was effected using an Avenue script supplied by Duncan Ray of Forest Research. The script applies response curves to the six ESC factors as shown in Figure 3.6. The suitability index is determined as the minimum value of the six factors (all varying from zero to one). In Figure 3.6 the uppermost curve, which shows accumulated temperature, also bears values of potential yield class on the ordinate axis. Yield class is determined by multiplying the potential yield class by the minimum suitability score from the other five factors. Raster maps of HSI for Scots pine and birch are presented in Figure 3.7.

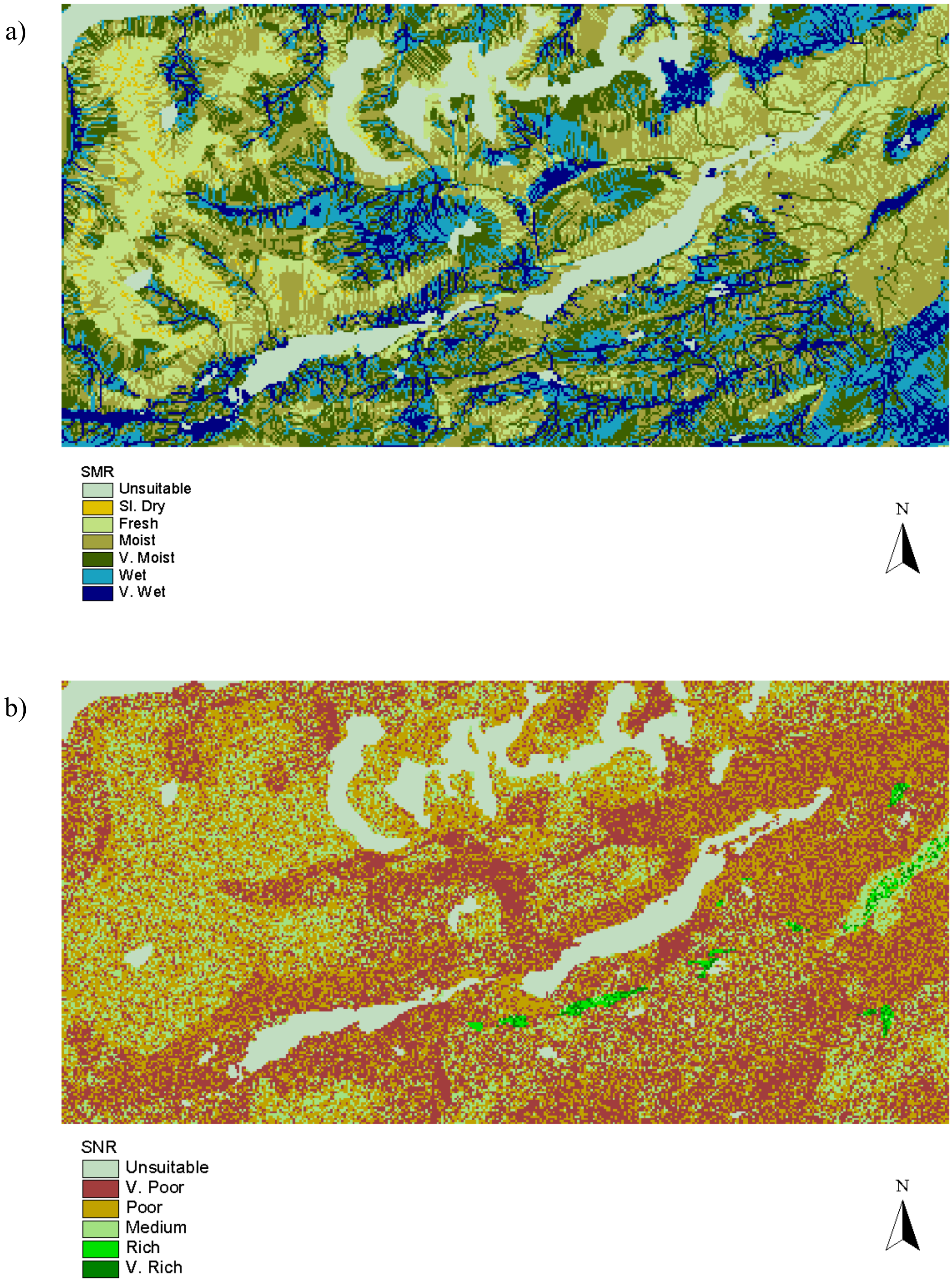


Figure 3.5 GALDR soil quality ESC variable rasters: a) SMR; b) SNR.

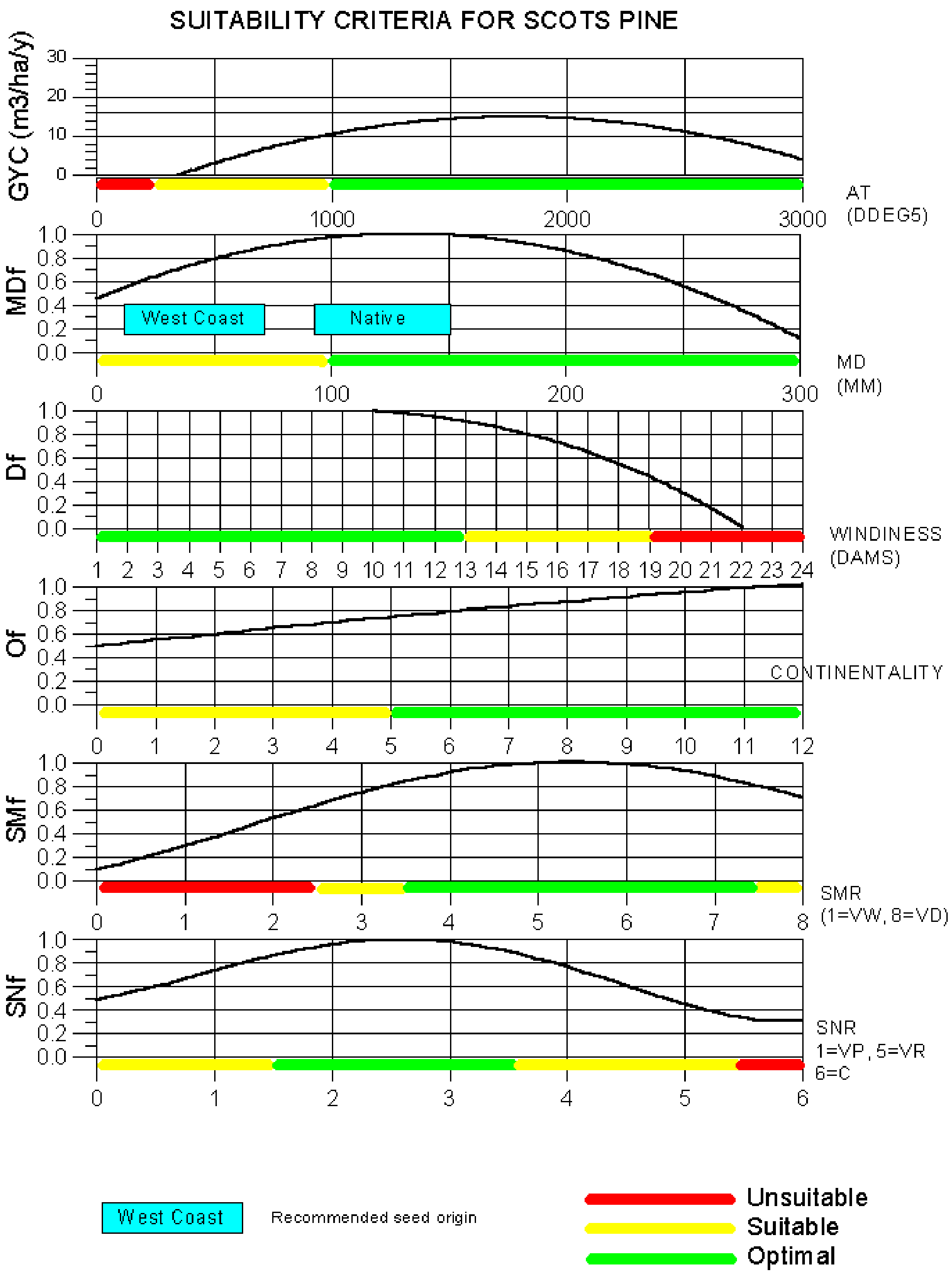


Figure 3.6 ESC Response curves for species suitability and yield class for Scots pine. The curves determine suitability according to the six ESC factors, which are from top to bottom: accumulated temperature, moisture deficit, windiness, continentality, SMR and SNR. Figure courtesy of D. Ray, Forest Research.

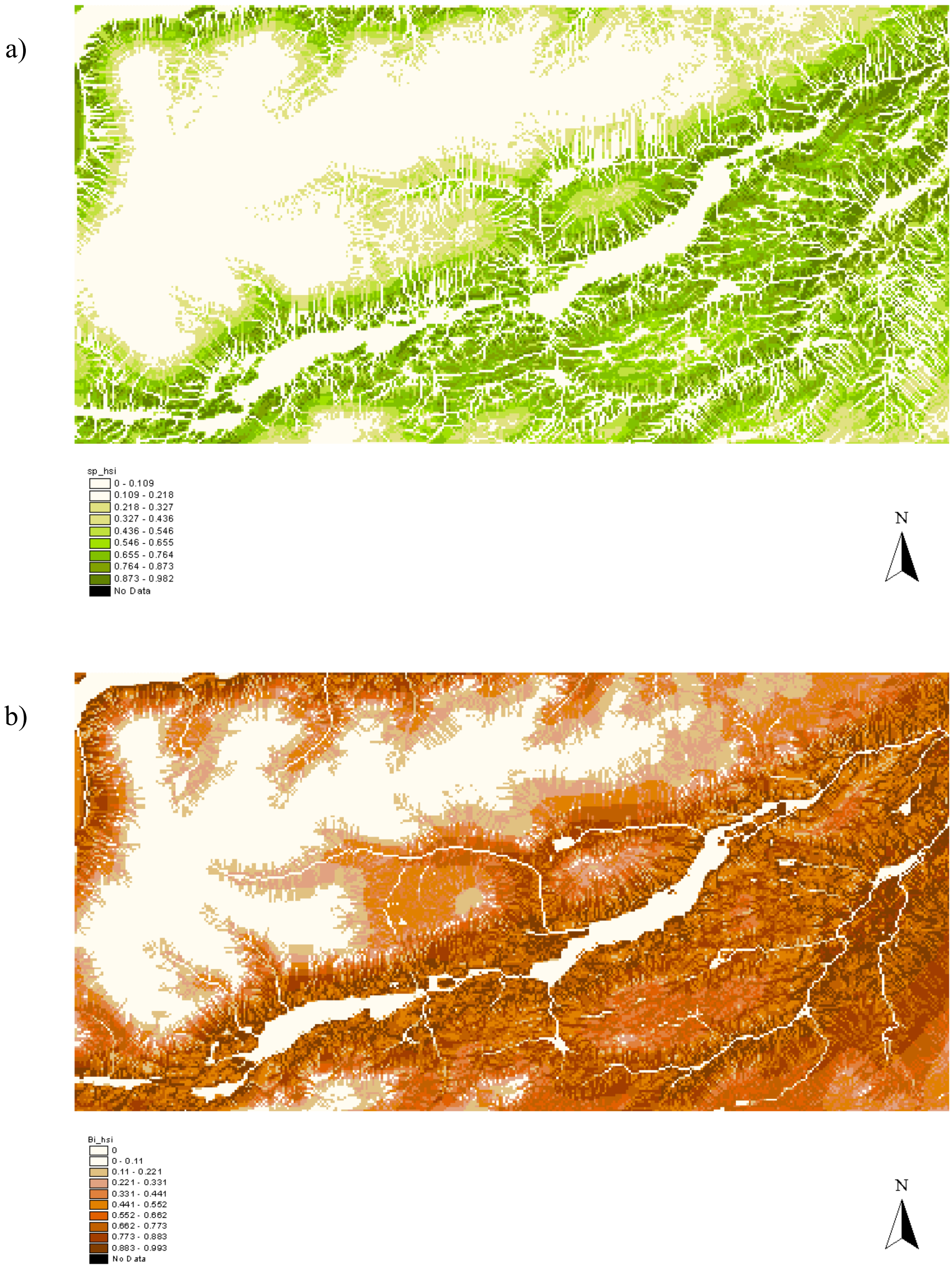


Figure 3.7 GALDR HSI rasters for: a) Scots pine; b) birch.

4 Landscape processes

This chapter provides detailed descriptions of the sub-models, which together comprise the dynamic behaviour of the GALDR model. Each sub-chapter describes one sub-model corresponding to a single SELES landscape event. Where appropriate, background theory is presented before the description of the sub-model itself. Discussions of the limitations of the sub-models are described separately in the Conclusions chapter.

Not all landscape events covered in the GALDR SELES model are covered in this chapter since some landscape events deal with administrative functions of the model such as initialization or output. However, all sub-models dealing with simulation of forest dynamics are included here.

4.1 Stand development – growth and mortality

4.1.1 Introduction

The stand development sub-model simulates growth and autogenic mortality of trees in established cohorts. Autogenic mortality here refers to death induced as a normal consequence of stand development in the absence of severe disturbance – i.e. density dependent mortality (self-thinning) and senescence. Allogenic mortality of established trees is effected by the wind disturbance sub-model (Section 4.2), whilst mortality of seedlings is covered by the establishment and grazing sub-models (Sections 4.4 and 4.5). The simulated growth of trees is of height only, since height is the only size measurement that has been applied to cohorts in the GALDR structure. In the course of simulation of growth and density dependent mortality, competition within and between species is also represented. The stand development sub-model also implements the trivial but essential routine of advancing the age of cohorts on each timestep. This sub-model acts on all established cohorts in the landscape but although interactions take place between cohorts of the same stand, interactions between cells are absent.

In the context of forest landscape dynamics as a whole, the processes of growth and mortality are perhaps the most predictable of all the landscape processes. It may be reliably observed that trees, once adequately established, will grow and eventually die. Furthermore, where regeneration occurs at reasonably high densities, density-dependant mortality is practically inevitable.

4.1.2 Height growth - background

Height growth characteristically follows a sigmoid pattern in trees (Oliver and Larson, 1996). Typically, rates are initially small, in keeping with the ability of the plant to capture resources. As the crown and root system grow, the ability of the plant to capture resources increases and so absolute growth rate also increases. In the later stages of growth, stresses caused by the large size of the tree cause height growth to slow.

In contrast to absolute growth rates, relative growth rates generally fall throughout the lifetime of the plant. Height growth effectively ceases at maturity, although diameter growth must necessarily increase until death.

Aside from this general pattern, growth rates depend on genetic traits as well as environmental factors such as light levels, soil moisture, temperature, nutrient availability and exposure (Botkin, 1993; Oliver and Larsen, 1996; Pyatt *et al*. 2001). Chronic exposure to defoliating invertebrates may also affect growth, but in pinewoods these are unlikely to cause serious damage over any significant period of time (Steven and Carlisle, 1959).

In general, height growth is more or less unaffected by side shade (trees will preferentially allocate photosynthates to height growth over diameter growth) but may be much reduced under high shade (Oliver and Larsen, 1996). Shade tolerant species may almost completely cease height growth under very dense shade. However, shade intolerant species (such as pine and birch) are less able to restrict height growth in this way and are more likely to respond to shade with increased mortality (Wright *et al*., 1998).

Height growth is of primary interest to foresters because of the relevance to timber production. Hence, height growth simulation is almost always a component of growth-yield models (see Section 2.2). In itself, height growth is usually only of secondary interest to ecologists, so it tends to be included in ecological forest dynamics models only as a means of simulating competition. In gap models (see Section 2.5), competition for light is the major process governing community dynamics so height growth is fundamental to their operation. The nature of the height growth simulation in gap models and UK growth-yield models is discussed below as background to the exposition of the GALDR height growth module.

Gap models

The following discussion is based on the description of JABOWA in Botkin (1993) but, as stated in that work, most subsequent models derived from JABOWA have used very similar procedures.

The *fundamental growth equation* for an individual tree is given in terms of volume growth as:

$$\delta\left(D^2H\right)=RL\left(1-\frac{DH}{D_{\max}H_{\max}}\right)f\left(\text{environment}\right) \qquad (4.1)$$

where R is the intrinsic rate of net assimilation, L is the leaf area, D is diameter at breast height, H is tree height, $f\,(\text{environment})$ is a function representing effects of climate, soil moisture and shading. The height, H, is defined to be a quadratic function of diameter, which (presumably) must be monotonically increasing for $H < H_{\max}$ whilst the leaf area, L, is assumed to be proportional to the square of diameter. Thus, it can be shown that height growth may be represented by the following differential equation:

$$\frac{dH}{dt} = R' f_1\left(H\right)\left(1 - \frac{f_2\left(H\right)}{f_2\left(H_{\max}\right)}\right) f\,(\text{environment}) \tag{4.2}$$

where R' is a constant and f_1 and f_2 are monotonically increasing functions of H.

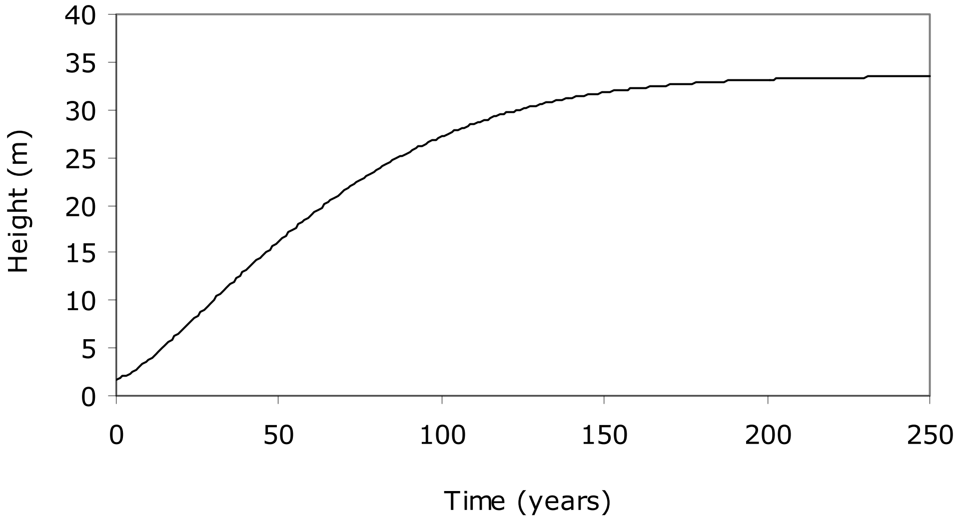


*Figure 4.1 Simulated height growth of sugar maple (*Acer saccharum*) according to JABOWA growth equations and parameter values from Botkin (1993).*

Since f_1 and f_2 are monotonically increasing, under constant environmental conditions, Equation (4.2) may be regarded as a modified logistic curve. For comparison, the standard logistic curve may be written as the differential equation in variables y and t:

$$\frac{dy}{dt} = ry\left(1 - \frac{y}{y_{\max}}\right) \tag{4.3}$$

where r and $y_{\max}$ are constant terms (r is sometimes termed *the intrinsic rate of increase).* A plot of height growth according to Equations (4.1) and (4.2) is shown in Figure 4.1, showing the similarity in form to the logistic curve.

UK growth-yield models

The Forestry Commission yield models (Edwards and Christie, 1981) are the standard growth-yield models used in UK forestry planning. The governing equations for the models are not given but output is presented in graphical and tabular forms for the major forestry species under a range of spacing and thinning treatments. The models are based on permanent sample plots established from 1919. The stand height measurement employed is the top height (defined in Section 3.3.4), which is effectively the mean height of the trees of largest diameter in the stand. Environmental effects on growth are aggregated into a single figure of site quality for each species: the yield class. The yield class determines the maximum height attained as well as the maximum rate of growth. Examples of yield model output for Scots pine and birch are shown in Figure 4.2.

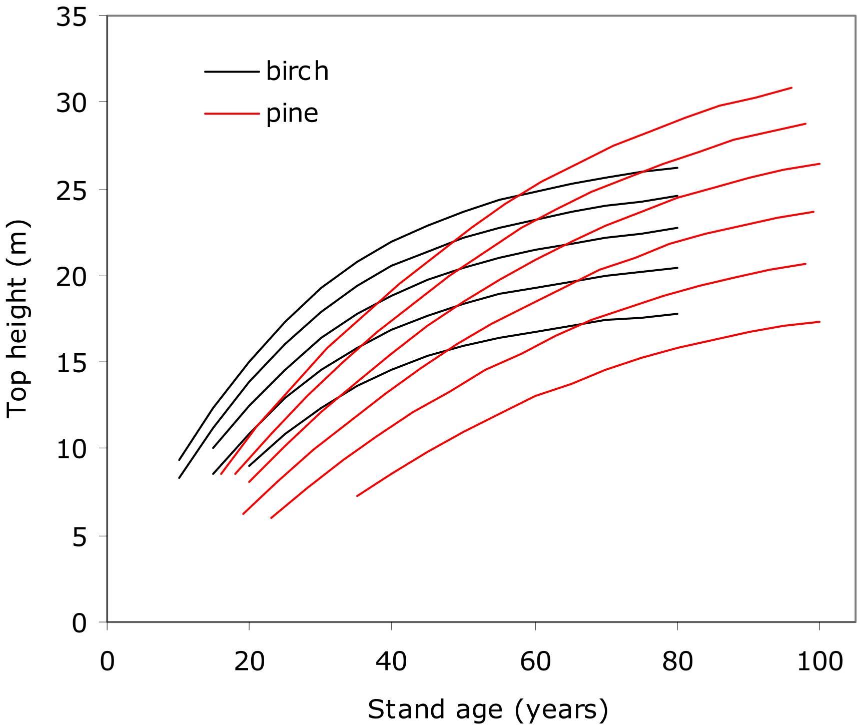


Figure 4.2 FC yield model output showing top height curves for Scots pine and birch with the full range of yield classes given for each species (pine: 4-14; birch 4-12).

4.1.3 GALDR height growth module

The approach taken in the GALDR simulation has been to approximate the FC yield model height values with a single function of time and yield class, parameterized according to species. The growth equation that has been used is the Gompertz equation, which takes the general form:

$$h(t) = Ce^{-e^{-B(t-M)}} \tag{4.4}$$

where *C*, *M* and *B* are positive constants in any time series. This function may be viewed as the result of assuming exponential decay in relative growth rate. Gompertz and logistic curves are commonly used to describe plant growth (Zeide, 1993); the Gompertz curve was chosen here because it has an asymmetric form, which appeared better suited to the shape of the yield model curves. Gompertz curves were fitted to the FC yield model tabular output for both Scots pine and birch over five yield classes using the nonlinear regression module of the GenStat program. The yield model output values for Scots pine, along with the fitted Gompertz curves, are shown in Figure 4.3. The time axis is shown extending into negative values; this is because the models will eventually be extrapolated beyond $t = 0$ since the yield model data is based on planted trees which are already a few years old at planting.

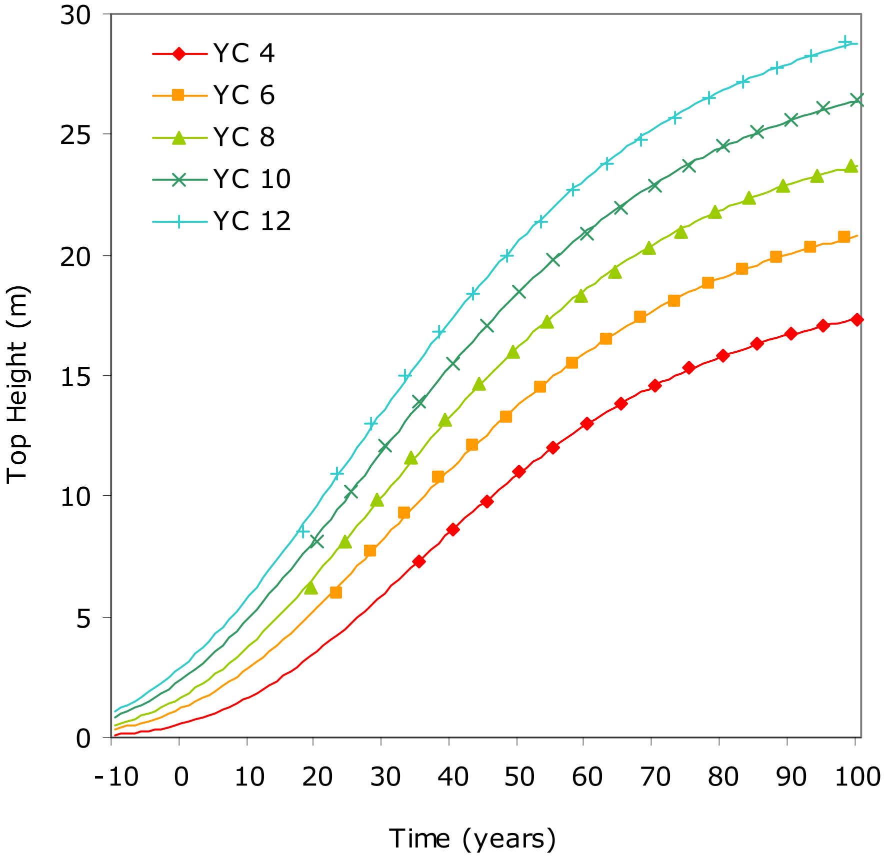


Figure 4.3 FC yield model output (points) and individually fitted Gompertz curves (lines) for Scots pine, yield classes 4-12.

Table 4.1 Gompertz parameter values resulting from regression of FC yield models for Scots pine.

Yield Class	C	M	B
4	18.86	33.60	0.03737
6	22.53	30.02	0.03580
8	25.54	27.84	0.03592
10	28.44	25.84	0.03498
12	30.87	24.29	0.03522

Curves for each yield class were regressed independently, giving separate sets of regression parameters (see Table 4.1 for those of pine) for each curve. To incorporate this family of curves into a single function, the parameters C and M were re-expressed as linear functions of yield class (Y) following linear regression. The third parameter, B, was only weakly dependent on yield class so this parameter was generalized by obtaining the mean value over the five yield classes. Thus, $C(Y)$ and $M(Y)$ may be written:

$$C(Y) = C_1 Y + C_0 \tag{4.5}$$

and

$$M(Y) = M_1 Y + M_0 \tag{4.6}$$

where C_0, C_1, M_0 and M_1 are species-dependent constant terms. The values of the growth parameters are given in Table 4.2.

Table 4.2 Values of Gompertz parameters.

Parameter	pine	birch
M_0	37.44	14.73
M_1	-1.14	-0.375
C_0	13.28	14.26
C_1	1.497	1.042
B	0.03586	0.05753

Plots of the Gompertz regression variables from Table 4.1 and the fitted lines are shown in Figure 4.4. On inspection, the data points for M and C can be seen to exhibit curvilinear tendencies. However, for the benefit of very minor improvements in accuracy it was not considered worthwhile to add extra parameters (e.g. second order terms). Similarly, the B parameter for pine could be represented more accurately by a linear function than a constant, but the practical advantages would be narrow.

As noted earlier, the yield model data are not derived from naturally regenerated trees, so the planted trees represented have a ‘head start’. To account for the age of planted trees and possible growth check in naturally regenerating seedlings, a lag of ten years was introduced into the growth equation.

Thus, the GALDR height growth equation may be written as:

$$h(t,Y) = C(Y)e^{-e^{-B(t-(M(Y)+10))}} \tag{4.7}$$

with $C(Y)$, $M(Y)$ defined as in Equations (4.5) and (4.6), and with values as shown in Table 4.2. Plots of this function (4.7) may be compared with the FC yield model output in Figure 4.5. It may be seen that the fit of the curves to the FC yield model output is not as good as for the individually fitted Gompertz curves shown in Figure 4.3. However, since assessment of site yield class is rarely very exact, these slight deviations are unlikely to be of serious consequence. In GALDR the yield class is estimated from ESC variables as described in Section 3.4.2.

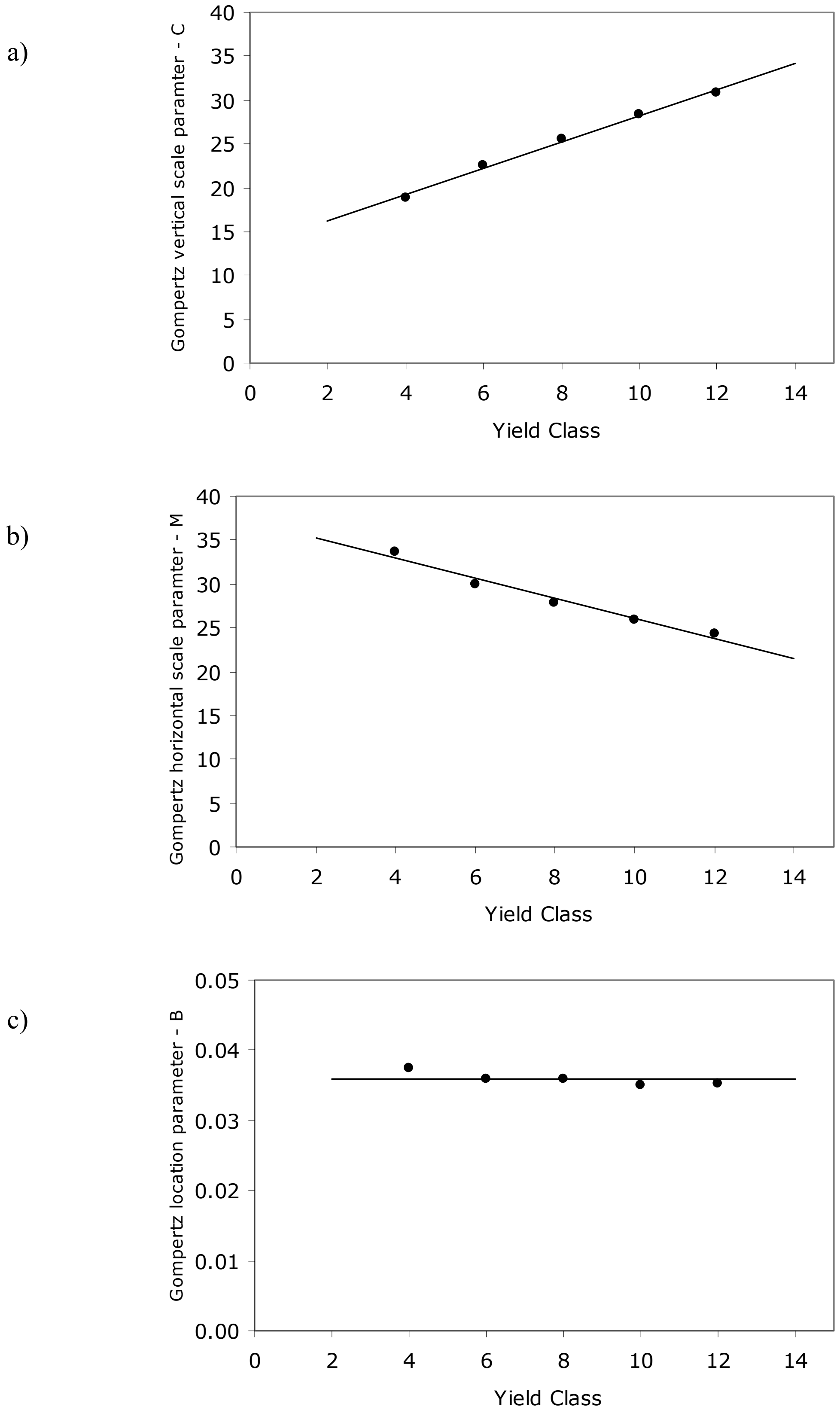


Figure 4.4 Plots of Gompertz regression parameters (a) C, (b) M and (c) B against yield class (points) and the fitted straight lines.

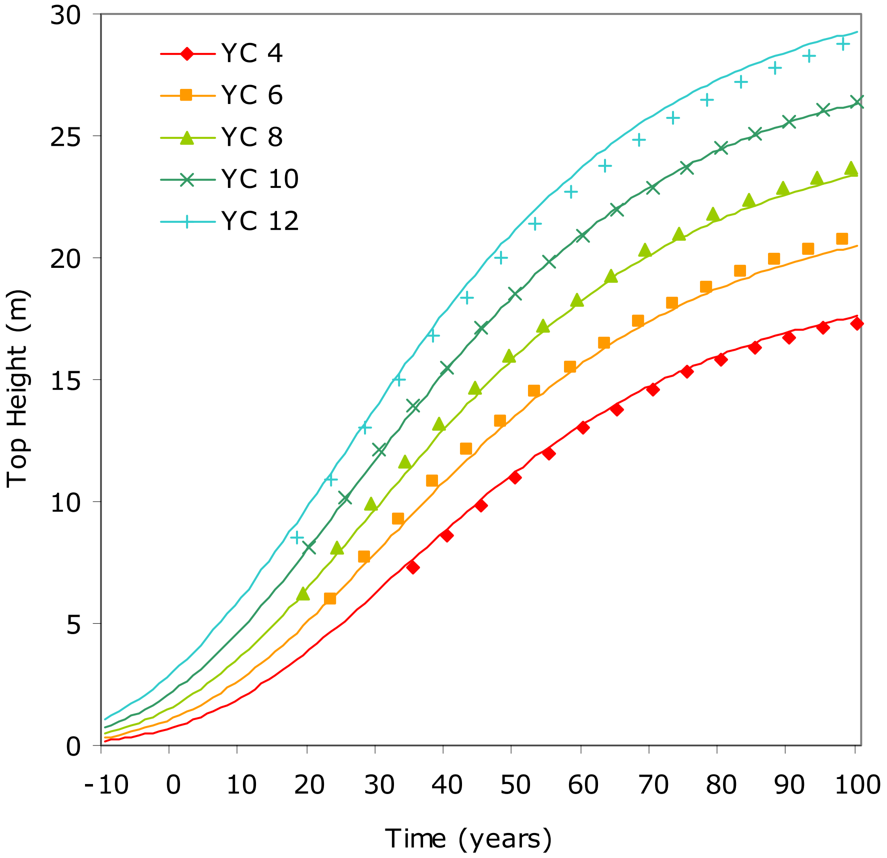


Figure 4.5 FC yield model output (points) and GALDR Gompertz curves (lines) for Scots pine, yield classes 4-12.

4.1.4 Density-dependent mortality – background

Density dependent mortality arising in even-aged stands through competition for resources is generally referred to as ‘self-thinning’. It is a corollary of the fact that resource usage increases with plant size that, in stands where resources are limiting, there must be a concomitant reduction in number of individuals for any increase in average plant size. The nature and generality of the self-thinning process has been much discussed by plant ecologists and foresters alike (e.g. Reineke, 1933; Wilson, 1946; Yoda *et al.* 1963; Westoby, 1984; Weller, 1987a,b; Zeide, 1987; Osawa and Sugita, 1989; Lonsdale, 1990; Weller, 1990; Weller, 1991; Zeide, 1991; Zeide, 1995; Enquist *et al.*, 1998).

Two important studies may be identified in the literature on self-thinning. The first is Reineke’s (1933) paper relating stem density to stem diameter in forest plantations; the second is that of Yoda *et al.* (1963) on the relationship between plant density and biomass in plants of various kinds. Despite the similarity of the subject matter, the two treatments are very different; Reineke’s rule was really intended as a tool for silvicultural management of even-aged plantation forests, whilst Yoda *et al.* were attempting to establish a new law of plant ecology.

Reineke’s self-thinning rule

The self-thinning rule of Reineke (1933) relates tree density, N, with quadratic mean diameter, D_q, (the diameter of a tree with mean basal area) in fully-stocked, even-aged stands of a single species:

$$N = KD_q^{\chi} \tag{4.8}$$

where K and χ are constant terms and χ is proposed to be equal to -1.605 for all species. Thus, Reineke developed the concept of a stand density index (SDI) which is calculated from

$$\ln(\mathrm{SDI}) = \ln(\mathrm{N}) + \chi(\ln(\mathrm{D_q})\text{-}1) \tag{4.9}$$

and has the property of being constant in fully stocked stands as long as (4.8) holds.

The 3/2 power law

Yoda *et al*. (1963) described changes in mean plant mass, w, and the number of plants per area, N, during closed canopy development of a singe-species even-aged stand as fulfilling the equation:

$$w = KN^{-\alpha} \tag{4.10}$$

where K and α are constant terms. Furthermore, it was suggested that the value of α is in every case equal to or nearly equal to 3/2. Thus, the relationship was described as 'the 3/2th law of self-thinning' (Yoda *et al.*, 1963; p.122). Equation (4.10) is linear with slope of -3/2 if plotted on log axes, thus the relationship between logarithms is sometimes referred to as the *thinning line*. The -3/2 exponent was derived from a number of described experiments and a theoretical model was proposed to explain it, which may be termed the *isometric* model (Weller, 1987b).

Isometric model of the 3/2 power law

The explanation of Yoda *et al*. (1963) relied upon two assumptions:

a) lateral growth is completely compensated for by self-thinning to maintain complete canopy closure;

b) during all stages of growth, all plant dimensions remain proportionally similar (isometric).

The first assumption may be used to relate the mean area covered by vertical projection of the crown (which we may term *cover*, for brevity), A, to plant density, N:

$$A \propto 1/N. \tag{4.11}$$

The second assumption allows a relationship to be drawn between plant volume, V, and mean cover:

$$A^3 \propto V^2. \tag{4.12}$$

If it is further assumed that the mean density of plant tissues does not change with stand development then (4.11) and (4.12) lead directly to the 3/2th law (4.10).

Significance and applicability of self-thinning rules

The 3/2 self-thinning law proposed by Yoda *et al*. (1963) was much celebrated by many plant ecologists for its generality, some even claiming it as the first true law of ecology (see Westoby, 1984; Weller, 1987a; Zeide, 1987). The self-thinning relationship was considered important because it was perceived to bind two major strands of ecology: ecosystem function and population ecology (Westoby, 1984). Initial enthusiasm for such a general law in ecology led to uncritical acceptance of the law until re-evaluation by Weller (1987a,b) and Zeide (1987) launched a fierce debate over its applicability and generality (e.g. Osawa and Sugita, 1989; Lonsdale, 1990; Weller, 1990; Weller, 1991).

This debate helped to clarify some of the disparate ways in which the 3/2 law was being applied. Weller (1990) divided the concept into three: the *interspecific size-density relationship* which defines an upper bound of yield-density combinations from a wide range of species; the *species boundary line* which defines a similar upper bound for a single species; and the *dynamic thinning line* which describes the straight line approached by an individual crowded stand. Weller also reviewed evidence to suggest that the dynamic boundary lines and species thinning lines often do not coincide (contrary to implications of Yoda *et al*. (1963)). This divergence of the self-thinning law into separate parts, along with convincing demonstrations by Weller (1987a) and Zeide (1987) to suggest that the exponent α may differ significantly from -3/2 has done much to erode the perception of the law's universality, although it may still be offered as a rule of thumb (e.g. Watkinson, 1997). Recent work has shown that the interspecific relationship may be better modelled with a value of –4/3 for the exponent α (Enquist *et al.*, 1998).

Zeide (1995) considered the rule of Reineke (1933) to be more robust than the 3/2 law, but still found it wanting. Zeide argues that stand density does not remain constant in self-thinning stands since 'as trees become older and larger, the size of a gap created by a fallen tree increases, while the ability of neighbouring trees to close the gap decreases' (Zeide, 1995; p. 266). As well as being problematical for

Reineke’s concept of stand density, this observation also runs counter to assumption (b) of the isometric model.

Allometric models of self-thinning

One of the major criticisms levelled at the 3/2 self-thinning law was that the isometric model used to explain it was hopelessly unrealistic. White (1981) attempted to reconcile the 3/2 self-thinning law with an allometric reworking of the explanation for trees. It was demonstrated that stem diameter, d, could be related to plant mass by the power law $w \propto d^{\delta}$ where δ is certainly less than three and frequently close to 2.5. Similarly, plant mass was shown to be related to diameter and height, h, as $w \propto (d^2h)^{\phi}$

with ϕ always less than one, whilst crown cover, A, was related to stem diameter as $A \propto d^{\varepsilon}$ with ε less than two. As Westoby (1984) notes, the scheme $w \propto d^{2.5}$, $N \propto d^{-1.6}$ fits White’s data if assumption (a) of the isometric model (above) is retained. (Perhaps strangely, reference was not made to the obvious similarity with Reineke’s (1933) rule; the likely reason is that Reineke’s paper, having been published in the forestry literature, was not consulted.) Weller (1987b) provides another model of self-thinning based on allometric plant growth but rejects the assumption that the final self-thinning equation should approximate the 3/2 law.

Self-thinning in gap models

Self-thinning in the usual sense of the term is not a particularly important process in gap models since they aim to replicate gap-phase rather than stand replacement dynamics. Furthermore, stem density of mature stands is effectively preordained by the neighbourhood size (commonly 10 × 10 m equating to 100 stems/ha). However, self-thinning of gap regeneration is effectively simulated by imposing a limit on the stem basal area that may be supported in the neighbourhood; growth of all trees in the neighbourhood attenuates as the threshold is approached and those that show poorest growth eventually die. This gives rise to a maximum size-density relationship equivalent to Reineke’s formula with $\chi = 2$.

4.1.5 Density-dependent mortality based on height

Analysis of the relationship between size of plants and their number has almost exclusively concentrated on mass, or less commonly, stem diameter, as the employed size measurement (Westoby, 1984; Zeide, 1995). However, the GALDR data framework was designed for only one size measurement – height – for each cohort.

In this section, mathematical models of self-thinning based on cohort height are presented. These models provide the basis for the density-dependent mortality module in GALDR, which itself is presented in Section 4.1.6.

To aid explanation of the theory behind these height-based models, it will be presented firstly for the simplest case: self-thinning in an even-aged single-species stand. Subsequently the theory will be presented for even-aged and uneven-aged stands of more than one cohort.

Self-thinning in an even-aged stand

One way that existing theories of self-thinning might be tied into the GALDR model would be to relate height to tree mass or stem diameter. The argument against such a course is that it merely adds convolution, since in terms of explaining self-thinning, mass or stem diameter may be seen as acting as surrogates for crown width or crown cover (Zeide, 1991). Stem diameter or mass may or may not be better predictors of crown width than canopy height but in the present case it is irrelevant since any quantification of such variables would be entirely dependent upon height.

Although accounts of self-thinning based on height-density relationships are almost entirely absent from the literature, Wilson (1946) presented a method of assessing stand density, principally as a means of guiding thinning regimes. Nonetheless, since the upper limit of normal stocking represents the point at which density-dependent mortality will become apparent, Wilson’s method may be inferred as a broad rule of self-thinning. The rule may be expressed as

$$N = Kh^{-2} \tag{4.13}$$

where N is number of trees per unit area, h is canopy height and K is a constant for each species. It may be noted that this relationship is in keeping with the naïve isometric explanation of the 3/2 self-thinning law proposed by Yoda *et al.* (1963). Furthermore, while the equivalent diameter-based rule arising from the isometric model has been discredited by White (1981), the above height rule does not contradict White's allometric model.

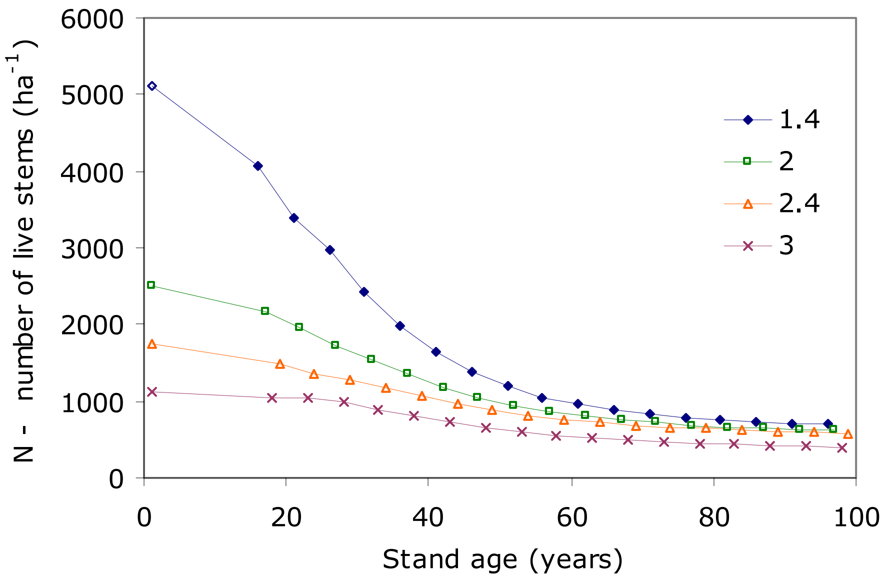
Weller's (1987b) re-examination of self-thinning and allometry represents the self-thinning relationship in the usual way in terms of stem density and plant mass, but estimates of allometric relationships are given that allow a height-density relationship of the form $N = Kh^{-\beta}$ to be extricated. The value of the parameter β may be calculated from mean values for allometric parameters estimated from either (a) forestry yield tables or (b) published studies of experimental and natural populations. Derived values of β are (a) 1.84 and (b) 2.12 but levels of variation in the allometric parameters were moderately high (standard deviations around 20-50% of mean values).

An advantage of using height as the size basis of the self-thinning model is that height growth is relatively independent of stem density (Wilson, 1946; Oliver and Larsen, 1996). Thus, density-dependent mortality may be seen as purely an *effect* of height growth. If diameter were used the situation would become considerably more complex, as diameter growth and stand density are interdependent.

The form of the GALDR self-thinning model has been partially based on theoretical considerations such as those presented above but it has also been informed by analysis of data from the FC yield models (Edwards and Christie, 1981). Weller (1987b) and Zeide (1987) have used yield table data in analysis of self-thinning relationships; the latter author considers yield table valuable because they make effective generalizations of trends observed in numerous sample plots.

The yield model dataset used is that of unthinned Scots pine of yield class 14. The yield models do not provide data for unthinned birch. Graphical representations of the yield model data are shown in Figure 4.6. The four line-plots show different initial planting densities. These are represented in the legend as values of planting spacing (expressed in metres), where spacing is defined as the inverse square of stem density. (Note however, that conversion to stems per hectare requires a multiplicative factor of 10^4.) The first data point of each plot is inferred from the stated planting density – i.e. it is not a measured value and thus differs from all subsequent data points of each plot. These initial values have been given an arbitrary height of one metre (the estimated data have not been employed in any analyses). Mortality may be interpreted from the gradient of the curves in Figure 4.6a. It can be seen that (at least initially) mortality increases with initial planting density. Furthermore, it may be observed that the curves inflect at around 20-30 years; this may be interpreted as the start of the phase in which density-dependent mortality compensates for crown expansion. Canopy closure is expected to occur at 15-20 years, but a lag exists as trees sort themselves into dominants, subdominants and suppressed trees before mortality attains maximum levels. The same reverse sigmoid curve shape in Figure 4.6b shows that this effect is not simply due to slow initial height growth. The curves may be described as passing through three phases: *pre-closure* in which no density dependent mortality occurs; *pre-equilibrium* in which the canopy has closed but mortality is still lagging; and *equilibrium* in which crown expansion is matched by mortality. A fourth phase, *post-equilibrium,* in which further mortality (density-dependent or not) is no longer matched by crown expansion, is not seen to be represented in the FC yield model data but must inevitably follow. The pre-closure phase may be seen in the first interval for the 3m spacing curves, but in other curves it is probably masked since the first measurement occurs after canopy closure.

Data for yield class 14 have been used exclusively since the site quality seems to have little effect on the nature of the self-thinning relationship, but higher yield classes show a larger portion of the self-thinning curve because growth is faster and progresses further (see Figure 4.7) a)



b)

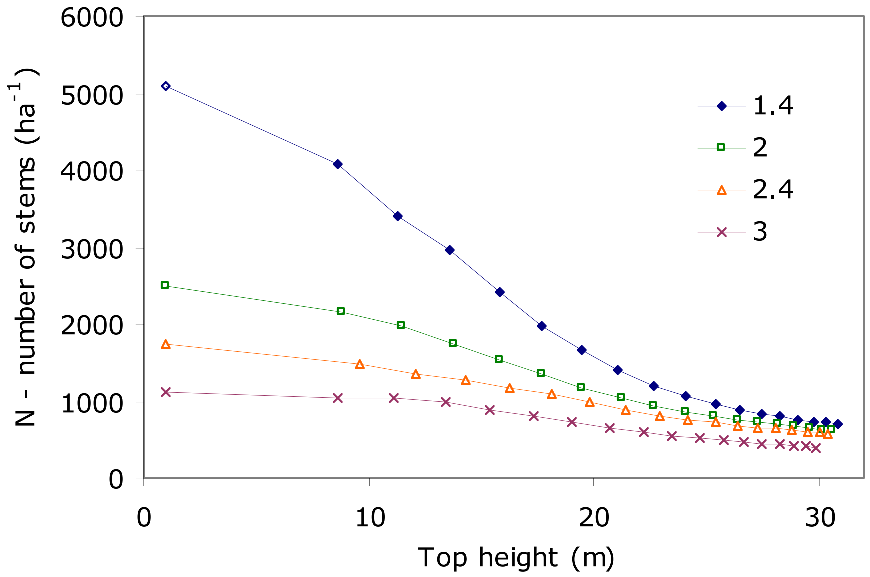


Figure 4.6 FC yield model representation of self-thinning for yield class 14 Scots pine in terms of (a) stand age and (b) top height. Legend shows initial density in terms of spacing (see text).

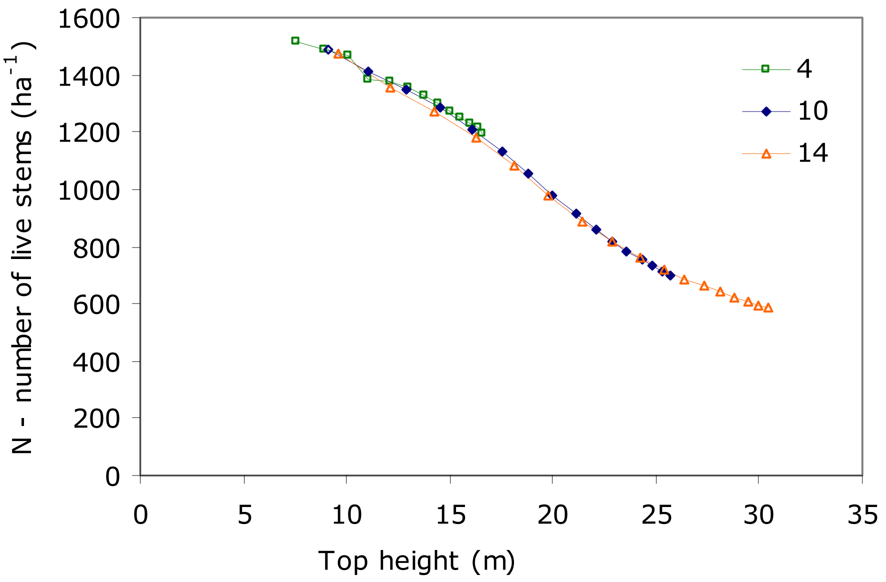


Figure 4.7 FC yield model data showing relationship of top height and stem density for 3 yield classes (4, 10 and 14).

To develop a model of self-thinning based on height growth an assumption must be made that height is related to the crown cover. In keeping with allometric models of White (1981) and Weller (1987b) it is assumed that this relationship may be expressed as a power function of the form $y = Kx^r$. It is well established that functions of this type provide good descriptions of relationships amongst dimension measurements in plants (Reineke, 1933; Whittaker and Woodwell, 1968; Curtis, 1971; Hutchings, 1975). This assumption leads to the following self-thinning equation

$$N = Th^{-\beta} \tag{4.14}$$

where T and β are positive constants. The above may be rewritten as a linear relationship of logarithms:

$$\ln(N) = \ln(T) \ - \beta \ln(h). \tag{4.15}$$

The value of β may thus be estimated from plots of logged height and density. (The value of T may also be estimated in this way, but it may not be the most practical way of doing so, since the estimation will be highly sensitive to the value of β). Figure 4.8 shows log-log plots of stem density against height for selected data from the FC yield model self-thinning dataset. In these plots the first four data points have been omitted to ensure that only the equilibrium stage of self-thinning is represented. The gradient terms from the regressions of these data are shown in Table 4.3. The four line-plots may be considered to approximate the dynamic thinning lines (*sensu* Weller, 1990) for each stand whilst the species boundary line will reside somewhere above all of the plotted data. Since the four plots of differing initial densities do not converge in Figure 4.6 or Figure 4.8, we can see that there is a lingering effect of initial density. Plots for initial spacing of 1.4 – 2.4 in Figure 4.8 show the expected steepening of the gradient with increasing initial density (i.e. decreasing spacing). The 3m spacing plot is anomalous in this respect; it is suspected that the inconsistency may be attributable to a small sample of 3m spacing permanent plots underlying the yield model output.

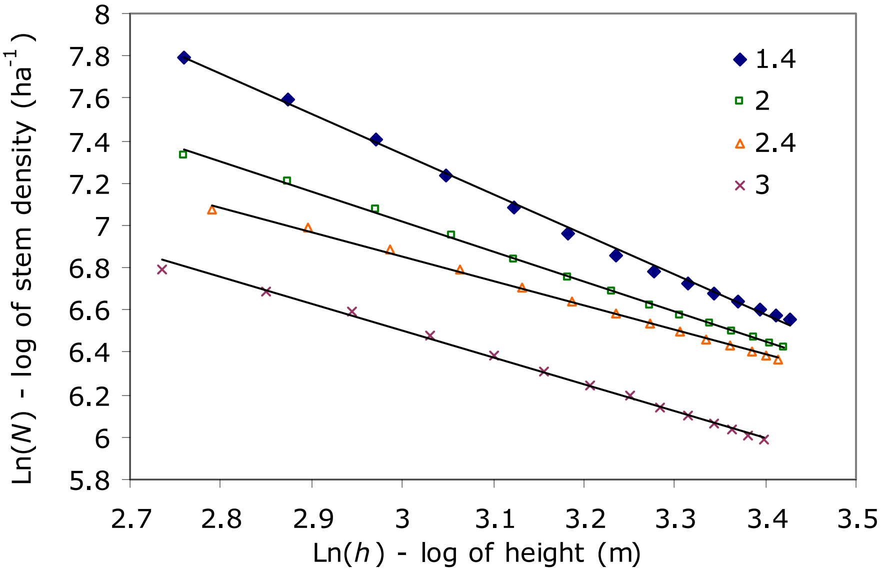


Figure 4.8 Log-log plots of density against height for the FC yield model data with regressed straight lines. The legend shows initial spacing in metres.

Table 4.3 Gradient terms for regressed lines shown in Figure 4.8.

Initial spacing (m)	Gradient term
1.4	-1.90
2	-1.42
2.4	-1.16
3	-1.26

The regression data from the log-log plots of height and stem density indicate that the most appropriate value of β for the species boundary line will be greater than 1.9. However, it is not possible to provide an upper bound for β without observing some convergence of thinning lines with differing initial spacing.

In the light of these data, and considering the theoretical bases provided by Wilson (1946), Yoda et al. (1963), White (1981) and Weller (1987b) discussed above, an integer value of two has been chosen for β. This provides an inverse square self-thinning equation identical to Wilson's (1946) rule, (repeated here as equation (4.13)). No claims are made here as to the precision or generality of the estimation of the exponent of (4.14) as -2. In terms of the FC yield model data, perhaps the best that can be said is that -2 is a plausible exponent. However, the choice of an integer value makes a good deal of sense in terms of simplicity as well as providing an understandable geometrical basis. The –2 exponent allows the boundary line to be represented as a linear relationship between spacing, *s*, and height:

$$s = Th. \tag{4.16}$$

A graph of the above self-thinning boundary line juxtaposed with the yield model self-thinning data is shown in Figure 4.9. The boundary line is shown with the default value for *T* of 0.115; the derivation of this value is explained later in the text. The boundary line thus indicates the bounds of possible stand dimensions; any point above the line represents a feasible combination of spacing and height, although stands close to the line may experience heavy density-dependent mortality. Points below the line are considered to represent stands that could not arise through normal stand development processes. The equilibrium phase of self-thinning may be seen as the portion of the curves which approximate straight lines parallel to the self-thinning line. The anomalous behaviour of the 3m spacing curve is very evident in these plots as it appears to be diverging from the other curves, which themselves, are apparently converging.

The proximity of any point to the boundary line may be expressed by a quantity that shall be termed the *stand density index* (SDI). The SDI of an even-aged stand may be defined as:

$$\rho = (Th/s)^2 \tag{4.17}$$

The purpose of the square term is to make SDIs of cohorts additive. Since (4.17) may be re-expressed as $(Th)^2N$, one cohort of uniform height may be conceptually split into two cohorts with N_1 and N_2 stems and the resulting partial SDIs, $(Th)^2N_i$, will sum to give the correct whole cohort SDI. Furthermore, since mean crown diameter is assumed to be roughly proportional to height, the SDI gives an approximate measure of the vertical projection of the canopy as a proportion of stand area. A graph showing isolines of SDI in *h-s* space is presented as Figure 4.10.

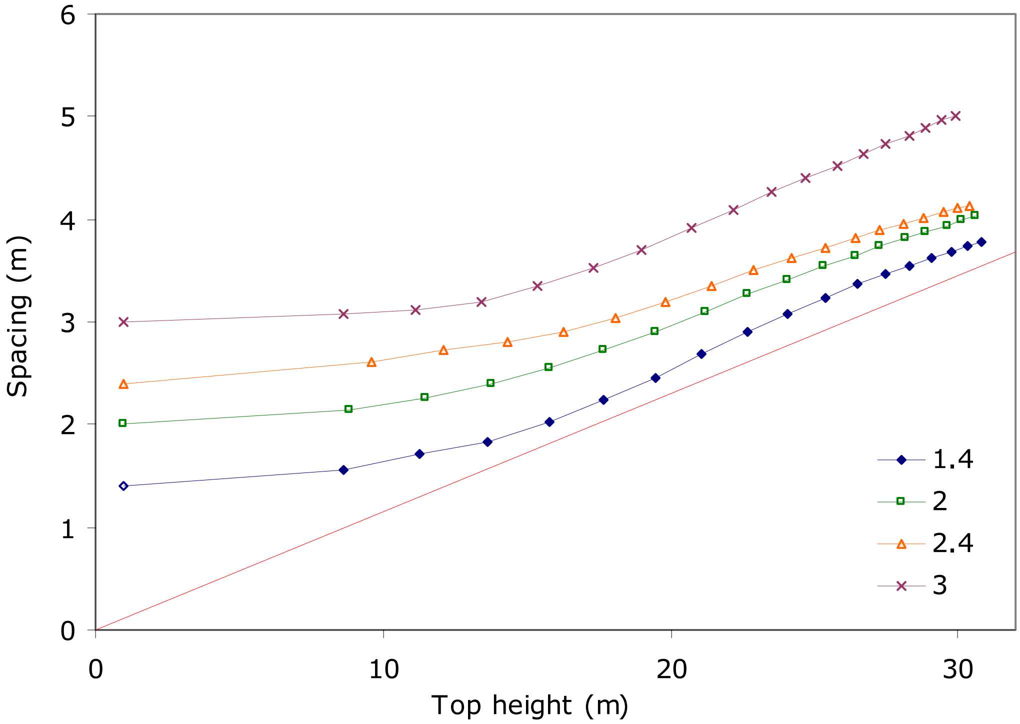


Figure 4.9 FC yield model data with thinning boundary line of Equation (4.16) shown in red. The legend shows initial spacing in metres.

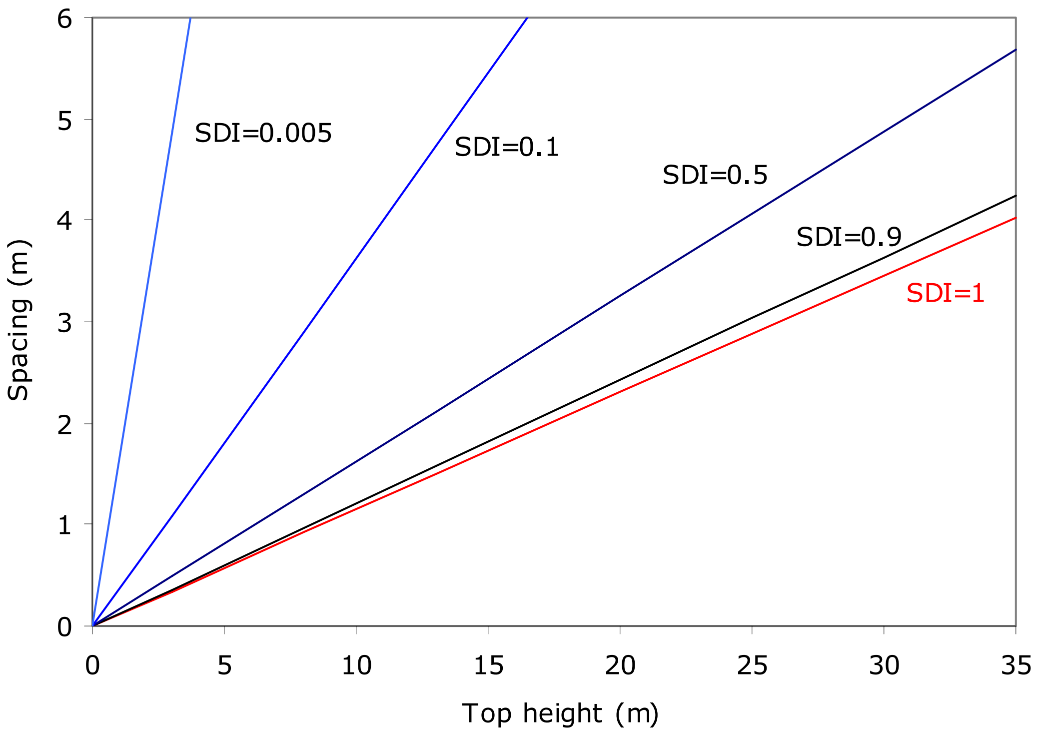


Figure 4.10 Stand density isolines in terms of top height and spacing.

Because the boundary line determines the maximum possible stand density, it determines the trajectory of any stand on the boundary line (i.e. fully-stocked; SDI =1), which will be to move upwards, along the boundary line. To determine the dynamic behaviour of stand densities above the boundary line the assumption is made that self-thinning rate will be determined by SDI (hence, mortality is literally density-dependent). This is essentially the same assumption that is made by Tang *et al.* (1994) for their model of growth and self-thinning, who define self-thinning rate by the equation:

$$\frac{d \ln N}{d \ln D} = -\beta \left(\rho / \rho_f \right)^{\gamma} \tag{4.18}$$

where N is stem density, D is average stem diameter, ρ is SDI (defined in terms of N and D and not standardized to give 1 for fully-stocked stands), ρ_f is the SDI of a fully-stocked stand (constant), and β and γ are species dependent constant parameters.

The GALDR self-thinning model may thus be considered analogous to that of Tang *et al.* (1994). The equation of self-thinning for under-stocked stands (i.e. SDI < 1) in GALDR may be written as:

$$\frac{ds}{dh} = T\rho^{\gamma} \tag{4.19}$$

where γ is a constant term. This satisfies the important condition that self-thinning of fully-stocked stands will take place along the boundary line, since when $\rho = 1$, $ds/dh = T$.

Choice of a value for γ was initially limited to integer multiples of ½ to ensure that the differential equation resulting from (4.19) would have terms in integer powers of h and s. A value of ½ was chosen for γ because it gave the simplest differential equation as well as the best fit to the yield model data. Thus (4.19) may be written as

$$\frac{ds}{dh} = \frac{T^2 h}{s} \tag{4.20}$$

which may be easily solved by separation of variables to provide the functional representation:

$$s = \sqrt{T^2 h^2 + s_o^2} \tag{4.21}$$

where s_o is a constant term equal to the value of s when $h = 0$ – i.e. the initial spacing. Plots of (4.21) are shown alongside FC yield model self-thinning data in Figure 4.11. It may be observed that the change in slope is more abrupt in the yield model data than the self-thinning model. It is hypothesized that the shapes of self-thinning curves in naturally regenerated stands would tend more towards the smoother curves predicted by (4.21). The reasoning for this is that natural regeneration will provide much greater variation in stem density than in the regularly spaced plantation. Thus, canopy closure will start earlier in the naturally regenerated stand, but it will also be a more drawn out process since (relatively speaking) gaps will be larger. Another interpretation of this is that the pre-closure, pre-equilibrium and equilibrium phases of self-thinning will tend to merge and overlap in the naturally regenerated stands.

However, it may be considered that the latter part of the equilibrium stage should be similar for artificially and naturally regenerated stands. For this reason, estimation of the thinning constant, *T*, was based on the fit of the self-thinning curves to the yield model data for the eight data-points of greatest height only. Goodness of fit was estimated by regression of spacing values from the yield model with spacing values predicted by the self-thinning model. Data from the 3m spacing plots were not employed in parameter estimation.

Since yield model data were available for non-thinned stands of Scots pine only, the same value of *T* was used for both pine and birch. This was considered to be a reasonable assumption since both species are similarly shade intolerant. However, Hynynen (1993) found self-thinning constants to be different when fitted to Reineke's (1933) equation. It is unclear how this difference in self-thinning on the basis of stem diameter might relate to any difference on the basis of height, but this aspect probably merits further investigation.

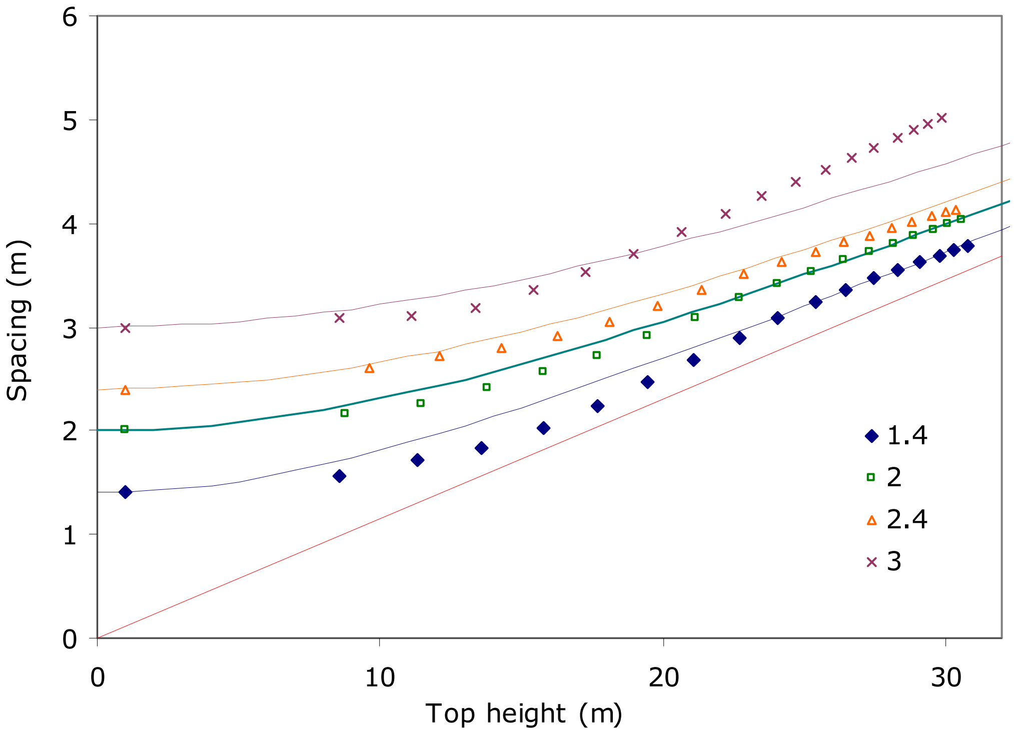


Figure 4.11 Line-plots of self-thinning curves of equation (4.21) fitted to FC yield model self-thinning data (points). The legend shows initial spacing in metres. The thinning boundary line is shown in red.

It may be noted that Equations (4.7) (see Section 4.1.3) and (4.21) together may define stem density in a single cohort stand as a function of time, *t*, and yield class, *Y*, since

$$
\begin{aligned}
\frac{ds}{dt} &= \frac{ds}{dh}\frac{dh}{dt} \\
&= \frac{T^2 B C^2 (Y) e^{-\left(B(t-M(Y))+1\right)e^{-B(t-M(Y))}}}{\sqrt{T^2 C(Y) e^{-2e^{-B(t-M(Y))}} + s_o^2}}
\end{aligned}
\tag{4.22}
$$

Thus, stem density may be written:

$$
N(t) = \left[\int \frac{T^2 B C^2 (Y) e^{-\left(B(t-M(Y))+1\right)e^{-B(t-M(Y))}}}{\sqrt{T^2 C(Y) e^{-2e^{-B(t-M(Y))}} + s_o^2}} dt \right]^{-2}
\tag{4.23}
$$

Equation (4.23) is unwieldy and the integration may be problematic, so in practice stem density is calculated according to difference equations as will be demonstrated later in the text.

Self-thinning in multi-cohort stands

Having constructed a model of self-thinning in single-cohort stands, the next step is to attempt to generalize and adapt this model to one of self-thinning in stands of more than one cohort. This may be considered relatively challenging compared to the previous step since (a) previous studies of self-thinning have almost exclusively dealt with even-aged monocultures, (b) suitable data on which such models might be based are difficult to come by, and (c) greater complexity in stand description will require to be matched by concomitant complexity in model behaviour. Thus, the multi-cohort self-thinning model will be based necessarily upon *a priori* reasoning.

Although there has been little work on non-uniform stands, White (1985) presented a paper on self-thinning in mixed-species stands. The major conclusion of this study was that the established self-thinning rules worked equally well for mixtures, considered as undifferentiated wholes, as for monocultures – but that each species behaves individualistically.

Weiner and Thomas (1986) characterize competition processes in terms of the balance of resource acquisition between plants of different sizes. *Relative size symmetric* competition occurs where resource acquisition is proportional to plant size and all individuals may affect the growth of their neighbours. If the effects of competition are disproportionate to relative size differences, the competition is said to be *relative size asymmetric*. In *completely* asymmetric (or *one-sided*) competition, growth of larger individuals is unaffected by smaller ones.

In the following discussion, two sets of assumptions will be presented with their resulting conceptual models. The first describes a set of cohorts with identical heights, so that the realized competition is assumed to be perfectly symmetric whether the competition mechanism be asymmetric or symmetric. The second describes a stand comprising cohorts of differing height, where competition is assumed to be completely asymmetric.

Symmetric multi-cohort self-thinning

Assume that the stand in question consists of *m* cohorts, denoted C$_i$ where *i* is an index from 1 to *m*. Let the stem densities and spacings of these cohorts be N_i and s_i respectively and let the height of all cohorts be *h*. Furthermore, let the stem density of the stand as a whole to be denoted N (= ΣN_i) and the corresponding spacing value to be *s*.

It is assumed that in this scenario, mortality is completely even-handed amongst cohorts. Thus,

$$\frac{dN_i}{dt}\bigg/N_i = \frac{dN}{dt}\bigg/N \quad \forall i \, . \tag{4.24}$$

Moreover, since

$$\frac{dN_i}{dh} = -2s_i^{-3}\frac{ds_i}{dh}, \tag{4.25}$$

Equation (4.24) holds if and only if

$$\frac{ds_i}{dh} = \frac{ds}{dh}\left(s_i/s\right) \quad \forall i . \tag{4.26}$$

The differential equation (4.26) may be solved if (a) it is assumed that the stand as a whole self-thins in the same manner as the single cohort case (i.e. Equation (4.20) holds), and (b) noted that

$$\frac{d}{dt}\left(s_i/s\right) = s^{-2}\left(s\frac{ds_i}{dh} - s_i\frac{ds}{dh}\right) = 0 \tag{4.27}$$

(i.e. s_i/s is a constant term). Hence, the solution of (4.26) may be written:

$$s_i = \left(s_{i_o}/s_o\right)\sqrt{T^2h^2 + s_o^2} \tag{4.28}$$

where s_{i_o} is the initial value of s_i. A graphical example is presented in Figure 4.12. Note that the slope of each cohort curve does not tend towards T, as does the entire stand curve, but instead tends to Ts_{i_o}/s_o . Note also that the curve for s is identical to a curve of a single cohort stand with $s = s_o = 6/\surd 13$.

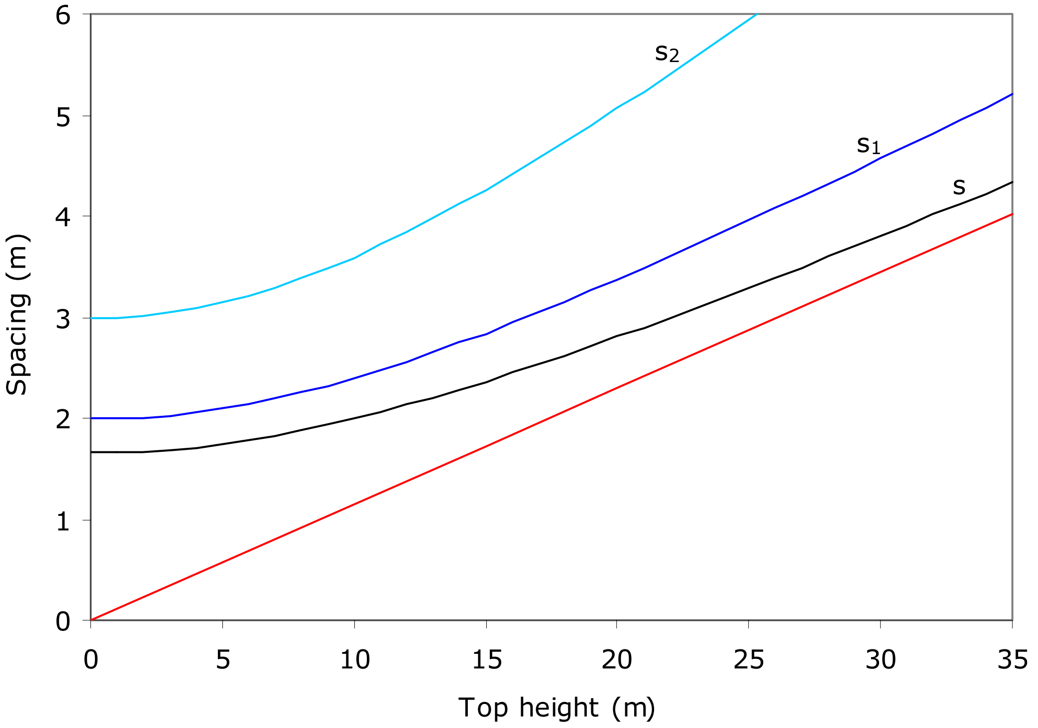


Figure 4.12 Self-thinning of two cohorts with symmetric competition. The blue curves show the spacing for the two cohorts, the black curve shows the spacing for the stand as a whole. The red line is the boundary line.

Asymmetric multi-cohort self-thinning

Consider a stand of m cohorts, as in the previous case except that the heights of the cohorts are different and are denoted h_i. The cohort indices may then be sorted in descending height order – i.e. $h_1 > h_2 > \ldots > h_m$. It is assumed here that the competition between cohorts is completely asymmetric, so the density of C_i will effect the mortality in C_j if and only if $i > j$.

Thus, self-thinning in the tallest cohort, C_1, will progress as if it were an even-aged stand in isolation. To accomplish this, a definition of density of individual cohorts is required. This will be the *partial stand density index* (pSDI), which may be defined as:

$$_p\rho_i = \left(T\,h_i / s_i\right)^2 . \qquad (4.29)$$

The SDI may then be defined as the sum of the pSDIs:

$$\rho = \sum_{i=1}^{m} {}_p\rho_i . \qquad (4.30)$$

Having established these definitions, self-thinning in C_1 may be represented by:

$$\frac{ds_1}{dh} = T\sqrt{{}_p\rho_i} \quad = T^2\, h_1 / s_1 \tag{4.31}$$

According to the premise of asymmetric competition, self-thinning rate in subordinate cohorts will depend upon density of all higher cohorts. The assumption made here is that in any 'upper' subset of cohorts, U_i defined $\{C_j\!: j<i\}$(i.e. all cohorts taller than C_i), the total rate of self-thinning amongst U_i will be equal to the self-thinning rate in an even-aged stand with SDI equal to the sum of pSDIs of cohorts in U_i. Allocation of mortality can then be calculated iteratively from self-thinning rates in C_1.

To proceed, the spacing of all stems in cohorts of U_i may be defined as:

$$\hat{s}_i = \left(\sum_{j=1}^{i} s_j^{-2} \right)^{-1/2} \tag{4.32}$$

and the *upper* SDI (uSDI) of U_i may be defined as:

$$\hat{\rho}_i = \sum_{j=1}^{i} {}_p\rho_j \ . \tag{4.33}$$

The total self-thinning in U_i may now be determined, according to the assumptions stated above, as:

$$\frac{d\hat{s}_i}{dh_i} = T\sqrt{\hat{\rho}_i} \tag{4.34}$$

(note that this reduces to Equation (4.31) when $i = 1$).

Then, the self-thinning rate of individual sub-ordinate cohorts may be determined iteratively, commencing with C_1, according to:

$$\frac{ds_{i+1}}{dh_{i+1}} = s_{i+1}^3 \left(\hat{s}_{i+1}^{-3} \frac{d\hat{s}_{i+1}}{dh_{i+1}} - \hat{s}_i^{-3} \frac{d\hat{s}_i}{dh_i} \right) \quad \forall i \geq 1 . \tag{4.35}$$

Equation (4.35) may be expanded into an equation expressed entirely in T, h_j and s_j (where $j \le i$) by means of Equations (4.32), (4.33) and (4.34). Solution of the resulting differential equation is non-trivial but may be obviated by calculating spacing differences via approximation of the difference equation with Equation (4.35) as demonstrated in Section 4.1.6.

An example of this self-thinning behaviour analogous to that represented in Figure 4.12 is shown in Figure 4.13. In this example, the two cohorts have almost the same height throughout the simulated life of the stand, though one is defined to be larger thus defining the asymmetry of the competition. Two scenarios analogous to the earlier symmetric example are possible, depending on whether the taller cohort is initially more or less dense than the lower cohort. Because the stands are practically of equal height there is no difficulty in the definition of the overall stand height. It may be noted that in both scenarios the *h-s* curve for the entire stand is identical to that in Figure 4.12 and the *h-s* curve for the tallest cohort is the same as if it were to comprise the entire stand. The trajectory of the sub-ordinate cohort is distinctly different to that in Figure 4.12, since its gradient does not converge to an asymptote but continues to increase throughout the lifetime of the stand. In simple terms, the lower cohort is undergoing self-thinning at a faster rate than the upper cohort because it is being ‘squeezed out’ by the relatively less constrained expansion of the crowns in the upper cohort.

4.1.6 Implementation of density-dependent mortality in GALDR

The aim of the density-dependent mortality module is to ensure realistic portrayal of the changes in stand density associated with the growth of trees represented therein. Of the two scenarios presented above, as yet only the asymmetric self-thinning model has been implemented. Attempts were made to unite the two approaches into a model of scaling symmetry, where competition would be symmetric between cohorts of equal height and asymmetric to various degrees depending on relative height differences between cohorts of unequal height. However, no practicable method of achieving this objective was found so it may be left as an object of further work.

At each timestep the height difference for each cohort is calculated as:

$$\Delta h_i = h_i(t) - h_i(t - \tau) \qquad (4.36)$$

where τ is the length of the model timestep in years (default value = 10).

The cohorts of all species are placed into an array sorted by height. Then, working through the cohorts in descending height order, the derivatives ds_i/dh_i may be calculated iteratively according to Equation (4.35). From this, the spacing difference may be calculated according to:

$$\Delta s_i = \frac{ds_i}{dh_i} \Delta h_i . \tag{4.37}$$

A new cohort spacing may be thus found, and hence the self-thinning mortality, $-\Delta_1(N_i)$, calculated (the minus sign is inserted because the change in stem numbers must be negative). However, this amount is not decremented from the cohort stem numbers until density-independent mortality has been evaluated (see next section).

An example of self-thinning in a multi-cohort stand is illustrated in Figure 4.14 where four cohorts initiate at 10-year intervals with successive cohorts increasing in initial density (the model timestep is one year in this example). The stand height, h, is an artificial variable (since the stand comprises cohorts of varying height) calculated as $s\rho^{1/2}/T$. It may be seen from Figure 4.14 that SDI exceeds the theoretical maximum value of one during the course of the stand development. This occurs because Equation (4.37) is actually an approximation since, if continuous functions were used, ds_i/dh_i would vary over the interval of the timestep. Furthermore, there is a bias in the approximation since ds_i/dh_i is calculated for the start of the interval only – it cannot be evaluated for the end because the new h and s variables have not yet been calculated. Improvement of the estimation would probably require another level of iteration.

Nevertheless, even in the most extreme cases, the discrepancy seems never to result in SDI values larger than 1.25 and the overall behaviour of the self-thinning process does not appear to be unduly affected.

4.1.7 Density-independent autogenic mortality

Other than through self-thinning, the principal cause of autogenic mortality will usually be old age. However, the lifespan of trees is not as well defined (Rackham,

1990) and density-independent mortality may occur at any time during the course of stand development. Mortality due to old-age generally arises as a result of an unfavourable balance of photosynthesis to respiration; the amount of photosynthesizing tissue is dependent on crown size, which stabilizes in middle age, whilst the quantity of respiring tissue continues to increase with the production of every annual growth ring. The final cause of tree death is often difficult to elucidate however, since mortality is commonly a complex and drawn out process involving a variety of agencies (Franklin *et al*., 1987). Old birch trees in Glen Affric are commonly seen bearing fruit bodies of the pathogenic fungi *Piptoporus betulinus* and *Fomes fomentarius* but often pathogenic fungi take hold in trees already weakened as a result of old-age (Rouvinen *et al*., 2002). Trees with stems or roots weakened by fungi may be blown down by relatively light winds. Insects, such as the pine shoot beetle (*Tomicus piniperdus*), may also contribute to mortality.

Tree mortality in the gap model JABOWA is modelled as two stochastic processes: *inherent risk of death* and *competition-induced* death (Botkin, 1993). The latter occurs as a result of reduced growth and may be considered analogous to self-thinning mortality in GALDR. The former process, inherent risk of death, controls tree longevity and is modelled as an exponentially distributed function whereby each tree is subject to a constant probability of death.

The exponential distribution did not seem suitable for GALDR, since any exponential function that predicts stand extinction at an age comparable with the maximum tree age also predicts very low densities of trees in middle and old age. Thus, an increasing hazard function was used for the density-independent mortality function in GALDR:

$$ {}_{e}\Delta_2\left(N_i\right) = -N_i\left(t/t_l\right)^2 \tag{4.38}$$

where ${}_{e}\Delta_2(N_i)$ is the expected absolute mortality due to density independent processes, t is the time since cohort initiation, and t_l is the longevity parameter for the species. A graph of expected relative mortality, $-{}_{e}\Delta_2(N_i)/N_i$, against time is shown in Figure 4.15. The increasing risk factor makes intuitive sense, at least for trees in old age where respiration costs will be increasing every year whilst photosynthesis stays relatively constant.

The actual absolute mortality, $-\Delta_2(N_i)$, due to density independent processes is modelled as a Poisson process with mean $-_e\Delta_2(N_i)$:

$$\Delta_2(N_i) = -\text{Poisson}\{-_e\Delta_2(N_i)\} \tag{4.39}$$

where the function Poisson$\{x\}$ returns a stochastic variable distributed according to a Poisson distribution with mean value x. The longevity parameter controls how long trees (and thus cohorts) may survive. Mortality must be complete when $t = t_l$, but cohorts expire well before this point. Default values for the longevity parameter are 600 for Scots pine and 200 for birch. These values give expected ages for cohorts of around 350 years for pine and 160 years for birch, depending on initial stem density and density-dependent mortality.

4.1.8 Total autogenic mortality and cohort extinction

The total autogenic mortality is determined simply as the most severe (i.e. largest absolute value) of the density-dependent and density-independent absolute mortality values:

$$\Delta N_i = \min\left(\Delta_1(N_i), \Delta_2(N_i)\right) \tag{4.40}$$

(the minimum function is used because the ΔN values are negative). The values are not summed because it is considered that the processes are intrinsically non-additive; any density-independent mortality talking place during self-thinning will contribute to the trees that must die to keep SDI below one rather than cause additional death. Figure 4.16 shows a graph of stem numbers against time illustrating the combined effects of density-dependent and density-independent autogenic mortality.

Cohorts are eliminated from state data when stem numbers fall to below a threshold value, $N_{\min}$. The default value for this parameter is five.

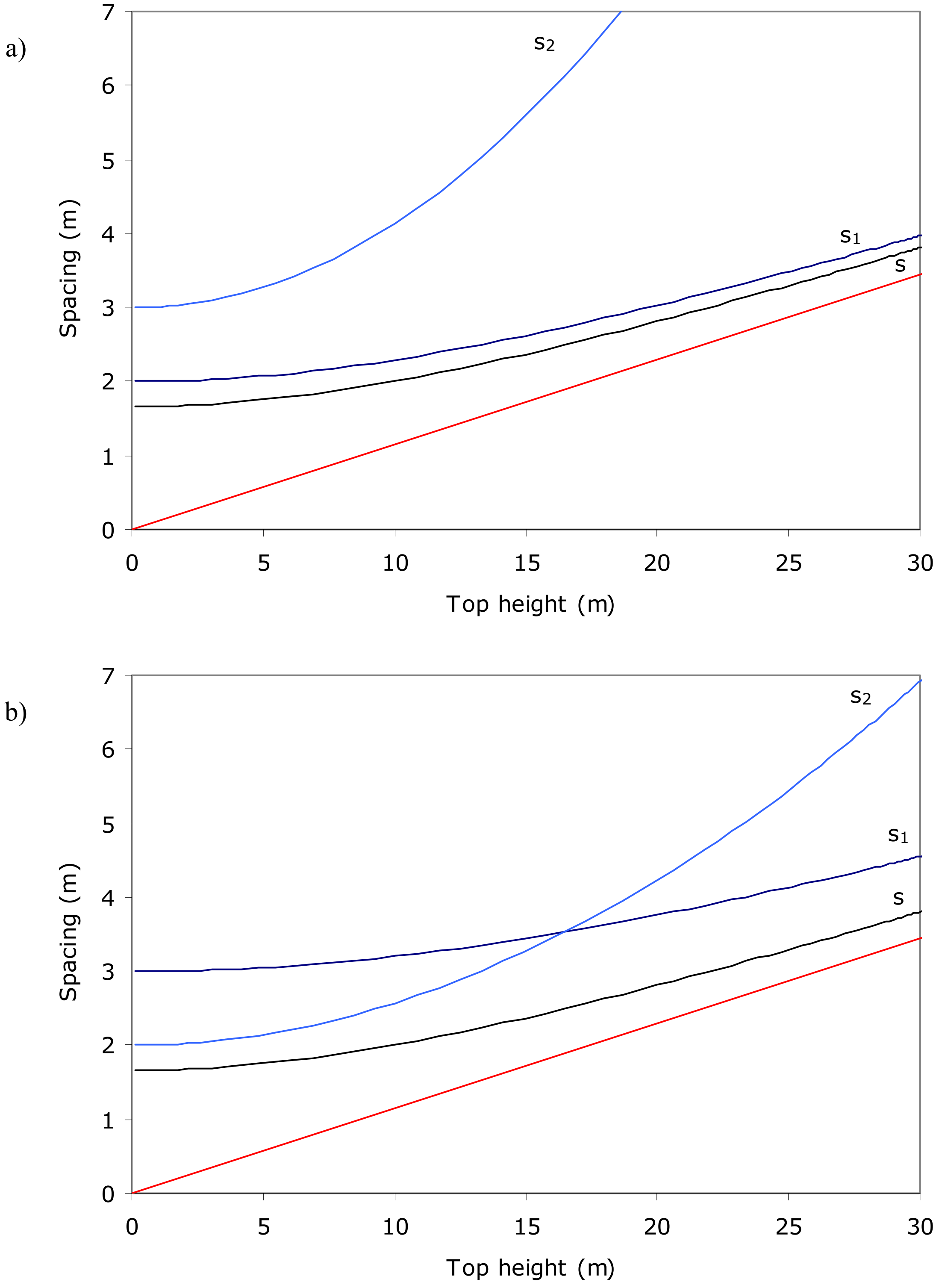


Figure 4.13 Self-thinning of two cohorts with asymmetric competition in which the two cohorts are of practically equal height and (a) the tallest cohort (s1) is initially most dense (b) the subordinate cohort (s2) is initially most dense. The blue curves show the spacing for the two cohorts, the black curve shows the spacing for the stand as a whole. The red line is the boundary line.

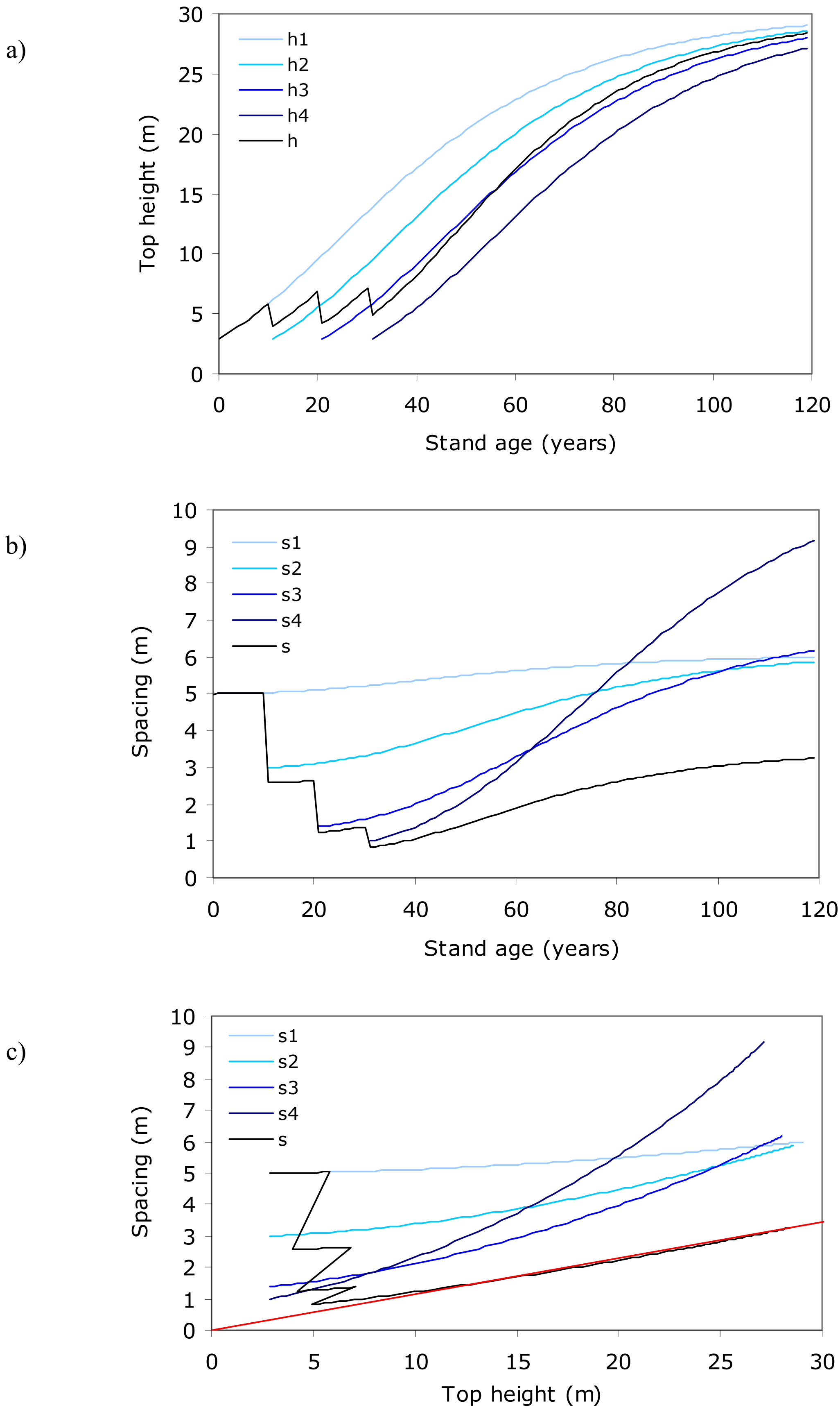


Figure 4.14 Example of self-thinning in a multicohort stand showing (a) height vs. stand age; (b) spacing vs. stand age; (c) spacing vs. height. The legends indicate the cohort index; in each the black lines indicate the whole stand value. The red lines show the boundary lines.

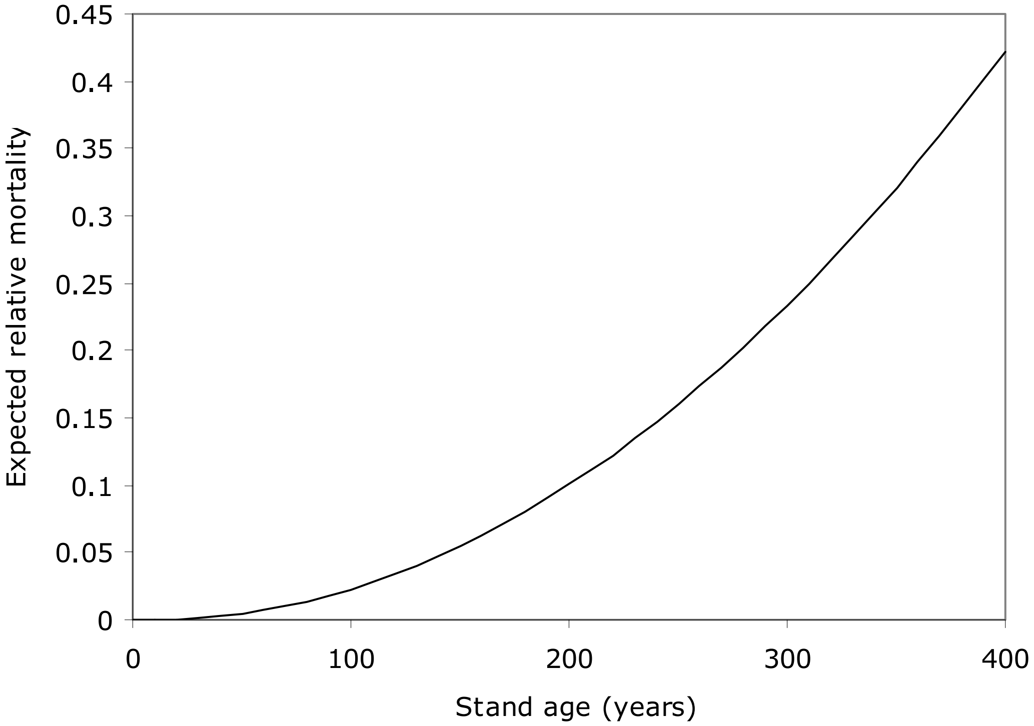


Figure 4.15 GALDR density-independent mortality function for Scots pine.

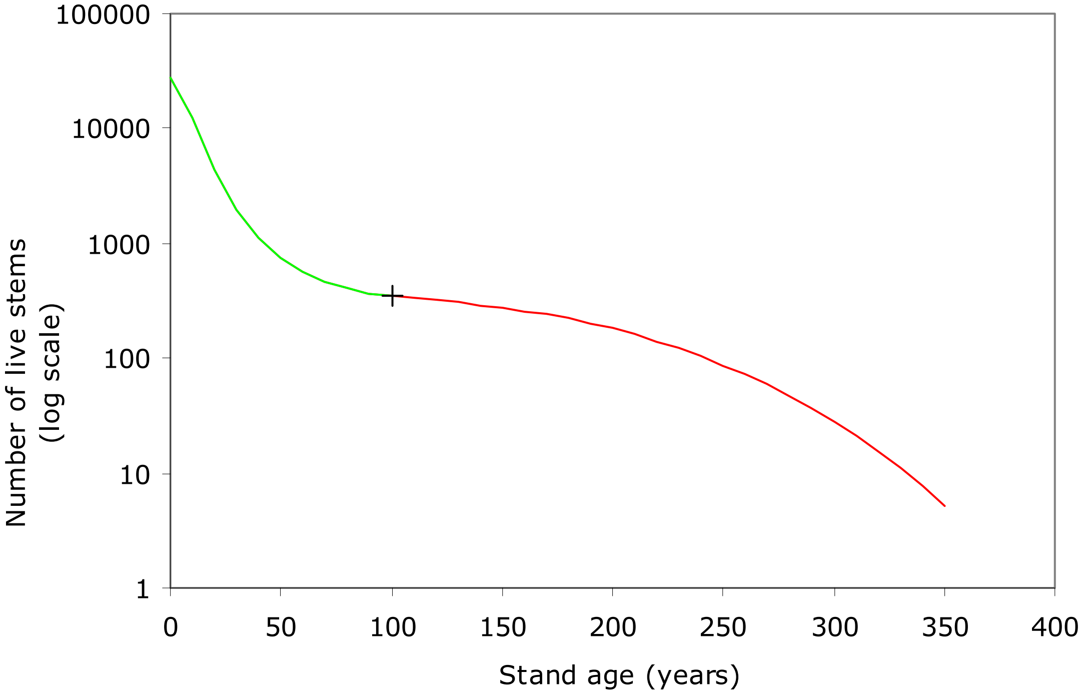


Figure 4.16 Changes in stem density during stand development in Scots pine– the dominant form of mortality is self-thinning in the portion of the curve before the cross (green), senescence in the latter part (red).

4.2 Wind disturbance

Wind has been identified as the principal natural disturbance agent in woodlands, for Britain as a whole (Peterken, 1996; Quine *et al*., 1999) and for Glen Affric in particular (Quine, 2003). To some extent, this conclusion is speculative since Britain lacks natural woodland in which a natural disturbance regime might be observed. However, wind storms frequently cause large quantities of damage to plantation forests in the uplands (Quine *et al*., 1999) and there is also evidence of prehistoric wind disturbance. For example, Anderson (1967) has reported remains buried in peat deposits containing trunks lying in a single direction, broken stems and tip-up mounds. Peterken (1996) also lists various instances of damage in native pinewoods, although Steven and Carlisle (1959) report that there is little evidence for catastrophic damage in pinewoods.

Effects of wind disturbance on forests

The frequency and intensity of disturbance events is a key factor in determining the structure and dynamics of natural forest landscapes (Jones, 1945; Pickett and White, 1985; Frelich, 2002). A distinction is often made between *gap-phase* and *stand replacement* dynamics, although in reality these are the end points of a continuous spectrum (Quine *et al*., 1999). In forests dominated by gap-phase dynamics, regeneration occurs in small-gaps produced typically by mortality of single trees, resulting in an intimate mixture of trees of many ages. Stand-replacement dynamics are exhibited where disturbances are severe (killing all or most trees) and extensive (from one to several hundreds or thousands of hectares; Canham and Loucks, 1984). This results in a coarse and patchy mosaic of roughly even-aged stands. Wind action may cause overthrowing or stem breakage of trees leading to both types of stand dynamics.

Quine *et al*. (1999) consider that both gap-phase and stand replacement dynamics may occur in close proximity to each other in hypothetical British natural woodland, the type of dynamics depending on topographic shelter as well as soil moisture conditions. Sheltered areas would rarely experience high wind speeds, so gap-phase dynamics would predominate. At the other extreme, exposed areas would be subject to frequent stand demolishing storms. Soil moisture may affect the stability of trees in two ways (Nicoll and Ray 1996): a high water table restricts rooting depth and hence the ability to resist overturning; also, wet soils tend to have lower tensile and shear strengths than dry soils.

Unlike disturbance due to fire, probability of wind disturbance is heavily dependent on stand age. Frelich (2002) states that stands in the early phases of stand development (stand initiation and stem exclusion) are not susceptible to wind disturbance and thereafter occurrence is random. This leads to a characteristic distribution of stand ages which is uniform until late stem exclusion phase and of negative exponential form thereafter.

A model of wind disturbance regime for Glen Affric is presented by Quine (2003) which predicts predominantly gap-phase dynamics in the valley bottom and in sheltered locations at higher elevations, stand replacement dynamics on the higher slopes and in exposed places and a intermediate zone where either disturbance pattern may occur. Additionally, the analysis predicts the occurrence of an upper zone, close to the treeline, where disturbance is rare because constant exposure to high winds causes adaptive growth and limits tree stature.

The wind climate in Britain

The oceanic climate of Britain is the windiest of anywhere in Europe (Troen and Peterson, 1989). The strong winds experienced in Britain are generally due to extra-tropical cyclonic systems (Quine, 2001). These systems generally follow a broadly defined eastward track, the centre of which often passes over north-western Britain. This results in a regional pattern of windiness characterized by higher wind speeds in the north and west than in the south and east of the country (see Figure 4.17). Strong winds associated with other mechanisms such as tornadoes, thunderstorms and slope winds are rare in Britain. Hurricanes do not occur in Britain.

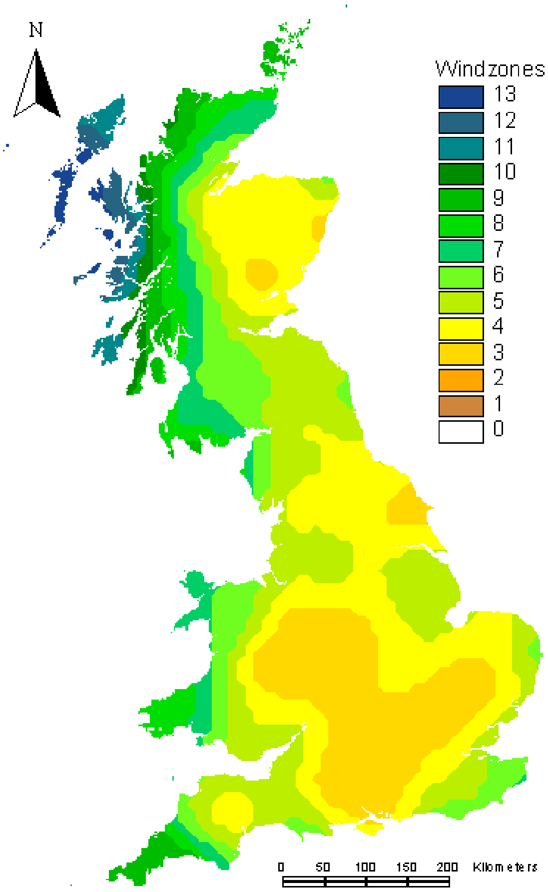


Figure 4.17 Wind zone map of Britain. (Courtesy of L. Sing, Forest Research.)

Horizontal differences of pressure occurring at a synoptic scale control a pattern of air movement known as the gradient wind (Linacre, 1992). The gradient wind operates in the upper air from a few hundred metres above the surface where the effects of topography and surface roughness are minimal. At lower elevations the wind speed and direction may be heavily influenced by topography and surface roughness (Quine, 2001). Topographic effects may include eddying and funnelling, and surface winds will generally be higher on aspects facing the wind (Frelich, 2002); surface roughness influences turbulence of the wind near ground level.

4.2.1 Existing approaches to modelling wind disturbance

Wind disturbance is a rarely modelled landscape process in dynamic simulations. Generally most FLDMs models seem to concentrate on fire as the principal agent of disturbance (e.g. Mladenoff *et al*., 1996; Waring and Running, 1998; Baker, 1999; Pennanen and Kuuluvainen, 2002). This would seem to reflect the fact that most forest landscape modelling has taken place in North America where the effects of fires may be particularly dramatic.

One FLDM that simulates wind disturbance as well as fire is the LANDIS model of Mladenoff *et al*. (1996). However, while the fire module of LANDIS has a whole paper (He and Mladenoff, 1999) devoted to its description, the wind module receives no more than a few lines in any published description of the model (see Mladenoff *et al*., 1996; He and Mladenoff, 1999; Mladenoff and He, 1999) and appears to be rather unsophisticated. The basis of the model is that stands of trees are assigned to five classes according to age and probability of windthrow is defined by these classes. It appears that there is no attempt to model the wind climate itself, but just the susceptibility of the stands. This may be acceptable in an area with little topography where wind shows little spatial pattern, but in an area of very variable topography like Glen Affric such a method would be over-simplistic. Frelich and Lorimer (1991) describe a landscape-level model of stand dynamics for deciduous forests in northern USA (STORM) but there is no spatial component in this model. STORM models windthrow stochastically with probability of disturbance increasing as cohorts pass through four size classes.

Despite the low incidence of wind disturbance as a modelled process amongst spatial forest dynamics models there are a few spatial models which predict wind speeds or windthrow risk to forests, albeit not as part of a FLDM.

DAMS

The standard model used by the UK Forestry Commission to predict wind speeds in Britain is DAMS (Detailed Aspect Method of Scoring; Quine and White, 1993). DAMS is an empirical model of site windiness produced from a multiple regression of rate of attrition of cotton tatter flags against geographic and topographic variables (Quine and White, 1994). Tatter flags are commonly used to gauge site windiness and their rate of attrition is well correlated with average wind speed (Jack and Savill, 1973). Average wind speeds can then be used to generate distribution functions from which probabilities of extreme winds may be calculated. DAMS was originally developed to be calculated manually from on-site field measurements of topex, however the method lends itself to calculation from a DTM using GIS (Bell *et al*., 1995) in which case the model output is a raster map at the same resolution as the input DTM.

The DAMS index of windiness is used by ForestGALES (Dunham *et al*., 2000; Gardiner and Quine, 2000), a non-spatial model of wind risk. ForestGALES calculates the probability of overturning or stem breakage for planted forest stands based on DAMS value and stand characteristics.

EXPOS

An interesting model to compare with DAMS is the EXPOS model of landscape exposure described by Boose *et al*. (1994), which is a component of a more complex model (HURRECON) for predicting patterns of hurricane damage. The model creates a Boolean map of the landscape representing areas that are exposed or protected from a given wind direction. Map loci are classified as protected if they fall within the wind shadow of upwind topography, assuming that the wind bends downward by no more than a fixed declination angle from the horizontal as it passes over a height of land. This method can be compared to a binary analogue of the aspect term in DAMS (see 4.2.2) but whilst DAMS is empirical and effectively fixed for the prevailing wind direction EXPOS is mechanistic (loosely) and can be calculated for any wind direction.

Airflow modelling

Airflow modelling is a highly mechanistic approach to wind speed prediction that uses theories of fluid dynamics to simulate the movement of an air mass over an uneven surface. The technique is used by the wind energy industry since it gives good quantitative predictions, but the disadvantage of the method is that is very computationally demanding.

Lekes and Dandul (2000) present a model of wind disturbance based on an airflow model. Wind Damage Risk Classification (WINDARC) uses an airflow model developed with the Computational Fluid Dynamics (CFD) program FIDAP to produce a map of terrain exposure. Terrain exposure is combined with soil type and various stand variables (proportion of spruce, height, age, and height/diameter ratio) to yield an ordinal value representing risk of wind damage.

British Standards Institute

The British Standards Institute (BSI) has produced a methodology for calculating average and extreme wind speeds for wind loading on built structures based on geographic position and local topography (BS 6399-2; BSI, 1997). While these methods do provide quantitative measures based on landscape attributes they are essentially feature-based and site-specific and therefore do not lend themselves to automated calculation from DTMs.

Suárez *et al*. (1999) compared the predictive ability of DAMS with two airflow models: WA^{S}P (Wind Atlas Analysis and Application Program) and MS-Micro/3. Model results were compared with observed wind speed data from six anemometers placed in an area of hilly terrain. The airflow models were found to be more accurate in exposed hilltop situations whereas DAMS performed better in more sheltered sites. The conclusion of the study was although more anemometers would be needed to make a definitive assessment of the relative ability of the models, the airflow models were not sufficiently better at predicting wind speeds to justify replacing DAMS.

GALDR uses a wind model based on the DAMS system of wind speed estimation because:

- it is well tested for British conditions;
- it has been used to calibrate models of windthrow (i.e. Dunham *et al*., 2000);
- it provides fine-scale spatial variation that may be evaluated using GIS;
- it is not overly computationally demanding .

An explanation of the calculation of DAMS is therefore provided in the next section.

4.2.2 Calculation of DAMS

The value of the DAMS index of windiness is calculated as the sum of six terms representing geographical or local topographical characteristics. Thus, DAMS may be expressed as Δ where

$$\Delta = \Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 + \Delta_5 + \Delta_6 \qquad (4.41)$$

The first term Δ_1 is based on a *wind zone* map of Britain (see Figure 4.17) and may be referenced by geographical co-ordinates. The wind zone map was derived empirically from the tatter flag data. The second term is a simple altitude factor which may be expressed as

$$\Delta_2 = 0.0178\,z \qquad (4.42)$$

where z represents elevation above sea level in metres.

The remaining four terms are topographic variables which may be summarized as follows.

- Δ_3 – **exposure**: this term is greatest for summits, plains and ridges and least for sheltered valleys and hollows.
- Δ_4 – **aspect**: greatest for aspects facing the prevailing wind; least for aspects facing away from the prevailing wind.
- Δ_5 – **valley funnelling**: greatest for long, steep-sided and open ended valleys; least for exposed areas.
- Δ_6 – **valley direction**: greatest for steep-sided valleys aligned with the prevailing wind; least for valleys running perpendicular to the prevailing wind.

The topographic variables are calculated by a method known as *topex*, an index of topographic exposure. The method of determination of the topographic variables for a position P is as follows (adapted from Quine and White, 1993; Quine and White, 1994).

From the point P, eight *topex sector values* are measured aligning with the principle compass directions (N, NE, E, *etc*.). Each sector value is measured as the angle of inclination from the horizontal to the skyline and may be denoted $\phi(\theta)$, where θ is the bearing of the sector in radians east of due north (i.e. N = 0, NE = $\pi/4$, E = $\pi/2$, etc.). Skyline angles are measured according to the landform rather than overlying vegetation. The minimum allowable value for topex sector values is zero.

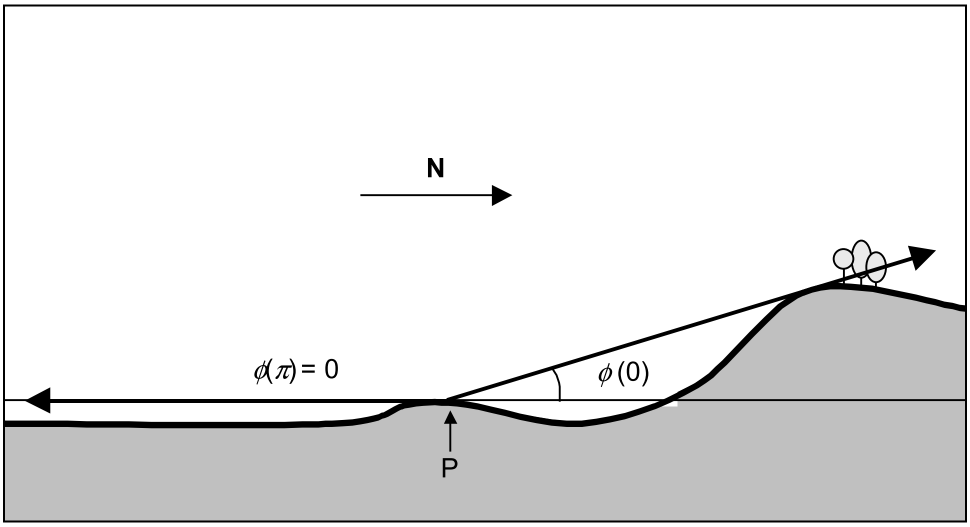


Figure 4.18 An example of calculation of north and south topex sector values.

Five derived values are calculated from the topex sector values as follows:

$$x = \sum_{i=1}^{8} \phi\left({}^{i\pi}/_{4}\right) \tag{4.43}$$

$$\mathrm{A}_1 = \sum_{i=1}^{8} \phi\left({}^{i\pi}/_{4}\right) \cos\left({}^{i\pi}/_{4}\right) \tag{4.44}$$

$$\mathrm{B}_1 = \sum_{i=1}^{8} \phi\left({}^{i\pi}/_{4}\right) \sin\left({}^{i\pi}/_{4}\right) \tag{4.45}$$

$$\mathrm{A}_2 = \sum_{i=1}^{8} \phi\left({}^{i\pi}/_{2}\right) \cos\left({}^{i\pi}/_{2}\right) \tag{4.46}$$

$$\mathrm{B}_2 = \sum_{i=1}^{8} \phi\left({}^{i\pi}/_{2}\right) \sin\left({}^{i\pi}/_{2}\right) \tag{4.47}$$

From these derived values the topex-based DAMS terms may be constructed. These are as follows.

$$\Delta_3 = \begin{cases} 0.00085x^2 - 0.1903x + 10.29 & \text{for } x < 100 \\ 0 & \text{for } x \geq 100 \end{cases} \tag{4.48}$$

$$\Delta_4 = 0.01077\mathrm{A}_1 + 0.02089\mathrm{B}_1 \tag{4.49}$$

$$\Delta_5 = 1.077\sqrt{A_2^2 + B_2^2} \tag{4.50}$$

$$\Delta_6 = 0.03779A_2 - 0.04099B_2 \tag{4.51}$$

4.2.3 GALDR wind disturbance sub-model

The overall strategy behind the windthrow model has been to use a modification of the DAMS methodology, called EDAMS (Event-based DAMS), to generate a windiness pattern, and then to use the Forestry Commission model of windthrow risk, ForestGALES to generate simple meta-models for stand stability.

The windthrow sub-model therefore consists of two components:

- **wind speed generation** (stochastic);
- **stand stability** (deterministic).

The wind speed generation component simulates the local wind climate. At each timestep the model generates a raster map of wind speeds corresponding to the most extreme wind event over the course of the timestep interval. The stand stability component calculates the minimum wind speed required to overturn the trees in each cohort. Windthrow occurs where the generated extreme wind speed for a cell exceeds the wind speed required for overturning one or more cohorts of that cell.

4.2.4 Wind speed generation

The process of generating a map of extreme wind speeds is as follows.

1. Assign a wind direction
2. Create a map of relative windiness associated with the assigned wind direction
3. Generate a pseudo-random number to act as a measure of the magnitude of the event
4. From the map of relative windiness, calculate the extreme wind speeds according to the event magnitude

Wind direction

Although wind direction at the surface will vary considerably over the landscape due to topographic effects, it is assumed that the overall wind pattern is governed by a gradient wind operating in the upper air (Linacre, 1992). The simulation of wind direction for the windthrow model is derived from Meteorological Office radiosonde data. Data from the upper air station at Stornoway Airport from the period 1990 to 2000 were used to create a probability distribution of wind direction. Wind directions were selected from soundings taken at an atmospheric pressure isobar at 85000 pascals, which corresponds to a mean height above sea level of 1414 metres with a standard deviation of 116 metres. Since the simulation of wind directions is for events of high wind speed, direction data corresponding to wind speeds of 30 metres per second or greater were used. Ideally data for even higher wind speeds would be used but, over the ten year period that data were available, this would result in too few data points. At a threshold of 30 metres per second 292 data points were available. A graph of the resulting probability distribution of wind direction is shown in Figure 4.19

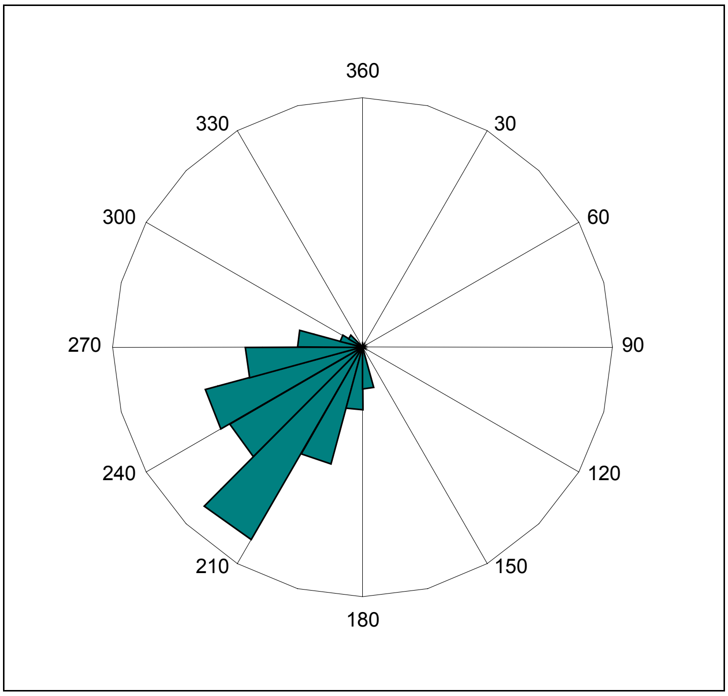


Figure 4.19 Probability density function for wind direction.

EDAMS

The principle underlying the formulation of EDAMS is that the pattern of windiness represented by DAMS should be the integrative resultant over time of some temporally varying windiness pattern. A further assumption is that the pattern of relative windiness is dependent on the gradient wind direction but not on the wind strength. In reality we might expect this not to be the case since, for example, patterns of turbulence will alter with varying wind strengths. However, wind speed prediction is an inexact science even in the case of the most complex airflow models and so there is little knowledge as to how the pattern would change with the strength of the gradient wind. Rejecting this assumption would necessitate adopting a more mechanistic approach such as airflow modelling which would be beyond the available computational capabilities and may not actually give better predictions. EDAMS therefore is expressed as a function of wind direction and topography. The formation of EDAMS is exactly the same as for DAMS except for those elements of DAMS that are related to wind direction, and may thus be expressed as:

$$E = \Delta_1 + \Delta_2 + \Delta_3 + E_4 + \Delta_5 + E_6. \qquad (4.52)$$

Note that, for an area the size of Glen Affric, the wind zone term, Δ_1, may be treated as a constant.

The two modified terms (aspect, valley direction) give values that are dependent on the orientation on local features of the landscape. These elements are both oriented toward the prevailing wind direction. Put more exactly, the aspect term is maximized where slope aspects are oriented 242.7° E of N (4.24 radians) and the valley direction term is maximized for valleys aligned with 246.3° E of N (4.29 radians). These directions are both approximately WSW and agree with the prevailing winds. The small difference between these two values is probably attributable to errors of the multiple regression of DAMS. In EDAMS these terms are replaced by terms which are maximized when landscape features are aligned with the input wind direction. The weighting of the directional terms should also be higher in EDAMS than in DAMS since the importance of the directional terms in the original tatter regression will have been diluted by the occurrence of wind originating from directions other than the prevailing wind direction.

- **DAMS Aspect term**

$\Delta_4 = 0.01077\ A_1 + 0.02089\ B_1$

$= -0.02350\ (A_1\cos(4.24) + B_1\sin(4.24))$ (4.53)

- **EDAMS Aspect term**

$E_4 = -0.02350\ 1/K_1\ (A_1\cos\theta + B_1\sin\theta)$ (4.54)

- **DAMS Valley Direction term**

$\Delta_3 = 0.03779\ A_2 - 0.04099\ B_2$

$= -0.05575\ (A_2\cos(2 \times 4.29) + B_2\sin(2 \times 4.29))$ (4.55)

- **EDAMS Valley Direction term:**

$E_5 = -0.05575\ 1/K_2\ (A_2\cos(2\theta + B_2\sin 2\theta)$ (4.56)

In the above equations K_1, K_2 are attenuation factors for aspect and valley direction respectively. The derivation of these factors is explained below.

Calculation of attenuation of directional factors

The factors K_1 and K_2 represent the factors by which DAMS underestimates aspect and valley direction terms respectively for the instantaneous pattern of wind speed governed by a single gradient wind direction. This attenuation of the directional terms occurs because DAMS represents (and was derived from) the combined effects of wind acting over an extended period. A method for deriving expressions for the attenuation factors and for calculating them from wind speed and direction data for the gradient wind is given below.

Assume that instantaneous flag tatter rate is proportional to wind speed and consider a set of points in a landscape where all DAMS terms are invariant except for aspect. Then consider a gradient wind represented by a vector $\mathbf{w}(t)$, a function of time (t), that acts over the landscape for a duration d. Let $\mathbf{w}(t)$ have magnitude $v(t)$ and direction θ and let $\bar{v}$ be the mean of $v(t)$ over d. Let $\mathbf{i}$ and $\mathbf{j}$ be north and east unit vectors respectively.

$$
\begin{aligned}
\text{tatter} &= \int_0^d v(t)\left(\lambda\left(\mathrm{A}_1\cos\theta(t)+\mathrm{B}_1\sin\theta(t)\right)+C\right)dt \\
&= \lambda\left(\mathrm{A}_1\int_0^d v(t)\cos\theta(t)\,dt+\mathrm{B}_1\int_0^d v(t)\sin\theta(t)\,dt\right)+C\overline{v}d \\
&= \lambda\left(\mathrm{A}_1\int_0^d \mathbf{w}(t)\cdot\mathbf{j}\,dt+\mathrm{B}_1\int_0^d \mathbf{w}(t)\cdot\mathbf{i}\,dt\right)+C\overline{v}d \\
&= \left(\lambda\frac{W}{\overline{v}d}\left(\mathrm{A}_1\cos\psi+\mathrm{B}_1\sin\psi\right)+C\right)\overline{v}d \qquad (4.57)
\end{aligned}
$$

where W is the magnitude and ψ is the direction of the vector $\int_0^d \mathbf{w}(t)\,dt$.

So the attenuation factor K_1 for aspect for the above wind pattern is the factor $\frac{W}{\overline{v}d}$.

K_1 can be calculated from historical wind data as below, where $\mathrm{P}(\theta)$ is p.d.f. for the occurrence of wind with originating direction θ, $v(\theta)$ is the mean wind speed in direction θ, $\overline{v}$ is the overall mean (non-zero) wind speed and $\hat{\mathbf{u}}_\theta$ is the unit vector with direction θ.

The relative wind loading $\mathrm{L}(\theta)$ is then defined as

$$
\mathrm{L}(\theta)=\frac{\mathrm{P}(\theta)\,v(\theta)}{\overline{v}}. \qquad (4.58)
$$

Thus, the aspect attenuation factor may be calculated as

$$
\mathrm{K}_1=\int_0^{2\pi}\mathrm{L}(\theta)\,\hat{\mathbf{u}}_\theta d\theta \qquad (4.59)
$$

and note that $\int_0^{2\pi}\mathrm{L}(\theta)\,d\theta=1 \quad \therefore \quad \int_0^{2\pi}\mathrm{L}(\theta)\,\hat{\mathbf{u}}_\theta\,d\theta\le 1$.

Using similar techniques the attenuation for valley direction may be calculated as:

$$K_2 = \int_0^{2\pi} L(2\theta)\,\hat{\mathbf{u}}_{2\theta}\,d\theta\,. \tag{4.60}$$

Upper air data from Stornoway Airport (1990-2000, 85000 pa) were used to calculate the attenuation factors. A graph of the relative wind loading $L(\theta)$ is shown in Figure 4.20. The calculated values for the attenuation factors for aspect and valley direction are shown below.

$K_1 = 0.5364$; $K_2 = 0.2565$

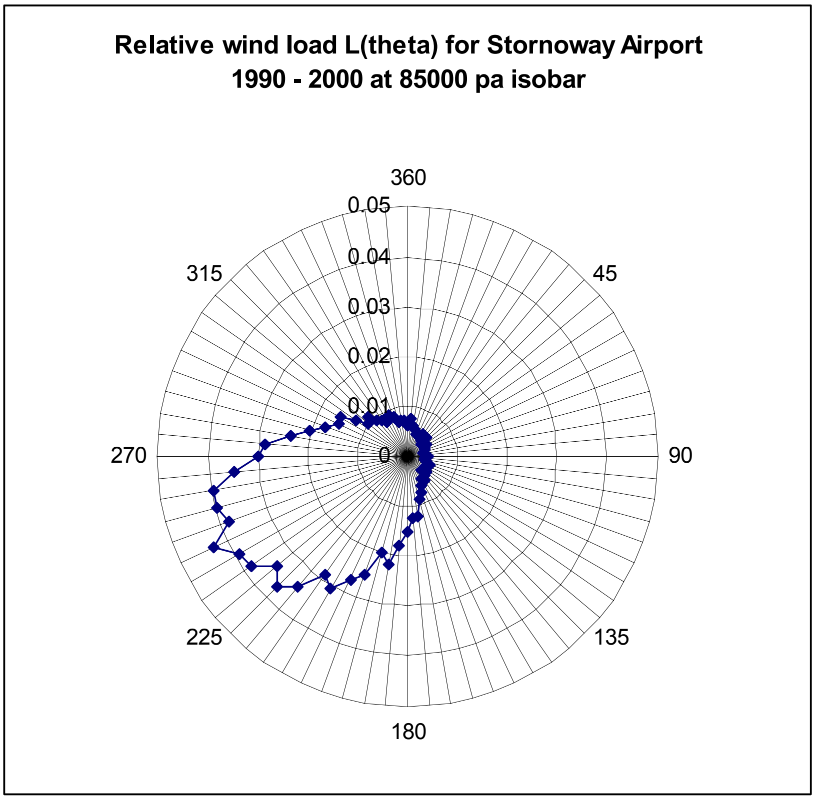


Figure 4.20 Relative wind loading L(θ) for Stornoway Airport (1990-2000) at 85000 pa isobar.

Calculation of extreme wind speeds from EDAMS

Since EDAMS values are on exactly the same scale as DAMS values, extreme values of wind speed can be estimated from EDAMS by replicating the methods used by Quine (2000) to obtain extreme wind speeds from DAMS. The method assumes that wind speeds at any given point can be represented by a two-parameter Weibull distribution with c.d.f.

$$P(v) = 1 - e^{-\left(\frac{v}{c}\right)^k} \tag{4.61}$$

where v is wind speed, c is the scale parameter and k is the shape parameter of the distribution. Quine (2000) has shown that a transformation of DAMS of the form

$$N = 4.592\, e^{0.08D} \tag{4.62}$$

(where D is DAMS output) is well correlated with the Weibull scale parameter c ($r^2 = 0.95$). The regression is shown below.

$$c = -0.185 + 0.317N \tag{4.63}$$

The shape parameter k shows no significant relationship with DAMS but can be assumed to be a constant value for any particular wind regime. A value of 1.85 is generally applied to maritime climates (ESDU, 1987).

Using these relationships the wind speed distribution at any point for winds acting from direction θ may be represented by a Weibull distribution dependant on values of EDAMS, E(θ).

$$\mathrm{P}(v) = 1 - e^{\left[-V/(-0.185+1.456e^{0.08\,\mathrm{E}(\theta)})\right]} \tag{4.64}$$

To obtain a distribution of the extreme (maximum) value over a given time period the method of ETSU (1997) is followed. This method derives a Fisher Tippett Type I (FTI) extreme value distribution from the parent Weibull distribution. The FTI has a c.d.f.

$$P(x) = e^{-e^{-a(x-U)}} \tag{4.65}$$

where x is the square of the wind speed, a is the scale parameter and U is the location parameter; then P(x) is the probability that $v_{\max}^2 < x$, where $v_{\max}$ is the maximum wind speed over 1 year.

The product *Ua* is generally assumed to be a constant over a regional scale and is termed the *characteristic value*. A value of 5 for *Ua* has been suggested for a wind climate such as that of Britain (ESDU, 1988). The value of the location parameter *U* can be derived from the scale and shape parameters, *c* and *k*, of the parent Weibull distribution as below.

$$U = \left[(-0.5903k^3 + 4.4345k^2 - 11.8633k + 13.569)c\right]^2 \qquad (4.66)$$

Thus, since $a = U/5$, we can obtain a fully parameterized FTI distribution for annual maximal wind speeds directly from EDAMS.

The Inverse Transform Method (ITM) has been used to generate stochastic variables distributed according to the FTI distribution. The basis of the ITM is stated below.

If f(x) is a p.d.f. of a random variable X , F(x) is the c.d.f. of X, $F^{-1}(x)$ is the inverse function of F(x), and U is a uniformly distributed random variable with p.d.f U(0,1): p(u) = 1 ∀ 0 < u < 1, then $F^{-1}(U)$ is a random variable with p.d.f. f(x).

Since SELES can provide uniformly distributed pseudo-random variables it is possible to generate variables distributed according to the FTI as follows:

$$v_{\max}^2 = U - (1/a)\ln\left(-\ln(x)\right) \qquad (4.67)$$

where x is drawn from the standard uniform distribution U(0,1). Furthermore, to create a distribution of extreme wind speeds over a longer timestep of *n* years we can use

$$v_{\max(n)}^2 = U - (1/a)\ln\left(-\ln(x^{1/n})\right) \qquad (4.68)$$

since $\mathrm{f}(x) = x^{1/n}$ is the p.d.f. for the random variable $X = \max(X_1 \ldots X_n)$ where $X_1 \ldots X_n$ are independent random variables drawn from standard uniform distributions U(0,1).

For a given wind event with unique direction θ, the pseudo-random uniformly distributed value x will represent the magnitude of the event; the same unique value will be used as the seed for the FTI distribution for all loci in the landscape.

Problems with attenuation factors

Preliminary simulation tests of the wind speed generation model with attenuation factors K_1 and K_2 have shown that the model produces wind speeds that are unrealistically high. When assessed over a long time interval, mean values for ten-year maxima at individual loci should show similar values whether calculated via DAMS or EDAMS, but in fact, the latter are significantly greater. Analysis of wind speed data from 3 mast-mounted anemometers in Glen Affric (see Quine, 2003) has shown that the EDAMS predicts *average* wind speeds more accurately if attenuation factors are used (Hope, unpublished data). It is believed that derivation of the FTI distribution from the parent Weibull distribution may be no longer valid when attenuation factors are used. Because of this, the attenuation factors have been reset to values of one in the default GALDR model. It is hoped that a reformulation of the FTI derivation can be discovered that allows attenuation factors to be used in future versions.

4.2.5 Stability

Stability is expressed as the critical minimum wind speed required to overthrow trees growing in each cohort – thus, the higher the value the more stable the cohort. Cohort stability is calculated as a function of cohort height and site wetness, $\mathrm{St}(h,F)$, where h is cohort height and F is Soil Moisture Regime (SMR) (derived from the ESC SMR map; see Section 3.4.2). The stability function is formulated as a meta-model of the ForestGALES stability model (Dunham *et al*., 2000). To create the meta-model ForestGALES was run with input parameters as shown in Table 4.4. Only Scots pine was used in the model runs, since data relating to stability for birch are scarce (Quine, 2003). Wind speeds were calculated for stands with top height and mean stem diameter calculated from stand age by the Forest GALES yield model. Stand ages were varied from 22 to 80 years and model runs were repeated for the three drainage class options of ForestGALES (‘poor’, ‘average’ and ‘good’). All other model input terms were kept as constant terms for the model runs (see Table 4.4). The resulting height and wind speed data are shown plotted in Figure 4.21. Although one would expect the curves to decrease monotonically, the plot for the poor drainage class shows a dip at about 12 metres height. This irregularity is thought to be due to model rounding errors (B. Gardiner, personal communication).

Table 4.4 Input values used for generating stability meta-models from ForestGALES.

Variable	Value
cultivation	notch
drainage	<*variable*>
soil	podzol
species	Scots pine
yield class	8
thinning	no thinning
initial spacing	3 m
edge	windfirm

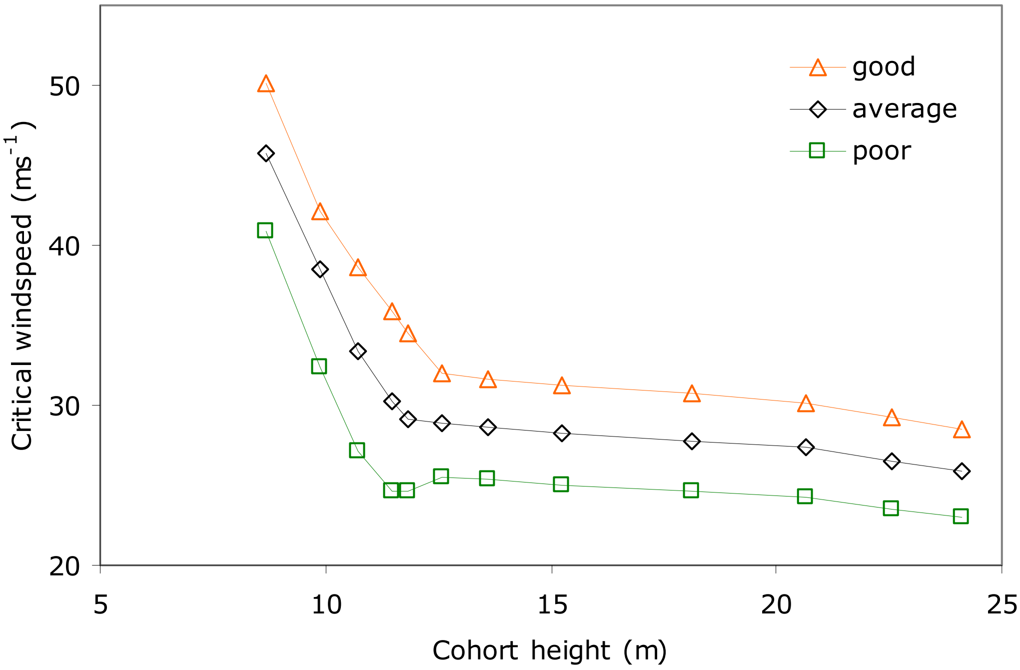


Figure 4.21 ForestGALES output showing critical wind speed for overturning against stand height. The legend shows ForestGALES drainage class.

Aside from the irreguarity in the ‘poor’ drainage plot, the curves show a marked ‘dog-leg’ shape. This shape is not easily reproduced by a single smooth curve so it was modelled using two linear relationships. Linear regression was performed on the ‘average’ drainge plot, resulting in the following function:

$$\mathrm{St}(h,F_{av}) = \max\{92 - 5.4h\ ,\ 32 - 0.24h\} \qquad (4.69)$$

where F_{av} is the SMR which corresponds to ‘average’ drainage. The ‘good’ and ‘poor’ drainage plots were modelled by applying multipliers; hence

$$\mathrm{St}(h,\ F_{poor}) = 0.88\ \mathrm{St}(h,F_{av}) \qquad (4.70)$$

and

$$\mathrm{St}(h,\ F_{good}) = 1.12\ \mathrm{St}(h,F_{av}). \qquad (4.71)$$

where F_{poor} and F_{good} are SMR vales corresponding to ‘poor’ and ‘good’ drainage classes respectively. Plots of the resulting model St(h,F) are presented in Figure 4.22 for $F_{poor,}$, F_{av} and F_{good}.

Generalizing Equations (4.69) - (4.71) over all values of F, the stability function may be defined for all soil moisture levels by

$$\mathrm{St}(h,F) = K_F\ (\max\{92 - 5.4h\ ,\ 32 - 0.24h\}) \qquad (4.72)$$

where K_F is defined by

$$K_F = \begin{cases} 1 - 0.12\left(F_{av} - F\right)/\left(F_{av} - F_{poor}\right) & \text{for } F < F_{av} \\ 1 + 0.12\left(F - F_{av}\right)/\left(F_{good} - F_{av}\right) & \text{for } F \geq F_{av} \end{cases} \qquad (4.73)$$

Furthermore, if F_{poor} and F_{good} are defined to be equidistant from F_{av} (they may as well be defined so, since the drainage classes are arbitrarily defined) such that

$$F_{av} - F_{poor} = F_{good} - F_{av} = F_d \qquad (4.74)$$

then (4.73) may be redefined as, more simply

$$K_F = 1 + 0.12\left(F - F_{av}\right)/\left(F_d\right). \qquad (4.75)$$

The default values of F_{av} and F_d used in GALDR are 6.5 and 2 respectively. Thus F_{av} corresponds to the boundary of the ‘moist’ and ‘very moist’ ESC category. F_{poor} corresponds to the ‘wet’/’very wet’ boundary whilst F_{good} is on the cusp of ‘fresh’ and ‘slightly dry’ (see Figure 3.4).

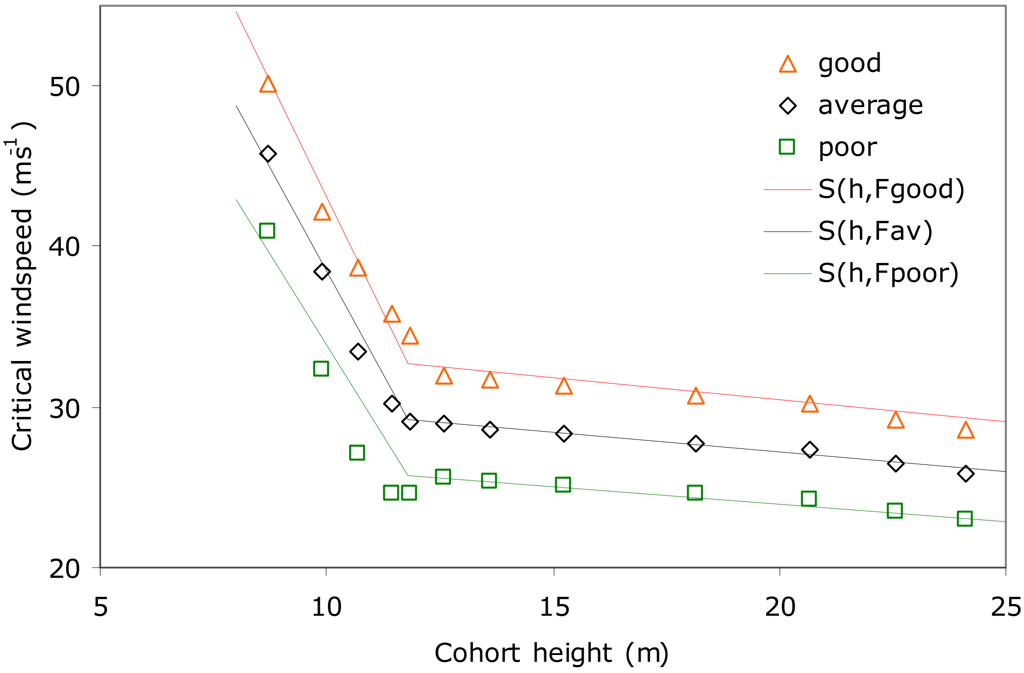


*Figure 4.22 ForestGALES output (points) and meta-model function St(*h,F*) (lines).*

4.3 Seed production and dispersal

4.3.1 Introduction

Seed dispersal is of immense importance to forest landscape dynamics since it provides the mechanism by which plant populations may expand onto formerly unexploited ground. The species currently considered in GALDR, pine and birch, have seeds dispersed primarily by wind. The seeds are winged – an adaptation that slows the rate of descent and allows the seeds to be caught in updraughts. Birds and mammals may incidentally disperse a small number of seeds of pine and birch, but this is likely to be a very minor mechanism compared to wind dispersal. Bird dispersed species, such as rowan and gean, are also present in Glen Affric, but these species are not yet included in the model. Seed dispersal of trees is especially pertinent to ecological restoration of wooded landscapes because British trees do not generally form a persistent seed bank (Hill and Stevens, 1981).

The vast majority of seeds dispersed by wind from pine and birch trees travel relatively short distances. Sarvas (1948) claims that the greater part of dispersed birch seed travels no further than two tree-heights in distance, whilst McVean (1963b) states that the majority of pine seedlings are found within 100 m of parent trees. However, pollen records from the early Holocene indicate that colonization of the post-glacial landscape relied on much larger dispersal distances (Birks, 1989).

Long distance dispersal events may be extraordinarily infrequent but their ecological consequences are likely to be disproportionately large (Nathan *et al.,* 2002a). By their very nature such events are difficult to observe and, consequently, difficult to simulate (Higgins and Richardson, 1999). Nathan and Muller-Landau (2000) suggest that mechanisms for long distance dispersal may be distinct from those operating for everyday dispersal. Furthermore, Nathan *et al.* (2002b) claim that, for wind dispersed tree seeds, mechanisms of long distance dispersal may be completely accounted for by considering effects of turbulent airflow lifting seeds above the canopy.

The purpose of the GALDR seed production and dispersal sub-model is to simulate the distribution of viable seed from parent stands. It may be conveniently divided into modules of seed production and seed dispersal. The production model estimates the number of viable seeds released from parent cohorts based on empirical measurements of seed production. The dispersal model relies on an adaptation of the micrometeorological model of seed deposition from a point source proposed by Greene and Johnson (1989). GALDR treats each seed-bearing cohort as a point source and produces a landscape distribution of seedfall for each species by summation over all source loci. Seed production and dispersal are calculated for each species separately.

A note on terminology

In keeping with common usage, the term ‘seed’ has been used here in place of the more technically correct ‘fruit’. The fruit of birch is technically designated as a nut or nutlet (Stace, 1997; Pelham *et al.* 1984) but these terms are rarely used (for birch) except in botanical descriptions.

4.3.2 Seed production – background

Seed production in trees is a highly variable process. There are very large differences between species. Variation within species may be both temporal and spatial, and may be influenced by climate and stand structure.

Considerable temporal variation in seed production (masting) is exhibited by birch species (Atkinson, 1992) as well as Scots pine (Carlisle and Brown, 1968). This phenomenon is sometimes interpreted as a passive response to climatic conditions in the flower development and pollination periods. An alternative hypothesis views it as an active strategy to satiate seed predators in masting seasons whilst limiting their population sizes by restricting seed production in other seasons. In any case, mast years in pine and birch should be sufficiently frequent to ensure at least one year of good seed production in any ten-year period; hence, masting is not simulated in GALDR.

Both birch and pine may produce empty seed in the absence of pollination (Carlisle and Brown 1968; Atkinson, 1992). Self-incompatibility in birch is effected by poor growth of the pollen tube in birch, and by early abortion of the embryo in pine. Koski (1975) estimated that 90% of all self-fertilized pine embryos abort.

Estimation of seed production

In the interior of moderate to large woods, seed rain (measured with seed traps) should equate to net seed production (i.e. less pre-abscission predation and other losses). Therefore, published figures of seed rain density within woodlands have been used as estimates of seed production per unit area of woodland. Another measurement sometimes reported is that of seed yield for collection purposes. These figures are likely to underestimate net seed production to some extent, since not all seeds will be collected and some seeds may have been released before collection.

Seed production in Scots pine

Seed production in Scots pine starts with flower (strobilus) production from August to October (Fletcher, 1992). The flowers lie dormant over winter and pollination occurs in late May or June of the following year. Pollen tube growth is slow, and is arrested over winter so that fertilization occurs one year after pollination. Embryo development proceeds over the autumn and the majority of seed is likely to be shed the following summer as the seed cones open.

Steven and Carlisle (1959) report a mean seed mass of 4.96 mg; Gordon (1992) provides a value of 165,000 seeds/kg (mean seed mass: 6.1mg).

McVean (1961b) recorded a seedfall of 4.5 viable seeds/m^2 in native pinewoods at Beinn Eighe National Nature Reserve (NNR), Wester Ross in a moderate seed year.

Mean seed fall values of 17 seeds/m^2 (range: 0-106 seeds/m^2) and 24 seeds/m^2 (range: 5-127 seeds/m^2) have been reported from Finland (Heikinheimo 1948; Lehto 1956; both cited in Miles and Kinnaird 1979a).

Carlisle and Brown (1968) report two measurements of Scots pine seed production: the quoted values of 2.6 and 10.0 kg/ha equate to 53 and 202 seeds per m^2 if Steven and Carlisle's (1959) figure for seed mass is used. It is not clear whether these figures arose though collection or measurement of seedfall.

Gordon and Faulkner (1992) give a range of 0.18 –8.6 kg/ha (equivalent to 3.6-173 seeds/m^2) for the quantity of seed that could be collected from commercial stands.

McNeill (1954) reports that in plantations of Scots pine, cone yields vary from 25 to 300 cones per tree, which was calculated to give seed rains of 15-200 seeds/m^2.

Seed production in birch

Development of birch flowers (catkins) begins in August with pollination commencing the following spring in late April or early May (Fletcher 1992). The seeds develop in the cone-like female catkins until July or August when the seed cones become pendulous and begin to release seed. The peak of seed release is in September and October (Miles and Kinnaird, 1979a).

Atkinson gives mean seed masses for various locations ranging from 0.19 to 0.21 mg for filled seed of silver birch and 0.21 to 0.43 mg for filled downy birch. Unfilled seed masses were significantly less (0.09 – 0.12 mg for silver; 0.12 – 0.22 mg for downy birch). Proportions of filled seeds range from <1% to 19% (in both species). In relation to the above figures, Gordon's (1992) figure of 1,900,000 seeds per kg gives a curiously high mean seed mass (0.53 mg), considering this value is meant to represent an average value for all birch seed used in Britain.

Sarvas (1948) recorded a maximum annual seedfall of 53,200 filled seeds per m^2 for silver birch woodlands in southern Finland. However, Sarvas considers this figure rather exceptional and suggests 2300 filled seeds/m^2 as an average for *good* seed years. A figure of 3050 seeds/m^2 is quoted for a three year period (= 1017 seeds/m^2 per annum). By contrast, in clear-cut areas the average seed rain was 340 filled seeds/m^2. Sarvas (1948) also reports that the germinability of the seed is best in good seed years, suggesting that the contribution of poor seed years may be very slight.

Miles and Kinnaird (1979a) supply measurements of seed rain taken over six years from woods of downy birch in Inverpolly NNR, Wester Ross. Mean annual values ranged from 3800 to 43,300 seeds/m^2 with a mean over all six years of 24,267 seeds/m^2. Viability of the Inverpolly seed was reported to be low, ranging from 2.5% to 15% (no average value supplied).

Gordon and Faulkner (1992) give a range of 3-20 kg/ha for the quantity of seed that could be collected in birch stands. Using Gordon's (1992) figures for mean seed mass (see above) and average viability (25%), seed production values of 570 – 3800 seeds/m^2 or 143 – 950 viable seeds/m^2 are obtained.

Maturation

Greene *et al.* (1999) make a case for using minimum tree size rather than age as the basis of a threshold for initiation of seed production. However, values for minimum size are rarely quoted in the literature whereas minimum ages are frequently given.

Atkinson (1992) states that birch may start flowering from 5-10 years but exceptional individuals may flower as early as 2 years. Nevertheless, these early reproductive efforts do not generally result in significant quantities of fertile seed. Evans (1988) gives 15 years as minimum seed bearing age for birch whilst Philipson (1990) gives 15-20 years as the minimum age for production of seed crops with regeneration potential for Scots pine. There has been some concern amongst managers of native pinewoods that production of viable seed may decline in older trees, though Nixon and Cameron (1994) reported only very slight decreases of cone production and viability with age. Likewise, Stewart *et al.* (2000) found no evidence for decline in seed production in birch.

Climate

In general, flowering is stimulated by warm dry weather (Nixon and Worrell, 1999). More specifically, seed production in pine has been found to be linked to mean temperatures and hours of sunshine in the year of fertilization (McNeill, 1954, Miles and Kinnaird, 1979a). Prolonged periods of rainy weather during pollination are thought to inhibit successful fertilization (Runions and Owens, 1996; Nixon and Worrell, 1999).

At the scale of the GALDR study area, the principal spatial variable affecting local climate is altitude. McVean and Ratcliffe (1962), Brown (1973) and Miller and Cummins (1982) have all reported inverse relationships between altitude and seed production or germinability for pine. Stewart *et al.* (2000) show a similar relationship for germinability for birch from Creag Meagaidh NNR (shown in Figure 4.23). Regression of this relationship gives

$$G = 66.1 - 0.09\,z \tag{4.76}$$

where G is percentage germinability and z is altitude in metres. These data are collected from one year only, so the absolute values may be poor indicators of average germinability over longer periods. Nonetheless, the relative variation of germinability with altitude is likely to be similar from year to year.

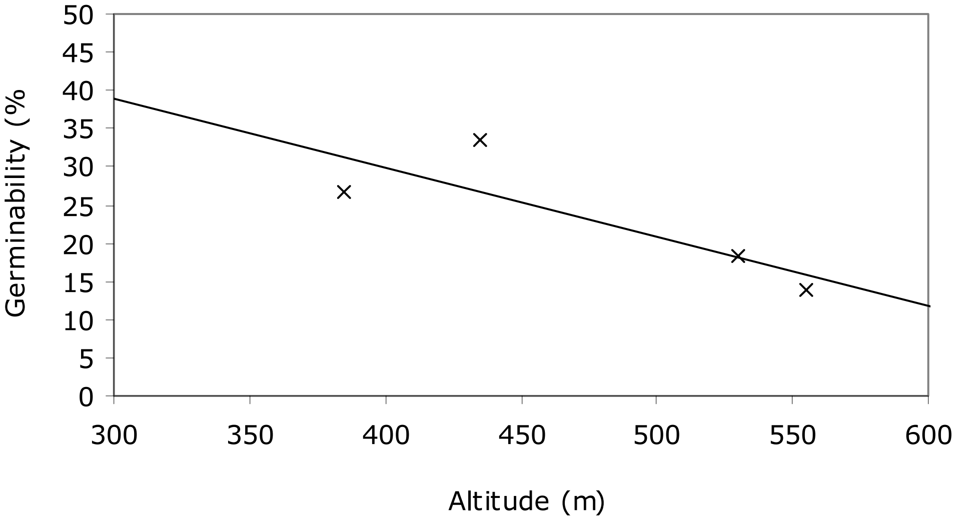


Figure 4.23 Relationship between germinability and altitude. Data points (crosses) are from Stewart et al. *(2000); a regression line is also shown.*

Stand density

The stem density of a stand influences seed production via effects of crown size and shape, light levels in the crown, and pollination success.

It is perhaps intuitively obvious that the seed production is likely to be related to the size of the parent plant as a whole; Greene and Johnson (1994) confirm that seed production is positively correlated with leaf mass or basal area of trees. However, flower production tends to be concentrated in those parts of the crown which are most exposed to sunlight (Mair, 1973). Thus, as long as pollen supply is not limited, seed production per tree is maximized for isolated trees (Nixon and Worrell, 1999). Closed canopy stands tend to show low productivity; thus, thinning of dense stands is generally prescribed to increase light levels, assist crown development, and hence encourage larger seed crops (Faulkner, 1992).

At low stocking densities, where individual crowns do not touch and hardly shade each other, total flower production may be expected to be directly proportional to the stem density. However, Boyle and Malcolm (1985) and Nixon and Cameron (1994) report slightly higher proportions of unfilled seeds and lower levels of germinability in the more isolated trees of small native pinewood remnants. Boyle and Malcolm

(1985) attribute this effect to higher rates of self-fertilization. Greene *et al.* (1999) note that such effects are frequently met amongst both conifers and broadleaved trees, but also state that no model of the phenomenon has been presented.

History of stand development will influence crown size and shape, and hence productivity. Stands that have grown at wide spacing from establishment stage will have wider and deeper crowns than those where density has been recently reduced to low levels (e.g. by heavy thinning).

Pre-abscission predation

The seed of Scots pine may be eaten by crossbills (*Loxia curvirostra* and *Loxia scotica*) and red squirrels (*Sciurus vulgaris*) (Steven and Carlisle, 1959; McVean, 1963b; Booth, 1984). Larvae of the pyralid moth (*Dioryctria abietella*) may consume some seed in the cones whilst the pine shoot beetle (*Tomicus piniperda*) may occasionally cause such extensive crown damage that flower production is impaired (Booth, 1984). However, insects are not generally reported as a major agents of seed loss in native populations of Scots pine.

Birch seed may be a principal food of siskins (*Carduelis spinus*) and redpoll (*Acanthus flammea*) (Newton, 1972). Birch seeds may also be destroyed by the gall midge *Semudobia betulae* (Miles and Kinnaird 1979a), although it is thought that this depletion is unlikely to account for more than 10% of annual production.

4.3.3 Seed production – model description

For each species, seed production per cohort is calculated as a baseline seed production value, Q^*, modified by three factors:

$$Q = Q^* \times Q_{age} \times Q_{alt} \times Q_{\rho} \qquad (4.77)$$

where Q_{age} is the parent maturity factor, Q_{alt} is the altitude factor and Q_{ρ} is the stand density factor.

Baseline production

Greene *et al.* (1999) provide a model for mean annual seed production (after pre-abscission losses to predation etc.), Q, based on basal area, B (in square metres), and mean seed mass m_s (in grams):

$$Q = 3067 m_s^{-0.58} B^{0.92}. \tag{4.78}$$

It is suggested that this formula may be applied to single trees as above or, in density terms, to stands. In the latter case, Q represents seedfall density (in seeds/m^2) and B represents stand basal area (as a ratio).

This formula may be applied to Scots pine and birch as follows. Basal area figures have been drawn from the standard forestry yield tables of Edwards and Christie (1981). Values were based on mature stands (oldest figures given) of average yield class (yield class 8 in both cases) with intermediate thinning and usual spacing (2m for pine; 1.5m for birch). Steven and Carlisle's (1959) figure for pine seed mass was used. Seed mass for birch was taken as the mean value of figures provided by Atkinson (1992) for mass of unsorted downy birch seed.

Table 4.5 Values of basal area, seed mass and resulting seed production as calculated by equation (4.78).

Species	Basal area (m^2ha^{-1})	Seed mass (g)	Seed production (m^{-2})
Downy birch	29	0.00016	1081
Scots pine	38	0.00496	189

These values, and the resulting seed production values as calculated using Equation (4.78), are shown in Table 4.5. The estimated values of seed production are clearly within the ranges of values quoted in Section 4.3.2.

In choosing default seed production values for GALDR, perhaps the most obvious method is to estimate average production and multiply by ten (the number of years in a GALDR timestep). However, from the point of view of serving the establishment model (Section 4.4), this is not necessarily the most appropriate measure. Since regeneration is expected to be spasmodic, the assumption has been made that regeneration will occur not more often than once per timestep per cell. Furthermore it is assumed that regeneration will generally follow after a ‘good’ seed year; thus the appropriate values of Q_0 are based on one year’s production, towards the upper limit of the distribution. Given the difficulty in unravelling the variation in values given in Section 4.3.2, the chosen default values (shown in Table 4.6) are somewhat arbitrary. Nevertheless, it was considered that the most important concern was that the values be of the correct order of magnitude and reflect important differences between the species. The figures given in Table 4.5 do not appear to show the differentiation seen in the upper limits of the seed ranges produced. This difference may be larger than a factor of ten if, as Sarvas (1948) suggests, temporal variability in birch germinability is correlated with seed production.

Table 4.6 GALDR default values for baseline seed production, Q^*

Species	Baseline seed production Q^* (m^{-2})
Downy birch	2000
Scots pine	200

Maturation

Although variation of production with age is probabilistic and gradual, for simplicity this factor is modelled as a step function as below.

$$Q_{age} = \begin{cases} 0 & \text{for cohort age} < age_{\min} \\ 1 & \text{for cohort age} \geq age_{\min} \end{cases} \tag{4.79}$$

In the current version of the model the age threshold, $age_{\min}$, is held as a global constant with a default value of 20. If more species were to be included in the model, it could easily be redefined as a species-specific constant.

Altitude

In the current version of the model, altitude is the sole proxy climatic indicator included. The relationship found by Stewart *et al.* (2000) has been used as the basis of the altitude model, though since it is here treated as a single factor on total production of viable seed it has been standardized to give a value of one at sea level. Thus the altitude factor is expressed as

$$Q_{alt} = 1 - G_{alt}\, z \qquad (4.80)$$

where z is altitude in metres and G_{alt} may be termed the *altitude-germinability parameter*, which has default value of 0.0014.

Stand density

The formula of seed production (4.78) proposed by Greene *et al.* (1999) is clearly at odds with the qualitative descriptions in the literature if used to predict seed production for a range of stand densities extending into conditions of complete canopy closure. (It may be reasonably supposed that this formula was not intended to cover such cases.) Furthermore, Greene *et al.*(1999) concede that, even when applied to single trees, the model overpredicts seed production for large basal areas. The presumption made here attributes this to the tendency for crown size to increase with basal area up to some maximum crown size, at which point basal area may continue to grow but crown size will stabilize or decline.

The modelling assumptions made by GALDR with respect to effects of stand density are that:

a) for low overall stand densities, seed production of cohorts will be proportional to their partial Stand Density Indices.(pSDI);

b) for any given species, seed production of *stands* will tend to be maximized when half-stocked (i.e. SDI = 0.5);

c) seed production of fully-stocked stands (i.e. SDI = 1) will be half that of half-stocked stands with similar composition.

It must be admitted that the two values of 0.5 used here, for both optimal stocking level and reduction of seed production in fully-stocked stands, are arbitrary. However, the qualitative nature of the data on this subject precludes more accurate parameter estimation. It is considered that this behaviour is broadly realistic, although the accuracy is difficult to assess.

On the basis of the above criteria, the stand density factor was formulated as

$$Q_\rho = {}_p\rho \, Q_{\rho L} \tag{4.81}$$

where ${}_p\rho$ is cohort pSDI and $Q_{\rho L}$ is the *limiting factor* of Q_ρ. The limiting factor is a quadratic function of the overall stand SDI, written

$$Q_{\rho L} = 2\rho^2 - 6\rho + 4.5 \tag{4.82}$$

where ρ is the SDI.

To aid comprehension of this treatment it may be helpful to consider the even-aged (single cohort) case. In such stands $\rho = \rho_p$, and thus Q_ρ becomes a simple cubic polynomial in ρ:

$$Q_\rho = 2\rho^3 - 6\rho^2 + 4.5\rho \, . \tag{4.83}$$

This relationship is illustrated in Figure 4.24 with the limiting factor $Q_{\rho L}$ included for reference. From the form of (4.83) it is clear that for low values of ρ, Q_ρ is roughly proportional to ρ. (Put formally, at $\rho = 0$, $Q_\rho = 4.5\rho + O_2(\rho)$; where $O_n(\rho)$ denotes terms of ρ of n^{th} order or higher.)

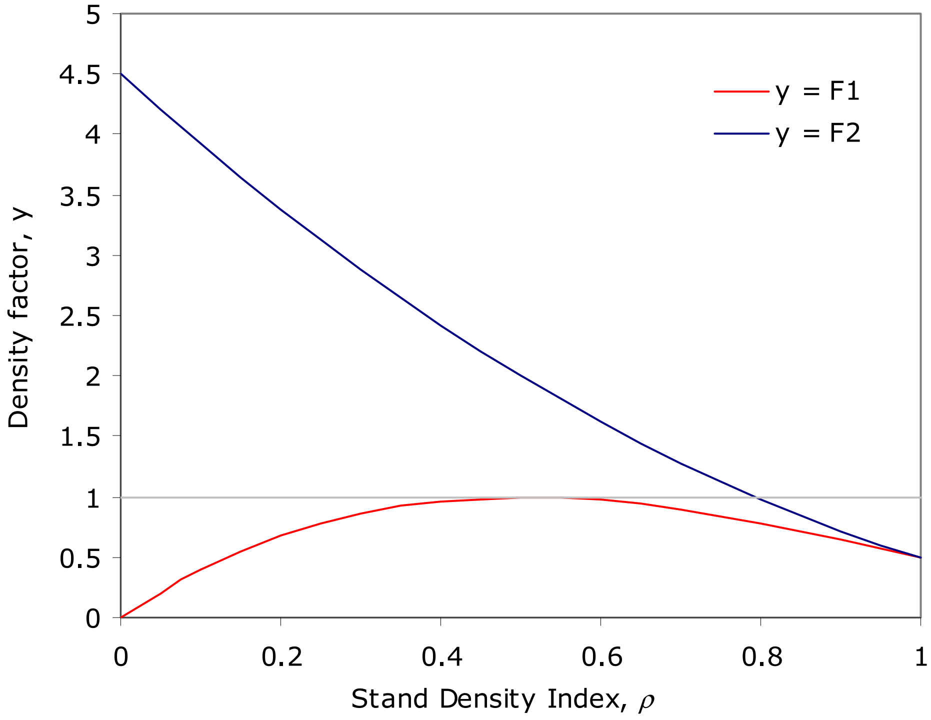


Figure 4.24 Seed production density factors for a single cohort stand.
$F_1 = Q_\rho$; $F_2 = Q_{\rho L} = Q_\rho/\rho$.

In the multi-cohort case, the situation is essentially the same, except that the limiting factor is no longer acting on the pSDI for the cohort.

As an example, consider a stand with three cohorts with pSDIs ${}_p\rho_1 = 0.1$, ${}_p\rho_2 = 0.5$ and ${}_p\rho_3 = 0.4$. Then $\rho = 1$ so $Q_{\rho L} = 0.5$ and this gives $Q_{\rho l} = 0.05$, $Q_{\rho l} = 0.25$ and $Q_{\rho l} = 0.2$. Thus, despite each of the cohorts being of low density, the contribution of each of them is reduced because the stand as a whole is fully-stocked.

At low values of ρ, the model shows broad agreement with that of Greene *et al.* (1999), Equation (4.78) since SDI is strongly correlated with basal area (at least in younger stands). However, as stands develop, SDI tends to stabilize whilst basal area continues to increase. This characteristic may in fact favour the use of SDI over basal area. On the other hand, there are other reasons why basal area would be more suitable if it were available as a variable; the current model takes no account of stand development history (see Section 4.3.2), but a model using basal area would be able to do so.

The value of calculating seed production of all cohorts in a stand may be questioned since the contribution to seed production made by understorey or subdominant trees is thought to be minimal (Greene and Johnson, 1994; Nixon and Worrell, 1999). However, if seed production were based only on the primary cohorts or tallest cohort, this may seriously underestimate seed production in certain stand compositions – e.g. where the largest cohort is of very low density. In such cases, the lesser cohorts may not represent an understorey in the usually understood sense. Nevertheless, the model could be said to underperform in stands that are fully stocked but where the lower cohort is not tall enough to realistically interfere with the seed production of a productive upper cohort. This is difficult to rectify other than by redesigning the model framework.

More complex models could be devised which examine the relative height position of the stands, however the current model is parsimonious with processing time as it uses cell values (pSDI, SDI) already calculated.

The current model does not simulate the dip in seed germinability associated with low stem densities and pollination limitation. This effect, however, could be incorporated relatively easily by modification of the limiting factor function, $Q_{\rho L}$. The modified function would probably need to take a cubic form.

4.3.4 Seed dispersal – theoretical background

Many publications provide figures of maximum dispersal distance (e.g. Smith 1900; McVean, 1963b; Sarvas, 1948; Nixon and Worrell, 1999; Harmer, 1999). These figures may refer to outright maximum distance for individual seeds, as evidenced by discovery of seedlings far removed from parent stands. Alternatively, they may refer to distances at which regeneration is likely to occur to some minimum stocking density. Either measure is of limited value in the context of spatial modelling where some measure of the distribution of seed is required – from the heavy seed rain under productive stands to very sparse rates of fall at greater distance from parent trees. To do this a mechanistic model of seed dispersal has been developed, based on the micrometeorological model of Greene and Johnson (1989). The theoretical background to the model is presented below.

Basic assumptions

Consider the case of seeds abscising from a height H onto flat ground and landing at a point at a distance s downwind of the source (illustrated in Figure 4.25). Let u be the average horizontal wind speed acting on the seed over its descent and F be the equilibrium descent velocity of the seed in still air. It is assumed that seeds are relatively light, with low terminal velocities, so that time taken to accelerate to terminal velocity (vertically), or wind speed (horizontally), is small compared with total descent time.

The descent time may then be expressed in terms of displacements and velocities in both vertical and horizontal components, giving rise to the equation:

$$Fs = uH\,. \tag{4.84}$$

Equation (4.84) can be used to predict dispersal distance from H, F and u. However, seeds are not expected to disperse to a constant distance from the source tree, because for each seed the three explaining variables will vary. In the present model only variation in u is used to describe the distribution of dispersal distances because in the majority of cases this will be largest source of variation. Also, variation in wind speed will differ according to place in the landscape whereas variation in H and F will tend to be the same everywhere.

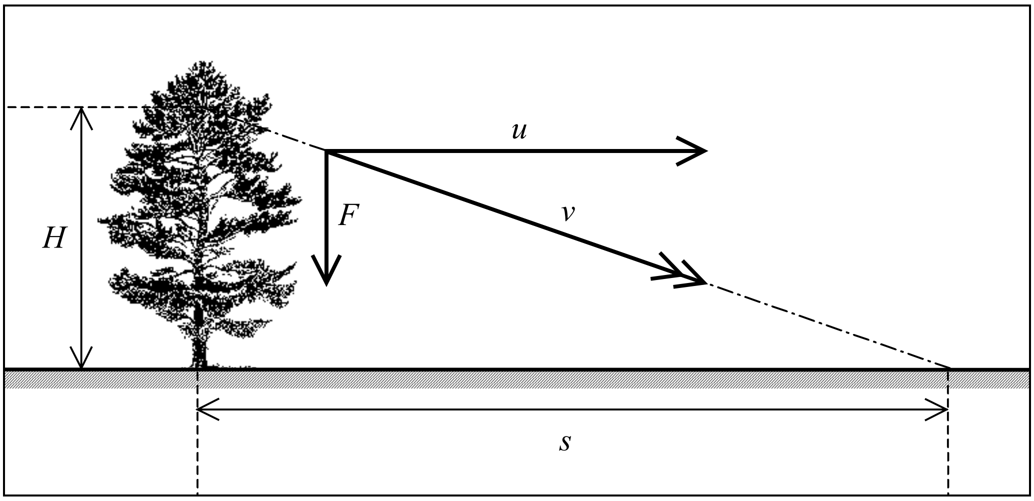


Figure 4.25 Seed dispersal from a point source. The dot-and-dashed line represents the idealized trajectory of a falling seed. Bold arrows are velocity vectors: F is seed terminal velocity; u is wind speed; v is resultant seed velocity. Double-ended arrows are lengths: H is height at which seed abscises; s is downwind horizontal displacement.

Distribution of wind speeds

In keeping with the wind disturbance model (see Section 4.2) it is assumed that horizontal wind speeds are distributed according to a Weibull model as in Quine (2000). The probability density function for u may be given as

$$p(u) = kc^{-k}u^{k-1}e^{-(u/c)^k} \tag{4.85}$$

where c is the scale parameter and k is the shape parameter of the distribution. This is a point of departure from the Greene and Johnson (1989) model, which uses a lognormal distribution for wind speeds, although the rest of the treatment is directly comparable.

Calculation of dispersal curve

If it is assumed that the probability of seed abscission is independent of wind speed then the frequency distribution of released seeds with respect to wind speed can be expressed as

$$\frac{dQ}{du} = Q\,p(u)\,. \tag{4.86}$$

Then, substituting equations (4.86) and (4.84) into (4.85) gives

$$\frac{dQ}{du} = Qkc^{-k}\left(Fs/H\right)^{k-1} e^{-(Fs/Hc)^k}\,. \tag{4.87}$$

The frequency distribution of wind deposited seeds with respect to their horizontal displacement from source may be expressed as the derivative of Q w.r.t. s. Then by the chain rule:

$$\frac{dQ}{ds} = \frac{dQ}{du}\frac{du}{ds}\,. \tag{4.88}$$

However, since (4.84) provides

$$\frac{du}{ds} = \frac{F}{H}\,, \tag{4.89}$$

the dispersal curve (*sensu* Green and Johnson, 1989) can be written

$$\frac{dQ}{ds} = Qk\left(F/Hc\right)^{k} s^{k-1} e^{-\left(Fs/Hc\right)^{k}} . \tag{4.90}$$

The Weibull generated dispersal curve may be compared with the lognormal derived curve of Greene and Johnson (1989). This is expressed as

$$\frac{dQ}{ds} = \frac{Q}{s\sigma_u\sqrt{2\pi}} e^{-\left(\frac{\ln\left(Fs/Hu_g\right)}{\sqrt{2}\sigma_u}\right)^2} \tag{4.91}$$

where u_g and σ_u are the geometric mean and standard deviation of the lognormal distribution of u (corresponding to c and k in the Weibull distribution) respectively. The curves are compared graphically in Figure 4.26. The curves are clearly broadly similar, although the lognormal-derived curve appears to be more strongly leptokurtic.

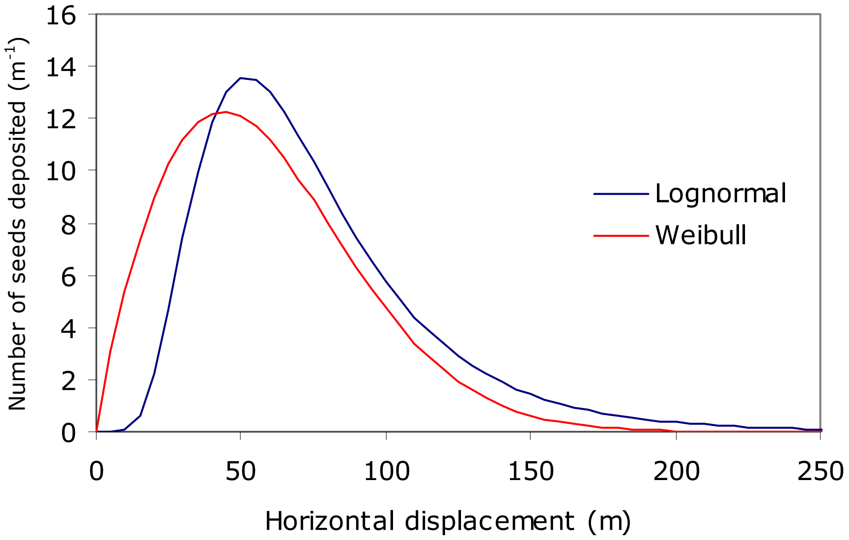


Figure 4.26 Comparison of dispersal curves based on lognormal and Weibull distributions of wind speed. Invariants: $Q = 1000$; $H = 20$; $F/u_g = F/c = 0.3$; $\sigma_u=0.5$; $k=1.85$.

Calculation of density distribution

To acquire the frequency distribution for *density* of seed (per unit area, a), the chain rule is invoked once again:

$$\frac{dQ}{da} = \frac{dQ}{ds}\frac{ds}{da} \tag{4.92}$$

and since

$$\frac{da}{ds} = \frac{d}{ds}\left(\pi s^2\right) = 2\pi s \tag{4.93}$$

it is possible to write

$$\frac{dQ}{da} = \frac{Qk\left(F/Hc\right)^k s^{k-2} e^{-(Fs/Hc)^k}}{2\pi}. \tag{4.94}$$

A comparison with the dispersal curve (4.90) is shown in Figure 4.27. Note that the density curve is monotonically decreasing with an undefinable value at $s = 0$, whereas the standard dispersal curve is definable everywhere, with a stationary point (maximum) at approximately 50m. Thus, the modal average of distance travelled by seed is around 50m but the highest densities occur at source.

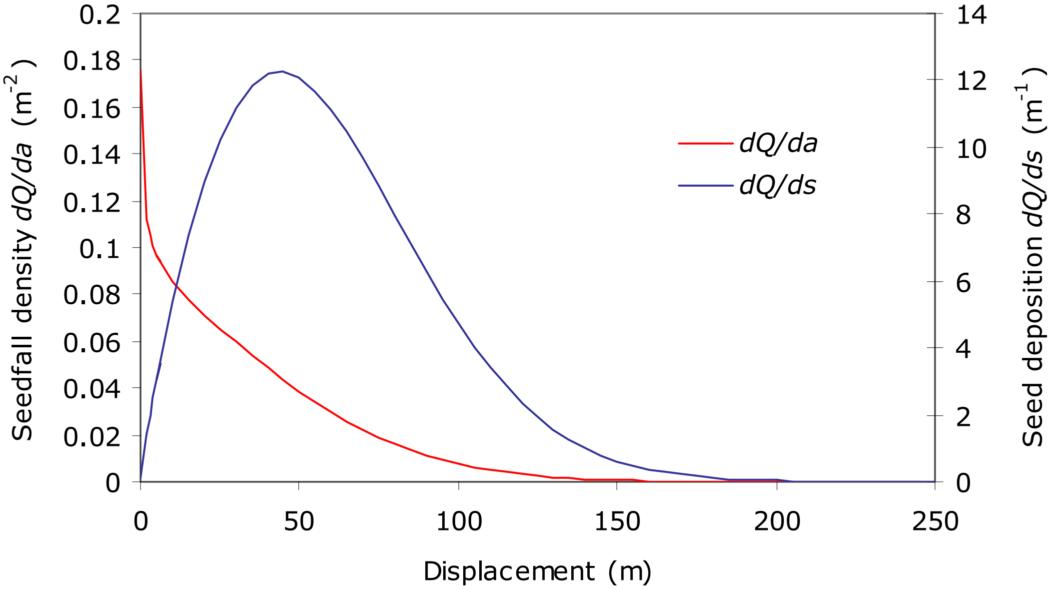


Figure 4.27 Comparison of dispersal curve dQ/ds with density curve dQ/da. Invariants: Q = 1000; H = 20; F/c = 0.3; k=1.85.

Non-random abscission of seeds relative to wind speeds

The above calculations assume that probability of seed abscission is independent of wind speed; however this assumption is intuitively incorrect. Greene and Johnson

(1992) demonstrate that abscission of *Acer saccharinum* samaras increase with increasing wind speed. The suggested reasoning is twofold:

a) development of the structures that facilitate abscission is hastened by conditions of low relative humidity, which in turn are associated with high wind speeds;

b) high winds induce mechanical deflection of seeds on their peduncles, weakening the attachment.

The same work shows that the probability of abscission is well correlated with the square of the wind speed. The authors further assert that these results should be broadly extendible to other tree genera. Greene and Johnson (1996) demonstrate that this assumption gives rise to an effective increase in wind speeds at which seeds abscise which may be approximated by application of a constant factor on the mean wind speed. This gives the equation

$$\overline{u}_a = \psi\overline{u} \tag{4.95}$$

where $\overline{u}$ is the mean wind speed, $\overline{u}_a$ is the mean wind speed for abscising seeds and ψ may be termed the *factor of non-random abscission*. Green and Johnson (1992) give a value of approximately 1.8 for ψ; whilst conceding that this function may alter for species other than *Acer saccharinum*, they suggest that it may be applied generally in the absence of further data. Hence, the value of 1.8 is used as the GALDR default. However, the value of ψ is properly a function of the horizontal turbulent intensity, which itself is inversely related to the median wind speed (Greene and Johnson, 1996). Therefore the use of a constant term to represent ψ is a simplification in this context.

4.3.5 Seed dispersal – model description

Seed catchment

GALDR calculates seedfall in each cell as a summation of seeds depositing from each cohort in the vicinity of the focal cell. The quantity d_{max} determines the maximum distance between seed source and deposition loci, and hence the number of cells, n_c, that may potentially provide seed supply for each collecting cell (see

Figure 4.28). The default value for d_{max} is 250m, corresponding to a catchment of 81 cells (the source cell may also be collecting a cell).

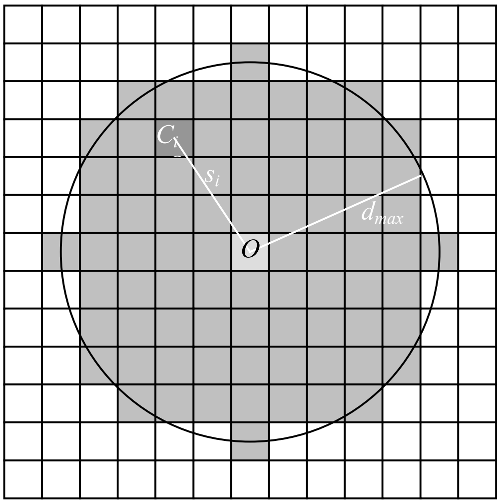


Figure 4.28 Catchment of seed source cells for collecting cell, O, defined by maximum dispersal distance d_{max}.

Calculation of seedfall density

Each of the cells C_1 to C_{n_c} may support up to m seed-bearing cohorts. Assuming that the total density of seed deposition at O is the sum of depositions from all cohorts in all catchment cells calculated according to equation (4.94), and modifying the scale factor of the wind distribution according to (4.95), the following expression gives the total number of seeds deposited.

$$Q = \sum_{i=1}^{n_c} \sum_{j=1}^{m} \frac{A Q_{ij} k \left(F / H_{ij} \psi c \right)^k s_i^{\,k-2} e^{-\left(F s_i / H_{ij} \psi c_i \right)^k}}{2\pi} \qquad (4.96)$$

where Q_{ij} and H_{ij} are the seed production and seed abscission height of the j^{th} cohort of cell C_i; s_i is the distance between C_i and O; and c_i is the Weibull c parameter evaluated at C_i. A is the cell area, equal to 2500 m^2 for a 50m grid.

Abscission height

The H_{ij} are calculated from the cohort heights under the assumption that the average height from which seeds are abscised is proportional to the cohort top height. Thus

$$H = \zeta h \qquad (4.97)$$

where h is cohort top height and ζ is a constant factor. The GALDR default value for ζ is 0.75, as used by Greene and Johnson (1995).

Displacement

With one exception, the displacement s_i is calculated as the Euclidean distance between cell centres. The exception occurs when $C_i = O$. In this case a non-zero value, d_0, is used as the average distance of dispersal. Thus, the displacement is defined

$$s_i = \begin{cases} d_0 & \text{if } C_i = O \\ \sqrt{(x_i - x_o)^2 + (y_i - y_o)^2} & \text{if } C_i \neq O \end{cases} \tag{4.98}$$

where (x_i, y_i) and (x_o, y_o) are the grid co-ordinates (in metres) of C_i and O respectively. The reason for the exception is that applying a value of zero to the displacement in (4.96) produces an infinite value for expected seed density because the annulus of possible dispersal loci is condensed to a single point. A default value of 0.3 for d_0 has been used in GALDR; this value has been found to balance intra- and extra-cell dispersal so that total dispersed seed equates to source quantity.

Weibull c parameter

The Weibull c parameter is evaluated, once only, for each cell at the initiation of the simulation; thereafter values of c are constant. No modification of c is made for dispersal direction, resulting in a radially symmetrical pattern of dispersal from any single point source (see Figure 4.29). There is a case for altering wind speed distributions to take account of prevailing winds, but this is offset by effects of relative humidity in the GALDR study area. Prevailing winds from the south and west tend to be associated with moist oceanic air-masses, but the less frequent easterly winds are more associated with drier continental air-masses. These drier winds will tend to cause more seeds to abscise (Mair, 1973), but the extent to which the effect counteracts that of the strength and frequency of the prevailing winds is difficult to determine. Because of this uncertainty, the simplest solution of radially symmetrical dispersal has been chosen.

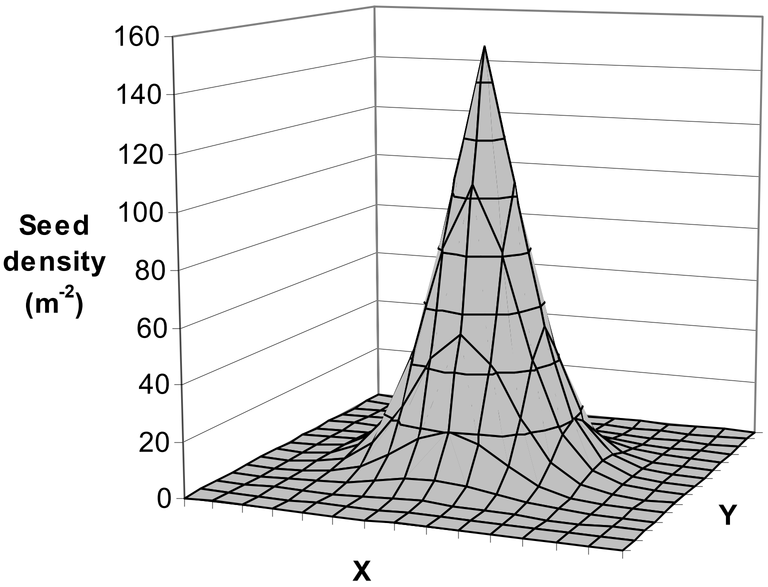


Figure 4.29 Surface plot of density of seedfall from a point source on a 50m grid, as described by equation (4.94) with s_i defined by *equation (4.98). The source is at the centre of the grid.*

Calculation of the Weibull *c* parameter follows similar methods to Section 4.2.4 inasmuch as the value is derived from a modified version of DAMS. Because the seed dispersal mode assumes that wind directions are uniformly distributed (i.e. just as likely to occur from one direction as another) the modification of DAMS involves removal of the directional DAMS terms to form ADAMS (Adirectional DAMS) defined as

$$\Omega = \Delta_1 + \Delta_2 + \Delta_3 + \Delta_5 \tag{4.99}$$

where Δ_i are as defined in Equation (4.41) (Section 4.2.2). Then the Weibull *c* parameter may be calculated as

$$c = -0.185 + 1.456\, e^{0.08\Omega} . \tag{4.100}$$

Seed terminal velocities

Estimation of the equilibrium rates of fall for seeds of each of the species is an important part of the parameterization of the model since dispersal distances are inversely proportional to terminal velocity.

The seed of Scots pine is reported as having a terminal velocity of 0.72 ms^{-1} (Denham, 1921; cited by Carlisle and Brown, 1968). Sarvas (1948) provides values of rates of fall for Scots pine, downy birch and silver birch. However they appear to be incorrect since they do not match the descriptions given in the text. He states that the rate of fall of silver birch seed 'is clearly below' (p.86) that of downy birch whereas the figures show the opposite trend. Seeds of silver birch tend to be lighter than those of downy birch (Atkinson, 1992) and the wings tend to be larger. On this evidence, it seems sensible to place more trust in Sarvas' text than his figures. No information is given on whether the seeds were filled or unsorted. Greene and Johnson (1995) provide a figure of 0.55 ms^{-1} for paper birch (*Betula papyrifera*) but, again, it is not stated whether this value is for filled or unsorted seeds. An experiment conducted by Brown (pers. comm.) has recorded a mean falling velocity of 0.60 ms^{-1} (sample size: 500) for unsorted seed of downy birch.

To help define the possible values for terminal velocity, an experiment was undertaken following the methods described by Greene and Johnson (1995) where terminal velocity of silver birch seeds collected from Guisachan Forest were measured. Seeds were released in still air from a height of 2.5m and timed over the final 1.5m of their descent with a stopwatch. Prior to release, seeds were sorted into filled and unfilled seeds by examination under a dissecting microscope. Because of the low proportion of filled seeds (approximately 1%), obtaining filled seeds was a time consuming process. Hence, the sample size of 20 seeds each of filled and unfilled seeds was lower than ideal. Mean falling velocities were 0.84 ms^{-1} for filled seed and 0.43 ms^{-1} for unfilled seed. Standard deviations were 0.17 and 0.13 ms^{-1} for filled and unfilled seed respectively. The difference between the means was statistically significant (ANOVA: $p<0.01$). This marked difference emphasizes the importance of stating whether measurements of terminal velocity are from sorted or unsorted seed.

The recorded value for filled seeds was higher than expected, since it is greater than that recorded by Steven and Carlisle (1959) for pine, the seed mass of which is much higher. Sarvas (1948) notes that despite this difference in weight, the rate of fall of downy birch is often 'slightly greater' than that of pine. Birch seems to be regarded as a more successful colonizer than pine, but this may be due more to the large quantity of seed released than the speed of descent.

These results, taken with Sarvas' (1948) assertion that rates of fall are greater in silver than downy birch, suggest that Brown's figure (0.6ms^{-1}) may not be representative of terminal velocity for *filled* seeds of downy birch. Equally however, there is likely to be variation in terminal velocity between populations at least as great as the variation in seed mass. Further measurement of falling velocity from other populations would therefore be desirable.

4.3.6 Model results

The SELES implementation of the model incorporates the production of a dynamic raster vector representing the seedfall density for each species. An example of an output raster map, rendered into a three-dimensional surface representation is shown in Figure 4.30.

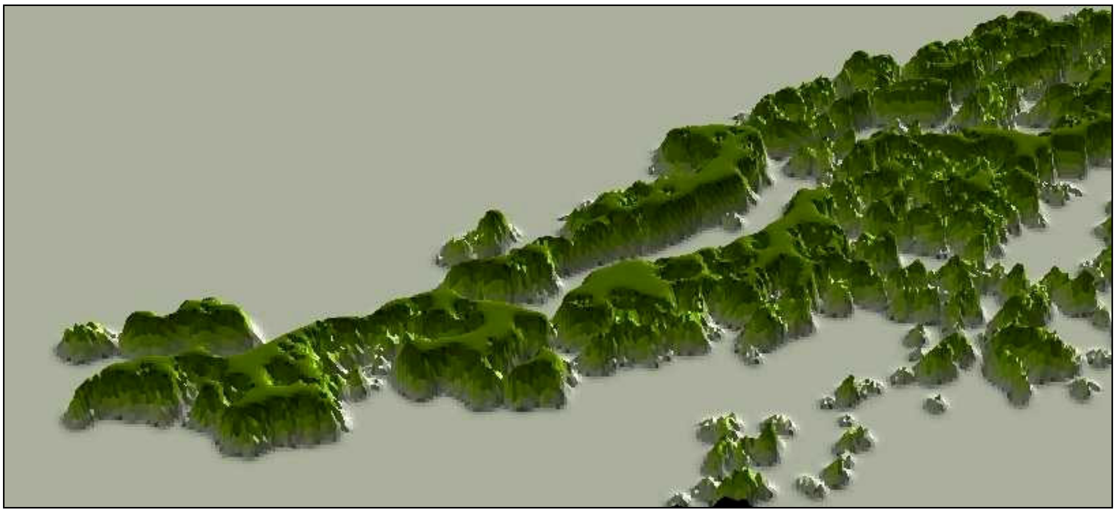


Figure 4.30 Three-dimensional surface representation of landscape seedfall density for Scots pine. The height of the surface (z-axis) denotes the number of seeds falling in that cell.

Experiments have been made for point sources on test grids to check that model output follows Equation (4.96).

4.4 Seedling establishment

4.4.1 Introduction

This section covers the germination of fallen seeds and subsequent establishment of seedlings. This process is a crucial aspect of the spatial dynamics of the forest because, whilst seed dispersal determines the potential for the forest to change its distribution in space, the establishment phase determines the realization of that potential. The determination of whether fallen seeds germinate and establish as new stands is a non-trivial exercise; the various factors that contribute to the success or otherwise of the process are outlined in the next section (4.4.2). The establishment sub-model is described in Section 4.4.3.

4.4.2 Background

There is a considerable quantity of literature on the subject of regeneration in native pinewoods and, to a lesser extent, birchwoods. Much of this work has concentrated on the role of grazing and browsing animals, or to a lesser extent, seed production. Of those studies that examine the establishment phase in particular, the key works are probably those of Steven and Carlisle (1959), McVean (1963b) and Miles and Kinnaird (1979a) with useful reviews provided by Harding (1981) for birch, and Cameron (1995) for pinewoods.

The factors influencing the success of natural regeneration may be summarized as follows. There is considerable overlap and interdependency among these factors.

1. Influx of viable seeds.
2. Predation on fallen seeds
3. Suitability of the substrate for seed germination.
4. Moisture regime of the seedbed and underlying soil
5. Nutrient regime of the soil.
6. Light and temperature regime.
7. Establishment of mycorrhizal associations.
8. Competition with other vegetation.
9. Damage to germinants and young seedlings by small animals and pathogenic fungi.
10. Damage to older seedlings by grazing and browsing animals.

The first point is dealt with in the seed dispersal section (4.3) while point 10 is considered in the section on browsing (4.5). The remaining factors will be dealt with under the following headings: germination and early growth; soils and vegetation; effects of a tree canopy; and damaging agencies.

Germination and early growth

Seeds of Scots pine show no dormancy and tend to germinate soon after dispersal between March and September, with a peak usually in May (Miles and Kinnaird, 1979a; McVean 1963b). Germination occurs more rapidly with illumination and the optimal temperature for germination is about 21 degrees Celsius (Sarvas, 1950). Germination failure occurs in seeds that are waterlogged or immersed in wet soil to any depth (McVean, 1963b). Seeds immersed in soils with better aeration are able to extend the hypocotyl to the surface from depths of up to 15 mm. The radicle is blunt and therefore will not penetrate heavily compacted soil surfaces.

In contrast to pine, birch seeds do exhibit dormancy. This may be broken by increasing day length or temperatures of over 20 degrees Celsius (Sarvas, 1950), thus favouring germination in the spring or summer following dispersal (Harding, 1981). Miles and Kinnaird (1979a) report that germination in the Scottish highlands commences in March and peaks in May or early June.

The principal differences between birch and pine seem to be associated with seed size and moisture relations. Sarvas (1948) reports that the quantity of food reserves in a seed of Scots pine is about twenty times that found in a seed of birch. Thus, in early development, pine seedlings are able to push the radicle deeper into the substrate than birch and so obtain more favourable moisture conditions. The upper layers of humus are apt to desiccation and Harding (1981) notes that birch seeds require high levels of relative humidity for successful germination. According to Sarvas (1948), these moisture requirements are crucial in determining the spatial distribution of birch regeneration, which may consequently be found in 'moist hollows and swampy forest lands' (p. 87). However, he notes that birch regeneration may also take place in dryer areas if the humus layer is thin or absent over bare mineral soil. Miles and Kinnaird (1979a) state that young birch seedlings are highly susceptible to drought whereas death from drought in pine is rare after hypocotyl extension. McVean (1961a) relates that pine seedlings (and saplings up to ten years old) may be killed by waterlogging of generally well-drained peats in periods of prolonged wet weather. Sarvas (1948) considers that the small size of the birch seedling and its sensitivity to moisture leads to a high dependency on climatic conditions, which is responsible for the highly unpredictable nature of birch regeneration.

The disparity in food reserves is also responsible for differences in the capacity of the hypocotyl to extend above a dense ground vegetation layer in dark conditions, so that photosynthesis may initiate. Maximum extension is reported as about 2 cm for birch and 8 cm for Scots pine (Miles and Kinnaird, 1979a).

Formation of mycorrhizal associations is thought to be crucial to the early growth of seedlings of both pine and birch (McVean, 1963a,b; Miles and Kinnaird, 1979a). Miles and Kinnaird (1979a) found that of 833 birch seedlings germinating on a wet peaty site in Inverpolly NNR, only five seedlings that had formed associations and showed good growth survived the first year. McVean (1963a) provides experimental evidence to suggest that mycorrhizal development is the cause of better seedling growth rather than an effect. Absence of mycorrhizal infection may often give rise to growth check, where seedling growth may be almost suspended.

Availability of mycorrhizal fungi appears to be heavily site dependent. Miles and Kinnaird (1979a) observe that inoculation may be prolonged on non-woodland soils whilst Harding (1981) states that association establishment is slowest on podzols and wet peats. Dimbleby (1952) found higher growth rates in birch saplings growing on the stumps of previously infected dead trees.

Soils and vegetation

Soil type and vegetation influence each other, so factors relating to either may not be readily extricable in the field. Nutrient status and moisture regime are the most important direct factors of soil in seedling establishment although other physical characteristics may also play a part (e.g. compaction). Direct effects of vegetation may be considered in terms of both floristic composition and physical structure.

Rodwell (1991a) notes the tendency for downy birch to regenerate more freely than pine on the wetter soils common in concave areas of undulating topography. Downy birch is generally regarded as a tree of wetter soils whilst silver birch is said to show a preference for more freely draining sites (Atkinson 1992). However both species can often be found on the same site and Rackham (1980) discerns no difference in ecological preference between the two species in eastern England. (However, the pattern of their distributions may be obscured heavily by fragmentation and anthropogenic influences in this region). Hill *et al.* (1999) place the three species in the following order of increasing preference for moist sites: silver birch, Scots pine, downy birch.

McVean (1963b) observes that pine seedlings are almost never found on brown earth soils despite the fact that plants grow well in cultivated soils of such types. This effect is attributed to the inability of pine to compete with other vegetation better suited to richer site types. Steven and Carlisle (1959) also note a marked tendency for birch to favour the better soils over pine. Hill *et al.* (1999) rank pine as more acidophilic than birch. (The two birch species do not seem to show differentiation in their preference for nutrient levels or soil acidity.) In fact, it seems that both pine and birch show a very broad amplitude of tolerance to soil pH levels (Carlisle and Brown, 1968; Atkinson, 1992), but birch appears to be the better competitor where nutrient availability is higher. There appears to be no evidence to suggest any difference between pine and birch in their ability to regenerate on soils with poor nutrient availability.

Both pine and birch will establish on peat soils, with birch regenerating on peat up to at least 60cm deep (Emberlin and Baillie, 1980). McVean (1963a) investigated growth of Scots pine on three peat types of different vegetation origin. The principal limitation to growth was generally levels of nitrogen or phosphorus, though on most peats this could be overcome if mycorrhizal associations could be formed. However, on some peats, usually colloidal peats derived from *Trichophorum cespitosum* and *Molinia caerulea*, nutrient levels were so low that growth of mycorrhizal fungi was inhibited. Henman (1961) considered that the best regeneration was to be found on peats of less than 10 cm depth, though establishment might occur on deeper peats after slow initial growth.

Kinnaird (1974) undertook a survey of birch regeneration in various vegetation types at three sites in the Scottish highlands. Density of young (< 1 year) seedlings was found to be greatest on cushions of *Sphagnum* (460 m^{-2}) followed by bare mineral and humus soil (130 and 117 m^{-2} respectively). Densities of 6-8 m^{-2} were found on mosses and litter, whilst very low densities (≤ 0.2 m^{-2}) were found amongst grasses, herbs, ferns and dwarf shrubs.

Association of birch seedlings with *Sphagnum* has been noted by others (e.g. Emberlin and Baillie, 1980), but Miles and Kinnaird (1979a) relate that the majority of seedlings germinating on *Sphagnum* are soon subsumed by the faster growth of the moss relative to the seedlings. However, Harding (1981) considers this an unlikely mechanism for the demise of such seedlings, and proposes instead that the high mortality is due to the inability of the developing radicle to find suitable substrate. McVean (1963b) has found abundant pine colonization on *Sphagnum-Eriophorum*-lichen hummocks but very slow subsequent growth and he considers the prospects for regeneration in *Sphagnum* dominated vegetation to be ultimately very poor.

Kinnaird's (1974) observation that regeneration is more plentiful in ericaceous than grassy vegetation is also borne out by McVean and Ratcliffe (1962) and Emberlin and Baillie (1980). The latter attributed the phenomenon to the fibrous mat of roots in the grass communities. Steven and Carlisle (1959), noting the paucity of pine regeneration in grassy communities, ascribe the effect to competition from the grasses as well as a tendency of such areas to attract grazing animals.

Various sources (Henman, 1961; McVean, 1961a; Kinnaird, 1974; Miles and Kinnaird, 1979a; Nixon and Worrell, 1999; Thompson and Milner, 2001) suggest that dense mats or wefts of pleurocarpous mosses such as *Hylocomium splendens*, *Pleurozium schreberi* and *Rhytidiadelphus* spp. present a considerable barrier to tree regeneration. This may frequently be combined with a dense litter layer. Seedlings attempting to establish in such vegetation are often killed by desiccation or else fail to raise their cotyledons above the moss sward. Miles and Kinnaird (1979a) also state that such vegetation tends to harbour high densities of mice and voles. Acrocarpous mosses (e.g. *Dicranum scoparium*) have been found more favourable to regeneration (Jones, 1948; McVean 1963b), though an exception to this may be found in *Polytrichum commune* (Henman, 1961) which forms tall dense stands. However, none of the acrocarpous mosses tends to form such extensive areas of dense growth as the pleurocarpous species.

Heathy vegetation dominated by *Calluna vulgaris* is often found in association with woodlands of pine and birch; heaths of one type or another often form the larger part of the ground available for colonization by trees. Upland heath vegetation is generally considered to be a plagioclimax which has been historically prevented from succeeding to woodland by grazing, burning or a combination of both (Gimingham, 1995). However, colonization of heath communities by trees may not be a straightforward or automatic process.

The classical description of heathland dynamics is Watt's (1955) portrayal of cyclical growth based on phased development of the *Calluna* plant. The now well known growth phases are summarized from Gimingham (1960) and Gimingham (1995) below.

Pioneer	Young plants colonize, often in association with a variety of other species. Normally up to 3-6 years after disturbance.
Building	Individuals merge to create a dense even canopy. Growth and competivity are at a maximum, resulting in exclusion of other species. 15-20 years old.
Mature	Gaps start to appear in canopy, allowing sufficient light for growth of bryophytes. Up to about 25 years old.
Degenerate	Principal branches die, leaving a large central gap. Peripheral branches may layer by the production of adventitious roots. 25 years and older.

However, this development may not progress in such well-defined phases at higher altitudes or on wet, peaty sites, where the majority of *Calluna* regeneration may be effected by layering (Gimingham, 1995; MacDonald *et al.* 1995).

Seedlings very rarely establish in the building or mature phases because of the height and density of the *Calluna* plants (DeHullu and Gimingham, 1984; Gong and Gimingham, 1984); these phases may occupy 20-30 years in a cycle of approximately 30-40 years. Tree seedlings may establish at the centre of collapsed plants in the degenerate stage (Miles and Kinnaird, 1979a). However, these niches may be elusive since the onset of the degenerate stage is typically marked by the establishment of a thick mat of pleurocarpous mosses with some species, such as *Pleurozium schreberi*, invading during the mature phase (Scandrett and Gimingham, 1989). Steven and Carlisle (1959) suggest that successful establishment may be found either in short *Calluna* (presumably either pioneer stage or under heavy grazing) or in the degenerate stage, if the mat of pleurocarpous mosses is absent.

Thus, only the pioneer phase appears to be inherently suitable for tree regeneration. However, extensive areas of this phase only come about through disturbance such as burning. Perhaps because of this, McVean and Ratcliffe (1962) claim that all dense stands of naturally regenerated pine currently found in Scotland result from establishment immediately following fire. McVean (1964) has observed that birch may also regenerate well on burnt heath. Fire is not the only disturbance mechanism however; Gimingham (1995) also notes extreme drought, heather beetle (*Lochmaea suturalis*) and lepidopterous larvae, such as winter moth (*Operophtera brumata*), as agents of large-scale gap-creation in *Calluna* stands.

Establishment amongst *Calluna* dominated vegetation may be further hindered by the production of a mycotoxin from the roots of *Calluna* that is inhibitory to mycorrhizal fungi (Robinson, 1972). It is considered that this influence may be crucial to the maintenance of heather dominance in certain communities, although the mechanism is not infallible since allelopathic effectiveness declines in the degenerate stage. Harding (1981) considers that *Deschampsia flexuosa* roots may also produce substances inhibitory to the growth of birch seedlings.

Generally, it seems that dense vegetation of any kind is detrimental to seedling establishment to some degree and that establishment is most successful in areas of bare ground or very sparse regeneration. Forest roads are often lined with dense tree regeneration establishing on cut embankments or spoil from road construction. Bare ground may be created by fire, mortality of mature plants including canopy windthrow, trampling by ungulates and excavations by moles (*Talpa europaea*) in the creation of their hunting galleries. However, the latter does not provide good opportunities for seedling establishment because the loose soil dries easily and is rapidly colonized by other vegetation (Miles, 1973). Disturbance by animal hooves will also only rarely produce areas of bare soil large enough to avoid recolonization by surrounding vegetation. Hester *et al*. (2000) found that areas of bare soil measuring 6 × 6 cm (experimentally created to emulate hoof-prints) did not even support good germination rates. Miles (1974) found young birch seedlings colonizing at reasonably high densities in experimentally bared areas of 25 cm^2, but eventual survival was low. Sarvas (1948) considered 50-100 cm^2 to be the minimum area of bare ground for successful birch establishment. Areas of ground disturbed by windthrown trees may give better prospects for regeneration. Kuuluvainen and Juntunen (1998) found 60% of pine seedlings and 91% of birch seedlings to be growing on areas of uprooting in an eastern Finland pinewood. Vickers and Palmer (2000) also found density of saplings to be associated with windthrow in Glen Tanar pinewood NNR

However, although bare mineral soil is often considered optimal for seedling establishment, frost-heave may cause heavy mortality in such situations; Miles and Kinnaird (1979a) found up to 25% mortality amongst Scots pine from this cause. The opinion of Henman (1961) was that bare mineral soil is sub-optimal because of problems with frost-heave and erosion due to rainfall, and that a covering of peat or sparse vegetation is desirable for seedling establishment

Various attempts have been made to predict the potential for tree regeneration in formally defined vegetation communities. Steven and Carlisle (1959) provide some indication of the regeneration potential of the communities described in their book. McVean (1963b) outlines the likelihood of regeneration or colonization of the vegetation communities described in McVean and Ratcliffe (1962). More formal schemes using the National Vegetation Classification (NVC) (Rodwell 1991a,b) are presented by Averis (1998) and Humphrey (2003) (also see Rodwell and Patterson, 1994). The study of Humphrey (2003) is specifically focused on Glen Affric and its principal vegetation types. The NVC communities considered most likely to support regeneration with reduction in grazing are M15, M25 and H10. Some wetter communities, such as M17, are considered unlikely to ever support regeneration, while other very marginal types (e.g. M19) might develop into ‘bog woodland’ with very low densities of slow growing trees. However, whilst it is widely presumed that over much of the Scottish highlands the limiting factor on tree regeneration is the abundance of grazing and browsing animals (and perhaps availability of seed in some heavily deforested areas), some authors (e.g. Fenton, 1997), consider the potential for regeneration to have been overestimated. A table from Humphrey (2003) showing hypothesized successional status and regeneration potential of the principal open ground communities in Glen Affric is included as Table 4.7.

Another way of predicting regeneration potential is by use of the Ecological Site Classification (ESC; Pyatt et al. 2001; see Section 3.4.2). This method classifies sites according to climate, soil moisture regime (SMR) and soil nutrient regime (SNR). Assessment of soil nutrient regime in the field is effected by analysis of the vegetation so methods based on NVC and ESC should show broad convergence. Thompson and Milner (2001) compared use of NVC and ESC on various heath and mire sites in the Scottish highlands. It was concluded that ESC appeared to be a better predictor of suitability than NVC on at least some of the sites examined. However, it seems likely that in certain situations this position could be reversed where vegetation types show differing resistance to invasion from tree species but underlying soil types are equally suitable for establishment and growth. For instance, ESC variables for dry heath and acid grassland show considerable overlap, but regeneration may be considerably slower on the grass communities (see above).

Soil conditions may also change over time, and vegetation is an important factor in soil development. Birch is often regarded as a ‘soil improver’, reducing soil acidity and facilitating development of mull humus (Atkinson, 1992). In contrast, pine (like most conifers) tends to encourage acidification, podzolization and development of mor humus (Miles, 1986). It is a central theme of McVean’s (1963b) paper that inappropriate land management in the Scottish uplands has led to impoverished vegetation and degraded soil conditions in native pinewoods, resulting in reduced regenerative ability. It was considered that intensive grazing and burning had reduced the broadleaved tree and herbaceous component of the vegetation leading to decreases in soil biological activity and promotion of mor humus development and *Sphagnum* growth.

Table 4.7 Tree regeneration characteristics of main heath and mire communities occurring as mosaics with woodland communities in Glen Affric (taken from Humphrey, 2003).

Community	Successional status	Colonising tree species	Potential woodland (from Rodwell, 1991a)
M11 *Carex demissa-Saxifraga aizoides* mire	seral at elevations <500m: succession to scrub climatic climax: elevations > 500m	birch, juniper, rowan	W19
M15 *Trichophorum cespitosum-Erica tetralix* wet heath	seral: succession to woodland	birch, pine, alder	W4 /W18d
M17 *Trichophorum cespitosus-Eriophorum vaginatum* blanket mire	climatic climax	none	None
M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire	climatic climax? possibly seral	pine, birch?	bog woodland?
M25 *Molinia caerulea-Potentilla erecta* mire	seral: succession to woodland	birch, willows	W4
H10 *Calluna vulgaris-Erica cinerea* heath	seral: succession to woodland	pine, birch	W18a/b
H21 *Calluna vulgaris-Vaccinium myrtillus-Spagnum capillifolium* heath	Possibly seral	pine, birch, willows	W18e

Damaging agencies

Miles and Kinnaird (1979a) report that woodmice (*Apodemus sylvaticus*) and other small rodents may eat considerable amounts of pine seed on the ground, with 100% losses of sown seed being recorded. Booth (1984) reports that regeneration may be negligible except in mast years because fallen seed may be eaten in such large quantities by small mammals, birds and insects.

Slugs (principally *Arion ater*) have been seen to be responsible for the death of very young pine germinants, particularly in wet areas or during prolonged wet weather (McVean, 1961a). Chaffinches (*Fringilla coelebs*) have been identified as the cause of a very particular type of damage in which the cotyledons are pecked off whilst still enclosed in the seed coat (Miles and Kinnaird, 1979a). Thompson and Milner (2001) also report browsing of birch seedlings by red grouse (*Lagopus lagopus scoticus*) on heather moorland. Slug damage is less problematic following lignification of the stem, but rodent damage may become heavy in the winter; Miles and Kinnaird (1979a) report up to 98% mortality in the first winter due to such causes.

Such mortality may not always be evident; Steven and Carlisle (1959) claim that biotic damage other than that effected by ungulates is not an important factor in the quantity of regeneration. They ascribe some non-lethal damage to capercaillie (*Tetrao urogallus*) and minor mortality to pine weevil (*Hylobius abietis*). Nixon and Worrell (1999) report that mortality due to *Hylobius* is less serious in naturally regenerated sites than in plantations.

Mortality from damping-off fungi such as *Pythium* spp. has been said to be minimal in open situations but may account for up to 90% of seedlings in shaded sites (Taher and Cooke, 1975). Nixon and Worrell (1999) consider that the needle cast fungus *Lophodermium seditiosum* may be a locally important cause of mortality in Scots pine.

Effects of a tree canopy

Scots pine, downy birch and silver birch are all widely regarded as shade intolerant trees (Carlisle and Brown, 1968; Atkinson, 1992). Hill *et al.* (1999) give all three species a shade tolerance ranking of seven, described as 'generally in well lit places, but also occurring in partial shade' (p.5). Of all British trees, only juniper and some uncommon *Sorbus* species are considered more shade intolerant on this scale. However, Ogilvy (in prep.) has conducted shade house experiments that have indicated that Scottish highlands origin Scots pine has shade tolerance equal to juniper, thus placing it in category eight of Hill *et al.* (1999).

Many observers have noted the reluctance of pine and birch to regenerate under their own canopies (e.g. McNeill, 1945; Steven and Carlisle, 1959; Henman, 1961;

McVean and Ratcliffe 1962; Miles and Kinnaird 1979a). Whilst most concede that in some circumstances limited regeneration may be found beneath light canopies, some (e.g. Nixon and Worrell, 1999) insist that conditions of full light are needed for the regeneration of shade intolerant species. Kinnaird (1974) found density of birch seedlings aged less than 1 year to be largely independent of tree cover but density of older seedlings was negatively correlated with tree cover. However, Emberlin and Baillie (1980) observed that not only was the distribution of seedlings unaffected by the presence or absence of a canopy, but that healthy saplings were found only within the woodlands. McVean (1961b) relates that Scots pine may regenerate under a reasonably full canopy in continental Europe but usually only in open forest in Scotland.

Such discrepancies may be due in part to the many complexities governing successful regeneration under canopies as well as differing conceptions of tree density and light levels in canopy descriptions.

The most obvious effect of a tree canopy on survival of subjacent regeneration is reduction of light levels. Indeed, whilst reduction in light levels is generally treated as the most important factor in determining the success of sub-canopy regeneration, the role of below-ground competition for water and nutrients remains poorly understood (Coomes and Grubb, 2000). McVean and Ratcliffe (1962), noting that birch may regenerate more successfully under canopies of other species, suggest root competition as an explanation, but evidence other than circumstantial appears to be wanting.

However, the effects of reduced illumination also may be considerably complex. All other factors being favourable, survival under low light levels is ultimately limited by the ability of the seedlings to photosynthesize. At light levels below the compensation point of the seedlings, where rates of photosynthesis and respiration are equalized, mortality is inevitable. At light levels above this threshold, less direct effects of shading may still influence ability of seedlings to establish. An important factor may be mortality due to damping-off fungi (see Section 4.4.2), which appears to be heavily dependent on light levels (Vaartaja, 1962; Taher and Cooke, 1975). Infection of pine seedlings with *Lophodermium seditiosum* has been said to be more serious beneath a pine overstorey since the mature trees act as a source of inoculum (Nixon and Worrell, 1999).

Although one might equally assume that mycorrhizal fungi would be more plentiful in areas with tree cover than open areas, formation of the mycorrhizal association has been found to decline with reduced light intensity (Bjorkman, 1942, cited in Miles and Kinnaird, 1979a). Reduced illumination may give rise to slower shoot growth and correspondingly slower root growth leaving seedlings more susceptible to drought and frost heave (Miles and Kinnaird, 1979a).

Vegetation differences associated with tree canopy may also influence regeneration. McVean (1961b) observed that the deep mat of pleurocarpous mosses and litter typically found in moderately stocked western pinewoods may persist for many years after canopy opening. Regeneration was found to be just as infrequent in the well-lit vegetation as in shaded vegetation of similar composition, leading to a conclusion that illumination under the canopy was not the limiting factor to seedling establishment (McVean1963b). McVean (1961b) concludes that it is the dense moss and litter mat, encouraged by the oceanic climate, that accounts for the differences in understorey regeneration between Scotland and continental Europe.

Whilst the presence of a mature canopy is almost universally treated as a negative factor for pine and birch regeneration, there may be some benefits from a light tree canopy. Miles and Kinnaird (1979a) regard protection from direct sunlight to be beneficial to birch regeneration on freely draining soils. McVean (1961b) considers that prolonged absence of canopy trees will encourage the growth of *Sphagnum* mosses and so reduce the suitability for pine regeneration. Booth (1984) considers that a certain amount of shade will help reduce the vigour of competing vegetation, although how this should not affect the tree seedlings equally is not explained. Other beneficial factors may be protection from wind and extremes of temperature, though these are more likely to be important to shade tolerant species.

Attempts at quantifying the effects of canopy openness on tree regeneration in Scottish upland woodlands have been made by Cameron and Ives (1997) and Vickers and Palmer (2000). Vickers and Palmer (2000) surveyed 39 plots (50 × 50 m) in Glen Tanar pinewood NNR for regeneration, assessing canopy cover by visual estimation in the field. Density of regenerating pine under 1 m tall was fitted to a quadratic model with a maximum at 20% canopy cover. Density of pine saplings over 1 m was found to be inversely associated with canopy cover (i.e. maximum at zero canopy cover). No regeneration was found in plots with over 72% canopy cover. Cameron and Ives (1997) used hemispherical photography to evaluate canopy openness in one hundred plots (2 × 2 m) along transects in Ballochbuie native pinewood. Weak correlations with canopy openness were found for both pine (r^2 = 0.29) and birch (r^2 = 0.12) regeneration. However, examination of the scatter-plots shows that the relationship may be heavily influenced by a large number of data points representing no regeneration. The form of the plots, which appear to display increasing variance in regeneration density with canopy openness, seems to indicate that canopy openness may act as a limiting bound for regeneration density. The lowest measured value of canopy openness was 30%; at this value only low densities of regeneration were found. It should be noted that both of the above studies were conducted in the ‘eastern’ group of pinewoods; McVean (1961b) notes that understorey regeneration is more common in these areas and suggests increased light intensity and reduced moss growth as factors.

The tendency for pine and birch woodlands to regenerate more successfully outside their canopies than inside has led to the observation (or speculation) that woodlands of this type are mobile in the landscape at large – the so-called ‘amoeboid habit’ referred to by Peterken (1986; p.16). This concept is by no means a modern one; a legal dispute in Ballochbuie Forest at the end of the eighteenth century prompted the remark ‘these highland fir woods shift their stances’ (Michie, 1904, quoted in Steven and Carlisle, 1959, p.160). However, a study of native woodland changes in Assynt (Noble, 1997), comparing estate maps of 1774 with contemporary boundaries, showed broad stability at the regional scale. Changes in the distribution of the woodland (primarily birch but with some pine, oak, hazel and aspen) consist of disappearance and contraction of some woodlands, with rather limited expansion and colonization of new areas. This pattern of change is almost certainly constrained by artificial boundaries but nevertheless agrees with Peterken’s (1986) concept of fluctuation around core areas and highlights the consideration of scale in descriptions of mobility.

4.4.3 Seed germination and establishment – model description

The objective of the establishment sub-model is to provide, at each cell and each timestep, an estimation of the numbers of each tree species regenerating and surviving until ten years of age. This quantity is then expressed as the cohorts aged 0-10 year of each species. Thus, the variable expressing the number of stems for 0-10 year cohorts is not intended to represent the number of extant seedlings in that cell. Rather, it provides the maximum number of seedlings that will be available to progress to the next age-class (subject to browsing and density-dependent mortality).

The success and extent of seedling establishment is contingent on the following spatial variables, which may be considered as the sub-model inputs.

1. **Canopy density** – derived from heights and numbers of stems of established cohorts.
2. **Habitat Suitability Index (HSI)** for each tree species.
3. **Yield class** for each tree species.
4. **Seed rain** – as calculated by the seed dispersal sub-model.

Establishment at any given locus is dependent upon factors for that locus only; i.e. there are no neighbourhood effects.

HSI and yield class are evaluated before model execution, as discussed in Section 3.4.2.

From the discussion in the background section (4.4.2) it is apparent that woodland regeneration in Scottish upland situations is inherently unpredictable. Thus, the normal condition will often be for no regeneration to occur. To reflect this, the logical function of the sub-model may be separated into two determinations for each species as follows.

1. Division of cells into regenerating and non-regenerating
2. Calculation of the quantity of seedlings establishing in regenerating cells

Regenerating and non-regenerating cases

For each species, the occurrence of regeneration is subject to the following deterministic criteria.

a) Seed rain for the species must be greater than zero.
b) Canopy density must be below a threshold value (see below).
c) The cell HSI value for the species must be greater than a constant threshold: $\mathrm{HSI}_{\mathrm{min}}$.
d) The cell yield class for the species must be greater than a constant threshold: $\mathrm{YC}_{\mathrm{min}}$.
e) The number of cohorts of the species on the cell must be less than the maximum number of cohorts, m.
f) The estimated number of seedlings of the species that *would* establish (see below) must be greater than a globally defined constant threshold: N_{min}.

Furthermore, the occurrence of regeneration is also subject to the following stochastic factor:

$$\Pr(regen) = R_i \eta_i^{\upsilon} \tag{4.101}$$

where Pr(*regen*) is the probability that regeneration will occur given that all deterministic criteria are satisfied; η_i is the local HSI of species i; υ is a species-independent global constant; and R_i is a species-specific global constant. The underlying assumption is that on suitable sites, seedlings will generally manage to establish despite adverse conditions whereas on less suitable sites adverse conditions will be more likely to overcome regeneration completely. Also, some species may be more susceptible to regeneration failure than others. However, under default parameter settings this stochastic element does not operate, since default values are: $\upsilon = 0$; $R_i = 1 \ \forall i$.

Criterion (f) is a pragmatic feature added as a consequence of point (e), which itself is a practical limitation of model structure. The result of omitting a lower bound on N would be the possibility that successive cohorts would be defined with very low stem densities. Potentially, the problem arises when all the available cohort positions are occupied yet the stand density is low enough for further regeneration to be theoretically possible. This leads to an unrealistic situation that may be termed *cohort-limited understocking*. There is a three-way trade-off between the value of $N_{\min}$, the maximum number of cohorts, m, and the level of cohort-limited understocking. Thus, if very large numbers of cohorts are employed, $N_{\min}$ may be reduced to one with no cohort-limited understocking. The problem may be largely avoided by choosing a value of $N_{\min}$ such that a stand consisting of m cohorts of one species only, each older than the next by one age-class, with the youngest 0-10 years, should have sufficient canopy density to preclude further regeneration. (This condition should apply at minimum yield classes for all species.) The default value of $N_{\min}$ is 50.

In the current version of GALDR, the inclusion of regeneration criteria (c) and (d) represents a redundancy, since yield class and HSI are linearly dependent. The threshold on yield class is included as another pragmatic measure to avoid cohort-limited understocking, which may be exacerbated by slow height growth. Default values for $\mathrm{HSI}_{\min}$ and $\mathrm{YC}_{\min}$ are 0.2 and 2.0 respectively.

Canopy density

The two reviewed quantitative studies of stand density and regenerative ability (Cameron and Ives, 1997; Vickers and Palmer, 2000) both suggest that a canopy cover of approximately 70% may act as a maximum value for the occurrence of understorey regeneration. Below this threshold, it appears that canopy cover might be negatively related to an upper bound on the density of regeneration. The usual measure of stand density used in GALDR is the stand density index (SDI). There are difficulties with using this index as a proxy for canopy cover. Vickers and Palmer (2000) relate that the relationship of (estimated) canopy cover to stem density is not linear, with 100% canopy cover occurring at much less than maximum stocking. Inevitable uncertainty arises from the generalization inherent in the GALDR stand depiction, which provides some representation of vertical distribution of the canopy, but none of horizontal. Thus, a partially stocked canopy (i.e. $\mathrm{SDI} < 1$) may be conceptualized as, at one extreme, a coarse heterogeneous mixture of dense canopy and 'gap' and, at the other extreme, a homogenous area of widely spaced trees (see Figure 4.31). The characteristics of regeneration in each of these idealized cases will differ, but there is no way to differentiate between them in the GALDR representation. Naturally regenerated stands tend not to follow either of these patterns but may fall somewhere on a spectrum between the two cases.

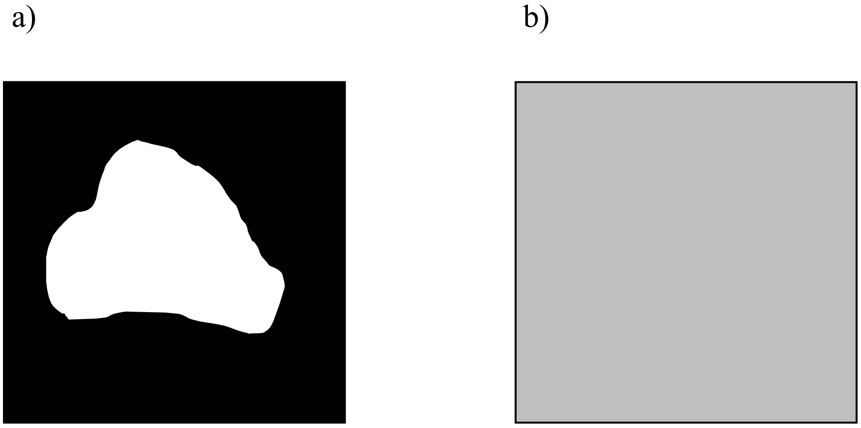


Figure 4.31 Alternative conceptualizations of spatial distributions of canopy density in partially stocked stands: (a) black and white, canopy gap model; (b) grey-scale, light even canopy model.

One problem that becomes apparent if SDI is used to determine the occurrence of regeneration is that SDI values may actually be quite low during the stem exclusion phase. In the model, mortality is high because of fast growth rather than high stand density. In real stands, light levels are at a minimum during stem exclusion phase because of strong canopy vigour. Thus, in simulation, if regeneration is to be allowed in the understorey reinitiation or canopy break-up phases, it will be also allowed in the stem exclusion phase. To some extent, this may not be entirely unrealistic, yet it may still be undesirable as modelled behaviour. Peterken (1996), writing on northern temperate forest dynamics generally, relates that stand initiation may take place over as much as 30 years and, since regeneration is invariably patchy, mosaics of groups in the stand initiation and stem exclusion phases may develop. The patchy or clustered nature of regeneration is also noted for pine and birch in Scottish upland situations (e.g. Fenton, 1985 in Glen Affric; Thompson and Milner, 2001). However, Peterken (1996) also notes that the stem exclusion phase generally results in a tightening of the age-class distribution since the younger and smaller trees die first. The GALDR self-thinning routine does replicate such a process in situations of protracted stand initiation. But depending on the balance of cohort densities, the subordinate cohort may survive to form a minor component of the mature stand.

Such subordinate cohorts may be considered largely irrelevant to overall stand structure since really they represent the tail end of the older cohort.

On consideration of the above, it is preferable to represent the patchy quality of regeneration at the grid-cell scale rather than attempt to incorporate it into the stand (within-cell) representation. That being the case, it may be considered undesirable to allow regeneration in the stem exclusion stage. In order to effect such behaviour a modified measure of stand density has been employed. The buffered SDI (bSDI) of the stand may be defined as:

$$\rho_b = \sum_{i}^{i=mn} \frac{N_i (Th_i + \beta)^2}{A} \qquad (4.102)$$

where i is an index on all cohorts of all species. In non-algebraic terms, the bSDI is similar to the SDI except that the canopy projection of each tree is augmented by a buffer of thickness β. The default value of β is 1m. The greatest differences between SDI and bSDI thus arise in stands with large numbers of small trees. A graph comparing the two stand density measures in a typical stand development sequence is presented in Figure 4.32. Note that bSDI may commonly take values larger than one. A parametric plot of SDI and bSDI is shown in Figure 4.33 with time since stand initiation as the parameterizing variable. It can be seen that for most values of SDI there are two corresponding values of bSDI: an ‘inward’ function for $t < 120$ and an ‘outward’ function for $t > 120$. The outward relationship is almost linear, but the inward curve peaks during the stem exclusion phase. The intention is that the difference between the two relationships reflects the differences in canopy vigour and density between younger and older stands.

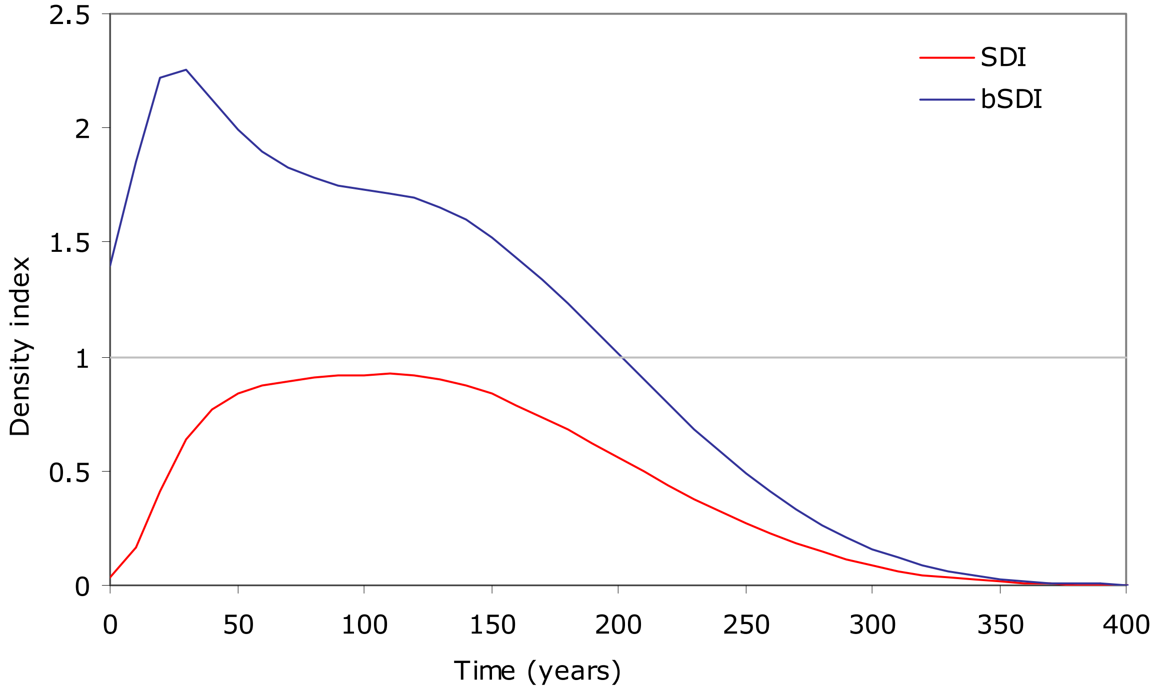


Figure 4.32 Plot of SDI and bSDI over typical single-cohort stand progression. Scots pine YC8; Initial stem density: 2500 m^{-2}.

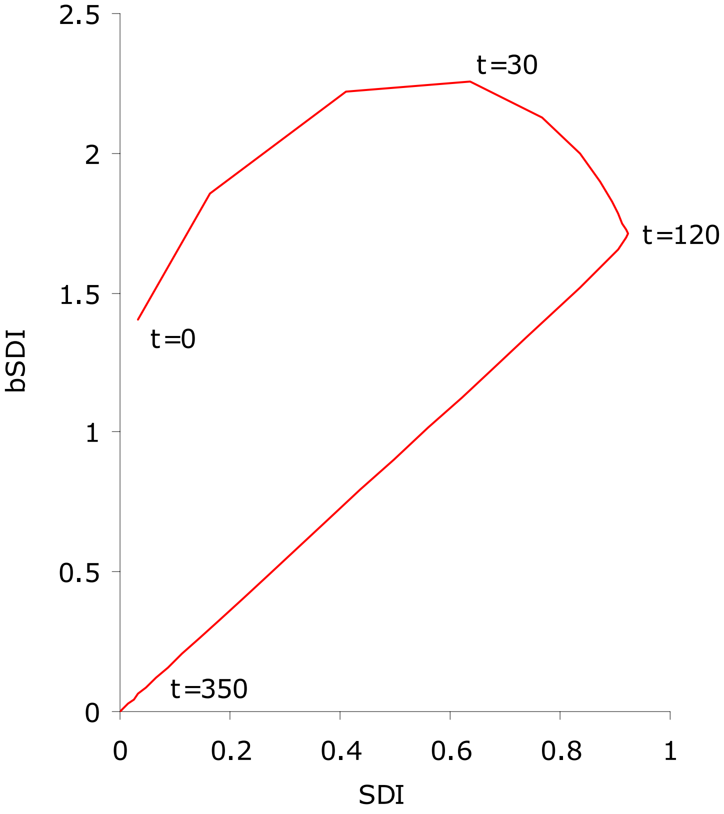


Figure 4.33 A parametric plot of bSDI against SDI with parameter t = time since stand initiation. Stand figures as for Figure 4.32.

Following the definition of the bSDI, regeneration criterion (b) may now be expressed as the following condition:

$$\rho_b < \rho_{b\,\max} \tag{4.103}$$

where $\rho_{b\,\max}$ is a species-independent global constant with default value of 0.8. In the case of the simulated stand development graphed in Figure 4.32, this condition would be reached 220 years after stand initiation when SDI = 0.44. If shade tolerant species were introduced into the model, the constant $\rho_{b\,\max}$ would be redefined as species-dependent.

Quantity of establishing seedlings

In those cases where regeneration is due to occur, the establishment sub-model must also determine how many seedlings of each species establish. This determination occurs in two stages: the first stage assessing the potential quantity of each species independently and the second determining the final number of each species establishing after comparison with the total potential numbers of all species.

In the first stage, the potential number of establishing seedlings is calculated for each species, *i,* as

$$N_i^* = E_i \eta_i^{\iota} q_i (1-\rho) \tag{4.104}$$

where E_i is the baseline establishment ratio (a species-dependent constant), q_i is the total seed rain of species i and ι is the regeneration suitability exponent, a species-independent constant.

The parameter E_i represents the maximum ratio of establishing seedlings to fallen seeds that could be expected under optimum field conditions in the study area. Note that it is not a measure of germinability, which is already factored into the seed production model (see Section 4.3.3) so that q_i represents only viable seeds. Default values are 0.1 for pine and 0.01 for birch. Estimates of default values were based on applying the seed production and dispersal model to areas of regenerating open ground studied by Thompson and Milner (2001) and comparing with measured numbers of establishing seedlings (Thompson, unpublished data). The values must be considered very approximate (i.e. to an order of magnitude) since: (a) seed rain was not actually measured in the studies; (b) none of the areas considered were in Glen Affric; (c) the concept of optimal site type is not well-defined. The low values reflect the fact that, even on optimal site types, the majority of seeds will fall on unsuitable microsites. The difference in establishment ratio between pine and birch is attributable to the large discrepancies in seed size and food reserves between the two species (see 4.4.2 - Germination and early growth; also Sarvas, 1948).

The dependency of numbers of seedlings on HSI is a reflection of the spatial variation inherent in any site. Unlike growth rate, which may vary continuously, establishment is a binary condition for an individual. A completely homogeneous site might be considered either suitable or unsuitable for establishment except for a very narrow window of site conditions where seed variability would be the major influence on the number of seedlings. However, in real conditions there will be a range of available microsites, which will vary considerably in suitability. The assumption made here is that in sites with high suitability, there will be a greater proportion of suitable microsites. However, the proportion of suitable microsites is not expected to vary with HSI in a linear manner (at least not for the current derivation of HSI, from ESC suitability). The nature of the relationship between establishment numbers and HSI is essentially unknown; as a first attempt a simple one-termed polynomial of order ι has been used. The default value for ι is two, making the relationship quadratic.

Note that the measure used for the proportion of the cell available for regeneration is $(1-\rho)$ rather than $(1-\rho_b)$. Thus, if conditions are favourable for seedling establishment the regeneration may bring the SDI up to the maximum value of one. This method probably overestimates the potential quantity of regeneration but was adopted in order to minimize occurrence of cohort-limited understocking.

Having established potential quantities of establishing seedlings for each species, the total density of regeneration in the growing space granted by the overstorey (the regeneration density index – RDI) is calculated as

$$\rho_r = \sum_{i=1} \frac{N_i^* \left(Th_i^*\right)^2}{A\left(1-\rho\right)} \qquad (4.105)$$

where i is an index over the regenerating species and h_i^* is the height of the regeneration of species i, calculated using the usual height growth equation (See Section 4.1.3) for a cohort of 10 years. Similarly, the total number of potential seedlings may be written as:

$$N^* = \sum_{i=1} N_i^* \ . \tag{4.106}$$

If the new cohorts were to establish with RDI > 1 the stand would then be overstocked (SDI > 1), which of course is not permissable. The total number of regenerating seedlings is also subject to an upper bound, a constant term $N_{\max}$, so that cohort stem numbers are kept within their memory allocations. The default value for $N_{\max}$ is 10,000.

To effect this, the number of seedlings establishing of all species is reduced by a respacing factor, defined:

$$R_s = \max\left\{1, \rho_g, N^*/N_{\max}\right\}. \tag{4.107}$$

Then the numbers of stems forming the regenerating cohorts of each species may be defined as

$$N_i = N_i^*/R_s \tag{4.108}$$

however, the cohort is only established if the number of establishing seedlings is greater than a threshold value, ${}_rN_{min}$.

4.5 Browsing

4.5.1 Introduction

By their effects on regenerating trees, large herbivores may be important determinants of woodland structure and dynamics (Miles and Kinnaird, 1979b; Gill, 1992). Mitchell (1990) has presented palynological evidence to suggest that changes in grazing regime have influenced long term changes in woodland structure and composition in Ireland. The effects of grazing and browsing may be particularly profound in Scottish upland woodlands, where the high density of red deer (*Cervus elaphus*) is thought to be the main factor preventing woodland regeneration (Miles and Kinnaird, 1979b; Staines, 1995). Watson (1983) reports that pine regeneration at Mar Lodge may have been almost completely suppressed since the 18th century. However, despite the undisputed negative effects of heavy browsing levels, the presence of herbivores at some level is thought to be beneficial to tree seedling establishment (Miles and Kinnaird, 1979b; Mitchell and Kirby, 1990). Furthermore, Margules and Usher (1981) consider moderate presence of grazing animals to be beneficial on account of their ability to diversify structure and species composition in vegetation communities.

As well as red deer, other important large herbivores in Scottish woodlands include roe deer (*Capreolus capreolus*) and domestic stock, whilst sika deer (*Cervus nippon*), fallow deer (*Dama dama*) and feral goats (*Capra hircus*) may be locally significant.

4.5.2 Mechanisms

The mechanisms by which large herbivores may affect woodland regeneration include browsing, grazing, bark stripping and trampling (Miles and Kinnaird, 1979b). *Browsing* here refers to offtake of woody vegetation, whilst *grazing* is the equivalent action for grasses and forbs.

Browsing

Browsing of tree seedlings and young saplings may often not be fatal. Saplings, especially of broadleaved species, may repeatedly resprout following intermittent browsing (Miles and Kinnaird, 1979b). Thus, Kinnaird (1974) found 31 year old seedling-sized saplings of birch amongst heather in Glen Feshie. Trees are often browsed more heavily after emergence from the field layer (Miller and Cummins,

1974) and the taller the field layer the longer trees may survive held in browsing check. Nonetheless, where browsing levels are high enough, seedlings and saplings will be killed by browsing. In Glen Feshie, Miles and Kinnaird (1979b) report 31% mortality over 4 years amongst unprotected seedlings of pine, birch, juniper and rowan compared with 4% mortality in exclosures.

Grazing

The action of grazing animals removing field layer vegetation may influence the ability of tree seedlings to establish in various ways (see Section 4.4). Miles and Kinnaird (1979b) observed mean depth of moss and litter layers increase from 2 to 8 cm following cessation of grazing in a Glen Feshie birchwood. Pigott (1985) has noted that the increased ground vegetation cover resulting from reduced grazing levels may lead to increases in bank vole (*Cleithrionomys glareolus*) numbers, which may also suppress tree regeneration. Thus, complete removal of all grazing animals often allows regeneration only of pre-existing suppressed seedlings and saplings (Miles and Kinnaird, 1979b).

Trampling

The observation that complete removal of grazing animals may hinder regeneration (e.g. Staines, 1995) led some researchers to conclude that the presence of the animals must help to create regeneration niches in the field layer; gap creation by trampling was one proposed mechanism (Dunlop, 1975; Miles and Kinnaird 1979a,b; Mitchell and Kirby, 1990). However, this hypothesis was untested until Hester *et al.* (2000) conducted a gap creation experiment and survey of birch regeneration at Creag Meagaidh NNR. Their finding was that germination success was low in experimentally created deer hoof-sized prints and that surrounding vegetation usually recolonized before seedlings had a chance to establish. The conclusion of the study was that trampling was only likely to be a significant factor on steep ground or where deer numbers were very high.

Bark stripping

The exact reason why animals strip bark is not known but Mitchell and Kirby (1990) state that both nutritional and behavioural factors may operate. Miles and Kinnaird (1979b) also suggest that the behaviour may be a response to requirements for roughage, minerals or vitamins as well as for general nutrition in the absence of other suitable food. Van de Veen (1973) found that bark stripping of young Scots pine coincided with the period in which heather was flowering and generally ungrazed. Miles and Kinnaird (1979b) consider that bark stripping is unlikely to be detrimental to mature trees except in cases where wounds may allow infection by pathogenic fungi.

4.5.3 Impacts

Deer density

Holloway (1967) observed that regeneration of Scots pine was successful where red deer densities were of the order of 2km^{-2} but that regeneration failed at densities of 25 km^{-2}. At an intermediate deer density of 6km^{-2}, damage occurred but did not completely prevent regeneration. At Abernethy pinewood, Beaumont *et al*. (1995) recorded increases of 20% in numbers of establishing seedlings, and reduction of proportion of browsed seedlings from 72% to 43%, following reduction of red deer density from 12 km^{-2} in 1989 to around 5 km^{-2} in 1992. Similar recovery in birch regeneration was observed at Creag Meagaidh NNR following reduction to 8 km^{-2}. Staines *et al.*, 1995).

However, prediction of impacts from densities is not straightforward (Staines. 1995; Staines et al, 1995; Hester *et al*., 1998; Palmer and Truscott, 2003). One difficulty with using animal densities as a hard measure of likely impacts is that herbivores do not distribute themselves evenly throughout the landscape. Thus, if they happen to congregate in areas of tree regeneration they may do more damage than would be indicated by their overall density at the estate level (Palmer and Truscott, 2003). Hester *et al*. (1998) conclude that ‘an outstanding problem with deer management has been a lack of information relating the severity of deer damage to deer population density’ (p.31).

Species preferences

Dzieciolowski (1969) found that red deer in Poland sought out Scots pine over other trees, followed by hornbeam (*Carpinus betulus*), birch, oak and alder in order of preference. However, Mitchell and Kirby (1990) caution that considerable variation is reported in species preferences; for example, juniper was found to be rarely browsed in Poland but highly sought after in north-west England. Trees that seem to be consistently preferred include aspen, willows and holly. Within herbivore populations, species preferences change seasonally with deer reported to take an increased proportion of woody vegetation during the winter (Putman, 1986). The species most liable to bark stripping are reported to be willows and aspen (Mitchell *et al.*, 1977).

4.5.4 Control

Whilst the level of grazing imparted by domestic stock is generally readily controllable in the course of normal stock management, the effects of wild herbivores such as red deer are more difficult to manage (Hester *et al.*, 1998). The usual methods of controlling red deer for the purposes of encouraging natural regeneration of woodlands are fencing and reduction of numbers by shooting (Staines, 1995). Less common practice includes provision of diversionary feeding in winter when deer habitually take the most browse. Miles and Kinnaird (1979b) report reductions in browsing levels at Inverpolly NNR in a winter where herbaceous growth was unusually vigorous and sustained. However, supplementary feeding may boost herbivore populations by reducing winter mortality, thus having the opposite effect to that desired.

Fencing

Fencing is the traditional method of excluding wild herbivores from woodlands. If carried out carefully it may be effective in excluding herbivores completely. However objections to the technique have been made (Beaumont *et al.*, 1995; Hester and Miller, 1995; Staines, 1995; Staines *et al.*, 1995) for the following reasons:

- complete absence of herbivores leads to reduction of diversity in vegetation and may hinder regeneration;
- they are a major cause of adult mortality for woodland grouse;
- they are visually intrusive and restrict recreational access;
- they are expensive to erect.

Very large fenced areas may sometimes be used (as in Glen Affric) so that populations of deer may be allowed within the fenced area and thus deer numbers may be more easily controlled in the absence of migration (Hester *et al.*, 1998). This may also help to reduce grouse mortality since fence length is less per unit area enclosed and fences in woodland interior may be avoided. However, the maintenance costs are likely to be high.

Shooting

Culling by professional stalkers is often the preferred option, particularly for control of deer numbers. A cull level of 15% has been proposed to keep populations of red deer stable (Mitchell *et al*., 1977). To reduce populations at Abernethy, Beaumont *et al*. (1995) used a cull level of 33% for hinds and calves, and 20% for stags. Often a particular deer density is aimed for (frequently around 5km^{-2}) but note comments in 4.5.3 above, regarding deer densities and impacts.

4.5.5 Spatial effects of grazing and browsing animals

Mitchell and Kirby (1990) note that upland woods are often confined to narrow bands on areas of steep ground. Very steep ground will generally deter grazing animals, although feral goats may browse on steeper ground than other ungulates (Hester *et al*., 1998). Areas of high soil fertility will generally contain higher proportions of palatable species in the field layer and may attract high numbers of grazing animals; however the high density of herbivores may be offset by the tendency of the animals to prefer grazing to browsing in such areas (H. Armstrong, personal communication). Hester *et al*. (1998) state that variation in habitat usage by ungulates is well recognized, but that effects on regeneration are still poorly understood.

Palmer and Truscott (2003) conducted a study of habitat usage and browsing levels by red and roe deer on Scots pine regeneration in Glen Affric and Glen Tanar. Local deer densities at the study site in Glen Affric, assessed using dung counts, were estimated to be in the order of 25km^{-2}; considerably higher than the overall site estimate of 2 km^{-2}. No relationship was found between availability of pine browse and habitat use at either site. In Glen Affric, a significant relationship was found between deer usage and a principal components analysis variable related to presence of shelter and high cover of heather and blaeberry (*Vaccinium myrtilis*). However since shelter was correlated with field layer composition these effects cannot be disentangled.

4.5.6 GALDR grazing sub-model

There are many effects of browsing that could be simulated as part of a model such as GALDR. These might include: varying levels of seedling mortality and/or growth check as a function of deer density; differential damage to tree species in relation to palatability; spatial variation of damage in relation to habitat factors such as topographic shelter, shelter from established woodland, field layer vegetation and habitual patterns of habitat use. However, the nature of all these relationships is presently quite unclear and lacking in quantification Hester *et al*., (1998).

Because of the lack of suitable knowledge on deer impacts, browsing in GALDR is represented simply by the specification of probabilities of damage. Simulation of damage is restricted to the reduction of stems from seedling stage cohorts (i.e. the first age class, 0-10 years). The proportion of stems killed is a stochastic variable defined according to the user-defined control parameters: $B_{\min}$, $B_{\max}$, P_b, and $P_{b\max}$. The parameters $B_{\min}$ and $B_{\max}$ control the minimum and maximum browsing levels respectively; P_b controls the probability of cells experiencing any browsing whatsoever; and $P_{b\max}$ controls the proportion of browsed cells that experience maximum browsing. All browsing control parameters may defined on the interval [0,1] but $B_{\max}$ must be greater than $B_{\min}$.

Thus if $P_{b\max} < 1$ the browsing level, B, may be determined by

$$B = \mathrm{X}(P_b)\left[B_{\min} + \left(B_{\max} - B_{\min}\right)\left(\min\left\{1, \mathrm{Z}/\left(1 - P_{b\max}\right)\right\}\right)\right] \tag{4.109}$$

where $\mathrm{X}(P_b)$ is a stochastic binary variable which takes a value of 1 with probability of P_b and zero otherwise and Z is a stochastic continuous variable with uniform p.d.f. on the interval [0,1].

If $P_{b\max} = 1$ the browsing level may be defined simply by

$$B = X(P_b)B_{\max}\,. \tag{4.110}$$

The values of the stochastic variables are independent between grid cells. Once the browsing level B is defined for a cell then stem numbers for all species in the seedling stage cohort are reduced by multiplication with the factor B (since, of course, $B \leq 1$).

The set of browsing control parameters may be defined for three zones. For example, some test runs of GALDR have used a raster map defining a zone within the fenced areas as well as areas of steep ground where browsing pressure may be lower than elsewhere (see Figure 4.34)

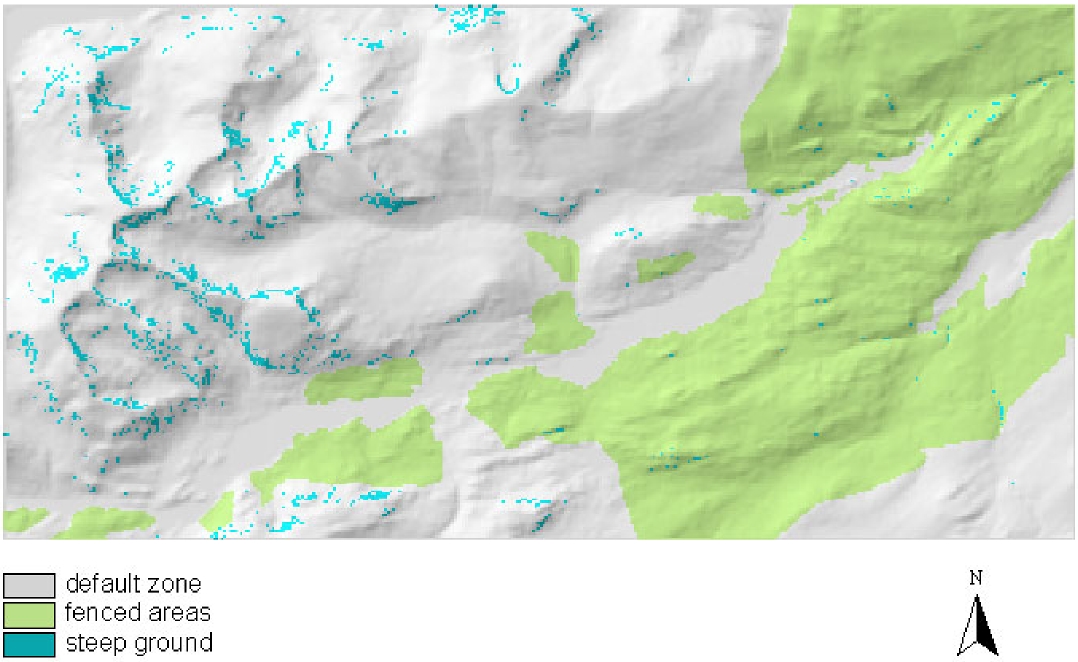


Figure 4.34 Raster map of browsing zones (see text for definition).

5 Sensitivity Analysis

5.1 Introduction and aims

The purpose of sensitivity analysis (SA) is to gauge the extent to which model output varies as a result of varying the model parameters. Some authors (e.g. Liu *et al.*, 1999) restrict the use of the term 'sensitivity analysis' to investigations of small changes in model parameters. The term 'uncertainty analysis' may then be used to describe investigations into the effects of larger input variations for parameters for which it is difficult to obtain exact values. Botkin (1993) takes a broader view. He states that '*a sensitivity test is a test that determines how great a change occurs in the value of an output variable with a change in the value of either an input variable or a parameter intrinsic to the model*' (p.159). In this chapter, 'sensitivity analysis' is used in the broader sense but the more specific sense of 'uncertainty analysis' is retained. The sensitivity of a parameter is taken to mean the degree to which output variables vary with respect to perturbation of the parameter. The tests presented here relate to 'intrinsic' parameters rather than input variables.

SA is often used to identify parameters that show particularly high or low sensitivity. Parameters with high sensitivity may be said to exhibit *amplification* of the effects of parameter variation. The opposite term *buffering* may be used of low sensitivity parameters. Botkin (1993) states a preference for parameters that display neither amplification nor buffering to great extent. Highly amplifying parameters are problematic because they require parameter values to be ascertained both accurately and precisely. However, if this aspect of the model behaviour is realistic then this may reflect some critical dependence inherent to the ecosystem. Discovery of such dependencies may provide useful insights and help focus future research effort. Similarly, identification of parameters with very low sensitivities may indicate model functions that may be omitted without impinging upon overall model objectives (Vanclay and Skovsgaard , 1997).

In the most uncomplicated cases, SA can be undertaken analytically by calculating model derivatives. However, for models that are more complex this is not possible since model output will originate from a number of separate processes and feedback loops. Instead, SA of complex models is undertaken by actually running simulations and observing the changes in model output that result from perturbing parameter values. For stochastic models, this will usually involve replication of simulations for each parameter value. The situation is more complicated again in the case of landscape dynamics models. Landscape model output may take the form of any number of output variables, all of which may be produced for each cell in the landscape and at each time interval throughout the simulation. The GALDR model is not oriented to a single output variable in the same way that (for example) a forest yield model or PVA model would be. For example, GALDR may run with up to forty dynamic rasters, each of 400 x 200 cells, with 100 model iterations. This equates to 320 million output values per run.

The aim of the GALDR SA is to gain a broad picture of the sensitivity of the model to its parameter values and to identify particularly sensitive or insensitive parameters.

The central part of the GALDR model uses twelve global parameters and ten species-specific parameters (see Table 5.1). This does not include parameters contained in some submodels or pre-processing routines such as ESC and DAMS calculations. Model infrastructure global constants such as cell size or maximum number of cohorts are also excluded.

Results of the analyses of ten parameters are presented in this chapter. Methods have not been completely standardized for all parameters but depend on the function of the parameter at stand and landscape levels and the degree of uncertainty in parameter estimation. In analysing species-specific parameters, variation has been confined to parameter values for birch only. This unilateral approach has been adopted to investigate the effects of differences in parameter values between species. Birch has been used rather than pine because its total coverage is less, and thus landscape effects appear more sensitive.

Table 5.1 Central parameters of the GALDR model. The asterisked SELES variables are not expressed in the same way as described in the text, but the function is identical. Default values relate to the parameters as described in the text.

Parameter name	Default value		Equivalent SELES variable	Function
Global parameters				
age_{min}	20		`*mature_age`	Age after which trees may set viable seed (years)
ψ	1.83		`abscise_bias`	Factor of non-random abscission
G_{alt}	0.0014		`alt_germ`	1st order term of germinability-altitude relationship
HSI_{min}	0.2		`*min_suit`	Minimum HSI value to allow regeneration
YC_{min}	2		`min_yc`	Minimum yield class to allow regeneration
β	1		`shade_buffer`	Buffer around SDI projection area of each stem in calculation of bSDI (m)
$\rho_{b\ max}$	0.8		`*min_gap`	Maximum value of bSDI to allow regeneration
${}_rN_{min}$	50		`min_seedlings`	Minimum number of seedlings needed to allow definition of new cohort
N_{max}	10,000		`*max_seedlings`	Maximum number of seedlings that may establish
N_{min}	5		`min_stems`	Minimum stems in cohort (cohorts with less are terminated)
υ	0		`sfrs`	Temporal stochastic regeneration index
Wind parameters				
k	1.85		`k`	Shape parameter (exponent) of Weibull distribution
Ua	5		`Ua`	Characteristic value (of wind regime)
Species- specific parameters				
	Pine	Birch		
F	0.72	0.5	`F`	Seed terminal velocities (ms^{-1})
Q^*	200	2000	`Q0`	Production of viable seeds (m^{-2})
E_i	0.1	0.01	`germ_ratio`	Baseline establishment ratio
R_i	1	1	`rgn_occur`	Temporal stochastic regeneration factor
t_l	600	200	`longlife`	longevity parameter: stand age at which mortality = 100% (years)
Growth model parameters				
M_0	47.4	24.7	`M0`	Constant term, Gompertz location parameter
M_1	-1.14	-0.375	`M1`	1^{st} order term, Gompertz location parameter
C_0	13.3	14.3	`C0`	Constant term, Gompertz vertical scale parameter
C_1	1.5	1.04	`C1`	1^{st} order term, Gompertz vertical scale parameter
B	0.0359	0.0575	`B`	Gompertz horizontal scale parameter

5.2 SA techniques and application to growth sub-models

5.2.1 SA for stand variables

At the stand level the growth sub-model is a real function of time and yield class differentiable with respect to all of its parameters. Hence it is possible to calculate the sensitivity of the height function analytically for each parameter.

The (relative) sensitivity of a function F to one of its parameters λ may be denoted S(F,λ) and expressed as

$$\mathrm{S}(\mathrm{F},\lambda)=\frac{\lambda}{\mathrm{F}}\cdot\frac{d\,\mathrm{F}}{d\lambda} \tag{5.1}$$

(Jørgensen, 1986).

This assumes that F is differentiable with respect to λ. Put less formally, the effect of a small change in λ by a factor of $(1+\delta)$ will be to change F by a similarly small factor of $(1+k\delta)$ where k = S(F,λ). Thus, for any parameter acting purely as a scalar multiplier on a function, the sensitivity of the function to that parameter will be unity. Large absolute values of sensitivity (i.e. $|S| > 1$) will occur where changes in parameter values are amplified in the parent function; buffering parameters will give rise to small sensitivity values (i.e. $|S| < 1$). Negative values occur where an increase of the magnitude of the parameter value gives rise to a decrease in the magnitude of the function. The advantage of using the relative sensitivity over that of using the absolute sensitivity ($d\mathrm{F}/d\lambda$) is that the value is not scaled to the value of the parameter and response value, so that comparisons can be made between functions and parameters.

The height-growth function presented in Equation (4.7) (see Section 4.1.3) may be expanded in full as

$$h(t,y)=\left(C_1 y+C_0\right)e^{-e^{-B\left(t-\left(M_1 y+M_0\right)\right)}} \tag{5.2}$$

where B, C_0, C_1, M_0, M_1 are non-negative parameters; t is time and y is yield class.

Clearly the outer exponent tends to unity as t tends to infinity, so the quantity $(C_1y + C_0)$ defines the maximum height of the cohort. The B parameter defines the stretch of the curve along the x-axis about the inflexion point, which is defined by $(M_1y + M_0)$.

Since $(C_1y + C_0)$ acts as a multiplier on a function of y and t, the sensitivities of C_0 and C_1 depend only on y and are independent of t.

$$\mathrm{S}(h, C_0) = \frac{C_0}{C_1 y + C_0} \tag{5.3}$$

$$\mathrm{S}(h, C_1) = \frac{C_1 y}{C_1 y + C_0} \tag{5.4}$$

Note that the sum $\mathrm{S}(h, C_0) + \mathrm{S}(h, C_1) = 1 \ \forall\, y$. The sensitivities of C_0 and C_1 for birch are shown graphically in Figure 5.1a. Yield classes for birch are not predicted to be greater than 12 in the ESC analysis but the x axis is extended to greater values to better illustrate the nature of the relationship. Figure 5.1b demonstrates the effects of altering the C_0 parameter by ± 10% on the height growth curve for yield class 6 birch.

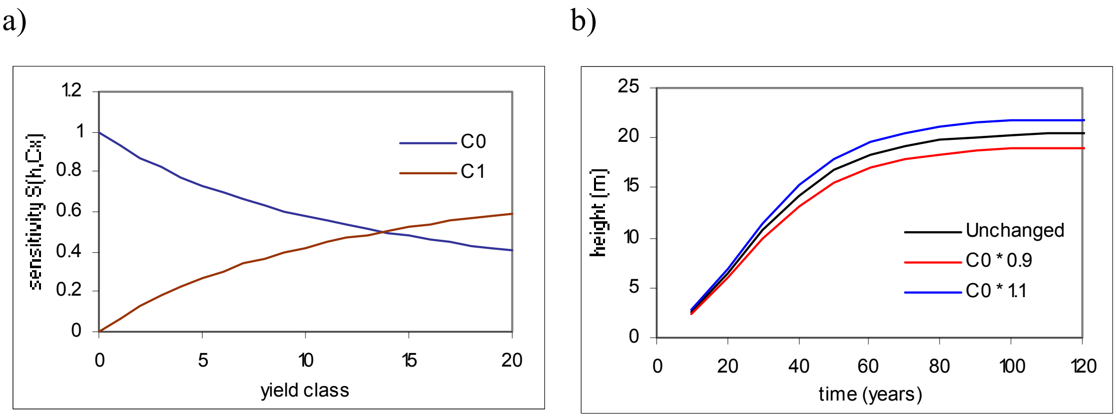


Figure 5.1 SA of growth parameters: (a) variation with yield class of the sensitivity of the cohort height growth submodel to C_0 *and* C_1 *parameter; (b) effects of perturbation of* C_0 *parameter on cohort top height of birch, yield class 6.*

The sensitivity of the B parameter is given by

$$\mathrm{S}(h, B) = B(t - M)\, e^{-B(t-M)} \tag{5.5}$$

where $M = M_1 y + M_0$. A graph showing sensitivity of h to B varying over time is shown in Figure 5.2a. Curves for yield classes 4 and 12 of birch are shown, demonstrating that yield class is not a major factor in determining sensitivity of this parameter. The equation and graph show that $\mathrm{S}(h,B) = 0$ when $t = M_1 y + M_0$. At this value of t the value of h is invariant under perturbation of the value of B. Figure 5.2b shows the height growth curve for yield class 6 birch with the B parameter altered by ± 10%. The point at which the three curves converge is the inflexion point: $t = M_1 y + M_0$.

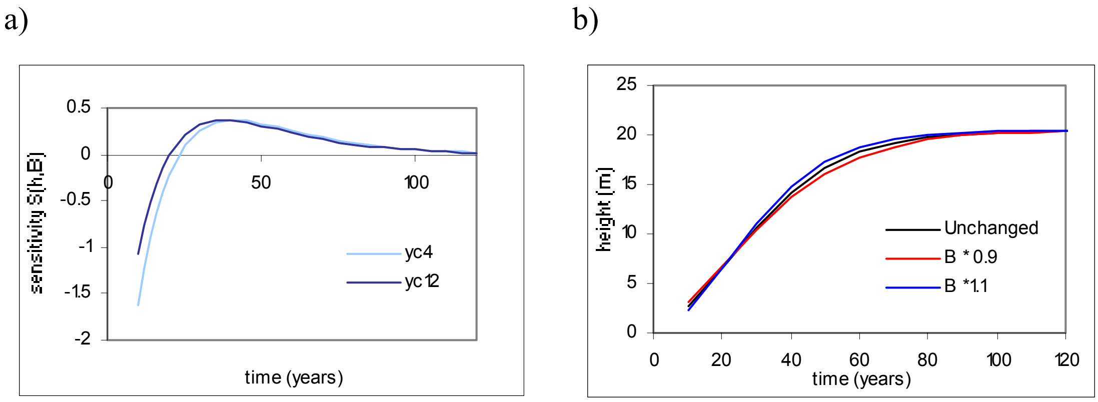


Figure 5.2 SA of Gompertz B *parameter: (a) sensitivity curves of cohort height growth submodel to* B *parameter, birch yield classes 4 and 12; (b) effects of perturbation of* B *parameter on cohort top height of birch, yield class 6.*

Sensitivities of the M_0 and M_1 parameters are given by the following equations.

$$\mathrm{S}(h, M_0) = M_0 B\, e^{-B(t-(M_0+M_1 y))} \tag{5.6}$$

$$\mathrm{S}(h, M_1) = M_1 B y\, e^{-B(t-(M_0+M_1 y))} \tag{5.7}$$

Figure 5.3a shows a graph of sensitivity of h to M_0 and M_1 over time; curves of birch yield class 4 and 12 are drawn for each parameter. The sensitivity of M_1 is highly dependent on the yield class value, though sensitivity values are relatively low over the entire range of ages. Predicted heights of year ten and twenty cohorts will be highly sensitive to variations in the value of M_0 but as cohorts age they become progressively less sensitive. Figure 5.3b illustrates the effect of ± 10% alteration of the M_0 parameter on the height growth curve for yield class 6 birch.

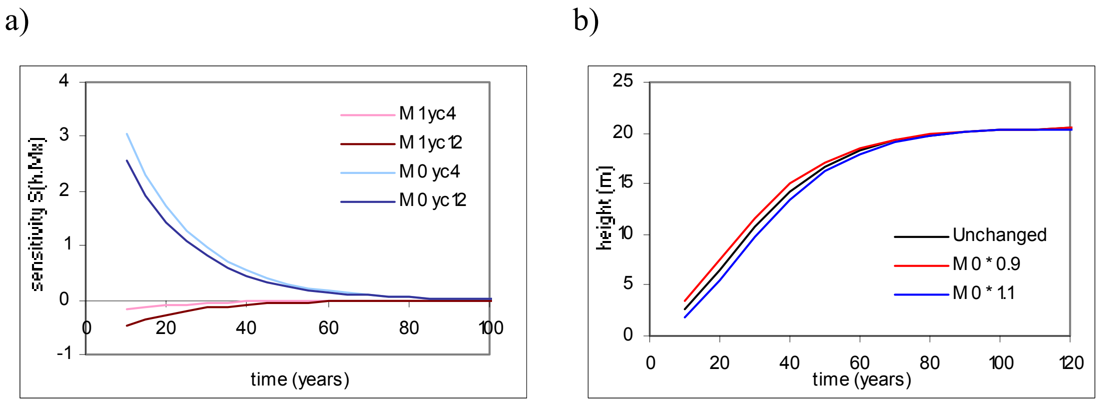


Figure 5.3 SA of Gompertz B *parameter: (a) sensitivity curves of cohort height growth submodel to* M_0 *and* M_1 *parameters, birch yield classes 4 and 12; (b) effects of perturbation of* M_0 *parameter on cohort top height of birch, yield class 6.*

5.2.2 Landscape level effects

The above sensitivity analysis of the height growth sub-model forms a preliminary investigation of the effects of variation of height growth parameters on the behaviour of the model. The analysis considers even-aged single-species stands in isolation, whereas the fully integrated landscape model contains many interacting mixed-species multi-cohort stands. A change in the nature of height growth will effects in turn on the following cohort properties:

- rate of self-thinning;
- competition with other cohorts (intra- and inter-specific);
- distribution of seedfall density;
- susceptibility to wind disturbance.

The overall landscape-level implications of such effects will also depend upon the intrinsic landscape pattern and dynamics.

The analytical method of investigating parameter sensitivity presented above cannot be used in the context of the entire landscape because of the sheer number of interactions between processes. This is compounded by the stochastic nature of some processes. In view of this intractability the most practical method of quantifying the effects of parameters is to actually perform simulations with altered parameter values. Because the model contains stochastic elements, it is necessary to replicate simulations for each parameter value. The number of replications for each parameter was ten in all cases. This level of replication appears to allow sufficient stochastic variation to assess differences between parameters, but allows simulation times to be kept within a reasonable limit (a few days to a week for each test). Leemans (1991) used five replications per run for his sensitivity analysis of the gap model FORSKA.

Figure 5.4 illustrates the effects on some landscape output variables of varying the C_0 parameter for birch only. In some cases, the effects of variation of the model parameter are obvious. For example, in figure Figure 5.4c there is almost complete separation of the responses due to parameter variation. Elsewhere, the effects may be slighter and may produce results in which differences due to parameter variation may not be discernible by visual inspection alone – e.g. Figure 5.4a. Various statistical methods are available to test whether mean responses of replicated runs differ statistically. Values from a single point in time may be tested using Analysis of Variance (ANOVA). Values from a sample of time points may be tested using Multivariate Analysis of Variance (MANOVA). Diggle (1990) provides methods for time series analysis including maximum likelihood estimation; such methods can be very powerful but implementation tends to be labour intensive.

In practice though, formal statistical tests may yield little benefit in sensitivity analyses of this kind because it is generally possible to follow the logical framework of the model to determine whether an output variable has a dependence upon a particular parameter. Where a dependency exists it will necessarily be possible to demonstrate a statistical difference between sets of output variables providing sufficient replications are used. (Exceptions may occur if stationary points exist on the parameter – response curves.) If variation of a parameter gives rise to a difference in mean output so small that statistical treatment is necessary to determine whether it is significant, then that fact alone is probably sufficient observation.

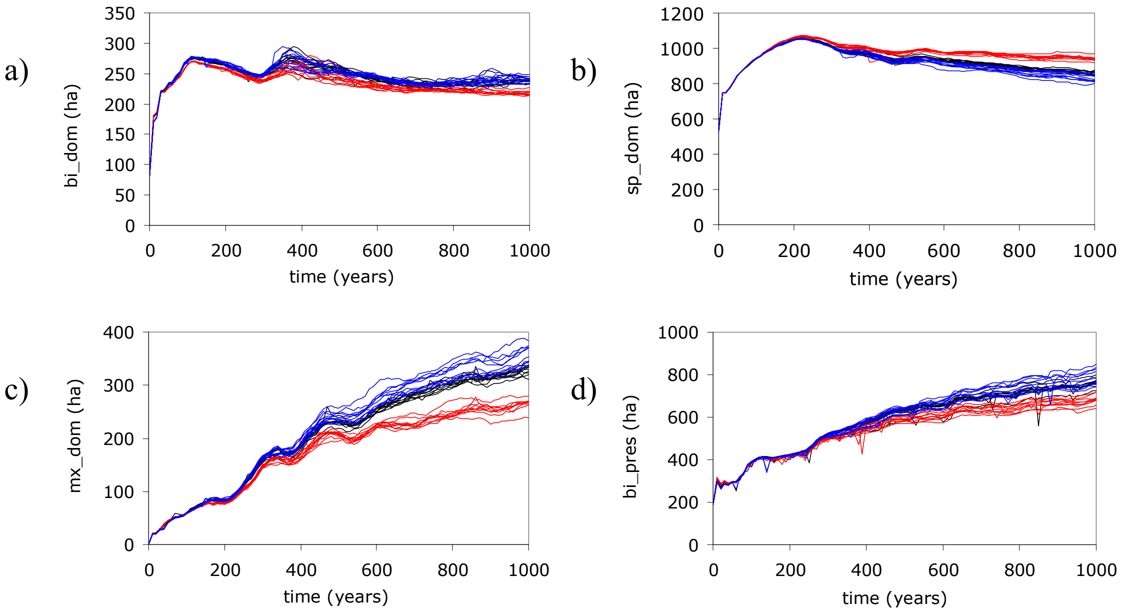


Figure 5.4 Time series graphs showing response of four GALDR output variables to perturbation of the C_0 *parameter (for birch only) by ± 10%. Each series shows ten replicates. Black plot – standard value of* C_0*; red plot – standard value less 10%; blue plot – standard value plus 10%. Ordinate axis represents area of woodland (a) dominated by birch; (b) dominated by pine; (c) with pine and birch codominant; (d) with birch present in any quantity.*

A peculiar feature of the sensitivity analyses illustrated in Figure 5.4 is the strong asymmetry of the response to positive and negative deviations from the standard value of C_0. This indicates a relatively high value of the rate of change for the value of sensitivity with respect to parameter value; i.e. small-to-moderate changes to the value of C_0 may result in large changes to the sensitivity of landscape metrics to further perturbation of the parameter. This asymmetry is peculiar to the landscape response, as it is not observable in the stand-level sensitivity analysis.

5.2.3 SA for landscape variables

Where sensitivity analyses are conducted using small perturbations a value of sensitivity (for the landscape variable with respect to the parameter) may be calculated which is analogous to that used for differentiable functions. Generally, let λ_0 be a standard value for a model parameter λ, and $\lambda_+ = \lambda_0 + \delta$ where $\delta > 0$; then L_0 may be defined as the value of the landscape variable L where the standard parameter value λ_0 is used and L_+ may be the value of L where λ_+ is used. Then we may estimate the sensitivity of L to λ as

$$S_+(L,\lambda) = \left(\tfrac{L_+}{L_0} - 1\right) \Big/ \left(\tfrac{\lambda_+}{\lambda_0} - 1\right) \qquad (5.8)$$

and accordingly,

$$S_{-}(L,\lambda)=\left(\tfrac{L_{-}}{L_{0}}-1\right)\Big/\left(\tfrac{\lambda_{-}}{\lambda_{0}}-1\right) \tag{5.9}$$

where L is calculated for both positive and negative perturbations, an unsigned value of sensitivity, S, may be calculated as the mean of S_+ and S_-.

If L were differentiable w.r.t. λ then S, as calculated above, would converge to the value calculated by differentiation as δ were reduced to zero; however for stochastic landscape models L will not be differentiable and very small values of δ will result in differences in L which are unnoticeable due to noise from the stochastic elements of the model unless very many replications are used.

Sensitivity estimates are shown for four landscape variables with respect to birch growth parameters C_0, M_0 and B in Figure 5.5. Some points of note include the following.

- In general, the sensitivities become greater over time. This is because the response is effectively cumulative as long as the landscape continues to change (we can expect that sensitivities would level out as the landscape reaches equilibrium).

- Changes in species dominance are in fact relatively trivial consequences of variation in height growth parameters since dominance is based on species pSDIs (partial Stand Density Indices), which in turn are calculated on the basis of cohort heights. However, species *presence* – the area of woodland containing any quantity of that species – is an indicator of wider influence. Figure 5.4c and Figure 5.5 show that presence of birch in the landscape is sensitive to C_0 and M_0 parameters.

- Sensitivities to B are generally lower than for C_0 or M_0. This may be attributed to generally low sensitivities in the stand level analysis (see Figure 5.2a) compounded by the sign of the sensitivity being negative in the early stages of stand development and positive thereafter.

- In all the analyses, the response of mx_dom follows the same sign as bi_dom. This is not an immediately obvious result, for whilst an increase in birch cohort heights will tend to lead to a transfer of cells from pine dominated to mixed, there will equally be a transfer from mixed to birch dominated. The fact that gains to mixed woodland are greater than losses may be a consequence of the landscape pattern.

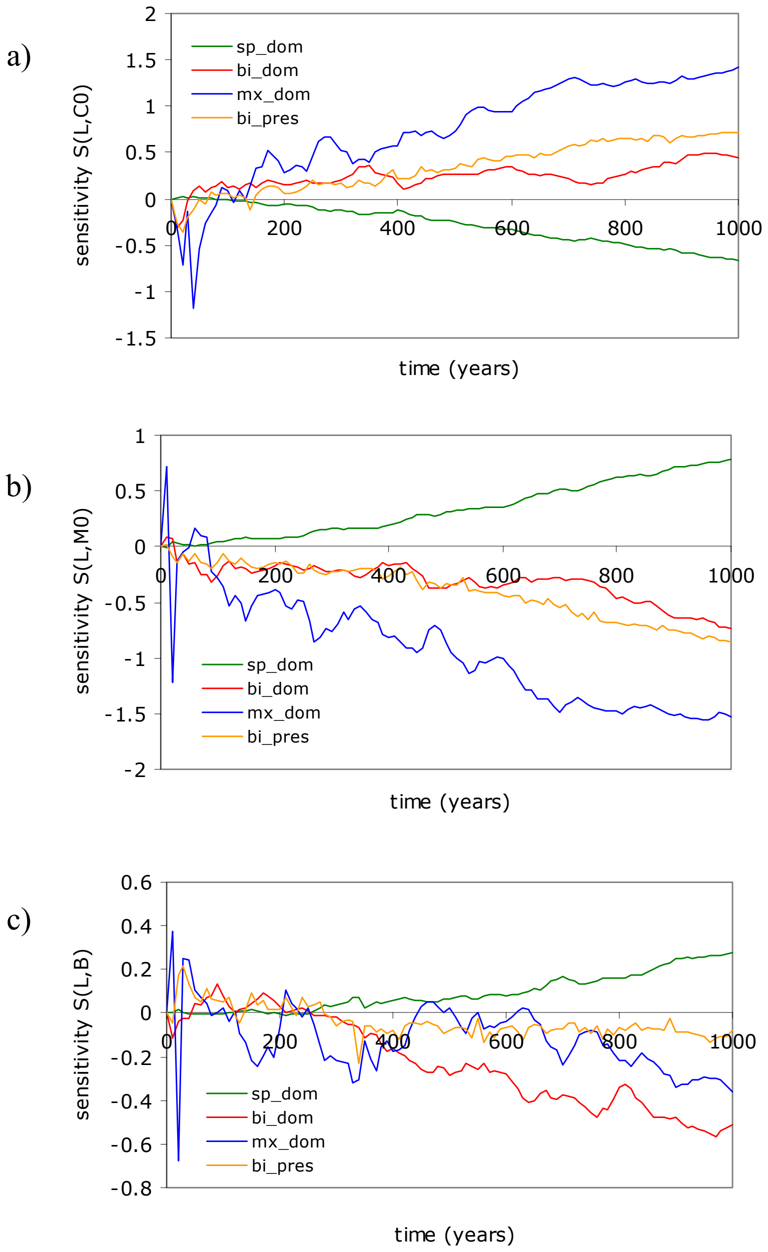


Figure 5.5 Graphs of sensitivity of four landscape variables to growth model parameters (a) C_0, *(b)* M_0 *and (c)* B. *The plots show mean values from ten replicates. Output variables are areas of woodland which are: dominated by pine (green plot); dominated by birch (red plot); codominant pine and birch (blue plot); with birch present in any quantity (orange plot).*

Figure 5.6 shows the effects of variation of the C_0 parameter on the output variable mid_age_bi. The interesting feature of these plots is the major differences in output behaviour over quite small parameter variations. The general behaviour of the output variable is periodic with period approximately 100 years. For the lower value of C_0 the pattern is strongly periodic with large amplitude. The higher value of C_0 results in a much weaker periodic pattern with much smaller amplitude. The middle value of C_0 yields a plot intermediate in these features.

The likely cause of this effect is that the strong periodic pattern is caused by the dynamics of birch in the absence of pine; by raising the value of C_0 the proportion of birch existing in mixture is also increased.

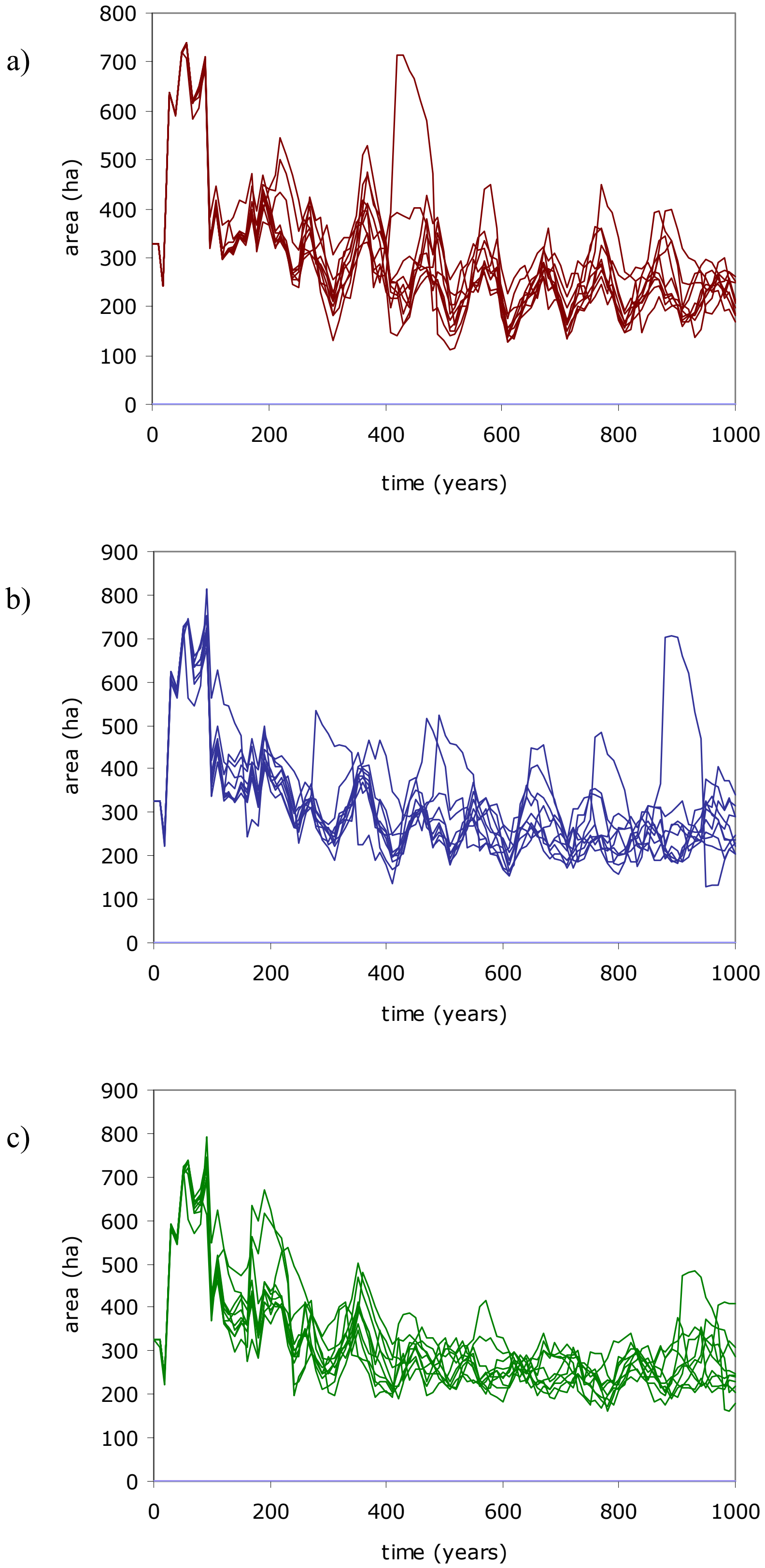


Figure 5.6 Time series graphs of the landscape variable mid_aged_bi under three values of the height growth parameter C_0*: (a) standard value of* C_0 *less 10%; (b) standard value; (c) standard value plus 10%*

5.3 Landscape-level sensitivity analyses

5.3.1 Default output

Simulations performed for the purposes of sensitivity analysis used a subset of the full landscape extent in order to allow a sufficient number of treatments to be carried out in a reasonable time. Excluding open water, this test area covers 1544.25 ha (= 6177 grid cells). The model output resulting from use of the default parameters (See Table 5.1) on this landscape is described below.

The overall trend in the output is that of woodland expansion. Figure 5.7 shows the development of woodland cover broken down into pine-dominated, birch dominated and mixed woodland. (A stand is classed as ‘dominated’ by one of the species if the sum of the pSDI for that species is greater than 80% of the SDI.) Figure 5.8 shows the amount of woodland in which any quantity of each of the species is present. The graphs show that maximum woodland cover is achieved approximately one third of the way through the simulation but that internal changes in woodland composition continue throughout the simulation. The major trend is gradual expansion of mixed woodland and birch presence. It is almost certain that both these quantities are underestimated in the representation of the initial state so to a certain extent these trends may be artificial. In the simulation, pine reaches its maximum extent relatively early, but the amount of pine-dominated woodland is eroded as birch gradually infiltrates through the landscape, converting pine-dominated stands to mixed stands in the process. It would appear, however, that the expansion of birch does not displace pine from stands completely as pine presence remains rather constant throughout the latter stages of the simulation.

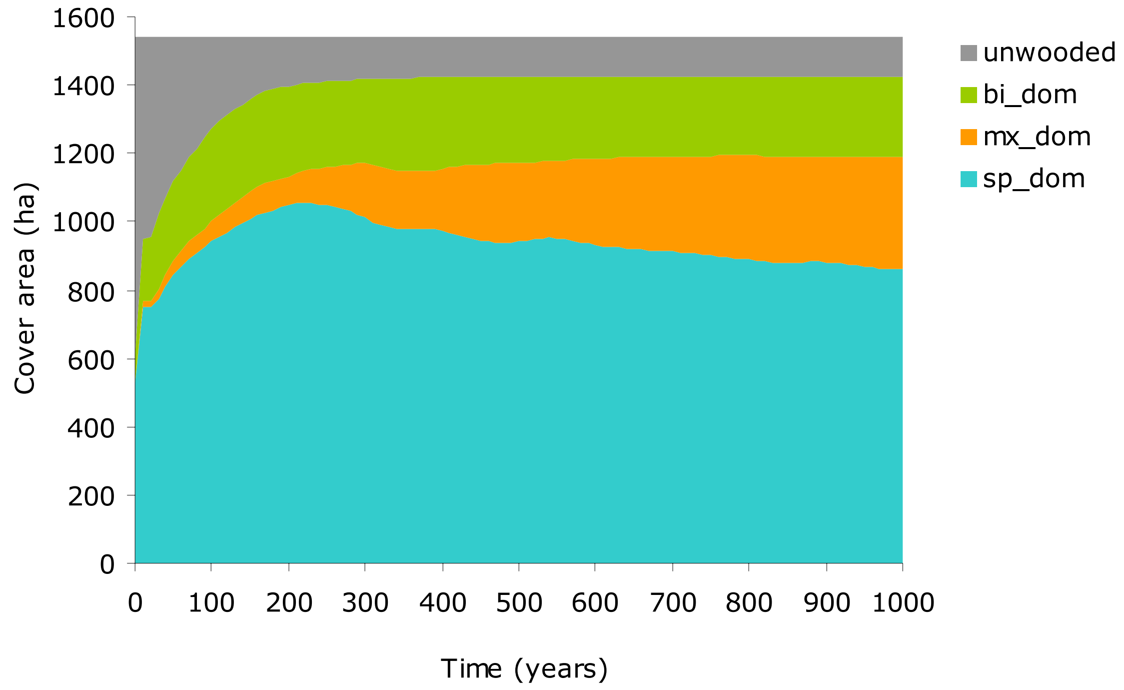


Figure 5.7 Area plot of default output for landscape-level sensitivity analysis. Areas of cover are represented by coloured areas on the graph. From the top down, these are: unwooded ground, birch-dominated woodland, mixed woodland, pine-dominated woodland.

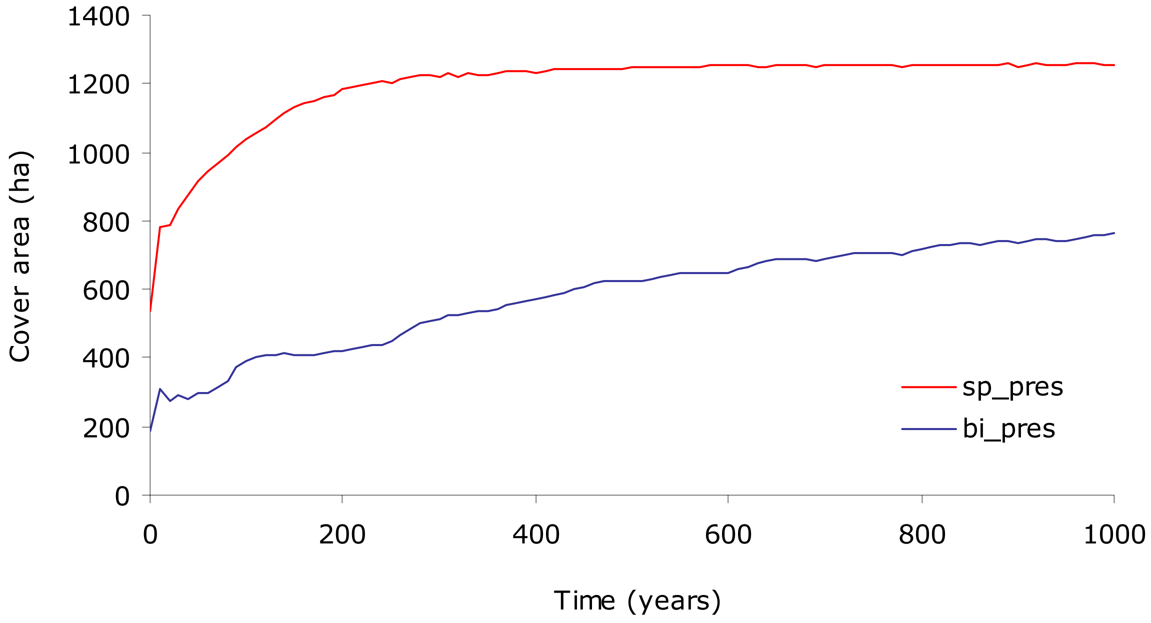


Figure 5.8 Line plot showing cover of pine and birch in default output for landscape-level sensitivity analysis. The legend shows: sp_pres – pine present in any quantity, bi_pres – birch present in any quantity.

5.3.2 Longevity

The t_l parameter determines the scaling of the mortality distribution for each species and hence the longevity of trees and cohorts (See Section 4.1.7). The relative difference in standard parameter values between species is greater for this parameter than any other in the GALDR model (pine – 600; birch – 200). Because of the importance of this parameter in determining separate characters for the two tree species, an uncertainty/behavioural analysis was carried out by varying the parameter value for birch. Variations were made to the birch parameters only, since the principal interest was in analysing the relative difference between the two species rather than looking at absolute differences. The model was run with three values: a standard value of 200 years and two non-standard values of 150 and 300 years. The non-standard values are intended to cover the upper and lower limits of the range of uncertainty. Figure 5.9 shows the effect of variation of the t_l parameter on the survivorship curve for an even-aged stand of yield class eight birch (stochastic effects excluded). The dominant mortality effect for the first 40-60 years is that of self-thinning, which is independent of the t_l parameter. Analysis of smaller variations in t_l gives a value of 0.69 for sensitivity of stand longevity to the t_l parameter.

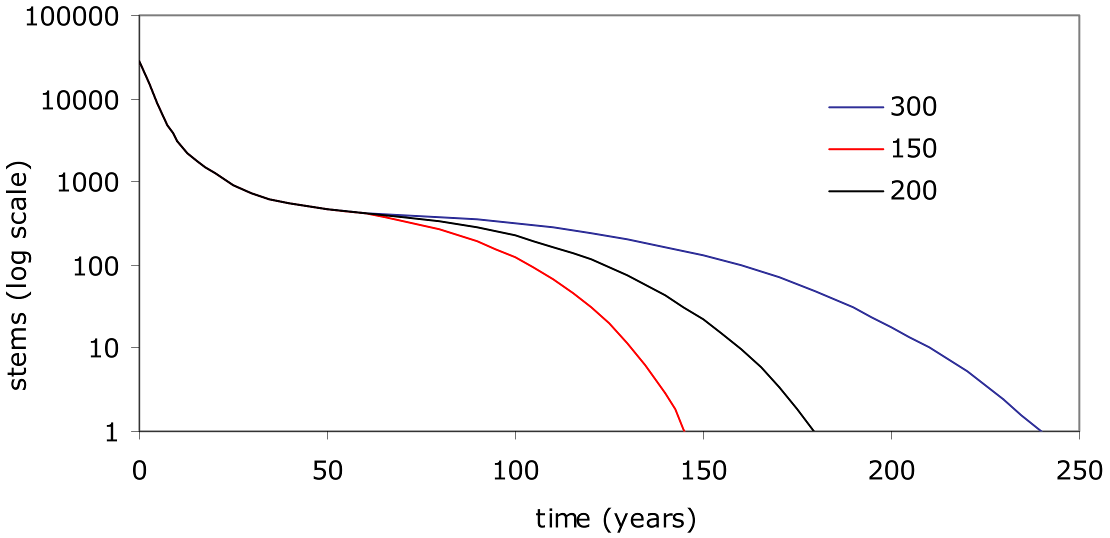


Figure 5.9 Decrease of number of stems over time for yield class 8 birch. Alternative plots show variation of t_l *parameter over three values (150, 200 and 300 years).*

Responses of four landscape output variables to variation in t_l are shown in Figure 5.10. Sensitivity values are high; for example the sensitivity of mx_dom to t_l increases over the 1000 years to a maximum value of 2.77. Differences of behaviour resulting from the altered parameter value are marked, especially in the latter stages of the simulation. For example, under the higher value of t_l, bi_dom is seen to be increasing towards the end of the simulation, whereas under the other values it is decreasing. Similarly, sp_dom increases under the lower value, but decreases otherwise. Under the lower value for t_l, bi_pres seems to stabilize at just over 500 ha, but under the higher value the quantity of birch in the landscape is still increasing at a rate of approximately 0.7 ha/a at the end the simulated period. There is, however, no noticeable effect on sp_pres.

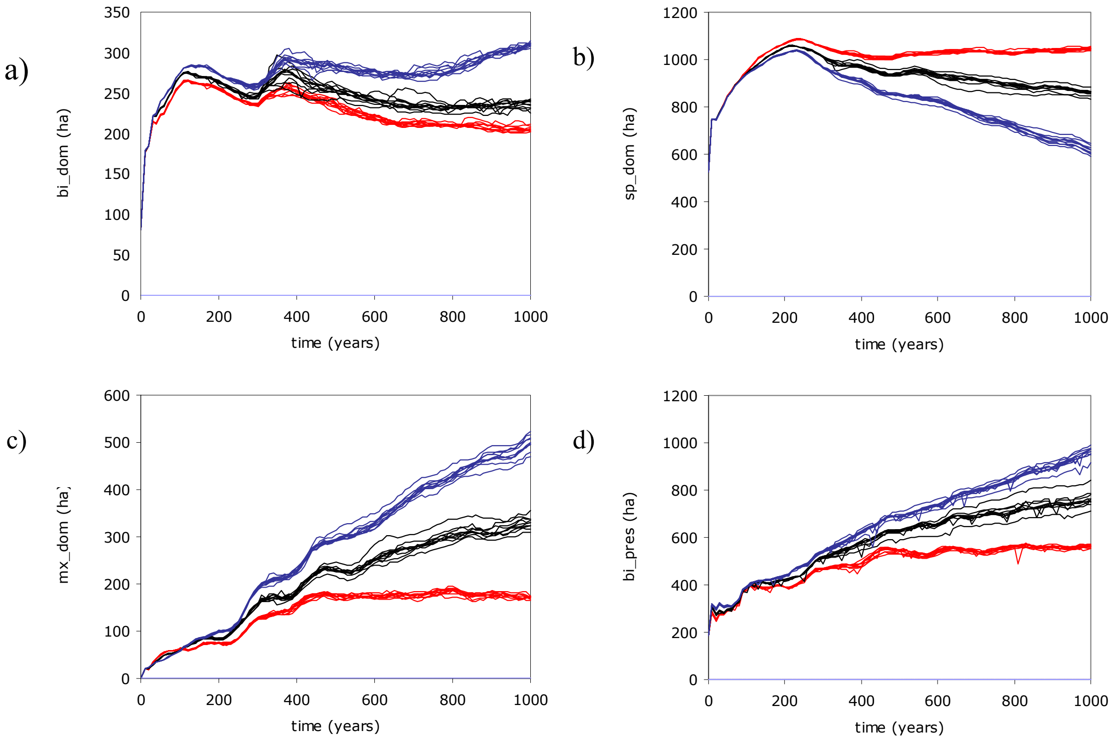


Figure 5.10 Time series graphs showing response of four landscape output variables to variation of the t_l *parameter for birch. Each series shows ten replicates. Black plot – standard value of 200 years; blue plot – 300 years; red plot –150 years. Ordinate axis represents area of woodland (a) dominated by birch; (b) dominated by pine; (c) with pine and birch codominant; (d) with birch present in any quantity.*

5.3.3 Terminal velocity of seeds

Uncertainty analysis on the terminal velocity parameter (*F*) comprised three sets of simulations using values for *F* of 0.5, 0.6 and 0.84 ms^{-1}. The first value is that reported by Greene and Johnson (1996) for *Betula paperifera*. The second is that measured for *Betula pubescens* by S. Brown (unpublished data) and the third is for *Betula pendula* as measured experimentally (see Section 4.3.5). Simulated dispersal curves based on the GALDR dispersal algorithm (see Section 4.3.5) are shown for the three parameter values in Figure 5.11. Generally, the effect of increasing seed terminal velocity is to shift seedfall towards the source.

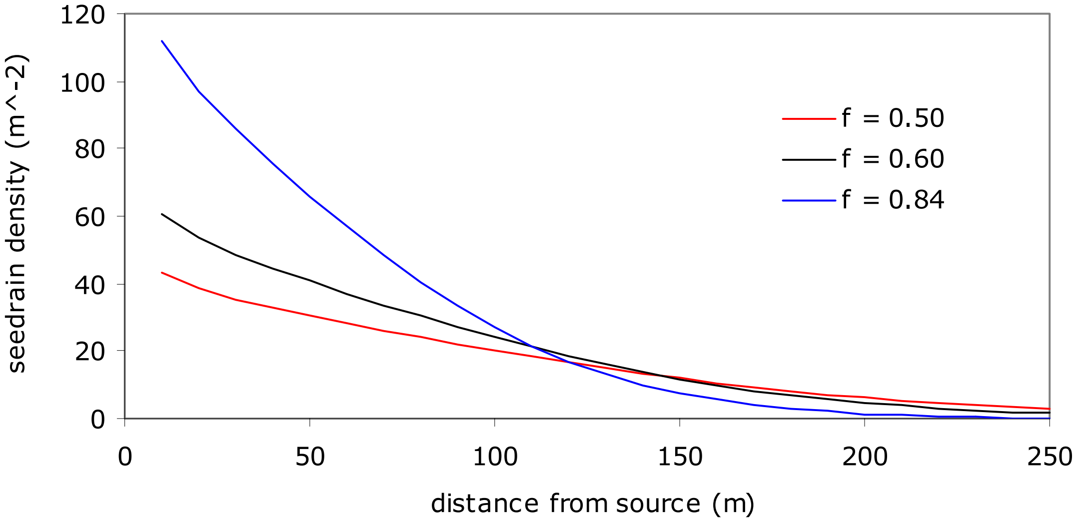


*Figure 5.11 The effects of variation of seed terminal velocity (*F*) on simulated dispersal.*

The landscape effects (Figure 5.12) are less easily interpreted. In the first two hundred years the pattern is similar for both bi_dom (Figure 5.12a) and bi_pres (Figure 5.12b) in that slower seed velocities give greater coverage. However, the situation completely reverses in the case of bi_dom in the latter part of the simulation where the correlation between seed velocity and area dominated by birch becomes positive. The effect on bi_pres is less marked, but at the end of the simulation it is clear that greatest coverage is attained when seed velocity takes the intermediate value. This reversal of the influence of seed velocity may be attributed to change in landscape structure; at the start of the simulation the two tree species tend to exist in unmixed stands and expansion of birch is mainly onto open ground. During this time expansion is favoured by longer dispersal distances. After two hundred years the landscape starts to fill up with woodland, more of the birch exists in mixture with pine and birch expansion is more often on the wetter sites within the pine matrix. At this stage, birch is better enabled to gain dominance of sites from pine if it can produce very high densities of seedfall – thus shorter dispersal distances become more competitive.

The most sensitive variables are bi_dom and mx_dom, but even for those variables, magnitudes greater than 0.5 are only occasionally attained.

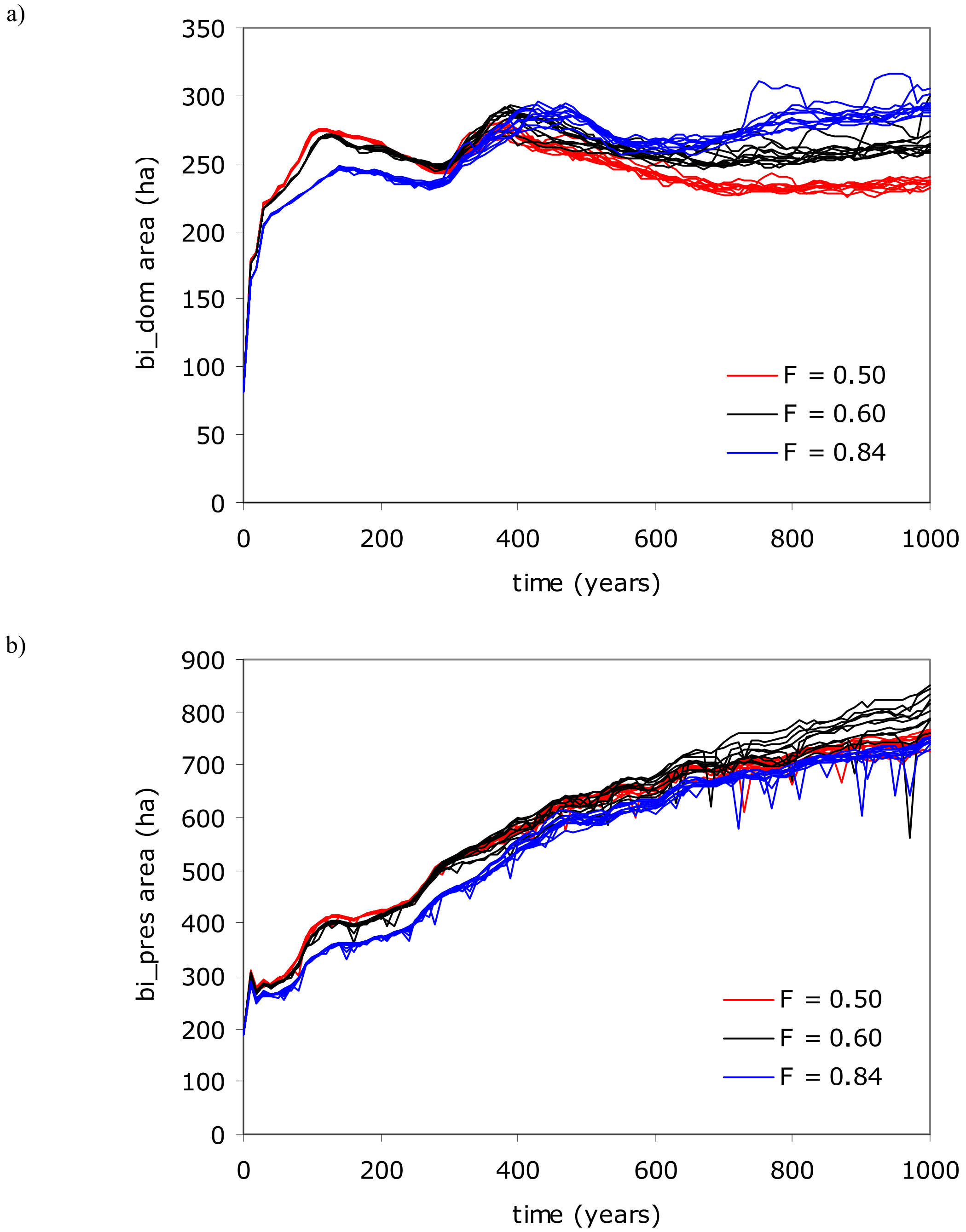


Figure 5.12 Response of landscape output variables; (a) bi_dom and (b) bi_pres to variation in seed terminal velocity. Each series shows ten replicates.

5.3.4 Baseline establishment rate

The parameter E_i determines the proportion of seeds that may germinate and progress to become seedlings. In the current version of the GALDR model, inclusion of both the E_i parameter as well as the Q^* seed production parameter represents a redundancy of function. Multiplication of E_i by a factor x, has an identical effect to multiplying Q_0 by x. The two parameters are both included to increase model comprehensibility and for potential developments in future versions. The default parameterization gives a rather low germination rate for birch, which effectively offsets the effects of the high seed production rate. However, rates of germination and seedling establishment are difficult to assess in the field over a wide range of site types so sensitivity and uncertainty analyses were performed for this parameter. Sensitivities for most variables were generally much higher than those for terminal seed velocity; those for sp_dom, bi_dom, mx_dom, and bi_pres all attained values between 1 and 2 towards the end of the simulation. Uncertainty analyses were carried out with birch : pine ratios for ($Q^{*}\times E_i$) set to 1, 3 and 10. In the latter case pine was eliminated from the landscape after about 800 years. With the ratio set to 3, pine was not completely eliminated by the end of the 1000 year simulation, but was reduced to under 300 ha and was declining by around 2ha/a. The results of these analyses are shown in Figure 5.13.

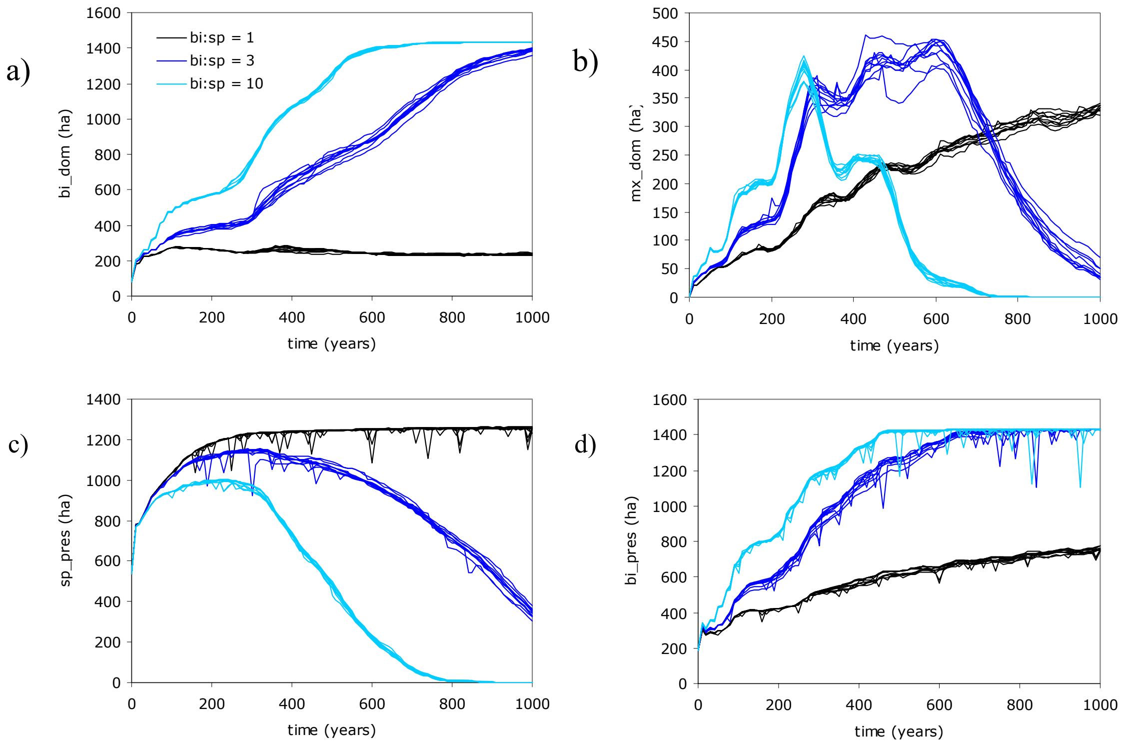


Figure 5.13 Response of four landscape output variables to variation of the E_i *parameter for birch. Each series shows ten replicates. Ordinate axis represents area of woodland (a) dominated by birch; (b) with pine and birch codominant; (c) with pine present in any quantity; (d) with birch present in any quantity. The values of birch : pine ratios of (*$Q^{*}\times E_i$*) are shown in the legend in (a).*

5.3.5 Sub-canopy regeneration

The $\rho_{b\,\max}$ parameter (see Section 4.4.3) determines the maximum stand density that will allow regeneration to occur in a cell. The determination of an appropriate value for this parameter is rather arbitrary, since there are no available data for parameterization of a multicohort model such as GALDR for gap size. An uncertainty analysis was carried out for five values of $\rho_{b\,\max}$ (illustrated in Figure 5.14). Sensitivities fluctuate over the course of the simulation but do not attain magnitude larger than unity. They are generally negative for variables relating to birch and mixed woodland abundance and positive for those relating to pine abundance.

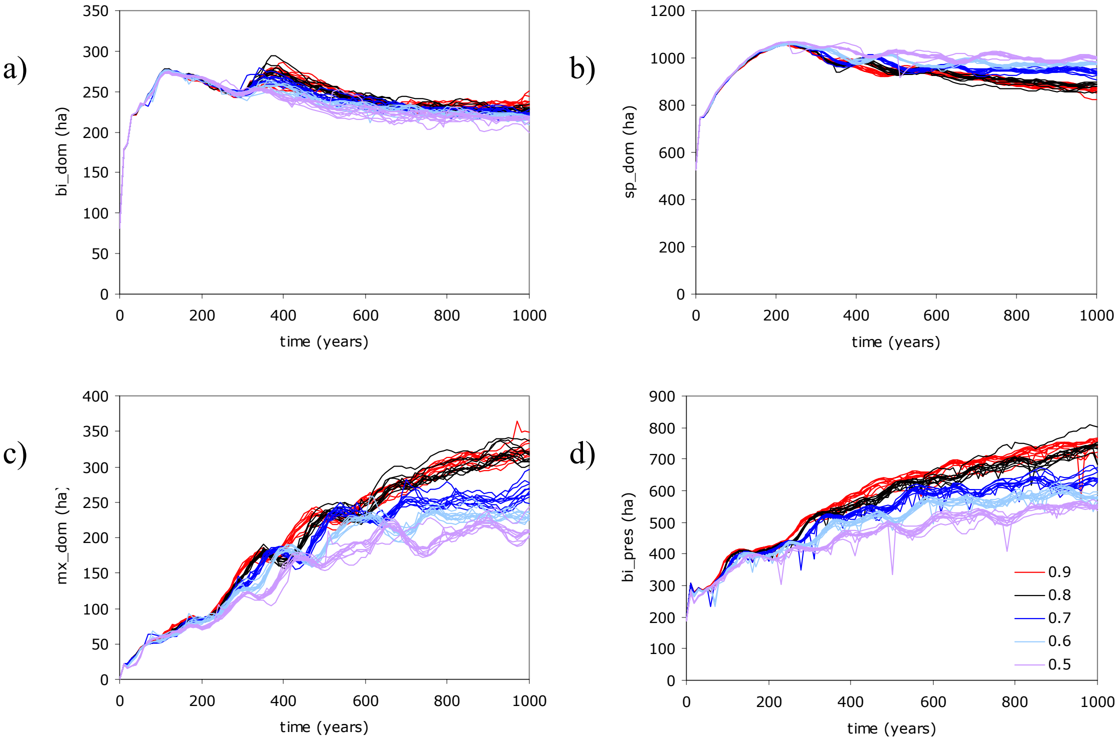


Figure 5.14 Response of four landscape output variables to variation of the $\rho_{b\,max}$ *parameter for birch and pine. Each series shows ten replicates. Ordinate axis represents area of woodland (a) dominated by birch; (b) dominated by pine; (c) with pine and birch codominant; (d) with birch present in any quantity. The legend ascribing plot series to parameter values is shown in (d).*

5.3.6 Frequency of regeneration

The default behaviour for GALDR is to initiate regeneration immediately on every cell that satisfies the conditions of site suitability, gap presence and seed availability. However, the parameter R_i allows the model behaviour to be modified to make regeneration a more spasmodic event (see Section 4.4.2). The occurrence or otherwise of regeneration on sites for which seed availability, soil type and light regime are all ostensibly favourable is difficult to anticipate. Determination of regeneration success in such circumstances is largely dependent on seedbed conditions (microsites), competition from field vegetation and extent of seed predation. These agencies are troublesome to model at landscape scales and are not explicitly simulated in GALDR. An uncertainty analysis simulation was performed with parameter value sets as shown in Table 5.2.

Table 5.2 Parameter values for uncertainty analysis of R_i

Simulation	R_i parameter value	
	Pine	Birch
run 1	1	1
run 2	3	3
run 3	10	10
run 4	6	2
run 5	2	6

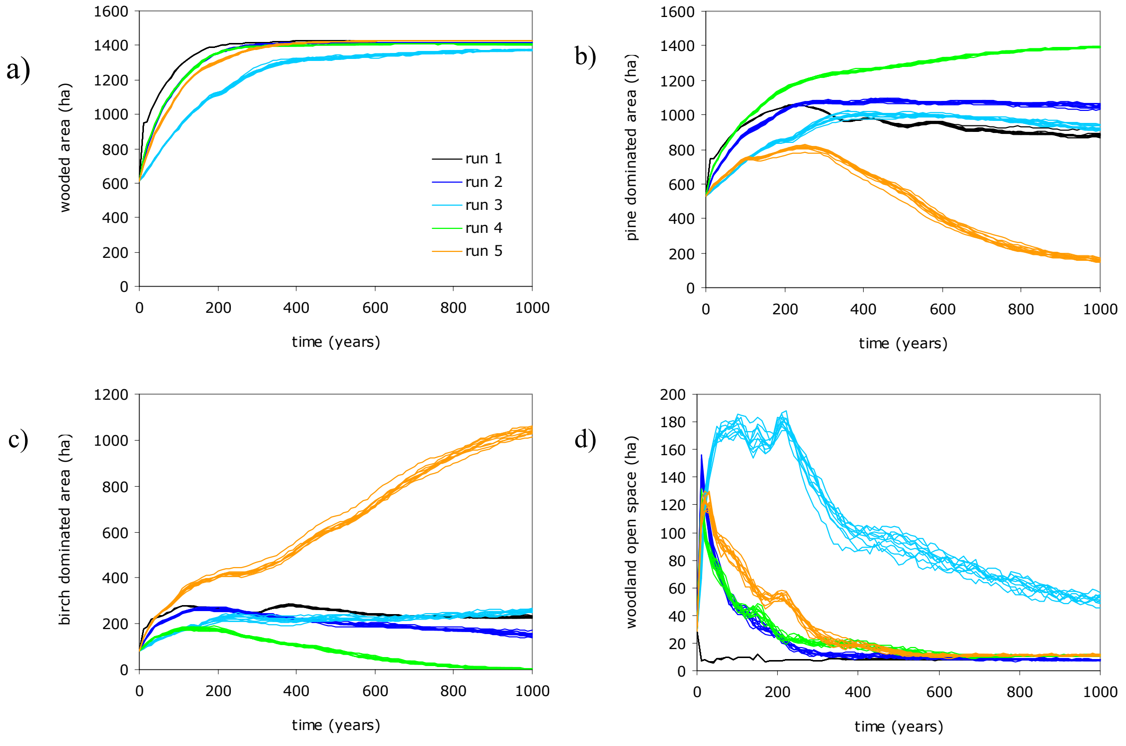


Figure 5.15 Response of five landscape output variables to variation of the R_i *parameter for birch and pine. Each series shows ten replicates. Output variables are: (a) wooded_ha; (b) sp_dom_ha; (c) bi_dom_ha; (d) w_open_ha. Legend shown in (a) relates to parameter sets defined in Table 5.2.*

If treated as a single parameter for both species, sensitivity to R_i is low (<0.2) for most output variables with the exception of w_open_ha which is highly sensitive in the early stages of the simulation (S = 9.5 at first timestep). Despite the low sensitivities however, this parameter is rather critical because of high uncertainty over appropriate values. Especially important in this respect is the relative difference between species. Figure 5.15 shows that a threefold advantage in R_i to either species confers significant competitive advantage in the long term, with the advantaged species tending to absolute domination of the landscape. Clearly, this level of advantage is not realistic over the entire landscape. A more refined model might attempt to incorporate the delayed regeneration effect as a site-specific variable rather than a global parameter.

5.3.7 Wind parameters

Whilst there are many constant terms used in calculations of the wind disturbance submodel, the parameters k (Weibull shape parameter) and Ua (characteristic value) are significant in that their values characterize particular wind climates. The value of k determines the shape of the pdf (see Figure 5.16). The sensitivity of the pdf to variation in k is represented in Figure 5.17. Sensitivity is modest at intermediate wind speeds but becomes very large in magnitude as wind speeds tend to zero or infinity. Large sensitivity magnitudes at small wind speed values are of little consequence since disturbance events depend on high wind speeds. However, the sensitivity at high wind speeds indicates the critical nature of this parameter for consideration of extreme wind speed events. The value of Ua does not influence the Weibull distribution at all but instead determines the central tendency of the Gumbel distribution of extreme wind speeds. Figure 5.18 shows the effects on the Gumbel distribution pdf of small changes to these parameters. It is clear that from (a) and (b) that variations in k produce more dramatic effects than similar variations in Ua. The sensitivity plot in Figure 5.18c demonstrates that sensitivity magnitudes become extremely large towards the tails of the distribution with k and Ua the more sensitive parameters for the right and left tails respectively.

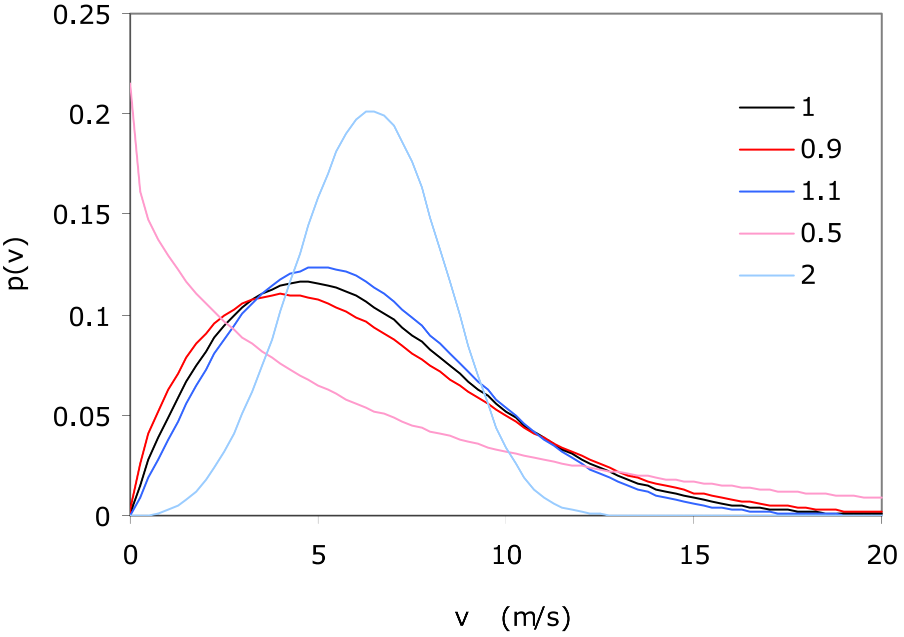


Figure 5.16 Weibull distribution (pdf) of wind speeds under variation of k *parameter (DAMS = 20). The legend indicates the ratio* k/k_{std} *where* k_{std} *is the default value (1.85).*

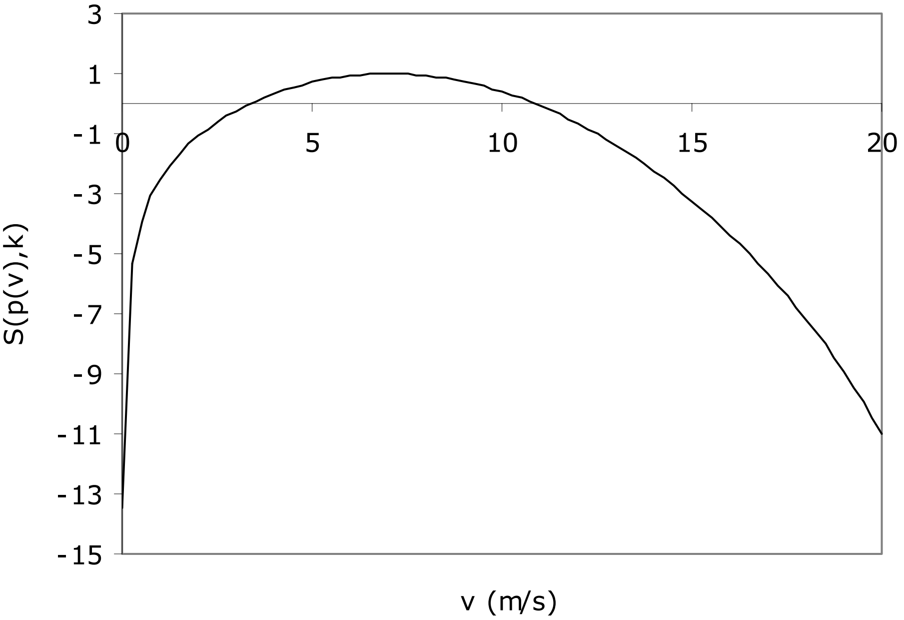


Figure 5.17 Sensitivity of the pdf of wind speed to the k *parameter (DAMS = 20)*

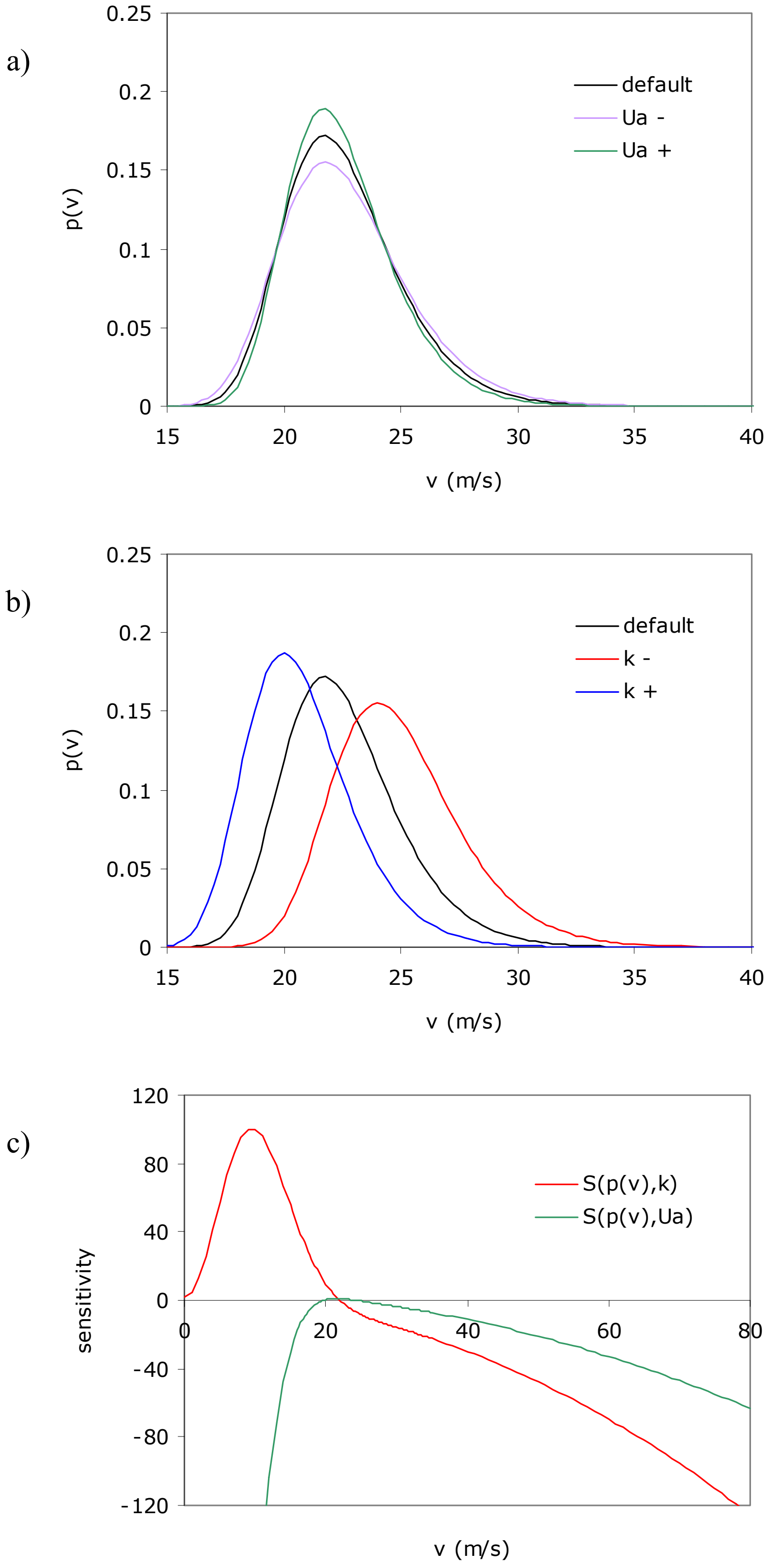


Figure 5.18 Effects of varying parameters on the Gumbel distribution pdf for maximum wind speeds (DAMS = 20). (a) ±10% variation of the Ua parameter (b) ±10% variation of the k parameter (c) sensitivity plots of S(p(v),λ) where p(v) is the extreme value type I pdf for maximum wind speeds and λ is taken by the parameters k and Ua.

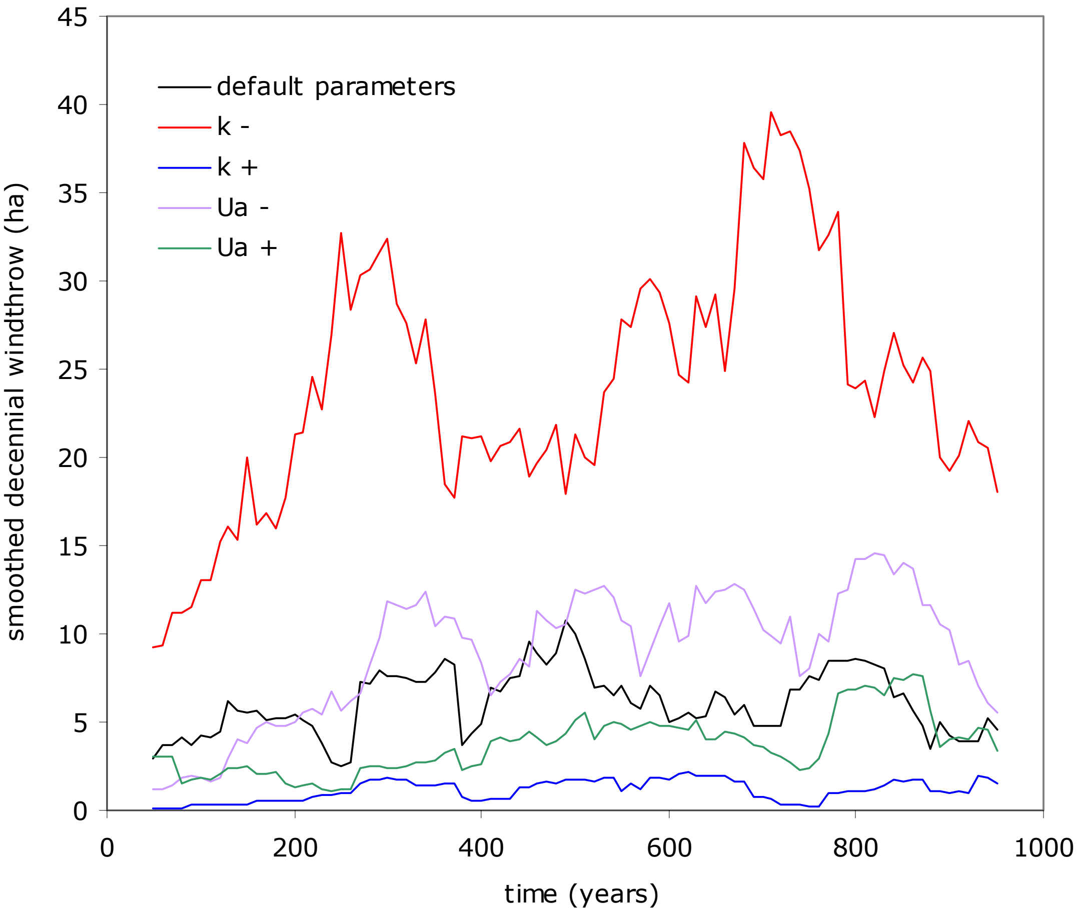


Figure 5.19 Effects of varying the k *and* Ua *parameters by ±10% on amount of windthrow over a 1000 year GALDR run. Series show means over ten replications.*

To investigate the landscape effects of these parameters GALDR was run with *k* and *Ua* parameters altered one by one by ±10%. A graph showing temporally smoothed data for mean area of windthrow per timestep is shown in Figure 5.19. The data were smoothed and averaged over all replications because the raw output data showed large variation and consisted of a large quantity of 'spikes' making interpretation difficult. The smoothing method was simply to replace individual timestep values with mean values from all timesteps within a 50-year radius. Even allowing for the smoothing and averaging over ten replication there appears to be considerable stochastic variation in the output although some temporal trends can be seen that appear to be common to all series. Sensitivity values do not show any discernible temporal trends. Means and standard deviations for sensitivity values are shown in Table 5.3 below.

Table 5.3 Mean standard and deviation for sensitivity of area of windthrow to wind submodel parameters

Parameter	Mean sensitivity	Standard deviation
k	-20.3	-4.35
Ua	9.2	2.6

These exceptionally high sensitivity values do not apply to all output variables. Total wooded area shows almost zero sensitivity. A sensitivity plot for area of old pine dominated stands (Figure 5.20) shows an intermediate case. Note the asymmetry between S_+ and S_- values. The dip in S_- values at approximately 500 years simulated time corresponds to a bottleneck in quantity of old pine.

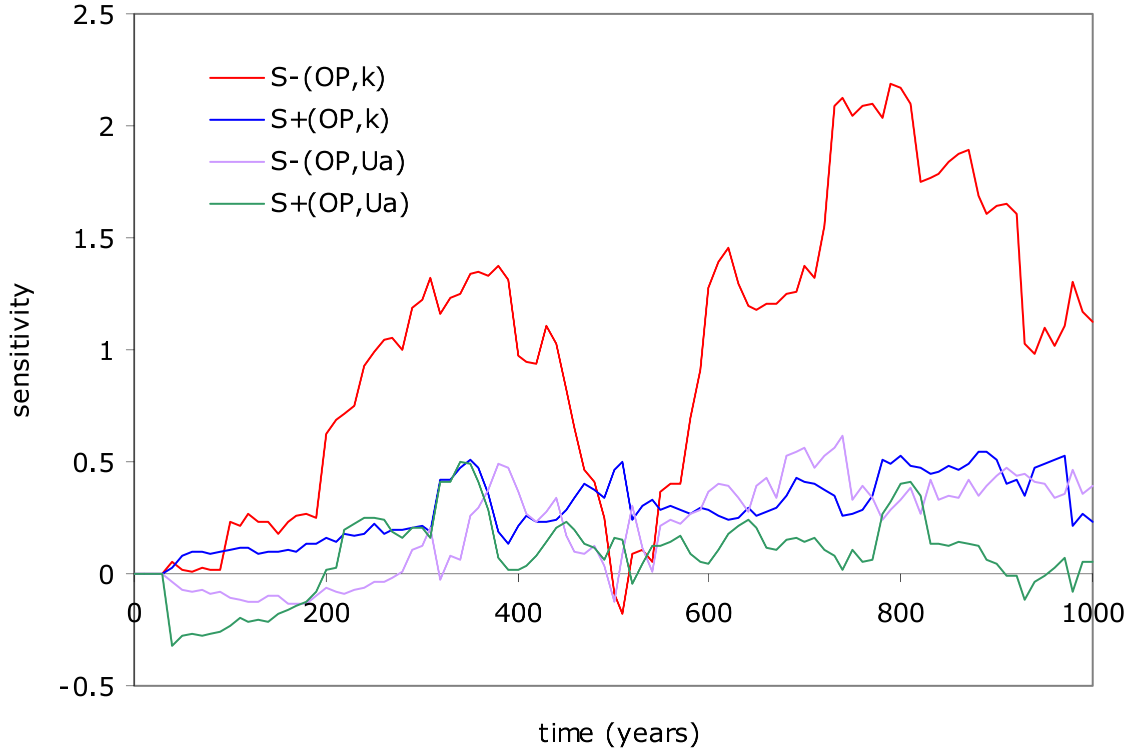


Figure 5.20 Sensitivity of area of old pine-dominated stands to k *and* Ua *parameters (mean values for ten replicated simulations).*

5.4 Conclusions

The first stated aim of the sensitivity analysis reported in this chapter was to gain a broad picture of the sensitivity of the model to its parameter values. Clearly, a complete tabulation of sensitivity of all output variables to all combinations would be unfeasible; however, the following generalities may be drawn from the analyses that have been performed.

- Some output variables, notably those representing total wooded area and area of pine dominated woodland, tend to be relatively insensitive to parameter variation.
- Sensitivity to species-specific parameters tends to be greatest for the output variable representing area of mixed woodland.
- Sensitivity values show a tendency to increase in magnitude over time indicating a cumulative nature for the effects of parameter variation.
- Sub-model sensitivity often gives some indication of overall model sensitivity (estimation of which can often be done analytically, without recourse to simulation experiments).

The second aim of the analysis was to identify parameters showing particularly high or low sensitivity. None of the parameters showed very strong buffering for all output variables; the lowest maximum sensitivities were for the growth model parameter B. Birch presence showed sensitivity of - 0.56 to B, which is large enough to suggest that the parameter serves some function.

Identification of amplifying parameters is straightforward; wind parameters k and Ua stand out clearly for their exceptionally high sensitivity values. This situation would appear to be unavoidable however, as high sensitivity is inherent in the prediction of extreme wind speeds. The best that can be hoped for in this respect is for better parameter estimation as more data on wind speeds are gathered. However, this would not dispel uncertainty relating to long-term changes in the wind climate.

In addition to the quantification of sensitivities, the sensitivity analysis provides a useful opportunity to examine the behaviour of the model and observe the effects of altering the underlying assumptions.

6 Lichen modelling

6.1 Introduction

This chapter demonstrates the use of the GALDR model and SELES to produce a predictive model of abundance for the epiphytic lichen *Bryoria furcellata*. The model has been called the Glen Affric Lichen Abundance Model (GALAM).

Glen Affric is nationally important for its lichen communities, containing nine nationally rare species and 30 nationally scarce species (B.J. Coppins, unpublished data). It is thought that the presence of many of the pinewood specialist species indicates a long history of habitat continuity. The concept of lichen species as ancient woodland indicators was developed by Rose (1974; 1976; 1992). Such indicator species tend to have poor dispersal, and so sites that have seen a discontinuity in provision of suitable habitat are often not re-colonized following re-establishment of favourable conditions. Rose developed the concept of the *index of ecological continuity* based on the number of ancient woodland indicator lichens present on a particular site. Since many lichen species are restricted in geographical range across Britain, different indices have been created for different parts of the country.

Because of the distinctive lichen flora found in native pinewoods, this habitat has its own index – the Native Pinewood Index of Ecological Continuity (NPIEC; Coppins and Coppins, 2002). Assessed according to the NPIEC, Glen Affric ranks second only to Glen Strathfarrar amongst the British pinewoods. Lichens are perhaps especially important in gauging ecological continuity in pinewoods because of the absence of plant indicators. Pitkin *et al.* (1995) state that no single embryophyte provides invariable indication of long-term ecological continuity in pinewoods (although appropriately chosen groups of species may reliably indicate ‘considerable age’). The non-lichenized fungi may also prove useful in this respect; Orton (1986) presents a list of c. 135 species of agaric fungi recorded from pinewoods, with around 43 species that may be restricted to Caledonian pinewoods. However, detection of non-lichenized fungi generally depends upon the production of fruiting bodies, which may be irregular from year to year.

The specialized habitat requirements and limited dispersal abilities of species such as *Bryoria furcellata* make them highly suitable as indicators of ecological continuity for old-growth forest habitat. Similarly, such species make good subjects of Spatially Explicit Population Models (SEPMs) based on Habitat Suitability Models (HSMs) derived from GALDR stand structure output. The limitation on dispersal ability will serve to highlight the influence of spatial and temporal connectivity of suitable habitat on the predicted abundance of the species. Thus, the ratio of the number of cells occupied by the focal species to the number of cells containing suitable habitat (the *occupancy*) may be considered to be a measure of the spatio-temporal connectivity of the habitat over the course of the simulation.

Most models of lichen growth concern the rates of growth of individual thalli of crustose species on rock substrates (lichenometry; see Winchester, 1984). However, the published literature does contain one described landscape model of lichen abundance (LA). Lichen Biomass Spatially Explicit Model (LIBSEM; Dettki, 2000; Dettki and Esseen, 2003) is a raster-based model of biomass dynamics for lichens of the genus *Bryoria*. Although the initial development of the Glen Affric lichen model was completed without reference to the LIBSEM model, the two models are similar in many respects. Both represent the spatial structure of the populations on a 50 m raster grid and use logistic models regulated by a carrying capacity based on habitat variables. The main differences between the models are that GALAM measures LA in terms of numbers of thalli of *Bryoria furcellata* only, whereas LIBSEM measures LA in terms of biomass of all *Bryoria* species. (Whilst biomass may actually be a more meaningful measure of abundance, counting thalli is a much more readily achieved survey method. More importantly, the rarity and protected status of *Bryoria furcellata* precludes the removal of specimens for weighing.)

LIBSEM has been parameterized by an extensive programme of fieldwork (Dettki and Essen, 1998; Dettki, 1998; Dettki *et al*., 2000) whilst GALAM relies on casual observations, expert opinion and analogy with other studies. On the other hand, the forest dynamics subroutine of LIBSEM is relatively simple compared to the GALDR model. The advantage of a more sophisticated habitat dynamics simulator should be the greater ability to predict over long timescales. Since the survival of old-growth lichens (as well as many other taxa) is crucially dependent on long-term dynamics, such studies may prove vital in informing successful conservation.

6.2 *Bryoria furcellata*

6.2.1 Description

Bryoria furcellata is a pinewood specialist, found in only four sites in the UK – all in old native pinewoods. (Of these, all but one are in the Beauly catchment group of pinewoods which includes Glen Affric, Guisachan Forest and Glen Strathfarrar.) The growth-form is fruticose (shrubby) and the appearance (see Figure 6.1) is rather small and spiky compared to the more common members of the genus, which tend to adopt a pendulous growth form.

Figure 6.1 Thallus of Bryoria furcellata *growing with* Imshaugia aleurites *(white) on bark of a mature pine tree (scale is approximately ×2.5). Pollan Buidhe, Glen Affric. Photo: J. Hope.*

The species is of conservation importance; it is nationally rare, occurring in only four ten-km squares in Britain and it is classed as 'vulnerable' on the British Red Data List. It is one of 30 lichen species appearing on Schedule 8 of the 1981 Wildlife and Countryside Act. Outside Britain the species is widely distributed, occurring in northern, eastern and central Europe, north and central America, the Himalaya and Japan (Purvis *et al*., 1992).

6.2.2 Habitat

One reason for the scarcity of *Bryoria furcellata* in Britain may be its rather particular habitat and substrate requirements. The following is quoted from the ecology section of the species dossier for *Bryoria furcellata* (O'Dare and Coppins, 1995) produced as part of the Scottish Cryptogamic Conservation Project.

‘In Scotland, *Bryoria furcellata* occurs in relict native pinewoods with eu- to hemi-oceanic, southern boreal conditions, on sheltered to moderately exposed, cool, rather wet foothills and local valleys. It requires fairly well-illuminated and ventilated situations, with some degree of shelter and humidity, and so appears to be restricted towards the valley bottoms and edges of bogs of the lower parts of relict native pine woodlands. It is found mostly on open stands of *Pinus* (twigs, bark and decorticated areas of trunk and branches), but also on *Betula* (twigs and small branches), moribund *Calluna* stems and twigs, and even old fence posts (Glen Affric).’

Following conversations with A.M. Coppins, the following further points regarding the habitat and substrate preferences of *Bryoria furcellata* are postulated.

- Substrate stability is likely to be important to successful colonization and growth. This may be one reason why younger pine trees generally do not support populations, since in the early, faster period of growth pine trees tend regularly to slough off bark plates. Older trees slough off bark much more slowly and develop cracks and fissures that provide sheltered conditions and a more stable substrate.
- Exposed pine lignin may constitute a preferred substrate over old bark. Of the populations of *Bryoria furcellata* that have been discovered, the number found on decorticate trees has been disproportionately high in comparison to the relative availability of bark versus lignin. This may be due in part to sampling bias, though there is reason to suppose that the high substrate stability of the lignin could be a causative factor.
- Whilst thalli are sometimes found on birch and heather, these may be sub-optimal substrates for *Bryoria furcellata* corresponding to the ‘sink’ in a source-sink system, where pine bark or lignin provides the source. Supporting evidence is provided by the observation that thalli are found on birch and heather only in the vicinity of mature pine trees and in woodlands with a long history of pine presence.

6.2.3 Dispersal characteristics

Notwithstanding this marked preference for old-growth pine stands, the scarcity of *Bryoria furcellata* is unlikely to be due entirely to lack of suitable habitat. There are 77 native pinewoods in Scotland, many of which could contain suitable habitat, besides stands of planted Scots pine which are starting to display old-growth characteristics (see Peterken *et al.*, 1992). It is therefore probable that poor dispersal may be responsible for its restricted British range. Dispersal of *Bryoria furcellata* may be via soredia – small propagules composed of a few cells of the algal symbiont bound by hyphae of the fungus – or by fragmentation of the thallus. Stevenson (1988) reports on three studies that conclude that thallus fragmentation is the most important mechanism for the initial colonization of forest stands by fruticose lichens (*Alectoria*, *Bryoria* and *Usnea* species).

Comparative studies on the dispersal and colonization abilities of *Alectoria sarmentosa* and *Bryoria* species (Dettki, 1998; Stevenson, 1988) have concluded that while species of *Bryoria* may disperse effectively up to 100 metres or more, *Alectoria sarmentosa* is an extremely poor disperser since thallus fragments tend to be larger, heavier and fewer. However, circumstantial evidence based on the current British distribution of *Bryoria furcellata* suggests that the dispersal capabilities of this species may be more akin to those of *Alectoria sarmentosa* than to the more common members of the *Bryoria* genus. The most common British *Bryoria* species is *Bryoria fuscescens*, which is extremely widespread across northern Britain and occurs on trees in a wide range of habitat types. By contrast, *Bryoria furcellata* is more restricted in its British distribution even than *Alectoria sarmentosa* and, for the Beauly catchment sites at least, populations of *Bryoria furcellata* are always associated with *Alectoria sarmentosa*.

Bryoria furcellata plants tend to be smaller than *Bryoria fuscescens* so it seems unlikely that the inequality in dispersal ability is attributable to differences in thallus fragment size. The reason for the poor dispersal of *Bryoria furcellata* may depend upon the species avoidance of wind exposure. Clearly, wind dispersed propagules will not travel so far when originating from sheltered locations. Also, *Bryoria furcellata* may be inhibited from ascending tree stems to the same heights as *Bryoria fuscescens*. Higher stem positions will confer many advantages for dispersal on account of higher wind speeds, greater variability of vertical component of wind speeds and longer duration of freefall for propagules.

6.3 Overview of the lichen model

GALAM consists of two parts, each corresponding to a SELES Landscape Event. The first part is the lichen habitat model (HSM), which predicts the distribution and quality of habitat suitable for *Bryoria furcellata*. The second part is the population model (SEPM), which predicts the actual abundance of the lichen (LA) over the suitable habitat. The model framework is shown schematically in Figure 6.2 (cf. Figure 1.1).

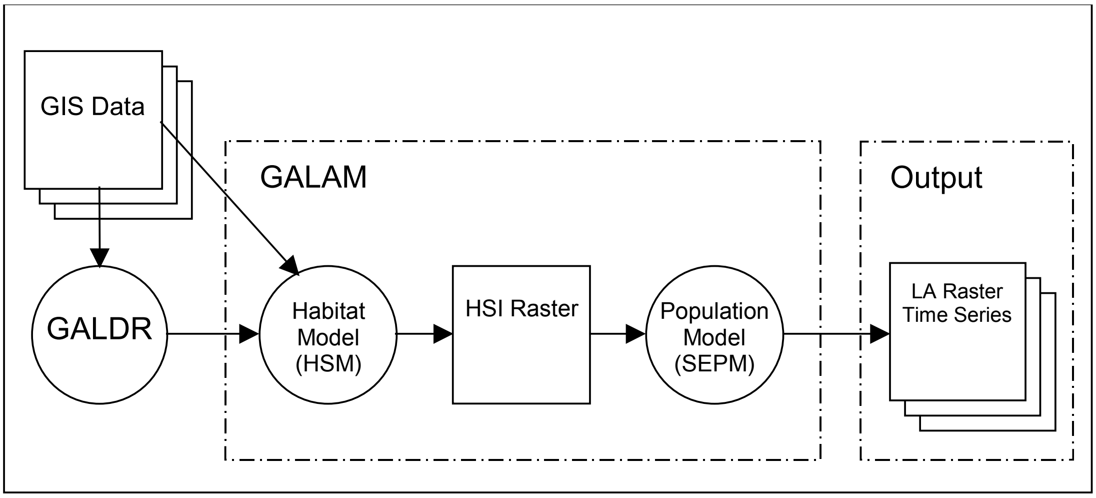


Figure 6.2 Diagrammatic representation of linkages in GALDR and GALAM. Squares represent datasets; circles represent models. Solid arrows show data flow

The output of the habitat model is a dynamic raster, of which cell values represent percentage Habitat Suitability Index (HSI) for *Bryoria furcellata*. The population model then uses the HSI to determine the carrying capacity of each cell. The population model simulates the species dynamics in the changing habitat and outputs a dynamic raster time series of LA in terms of numbers of thalli. The model also outputs seven global statistics derived from the habitat and LA rasters (shown in Table 6.1).

Table 6.1 GALAM global statistics output.

Variable	Description	Definition	Units
ALC	Area colonized by lichen	Area of cells where LA > 0	ha
TLA	Total lichen abundance	Σ LA	no. thalli
MLA	Mean lichen abundance	TLA / ALC	no. thalli
ASH	Area of suitable habitat	Area of cells where HSI > 0	ha
THS	Total habitat suitability	Σ HSI	-
MHS	Mean habitat suitability	THS / ASH	-
LHO	Lichen habitat occupancy	ALC / ASH × 100	%

6.4 Habitat Suitability Model

As for the main GALDR model, the HSM is calculated for cells of a grid of resolution 50 m × 50 m. The quality of the habitat is expressed as a Habitat Suitability Index (HSI) for each cell, taking percentage values from between zero and one hundred. An HSI of zero indicates that the habitat is completely unsuitable for the target species. An HSI of 100 indicates that the cell provides the greatest habitat provision possible (number and extent of suitable niches at a maximum) within that general geographic area.

The factors used in determining habitat suitability are as follows.

Factors determining substrate availability, calculated for each cohort:

- Species
- Cohort age
- Number of stems

Factors determining environmental suitability, calculated for entire cell:

- Light regime
- Wind regime

The number of thalli that may be supported by each cohort is calculated on a cohort-by-cohort basis and then summed over all cohorts to yield a figure for the entire stand. This number may be reduced by multiplication with the *environment factor*, which is calculated as the product of the illumination and wind factors. Logistic relationships have been used to model the effects of these factors (as well as the cohort age factor), thus providing a smooth transition from ‘suitable’ to ‘unsuitable’ habitat.

In contrast, the LIBSEM model uses only stand age and ‘edge effects’ to quantify habitat suitability for *Bryoria* species. The edge effects, which are always negative, represent combined effects of differing light, wind and humidity levels at the forest edge.

6.4.1 Phorophyte species

On the basis of the discussion in Section 6.2.2, only cohorts of pine are considered in the provision of substrate. Therefore birch cohorts are ignored at this stage of the model, but they will influence the wind and light regimes at the entire stand level.

6.4.2 Cohort age

It is assumed that the number of thalli that could be supported by a tree will increase with age. The assumption is based on observation and may be explained by three factors. These are that, in general, older trees are:

- larger, allowing more potential microhabitat niches;
- slower growing, so providing more stable substrate;
- more likely to contain deadwood and exposed lignum.

A logistic model is used to describe the relationship between cohort age and the number of thalli that could be supported by each stem in optimal conditions (denoted H_{age}). The formula is given below and is represented graphically in Figure 6.3.

$$H_{age} = 10\left(1 + e^{-\frac{1}{20}(age-200)}\right)^{-1} \qquad (6.1)$$

(Note that H_{age} is effectively zero for ages of 100 or less.)

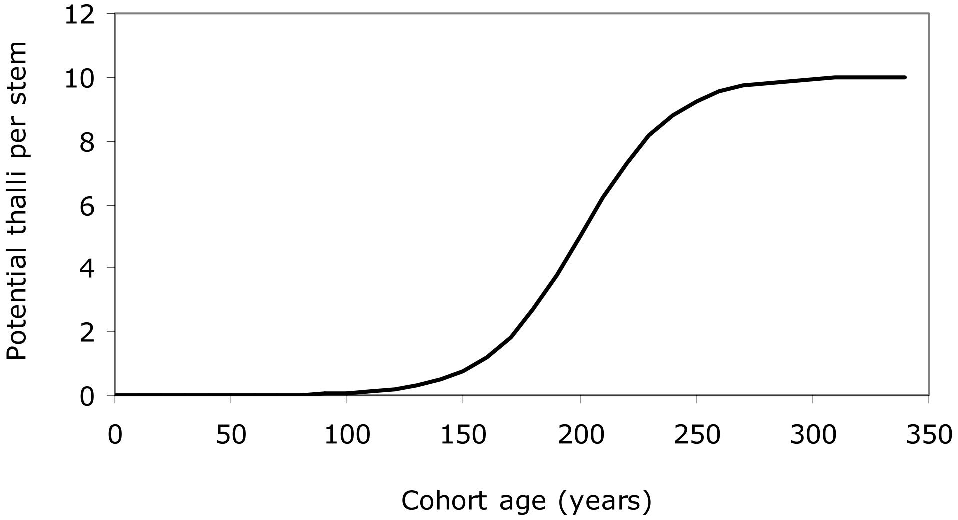


Figure 6.3 Relationship between stem carrying capacity and cohort age.

By way of comparison, the age relationship used in LIBSEM is shown algebraically below as Equation (6.2) and graphically in Figure 6.4.

$$Biomass = \begin{cases} 0 & | \, 0 \le age \le 29 \\ -4.54\times10^{-6} age^3 + 1.63\times10^{-3} age^2 - 4.31\times10^{-2} age & | \, 29 < age < 250 \\ 20.5 & | \, age \ge 250 \end{cases}$$

(6.2)

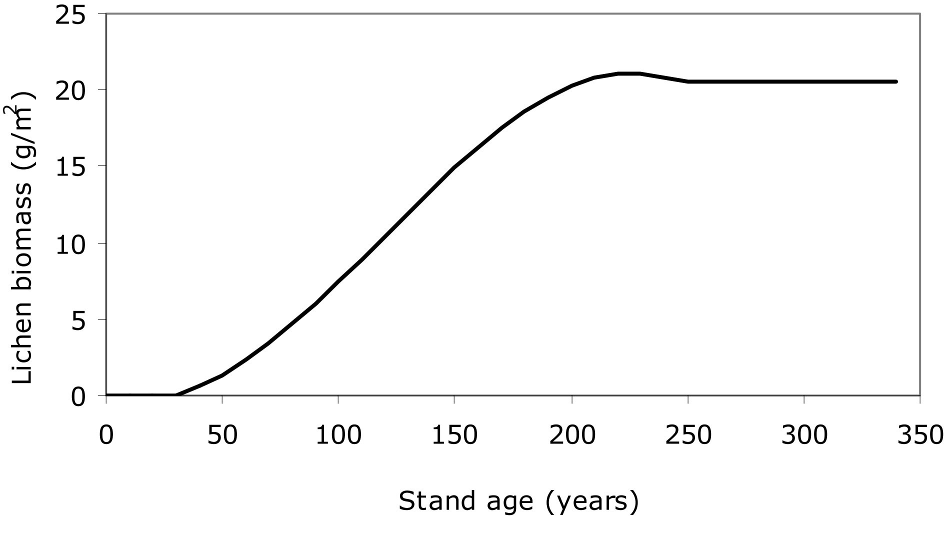


Figure 6.4 Empirical relationship of biomass of Bryoria *species against forest stand age used in LIBSEM model (after Dettki and Esseen, 2003).*

The points of note in the comparison are as follows.

1. Whilst the distinction between biomass and numbers of thalli is probably not particularly critical here, it is important to note that the GALAM abundance is per tree stem whilst the LIBSEM abundance is per unit area. Assuming that self-thinning operates in the young stands surveyed by Dettki and Esseen (1998), the corresponding per-stem abundance values for the LIBSEM model would be relatively less for younger stand ages than those of the per unit area relationship.
2. In the LIBSEM model, stand age acts as a surrogate for light, ventilation and humidity as well as representing the suitability of the trees as substrate.
3. Despite somewhat dissimilar mathematical and conceptual constructions, the two curves follow a similar, broadly sigmoid, shape.
4. The minimum age for suitable habitat is much younger in the LIBSEM model. This agrees with observations that *Bryoria fuscescens* generally colonizes younger trees than *Bryoria furcellata* does (but see also note 1, above).

6.4.3 Light regime

As stated in 6.2.2, *Bryoria furcellata* requires fairly well-lit conditions for survival. In GALAM, the stand density index (SDI) has been used as a surrogate for light levels within the stand. The *illumination factor*, H_{light}, is determined as a logistic function of SDI (here given as a percentage).

$$H_{light} = \left(1 + e^{\frac{1}{4}(\mathrm{SDI}-15)}\right)^{-1} \tag{6.3}$$

The threshold value of 15% SDI has been estimated from stand characteristics of known locations for *Bryoria furcellata*. Neighbourhood effects of illumination have so far not been included. Such effects could take account of tree heights and stocking densities of immediately adjacent cells.

The logistic relationship for light regime may not be suitable for some lichen species, which may be damaged or killed by higher light intensities. Gauslaa and Solhaug (1996) suggest that some old-forest indicator species (particularly those of the *Lobarion* community) may be especially susceptible to effects of photoinhibition. However, observations of *Bryoria furcellata* thalli on unshaded trunks of dead pine trees on south facing slopes may indicate that this species is not limited by overillumination.

6.4.4 Wind regime

It is proposed that the wind regime plays a major role in determining the suitability of habitat for *Bryoria furcellata*. The species dossier (O'Dare and Coppins, 1995) implies that the requirement for shelter from wind is important in determining local distribution (see Section 6.2.2).

The effects of exposure to wind on lichen growth and survival can be summarized in four points (A.M. Coppins, personal communication):

1. Mechanical agitation of the thallus
2. Temperature reduction due to wind-chill
3. Reduction of ambient humidity levels
4. Rapid drying of the thallus after precipitation

The approach taken to modelling the effect of wind exposure has been to modify the DAMS model to produce a measure of windiness within stands.

The usual model for describing the wind profile within a stand of trees (or indeed any tall crop) is by an exponential relationship:

$$u_z = u_h e^{-\alpha(1-z/h)} \tag{6.4}$$

where h is the height of the top of the canopy, u_z is windspeed at height z, u_h is windspeed at height h, and α is a constant term.

The constant term α is dependent upon the permeability of the canopy to airflow, and hence related to the canopy density. White (undated) found that in stands of Sitka spruce, good relationships with α could be drawn with either Leaf Area Index (LAI) or the ratio of tree spacing and height. A formula for the latter relationship is given below:

$$\alpha = -2.4\ln\left(s/h\right) + 1.62 \tag{6.5}$$

To simplify the algebra an assumption can be made relating to the region of interest on the tree stems. O'Dare and Coppins (1995) report that thalli occur at a vertical height from the ground from about 1m to at least 2.5 m, but that the limitation of inspection from ground level precludes determination of an upper limit.

Under the assumption that thalli can colonize the lower third portion of the stem, we can use (6.4) to calculate the wind speed for the middle of this zone as

$$u_z = u_h e^{-5\alpha/6} \tag{6.6}$$

Then substitution of (6.5) into (6.6) gives

$$\begin{aligned} u_z &= u_h e^{2\ln(s/h)-1.35} \\ &= 0.26\, u_h \left(s/h\right)^2 \end{aligned} \tag{6.7}$$

which can be expressed in terms of the SDI as

$$u_z = 0.26\, u_h \frac{T^2}{\mathrm{SDI}}. \tag{6.8}$$

With the expression in this form it is clear that the relationship will not be valid for very low density stands where SDI < $0.26\ T^2$. (In such cases, wind speeds would be predicted to be higher within the canopy that at the top of the canopy, which is clearly unrealistic.) A simple indicative measure of within stand windiness is presented as WISDAMS (Within-Stand DAMS) below:

$$\mathrm{WISDAMS} = \frac{\mathrm{DAMS}}{1+\left(\mathrm{SDI}/\mathrm{SDI}_{0.5}\right)} \tag{6.9}$$

where $\mathrm{SDI}_{0.5}$ is a constant term. This expression has the following characteristics.

1. As SDI → 0, WISDAMS → DAMS

2. WISDAMS = DAMS/2 when SDI = $\mathrm{SDI}_{0.5}$

3. For denser stands, WISDAMS is approximately inversely proportional to SDI

Accurate prediction of wind speeds in very open woodland poses a complex problem since the habitat represents an intergrade between two habitat types normally modelled in two different and disparate ways. Vertical wind speed profiles in denser woodland is normally modelled as an exponential relationship as above whereas in open situations the wind profile is generally represented as increasing logarithmically. Construction of a hybrid model to predict wind speeds accurately would present many difficulties of definition and would result in an algebraically unwieldy expression. Thus, the above model has been used as the simplest solution to the problem of deriving *indicative* values of windiness. As with DAMS, the scale of WISDAMS is arbitrary – the limits for suitable habitat being set by calculating WISDAMS values for sites known to contain *Bryoria furcellata* in Glen Affric. The only parameterization needed in the WISDAMS model is determination of the value of $SDI_{0.5}$ – the stand density that reduces wind speeds to 50% of open situations. Such determination could be made by siting anemometers or tatter flags in pinewood stands of varying density as well as in similar open sites. In the absence of such data however, a provisional value for $SDI_{0.5}$ of 0.1 has been used.

Wind effects of neighbouring vegetation

With a grid resolution of 50 metres, the density of forest vegetation surrounding that of any particular locus will have an important influence on the windiness of the focal cell. Vegetation bordering on the south, south-west and west will be particularly important. For this reason, a modified indicator, WISNDAMS (Within-Stand Neighbourhood DAMS), is used as the actual indicator of windiness in gridcells. WISNDAMS is defined as the mean value of WISDAMS over the focal cell and its three adjacent neighbours to the south, south-west and west. The neighbourhood effect thus serves a similar function as the LIBSEM edge effect for wooded cells bordering non-wooded cells to the south or west.

Combined wind effects on habitat

The effect of the WISNDAMS indicator is modelled as a logistic response with inflexion point at the threshold windiness value. A formula for the wind factor, H_{wind}, is given below.

$$H_{wind} = \left(1 + e^{(\text{WISNDAMS}-10)}\right)^{-1} \tag{6.10}$$

6.4.5 Factors excluded in determination of suitable habitat

Altitude and temperature

Because of the very restricted range of *Bryoria furcellata* in Britain, it is impossible to gauge the potential altitudinal range of the species. In practice, the species may be restricted to lower altitudes by wind exposure. It is also possible that accumulated temperature is a limiting factor in suitably sheltered habitat at higher altitude, though it is equally possible that tree growth would be affected before lichen growth. Extreme winter cold has been shown to affect survival of some lichen species (Laundon, 1966), however *Bryoria furcellata* has been recorded from latitudes of up to 64°N in Yukon, Canada so extreme cold is unlikely to be limiting.

Precipitation

Rainfall has been shown to be an important factor for many lichen species (Topham, 1977; Armstrong 1973). Since Glen Affric shows a strong precipitation gradient from east to west, this factor may be important in determining the distribution of *Bryoria furcellata*. However, the nature of the relationship varies with species so that it is not possible to form, *a priori,* a conceptual model for a particular species. A study of precipitation levels at the known sites for the species in Europe and North America might indicate whether the factor is likely to be important.

6.4.6 Calculation of Habitat Suitability Index

The ultimate product of the habitat model is the HSI, calculated for each raster cell as follows.

$$\begin{aligned} \mathrm{uHSI} &= H_{wind} H_{light} \sum_{i=1}^{m} N_i \left(H_{age} \right)_i \\ \mathrm{HSI} &= \max\left(100\,,\,\mathrm{uHSI}\right) \end{aligned} \tag{6.11}$$

where m is the number of pine cohorts, N_i is the number of stems in cohort *i*, and H_x are habitat factors for light, wind and cohort age.

6.5 Population model

The GALAM population model simulates changes in the number of thalli of *Bryoria furcellata* predicted to occur in the cells that contain suitable habitat. The functioning of the model can be thought of comprising two processes: intra-cell population dynamics and colonization of new cells (inter-cell dynamics).

6.5.1 Intra-cell population dynamics

The assumptions upon which the population model is based are as follows.

1. In cells of suitable habitat, small populations will tend to grow at a rate proportional to the population size.
2. In cells with stable habitat quality, populations will reach an equilibrium point determined by the carrying capacity of that cell.
3. As populations approach the carrying capacity of the cell, growth will slow as available niches become more marginal.
4. Changes in habitat quality will be reflected by changes in the local abundance.

Thus, the dynamics of a population of *Bryoria furcellata* within a particular cell are modelled by a logistic difference equation, where the carrying capacity of the cell is determined by the HSI of the habitat model. The number of thalli that might be supported in a 50 × 50 m quadrat in optimal habitat has been estimated to be in the order of one hundred, so in this case the carrying capacity is defined as numerically identical (though conceptually separate) to the percentage HSI.

The population model can be expressed by the following difference equation:

$$N_{t+10} = N_t + rN_t\left(1-\left(N_t/K\right)\right) \qquad (6.12)$$

where N_t is the LA at time t, r is the intrinsic rate of increase (constant) and K is the carrying capacity, which will be set equal to the HSI for the cell and will change over time. Since the model timestep is ten years, the difference equation is of first order.

The LIBSEM model also uses the logistic difference equation *form* to simulate annual biomass accumulation in cells. However, in this model the intrinsic rate of increase is not constant, but is expressed as the sum of immigration and net biomass growth. The latter is calculated as the difference between total annual production and litterfall, where total production is proportional to the standing crop, and litterfall is a function of standing crop and carrying capacity (see Dettki and Esseen, 2003). Thus, in the absence of immigration and under conditions of constant carrying capacity, net biomass growth follows a logistic-like trajectory whilst the standing crop biomass of the cell grows in a similar manner to a Gompertz difference equation.

Growth curves for LIBSEM and GALAM are shown for comparison in Figure 6.5.

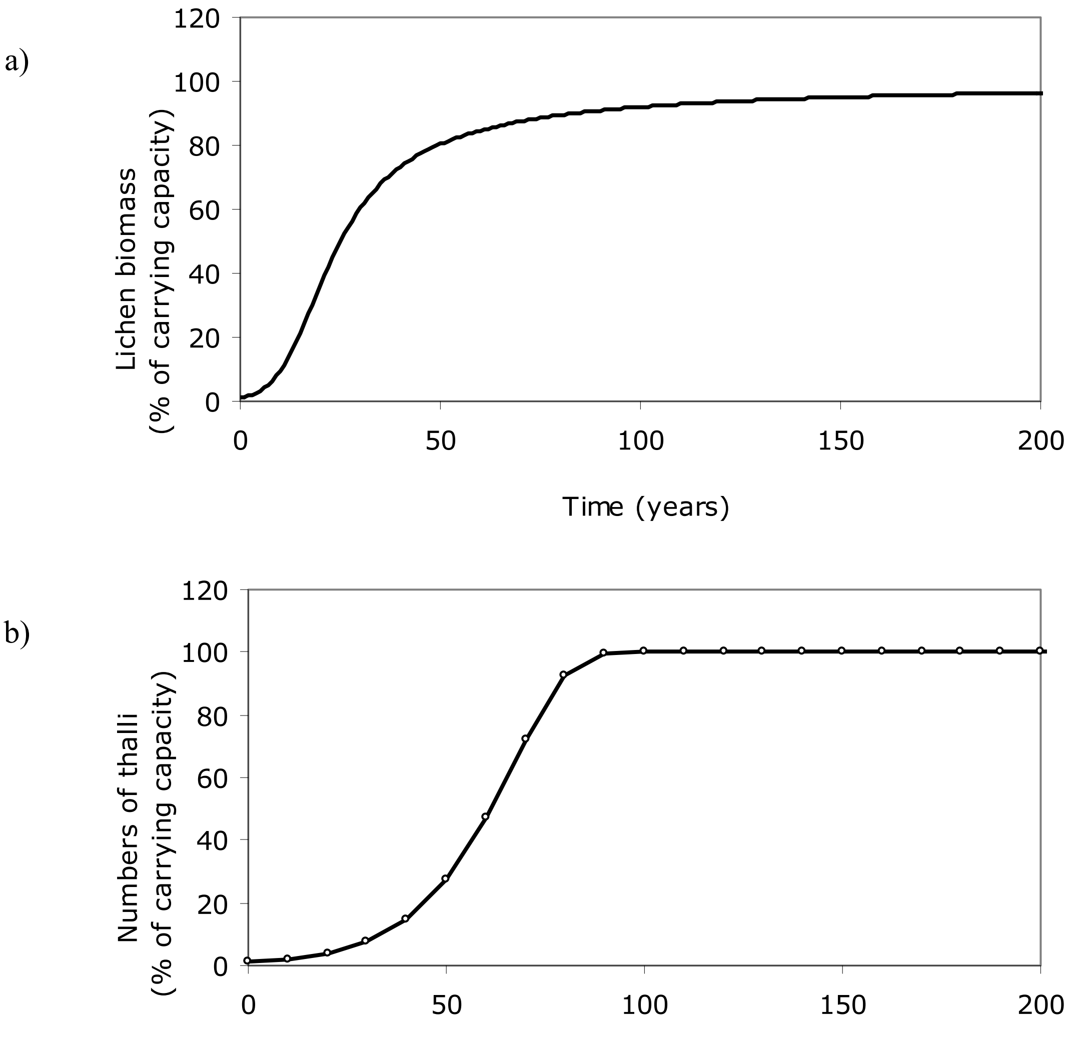


Figure 6.5 Growth curves for (a) LIBSEM (with annual growth rate of 0.08) and (b) GALAM (with r=1.0) in the absence of immigration and under conditions of constant carrying capacity. For comparison, LA values are shown as percentages of carrying capacity.

For the chosen parameters, growth rates of the two models are broadly similar; LIBSEM takes 84 annual timesteps for the biomass to accumulate to 90% of carrying capacity, whilst the same percentage abundance is achieved in eight ten-year timesteps of GALAM. Although LIBSEM is essentially simulating individual thallus growth as well as within-cell dispersal and colonization, the beginning and end-points of the process can be considered to be identical between models.

Since there are no field-based population studies of *Bryoria furcellata*, the appropriate population growth rate is difficult to estimate. For this reason, a value of 1.0 for r has been used as the baseline figure since this gives good agreement with the LIBSEM model (as shown in Figure 6.5). However, since intra-cell population growth is dependent upon dispersal, we may expect growth rates for *Bryoria furcellata* to be slower than for *Bryoria* species in general. Whether or not this is the case will depend upon whether *Bryoria furcellata* is a poor disperser at all scales or simply ill-adapted to long distance dispersal. Currently this is not known.

6.5.2 Colonization of new cells

A stochastic model has been used to simulate dispersal and subsequent colonization. The range of possible dispersal has been limited to cells adjacent (including diagonally adjacent) to the source cell. The model assumes that in cases where the source cell contains the maximum abundance of thalli and the destination cell contains optimal habitat, then probability of successful colonization will have a maximum value (denoted $P_{\max}$). The default value for $P_{\max}$ is one. The number of propagules arriving at the destination cell will be proportional to the number of propagules arising from the source cell, which in turn can be assumed to be proportional to the number of thalli. Furthermore, the probability of a propagule establishing successfully in the destination cell will be proportional to the abundance of suitable substrate, which is taken to be directly related to the HSI in the destination cell.

Thus in formal terms, the probability of colonization occurring from cell i to cell j may be denoted P_{ij} and calculated as follows:

$$P_{ij} = P_{\max}\left(\mathrm{HSI}_j/100\right)\left(N_i/100\right) \tag{6.13}$$

where HSI_j is the HSI in cell j and N_i is the number of thalli in cell i.

When successful colonization is deemed to have occurred, the LA in the destination cell is set to a value of one. Subsequent colonization events in cells already supporting populations are disregarded since the resulting augmentation in population size is likely be insignificant in relation to changes in population size attributable to within cell dynamics.

The dispersal element of GALAM is more basic than that of LIBSEM which uses a power law relationship to effect dispersal up to a maximum distance of 200m (i.e. four grid cells). Whilst this approach would be simple to implement (using similar algorithms to those used for GALDR seed dispersal; see Section 4.3), it is not considered to be necessary on account of the presumed poor dispersal abilities of *Bryoria furcellata*. LIBSEM also incorporates a ‘regional dispersal’ biomass input into each cell, which can be considered analogous to Greene and Johnson’s (1995) ‘background deposition’ for tree seed dispersal.

6.5.3 Initial conditions

Bryoria furcellata is known to exist with certainty at three locations in Glen Affric: Pollan Buidhe, to the south-west of the head of loch Beinn a’ Mheadhoin; in a research plot south of Coille Ruigh na Cuileig; and across the River Affric from the car park at Dog Falls. However, these records are the product of somewhat *ad hoc* sampling rather than concerted search action, so it is likely that the species is distributed reasonably widely in suitable habitat throughout the glen. For the purposes of simulation, the initial distribution is established as a one-fifth random sample of all cells with non-zero HSI. Initial values of LA are determined to be equal to carrying capacities at the start of the simulation. However, it should be noted that the locations with known populations do not appear as suitable habitat when the model is loaded with initial state. This is because the baseline data for species distribution, age class distribution and stocking densities are highly generalized and do not reflect accurately the small-scale variation in habitat that is actually present. These problems are discussed further in Section 7.4.

6.6 Simulations

6.6.1 Model parameters

Initial simulations of GALAM with GALDR parameters set to baseline values resulted in predictions of rapid extinction of *Bryoria furcellata* (see Figure 6.6). The cause of the simulated extinction was reduction in habitat provision caused by dense regeneration increasing SDI and thus casting heavy shade. However, as already stated (Section 4.4.2), there is gross uncertainty over the nature and extent of tree regeneration in upland areas, so this first result should not be treated instantly as a harbinger of doom for light sensitive lichens in Glen Affric.

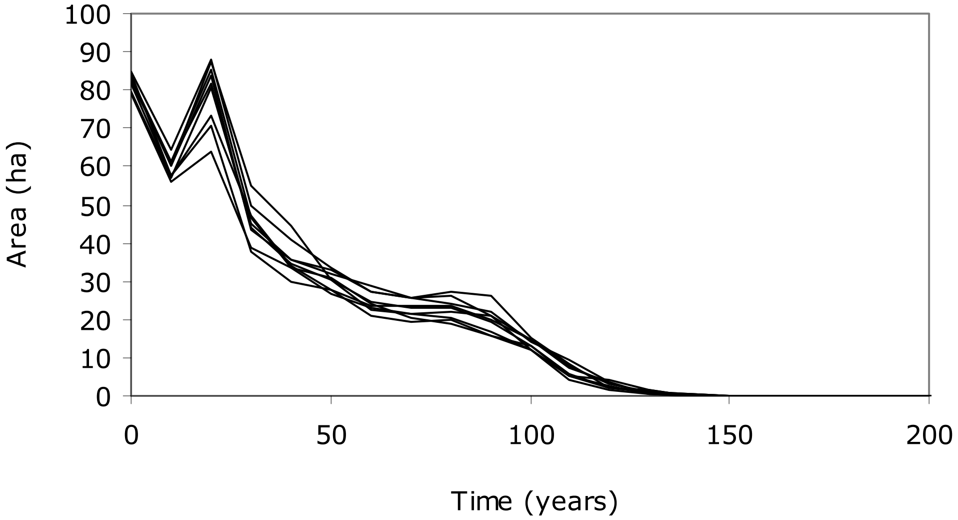


Figure 6.6 Simulated area of cells occupied by Bryoria furcellata *(output variable: ALC) with ten replicated GALAM runs using GALDR baseline parameters.*

In fact, given that we presume that *Bryoria furcellata* has been present in Glen Affric for several centuries at least, the balance of probabilities seems to indicate that the GALDR baseline regeneration parameters are unrealistic. However, this is only one of several conclusions that might be drawn. It might be that elimination of browsing animals would actually promote regeneration to such an extent as to threaten the continuing presence of *Bryoria furcellata*. Also, the predicted constriction of available habitat is contingent upon the initial age-structure data as well as the choice of regeneration parameters.

Various combinations of parameter alterations were tested for their propensity to sustain modelled populations of *Bryoria furcellata* over a one thousand-year period. From this, two parameter sets were assembled to be used as standard parameter sets for GALAM runs. These sets are labelled PL1 and PL2; deviations from GALDR baseline parameters are shown in Table 6.2. In terms of the performance of lichen populations, the parameter sets PL1 and PL2 can be envisaged as pessimistic and optimistic respectively

Table 6.2 Parameter sets for GALAM simulations

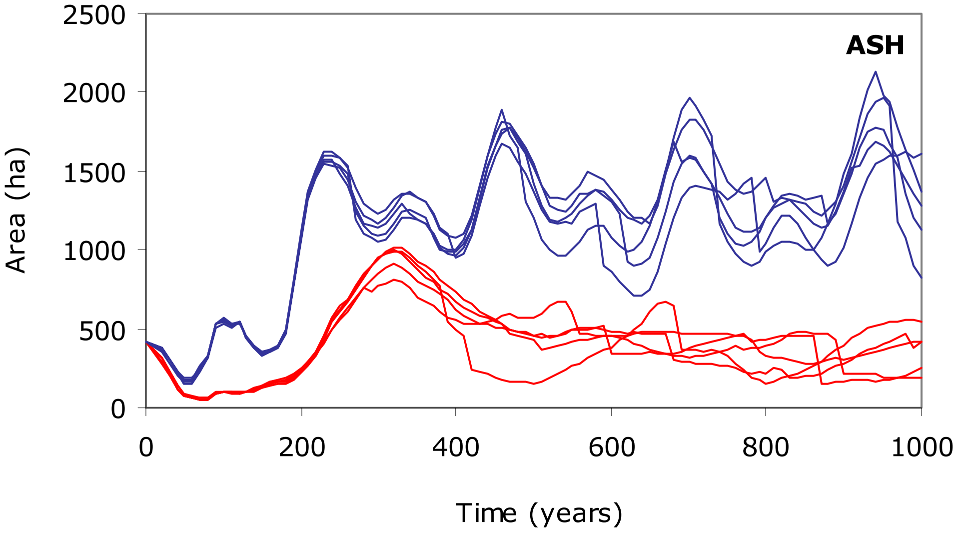
Parameter	Baseline value	PL1 value	PL2 value
υ	2	3	3
R_1 [pine]	1	1	3
R_2 [birch]	1	1	3
$\rho_{b\,\max}$	0.9	0.9	0.8
β	1	1	2

6.6.2 Global statistics

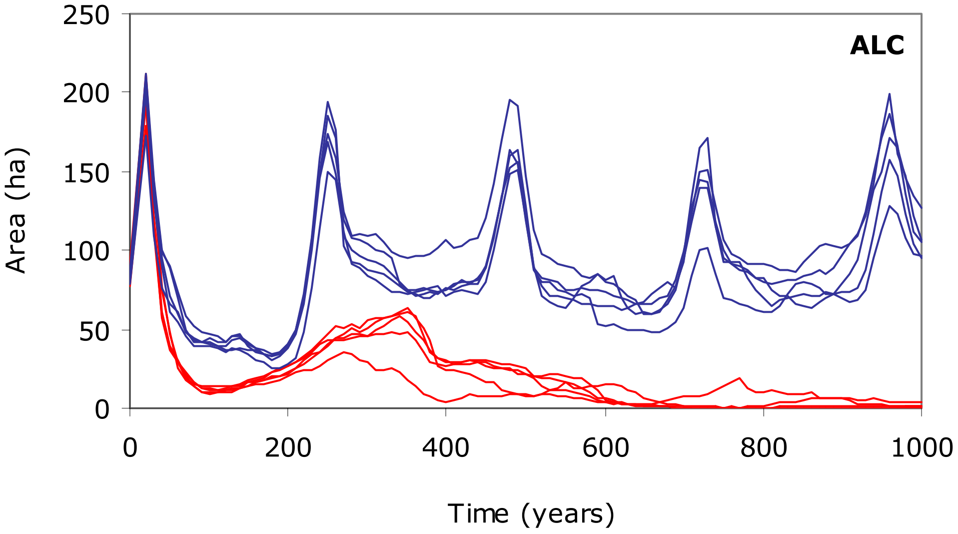
Results from a set of model runs of GALAM with these parameter sets are shown in Figure 6.7. Output was replicated five times for each parameter set. For both optimistic and pessimistic scenarios there is a pronounced bottleneck in habitat availability (ASH; Figure 6.7a) from 30 to 90 years simulated time. Thereafter, the two ASH trajectories diverge with PL2 showing a marked periodic pattern and much higher values than PL1. The periodicity associated with the PL2 parameter set may be attributed to the combination of largely even-aged initial state with greater lag times between canopy break-up and understorey reinitiation stages. The area of cells occupied by *Bryoria furcellata* (ALC; Figure 6.7b) initially shows sharp rises as seed cells (those initially allocated non-zero populations) colonize adjacent habitat, but falls sharply when habitat provision declines. The initial habitat bottleneck restricts the range of lichen within the focal area and thus when habitat provision rises after 200 years simulated time, the colonized area also recovers, but occupancy levels (Figure 6.7c) remain under 20% for the rest of the simulation.

Although the area of suitable habitat is much greater in the optimistic scenario it is interesting that MHS values are actually greater in the pessimistic scenario (Figure 6.7d); though this is not reflected in the MLA plot (Figure 6.7e). Another peculiar feature of the output is that TLA (Figure 6.7f) shows periodicity of different frequency to that of ALC. To understand this, and other more subtle characteristics of the habitat and population dynamics, it is necessary to examine the spatial output.

a)



b)



c)

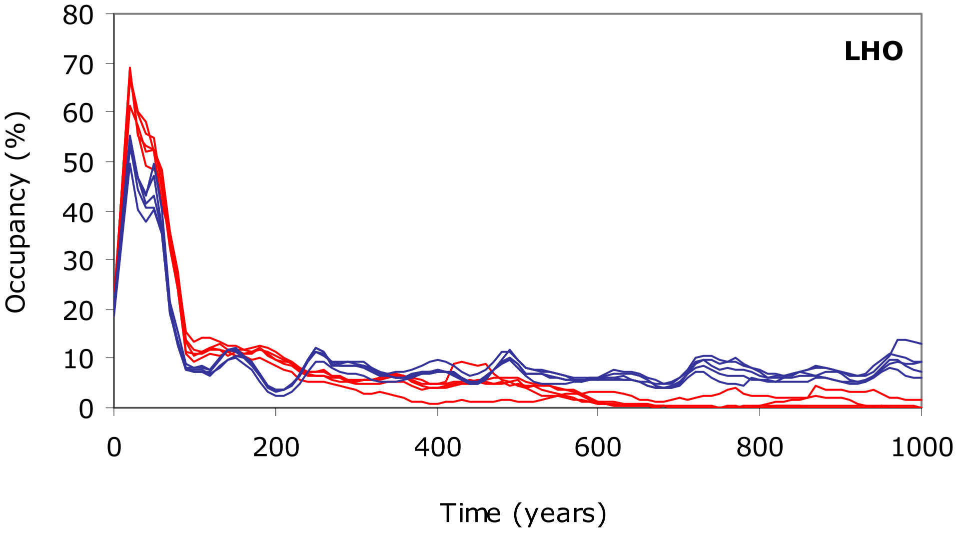


Figure 6.7 Time series of various output variables from GALAM with parameters set as PL1 (red) and PL2 (blue) with five replications for each parameter set. Output variables plotted are: (a) ASH – area of suitable habitat; (b) ALC – area of colonized cells; (c) LHO – percentage occupancy. (Continued on next page.)

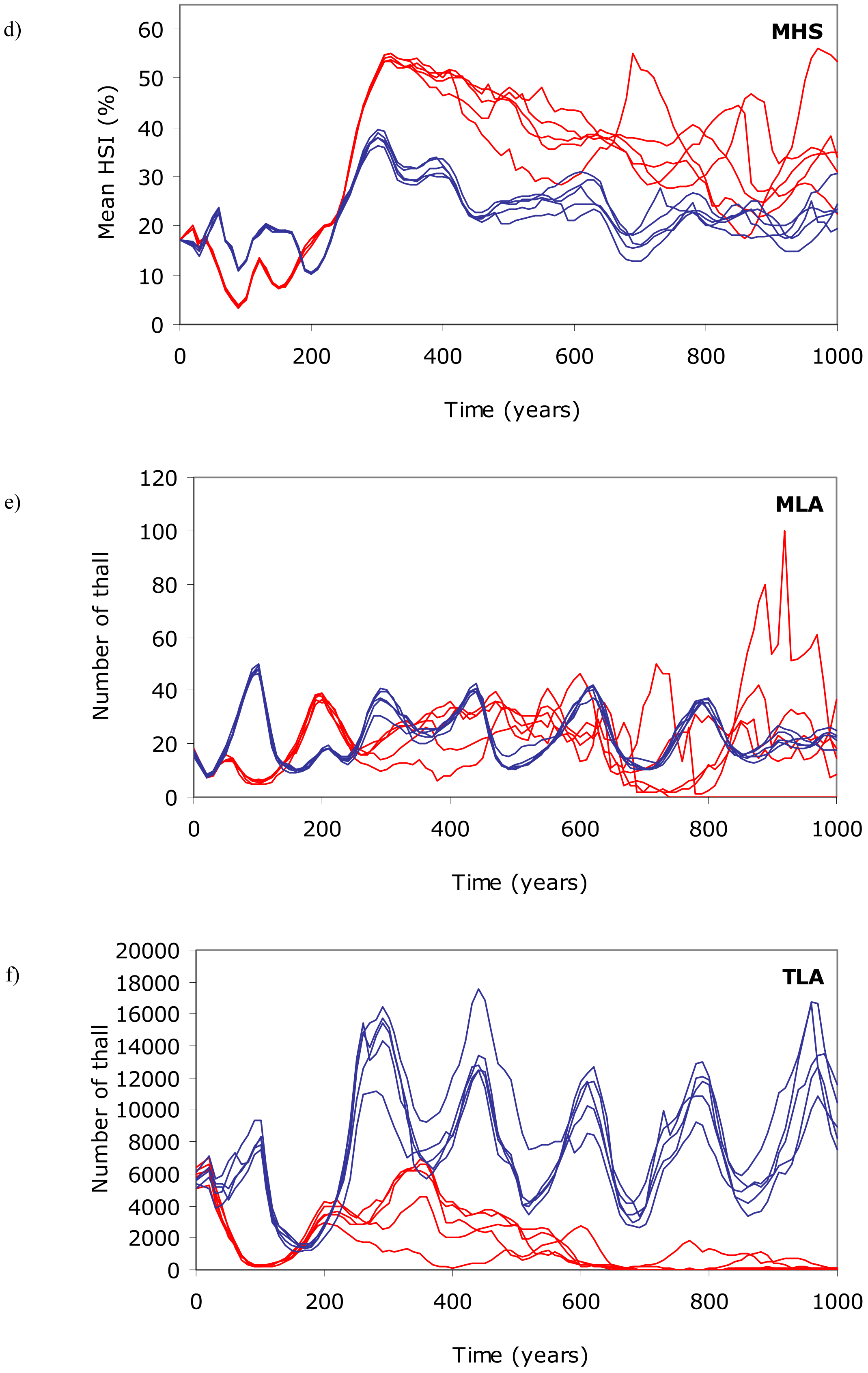


Figure 6.7 (Continued) Output variables on this page: (d) MHS – mean HSI for cells with suitable habitat; (e) MLA – average LA for colonized cells; (f) TLA – summed LA over entire landscape.

6.6.3 Raster output

Selected excerpts from the time series of LA and HSI raster maps from an ‘optimistic’ simulation (PL2 parameters) are shown in Figure 6.8. The initial distribution of habitat and abundance is shown in Figure 6.8a; this shows the distribution of habitat as consisting of a few, mostly rather well-defined, patches. The initial pattern of colonization can be seen to be randomly distributed throughout the available habitat. After 20 years of simulation time the seed cells have colonized much of the surrounding habitat, but the two habitat patches to the south of Loch Affric (around Creag na Caillich and Loch Salach a’ Ghiubhais) disappear. This is due to the presence of a dense young understorey present in these patches in the initial state; after 20 years, this understorey creates unsuitable lighting conditions. 100 years into the simulation suitable habitat has redeveloped over large areas to the south of Loch Affric, but this habitat is completely uncolonized because of the lack of sufficiently proximal source populations. In fact, suitable habitat located to the south of Loch Affric is continually unutilized for the remainder of the simulation.

Comparison of the initial LA distribution with those at 300, 600 and 900 years reveals that the lichen makes very little range expansion. It is largely restricted to the same broad locations throughout the simulation, although the range expands and contacts according to the area of suitable habitat in the vicinity of the major aggregations of LA. Furthermore, it can be seen that when habitat becomes more scarce the populations tend to contract to the same core areas which act as refugia. These refugia correspond to areas with rather low HSI values for Scots pine (see Figure 3.7a). In such areas pine regeneration is sparser, so the stand is less likely to become so dense that *Bryoria furcellata* is shaded out. So, the loci used by the lichen can be categorized into two types: the low pine HSI persistent refugia and the high pine HSI ephemeral habitat. Utilization of the ephemeral habitat is opportunistic and evanescent so LA rarely gains substantial values in such loci in the way that it may in the persistent habitat.

The periodic patterns shown in Figure 6.7 can be explained by comparing the areas used by the lichen with the initial raster for the primary cohort of Scots pine. The majority of cells regularly occupied occur in the large area with primary pine cohort originating in 1840 AD. Thus the habitat dynamics within these areas tend to be synchronized (at least at first). However, because regeneration is much less abundant in the core *Bryoria furcellata* habitat, stocking densities are lower throughout the stand cycle and hence regeneration may occur earlier in the life of the previous generation. Since the bulk of the entire population of the lichen is found in the persistent habitat, LA in these cells provides greatest influence on TLA and MLA. On the other hand, ALC is more dependent upon the dynamics of the ephemeral habitat, where, because stocking densities are higher, generation cycles are longer. Thus, the difference in frequencies of periodicity between ALC, TLA and MLA is explained. The plot of ALC follows that of ASH because the lichen populations are all contained in a region where the habitat dynamics are determined by a single cohort, and that age-class dominates the landscape as a whole. Furthermore, it can be seen that values of MLA are larger in the pessimistic scenario than the in optimistic because a larger proportion of occupied cells utilize the persistent habitat in the pessimistic case.

a) Start of simulation (t = 0). HSI above; LA below.

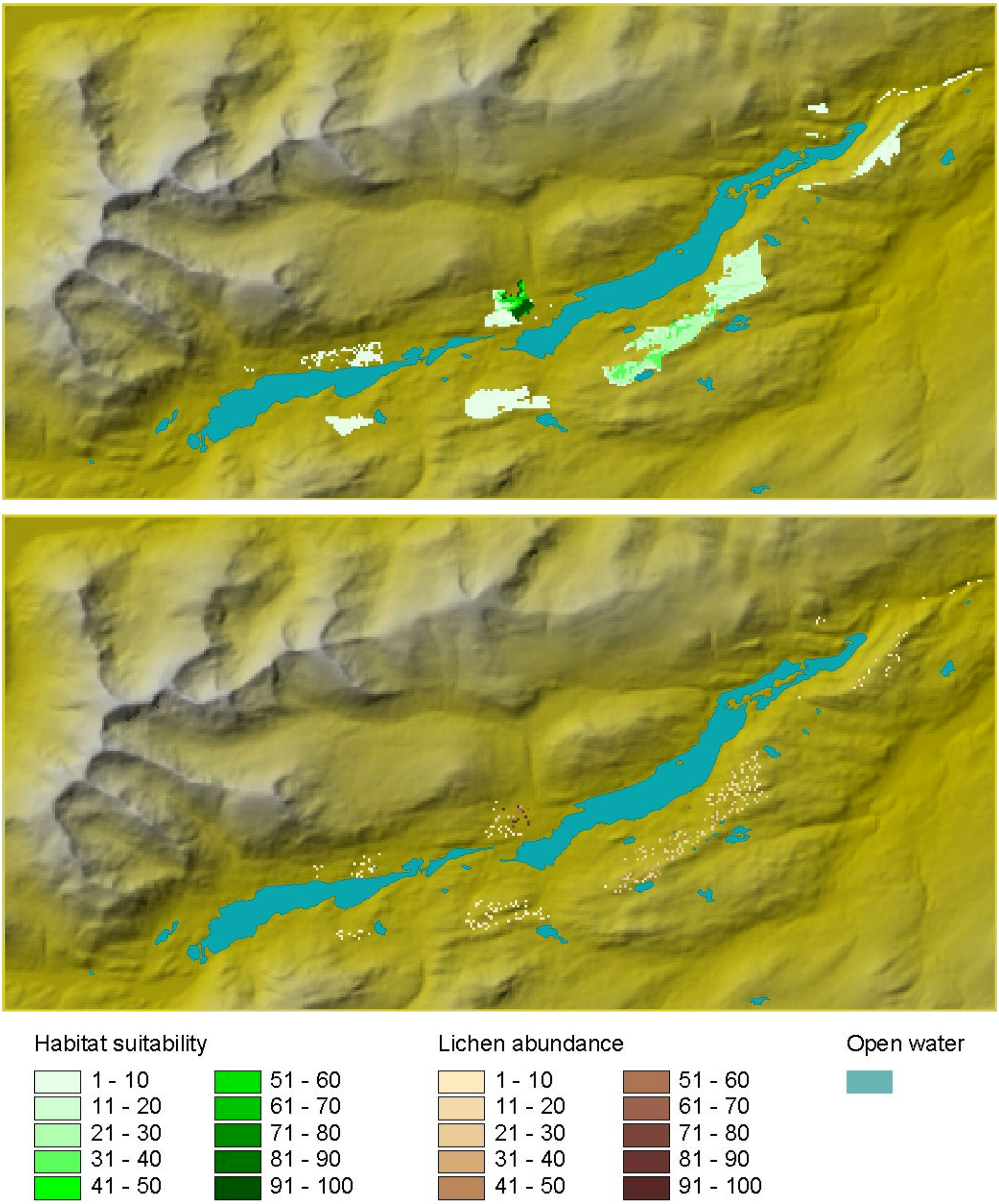


Figure 6.8 Raster output from GALDR with GALAM from simulation using PL2 parameter set. Successive scenes show maps for HSI and LA at different points in the time series (t = x).

(b) 20 years. HSI above; LA below.

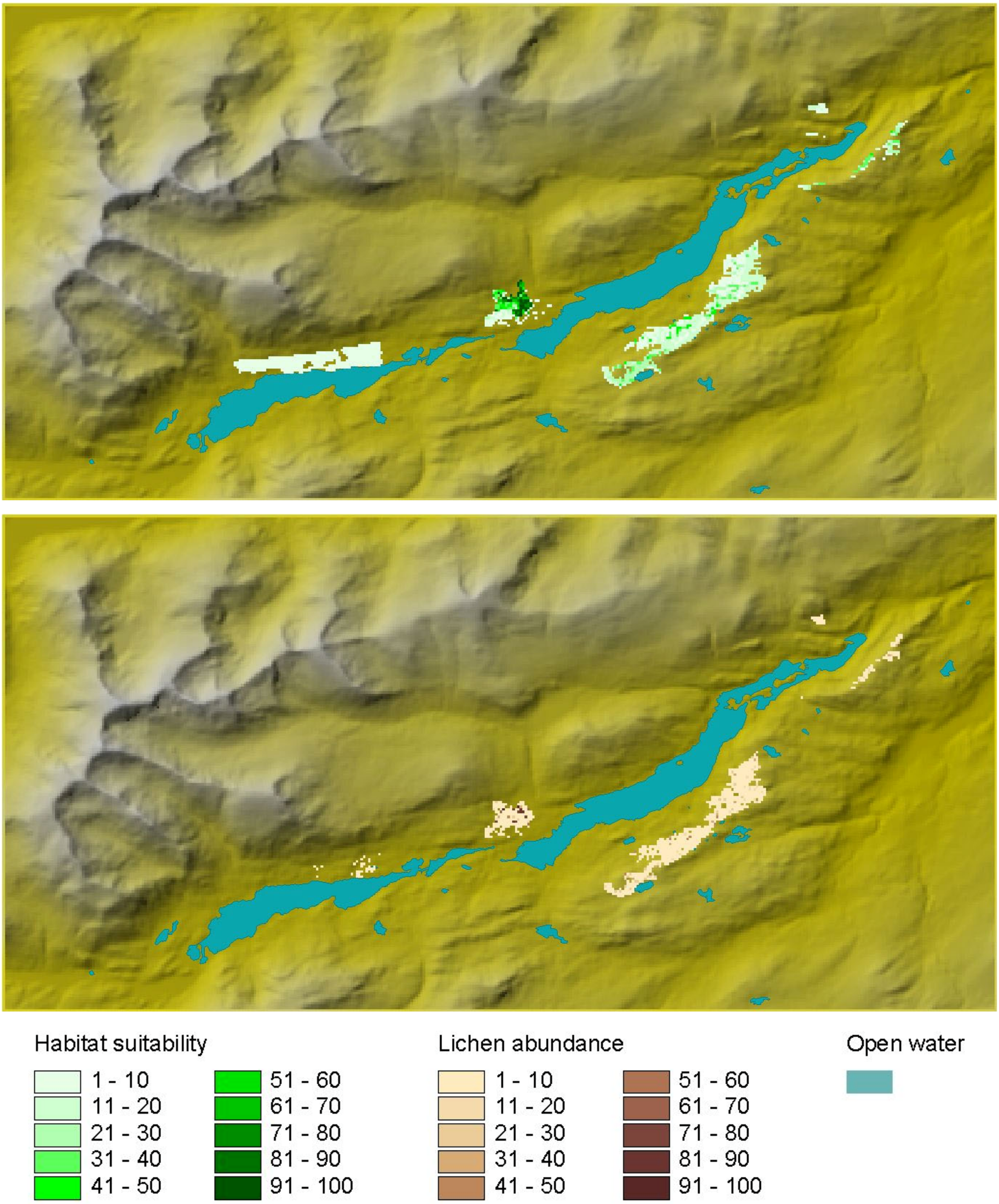


Figure 6.8(continued)

(c) 50 years. HSI above; LA below.

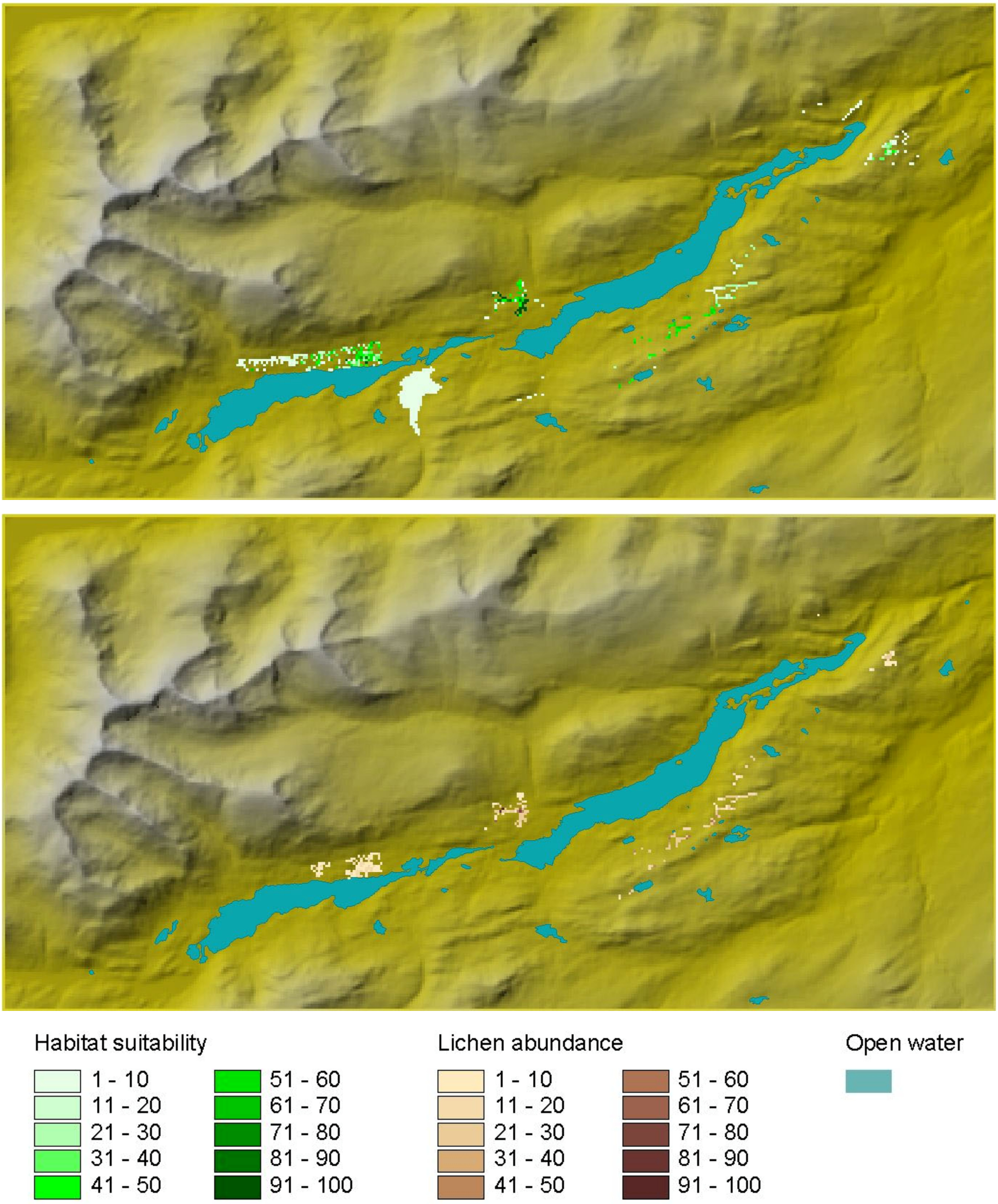


Figure 6.8(continued)

(d) 100 years. HSI above; LA below.

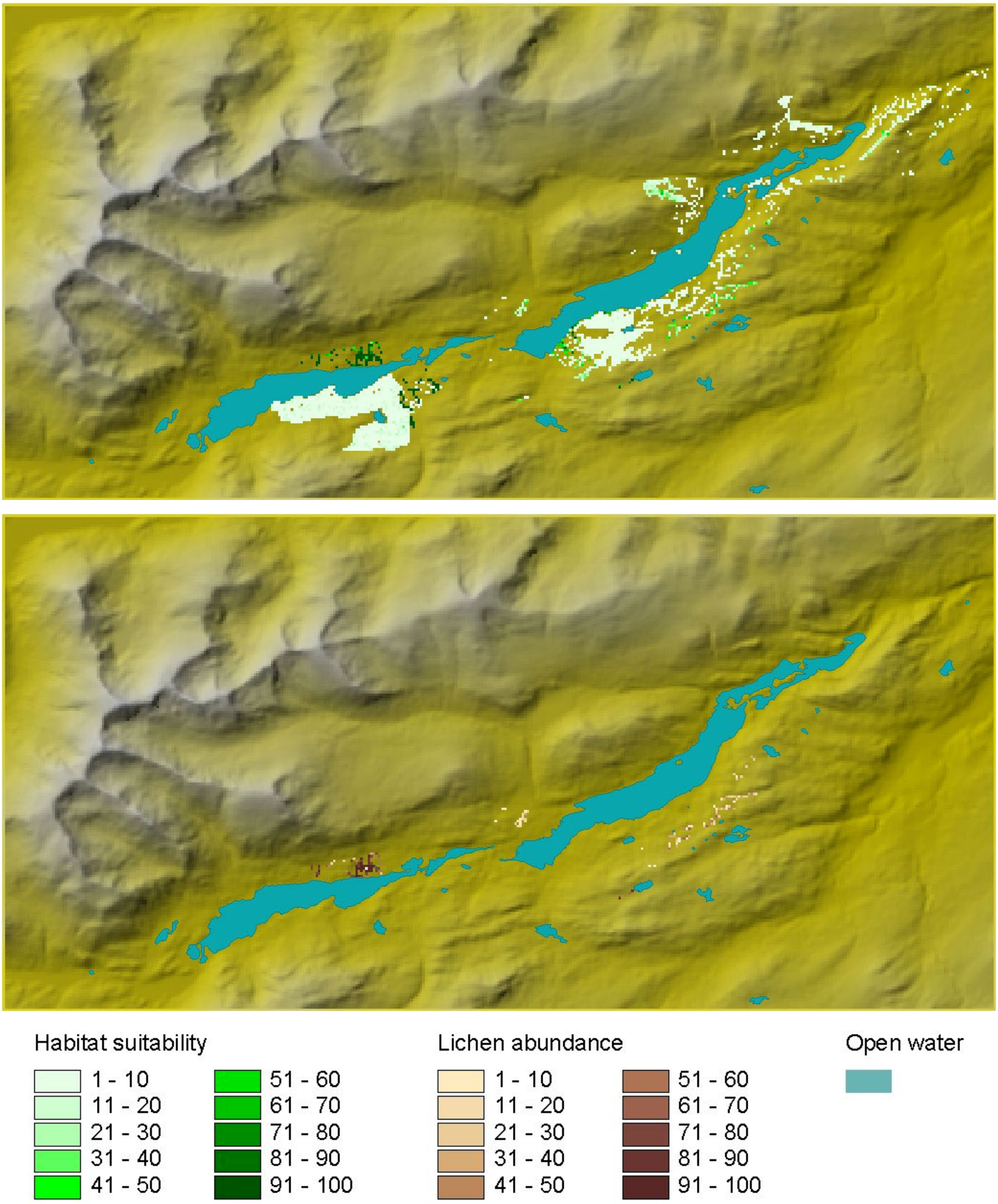


Figure 6.8(continued)

(e) 150 years. HSI above; LA below.

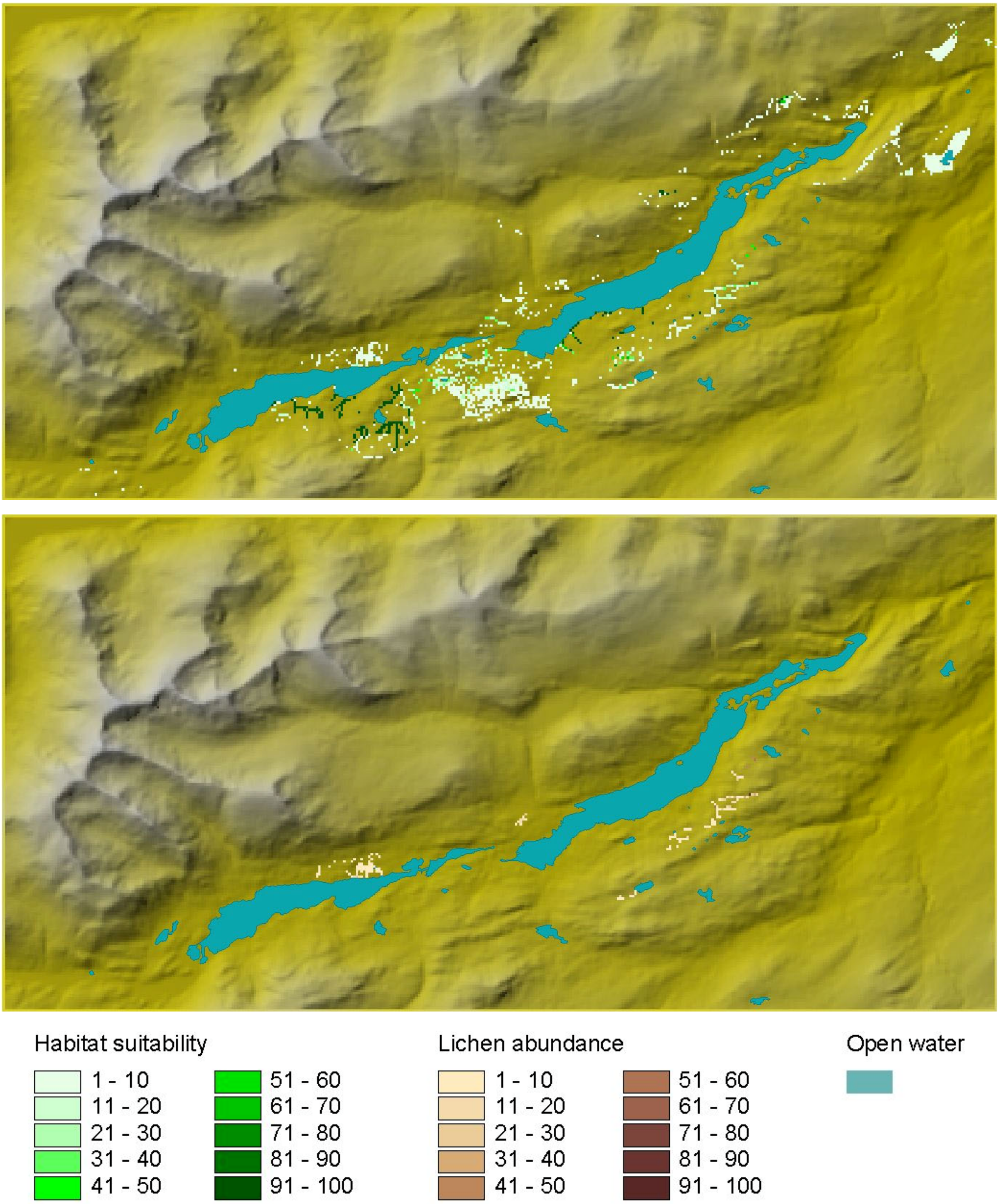


Figure 6.8(continued)

(f) 200 years. HSI above; LA below.

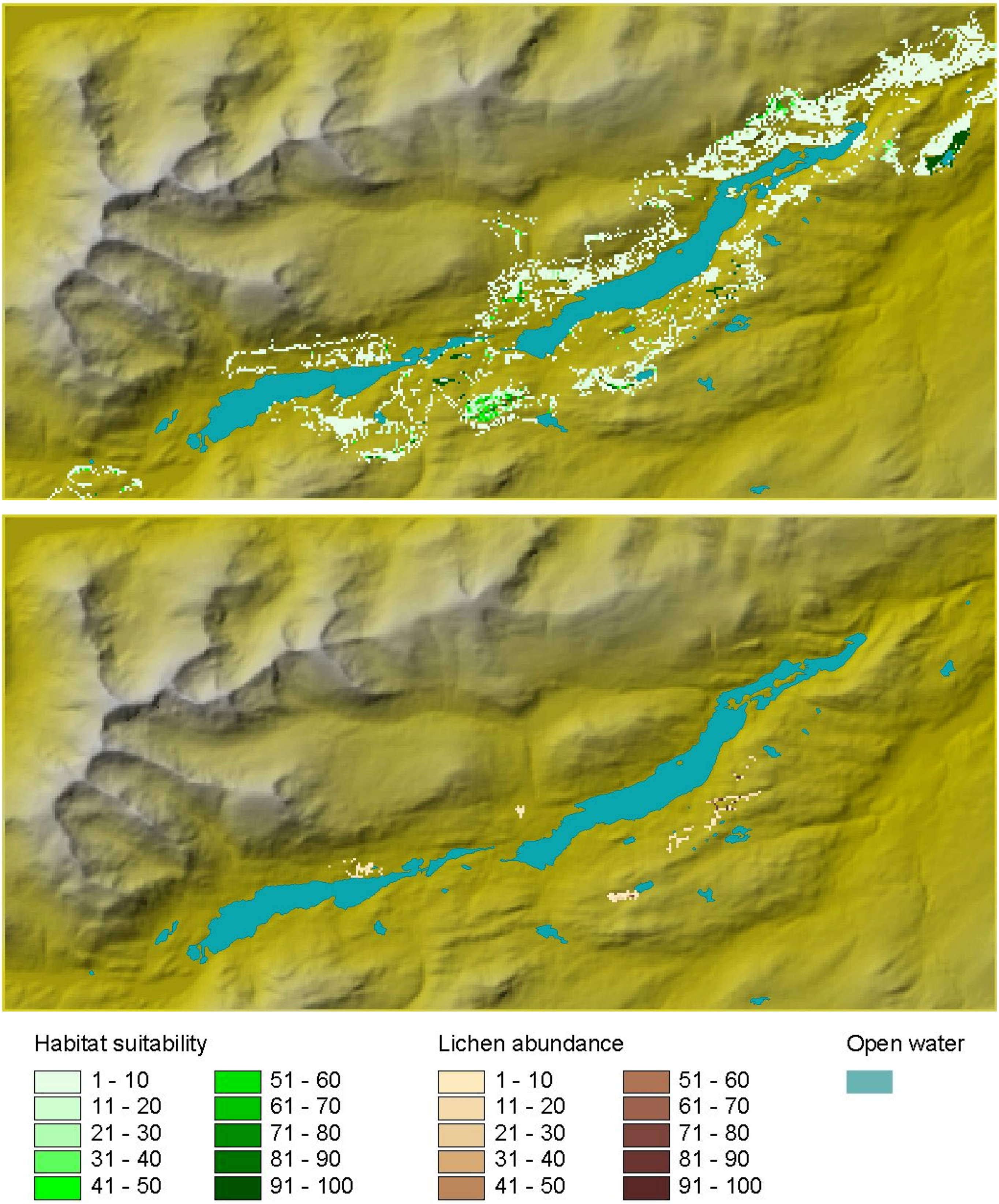


Figure 6.8(continued)

(g) 250 years. HSI above; LA below.

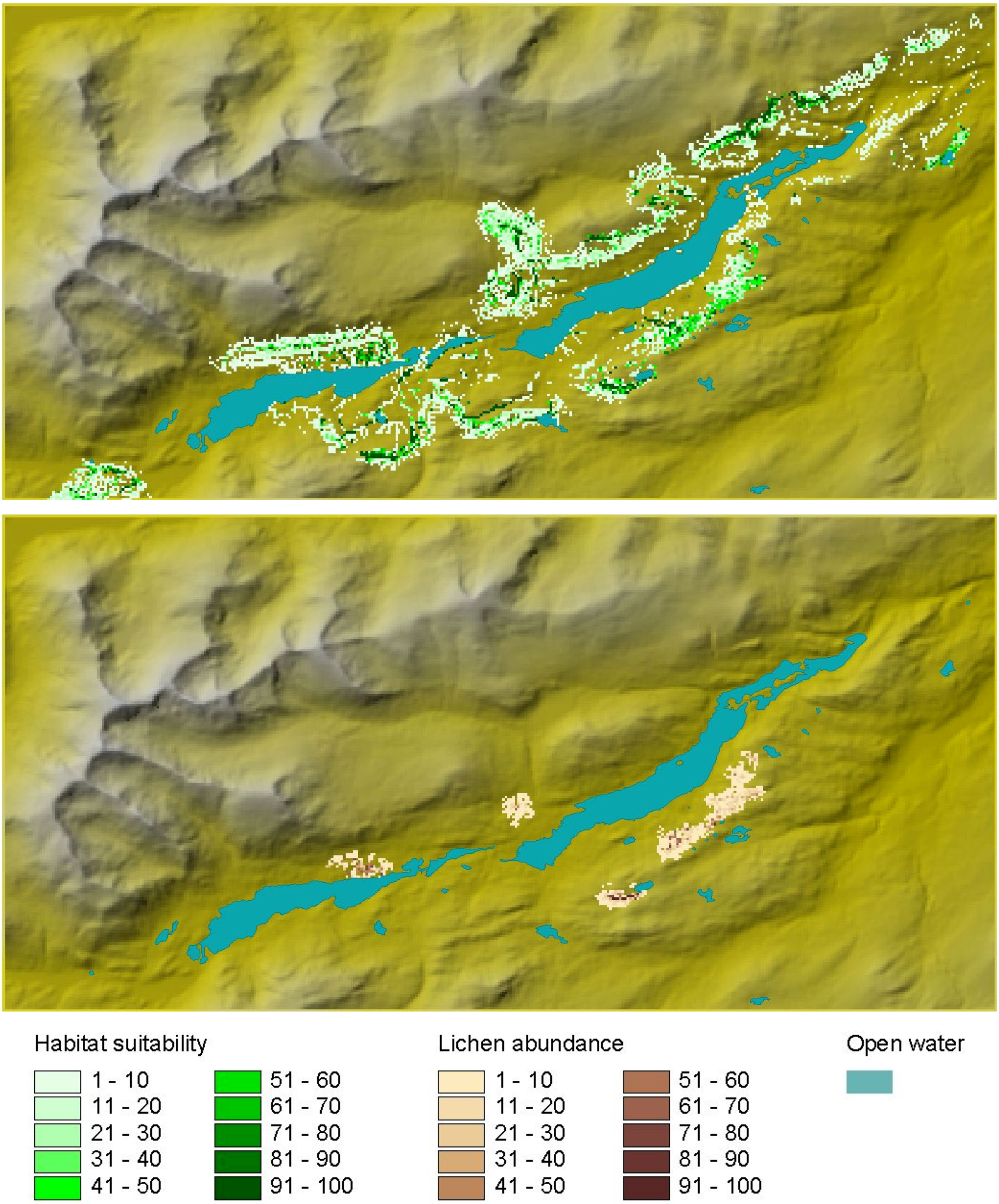


Figure 6.8(continued)

(h) 300 years. HSI above; LA below.

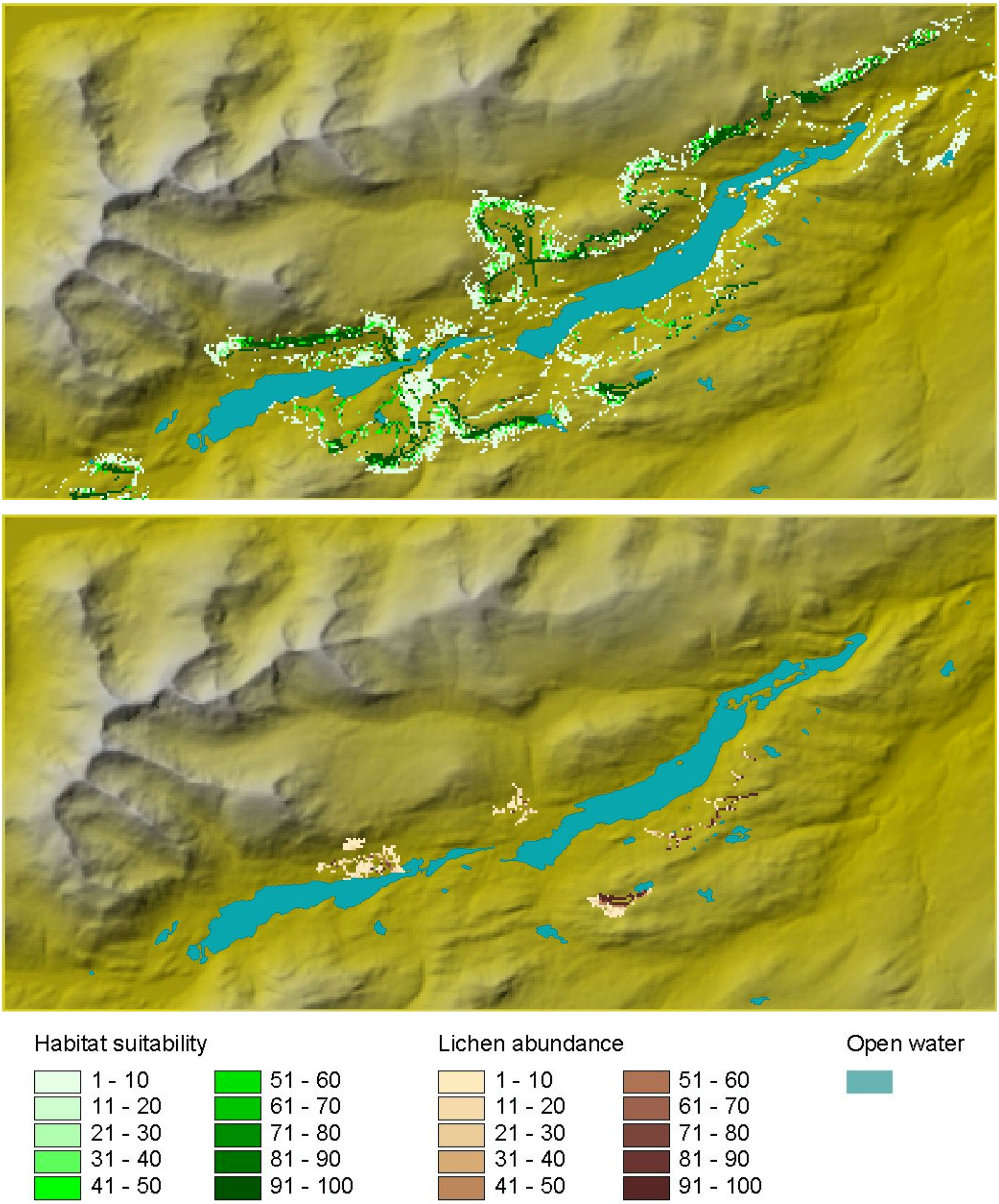


Figure 6.8(continued)

(i) 600 years. HSI above; LA below.

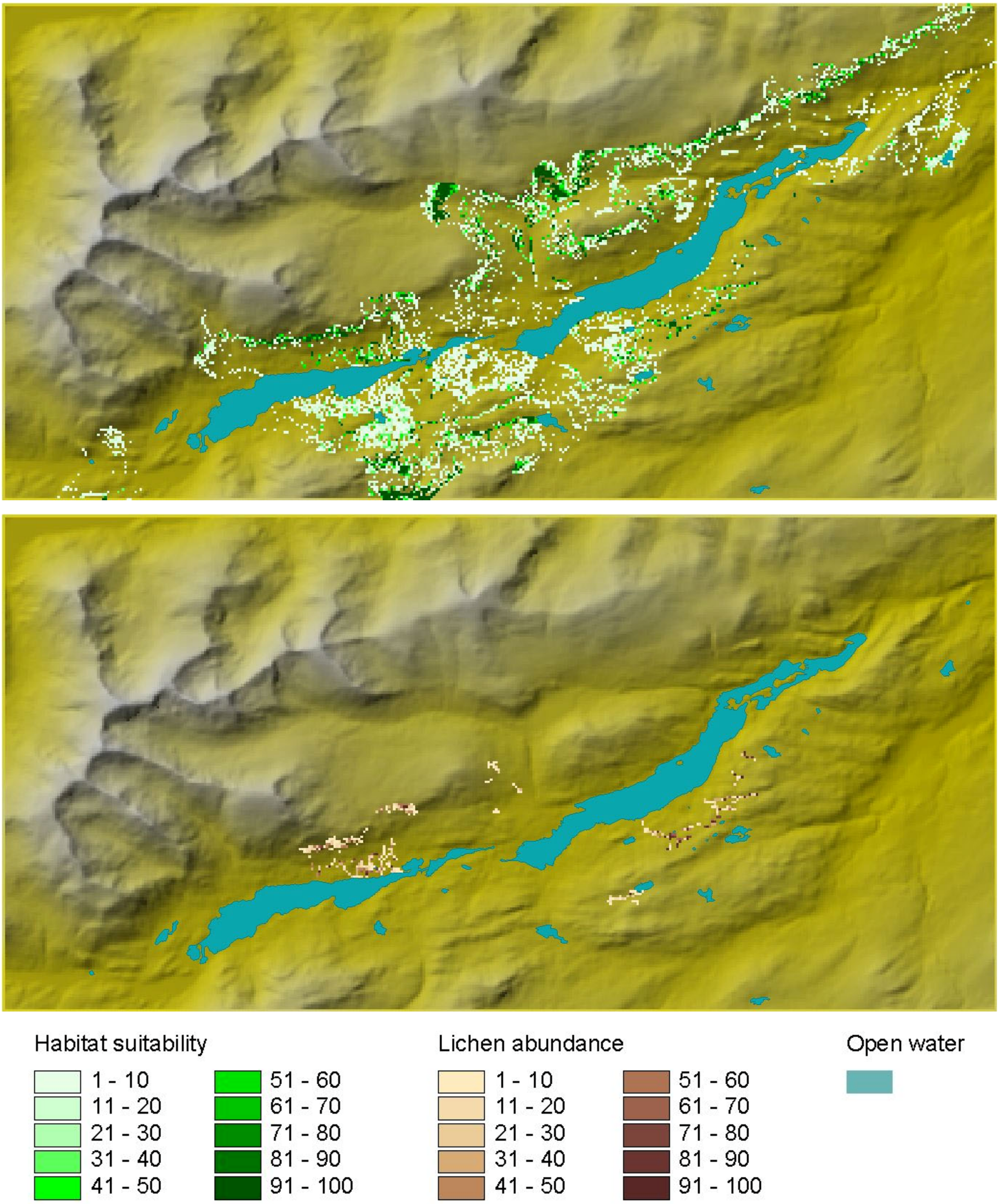


Figure 6.8(continued)

(j) 900 years. HSI above; LA below.

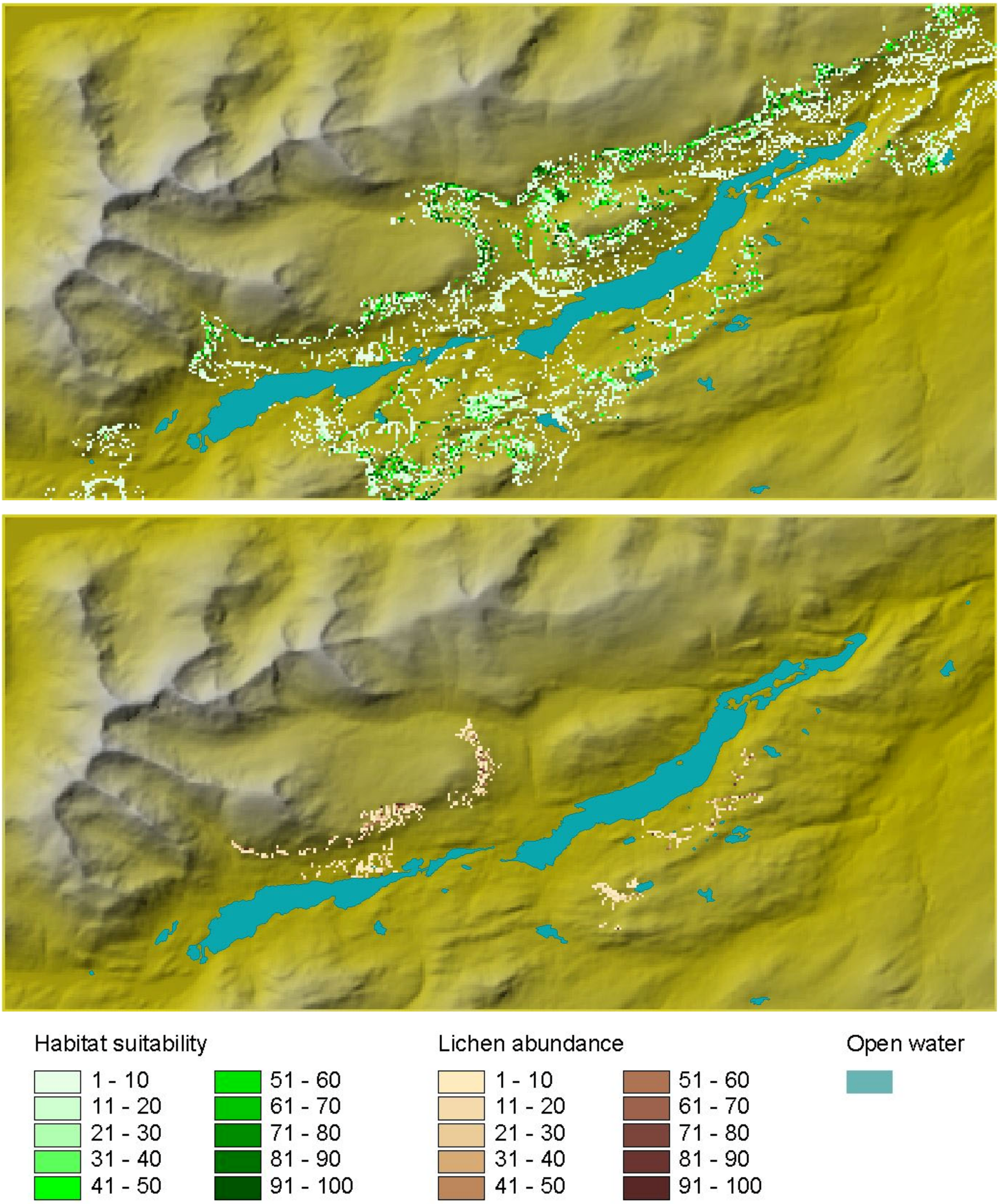


Figure 6.8(continued)

6.7 Discussion

6.7.1 Critique of the approach and potential for improvement

Since landscape modelling of species abundance often stops at the habitat suitability stage (e.g. Pausas *et al*., 1997; Riiters *et al*., 1997; Debeljak *et al*., 2001; Gurnell *et al*., 2002), one might question the usefulness of adding a population model. Certainly, using a population model on top of a habitat suitability model increases the complexity of the modelling system and creates additional sources of uncertainty. However, the simulations presented in Section 6.6 suggest that provision of suitable habitat may be a poor predictor of species presence or abundance. The maps presented in Figure 6.8 (Section 6.6.3) show that suitable habitat may remain unoccupied if there are no links to populations that might act as a source of colonizing propagules. Thus, it may be seen that the spatio-temporal connectivity of the habitat is equally as important as the quantity of suitable habitat present in the landscape. Moreover, the spatio-temporal connectivity must not be assessed arbitrarily, but must be related to the vagility of the organism. The most effective way of doing this is to use a SEPM. In general, the appropriateness of using a SEPM as well as a HSM may be seen to depend on the vagility of the focal species in relation to the scale of the study. Highly vagile species may ‘perceive’ even highly spatially fragmented landscapes as being connected (D’Eon *et al*., 2002), in which case the use of a HSM alone may be sufficient.

Since GALAM is essentially a model in development, it is not surprising that there are many elements that could benefit from further work and improvement. The limitations of the model need not be seen as purely negative, since they may serve to inform future research work, but appreciation of the nature of the limitations is necessary before further interpretation of model results can be made.

First, distinction must be made between limitations of GALAM and those of GALDR, the forest dynamics model that drives it. As has been shown, predicted landscape-level performance of *Bryoria furcellata* is subject to great uncertainty as a result of more basic uncertainty over the realistic representation of tree regeneration. However, this uncertainty, whilst undoubtedly militating against the use of the model as a strict predictor of future population sizes, cannot be considered a limitation of the GALAM model. Indeed, one should expect the performance of a light sensitive epiphyte to be contingent upon frequency and density of regeneration. Similarly, whilst there are certainly shortcomings in the representation of initial habitat distribution (not least because it does not include all of the currently known localities for the species), these can be attributed to the quality of the data used for initializing the GALDR model.

Nonetheless, the initial distribution of LA used in the model is only partially dependent on the initial GALDR spatial state. Some errors of omission may be unavoidable given an inadequate habitat map, but errors of commission may also be considerable, and these may be correctable by more detailed survey for *Bryoria furcellata* in Glen Affric. Naturally, it would be desirable to match improvements in initial state data for the GALDR model with commensurate enhancement of the GALDR initial state. If, however, the model is to be used directly to inform species conservation actions, a thorough survey of current species distribution will be essential.

Probably the most significant limitation of GALAM is the lack of any formal testing beyond verification of model logic. Testing models of long timescales and large spatial extent presents particular difficulties; however, it should be possible to test individual components of the model to some extent. The results of testing may also provide for better estimation of parameter values.

The most realizable tests are likely to be those of the components of the HSM. A useful test of the relationship of habitat quality with phorophyte age would be to compare stem cores from trees with and without *Bryoria furcellata*. If further locations for the species were to be revealed by further survey, the relationship of abundance to SDI could be tested. It may be worth investigating the use of tatter flags to test within-stand wind speed relationships.

Testing the SEPM is a more difficult proposition, but an equally important one for long-term prediction. Both elements of the population model (intra- and inter-cell population dynamics) effectively simulate dispersal at two different scales. Unfortunately however, the methods of Dettki and Esseen (1998) are likely to be inadequate for quantifying dispersal of *Bryoria furcellata*. Overall LA values are many times lower for *Bryoria furcellata* in Scottish pinewoods than for all species of *Bryoria* in Swedish old-growth stands so traps for thallus fragments are unlikely to yield enough *Bryoria furcellata* to be useful. Additionally, identifying thallus fragments to species will be problematical where soralia are absent. Instead, the most practical method of quantifying local dispersal and colonization may be to undertake long-term monitoring programmes of trees and stands. Comparison of photographs of trees in Pollan Buidhe taken from 1995 and 2003 indicate that lifespan of individual thalli is likely to be under ten years, suggesting that dispersal over short distances may be quite frequent in relation to the model temporal resolution.

Improvements could also be made to the representation of habitat and populations at the cell level. A more logically robust method would be to represent both habitat and populations at the cohort level rather than for the entire stand. This would involve setting HSI and LA values for each cohort, and would involve significantly higher dynamic state and processor usage. The advantage over the present model would be that colonization of younger cohorts would be simulated explicitly. However, such sophistication would probably be only worthwhile once the present model has been subject to some validation and refinement. Other modifications that could be made include stochastic intra-cell population dynamics that permit extinction of small populations, and a regional dispersal sub-model similar in concept to that of LIBSEM.

6.7.2 Interpretation of the results

Whilst it may seem obvious that the purpose of this section might be to give some long-term prognosis for the continuing survival of *Bryoria furcellata* in Glen Affric, this is not possible at present. Too many uncertainties exist in terms of representation of present conditions, the nature of woodland dynamics in Glen Affric (particularly of regeneration) as well as habitat requirements and dispersal characteristics of *Bryoria furcellata* itself.

Nonetheless, the model indicates the importance of persistent habitat that might be provided by areas of ground that are marginally suitable for Scots pine and so never regenerate at high density levels. Optimal habitat may be provided by very heterogeneous sites with an intricate mosaic of dry ground and very boggy ground too wet even for downy birch. However, representation of complex site conditions of this nature is not possible in the current version of GALDR and is likely to be challenging to any landscape modelling approach.

In the present model, the habitat provided by drier ground of higher suitability for pine contributes rather little to total landscape LA or to the persistence of the species in the landscape as a whole (both are mainly determined by the distribution and dynamics of the persistent habitat). However, this situation may be altered if a less even-aged age-distribution were to be used as initial state. The ephemeral habitat may also be considered to take a more active role in the overall habitat dynamics if long distance dispersal is an important mechanism.

6.7.3 Conclusions

Despite uncertainties over model behaviour and data quality, the model results emphasize that quantity and timing of tree regeneration is likely to be critical to the future performance of *Bryoria furcellata* in the landscape as a whole. In general terms, this conclusion could be easily deduced without the use of a landscape model. However, GALAM provides a structure for further exploration of this supposition in a formal manner. The ultimate aim of the modelling project is to act as a tool to support evaluation of alternative management scenarios; such utility is possible even under high levels of uncertainty. In such contexts, it is the relative performance under the range of scenarios that is important, rather than the absolute performance under any one of them. That is not to say that data quality and model realism are not important, but rather that, in the absence of other means of evaluation, a model in development may be consulted provisionally whilst improvements are sought.

Whilst it is hoped that *Bryoria furcellata* may act as an umbrella species for other lichens of conservation importance in Glen Affric, it should not be interpreted as acting as an indicator of total biodiversity. As Jonsson and Jonsell (1999) point out, diversity of different groups of species do not necessarily correlate, so indicator species should be chosen from a range of species groups. In time, it is hoped that GALAM will be complemented by other species models compatible with the GALDR forest model.

7 Conclusions

7.1 Introduction

The aim of the project as stated in Section 1.5 was to develop a FLDM for Glen Affric that would predict change in habitat characteristics relevant to a range of key species, and hence allow further predictions of population dynamics for these species. In addressing this objective, two models were developed: GALDR, a FLDM for Scots pine and birch (see Chapter 3); and GALAM, a landscape SEPM for the lichen *Bryoria furcellata* (Chapter 6). The linkage of the lichen SEPM with GALDR confirms the feasibility of the original objective.

Undoubtedly however, the major limitation on the level of confidence that might be placed on the ability of these models to predict habitat and species populations into the future is the lack of any formal testing. Indeed, whilst certain elements of the models may be simplistic, unless tested, it is impossible to say whether they are over-simplistic or not. However, to test GALDR as a whole, over the whole landscape and for appropriately long timescales is obviously impractical. Thus, a realistic testing programme would consist of tests of individual sub-models or modules conducted at lesser spatial and temporal scales. If confidence can be placed in the performance of the sub-models then the performance of the whole model may be judged entirely on the deductive reasoning that predicts emergent behaviour at the landscape scale.

Although the job of formal, quantitative testing is beyond the scope of this work, some evaluation of the GALDR model can be made by examination of the logical reasoning and assumptions made in the construction of the various elements of the model.

7.2 Critique of the GALDR model

In this section, the GALDR model as a whole is reviewed critically. Limitations and potential for improvement are identified.

7.2.1 Overall design

The description of the GALDR model in Chapters 3 and 4 reveals its nature to be distinctly chimerical. The landscape-scale scope and cohort-based structure owes to

VAFS-LANDSIM (Roberts, 1996a) and LANDIS (Mladenoff *et al*, 1996). Consideration of cohort density has been taken a step further than Pennanen and Kuuluvainen's (2002) FIN-LANDIS modification of the original LANDIS model. The inclusion of height as a cohort variable brings the GALDR model closer to the gap model design of Botkin et al. (1972) than any of the aforementioned FLDMs. The simulation of competition in particular shows similarities with gap models but in GALDR this is integrated with a self-thinning model that has been inspired by previous models of Wilson (1946), White (1981), Weller (1987b) and Tang *et al.* (1994). Seed dispersal is based explicitly on the dispersal model of Greene and Johnson (1989).

Most of the above models originate in the ecological literature (Wilson, 1946 is an exception); however the GALDR model also incorporates models designed by and for the forestry sector. The height growth and self-thinning models are based on output from the Forestry Commission yield models (Edwards and Christie, 1981). Site conditions are represented using the ESC system of Pyatt *et al.* (2001) whilst the wind model is heavily reliant on the wind speed model DAMS (Quine and White, 1993) and the stability and wind risk model ForestGALES (Dunham *et al.*, 2000).

The most characteristic feature of the GALDR model is the representation of cohort structure. The cohort representation is a powerful simplification of the population structure of trees in a stand, allowing faster simulation and a more tractable model than would be possible by attempting to use an individual-based model at landscape scales. GALDR differs from VAFS-LANDSIM, LANDIS and FIN-LANDIS in that it allows fewer cohorts per cell, but represents the cohorts in much more detail. The advantage of this is that it allows far more precise definition of cohort types than would be possible using LANDIS-type cohorts. For example, modelling the particular habitat requirements of the lichen *Bryoria furcellata* (see Section 6.2) would be very difficult using LANDIS, feasible but problematic with FIN-LANDIS, but is relatively straightforward with GALDR.

The major limitation of the GALDR cohort representation is that fine scale gap-phase dynamics are not modelled easily because mortality and recruitment both occur nearly continuously, and the number of age-classes present may be high.

Where the dynamic behaviour of the model dictates such dynamics (e.g. low rates of establishment and lack of catastrophic disturbance) the representation of the structure may be poor and the model is said to exhibit cohort limited understocking (see 3.3.4). However, although there can be no definite knowledge on the structure and dynamics of British natural woodlands (see Peterken, 1996), it may be noted that GALDR is well adapted to simulate the hypothetical dynamics proposed by Humphrey (2003) for Glen Affric.

7.2.2 Stand development sub-model

Limitations of the stand development sub-model are considered below under the headings of the three modules that compose the sub-model.

Height growth module

The GALDR height growth models can be seen to make good approximations to the FC yield models. These yield models are well-established and widely used, giving confidence to their use in the present context, where accuracy may be less important than in the production forestry context for which they were designed. Inaccuracies are most likely to arise through yield class estimation, though this is not a limitation of the growth model as such. The reliability of the GALDR height-growth model might also be called into question where it operates beyond the data-range of the yield model. This may occur where the ESC model predicts yield classes lower than 4, as well as in predictions of height growth of young cohorts (less than 20-30 years). Low yield classes are unlikely to cause many problems since regeneration is excluded on sites with yield class less than two. The prediction of early growth is more likely to be a source of unrealistic behaviour since it is not based on any field data. This phase of growth is also likely to be the most unpredictable since growth check may arise through browsing or lack of mycorrhizal inoculation on very infertile soils (Miles and Kinnaird, 1979a,b).

Although it is not considered a major limitation at present, some form of dependency on shading would certainly need to be incorporated into the height growth model if shade-tolerant species were to be included in the species list. The current assumption is that highly shade-intolerant species such as pine and birch do not significantly reduce height growth under shade.

Density-dependent mortality

The density-dependent module is more speculative than the height growth model, and thus less confidence can be placed in it. It would be desirable to validate the GALDR model with independent data, preferably data from semi-natural stands of Scots pine and birch. The major inconsistency in the current formulation is the asymmetry of competition between cohorts with very similar heights. (Although it may be noted that this assumption is completely analogous with Botkin's (1993) treatment of trees, where all of the leaf area is assumed to occur at the very top of the crown.) It seems likely that a solution to this problem could be brought about if more time were spent on developing the mathematics of multi-cohort self-thinning. The desirable next step in the development of this module would be a model in which the rate of self-thinning was dependent upon the level of vertical crown overlap. To make a significant improvement to the model however, some data on self-thinning in two-cohort stands will be required.

Whilst the height growth module would require some minor modifications if shade tolerant species were to be included in GALDR, the density-dependent module would require major review. It may be anticipated that the concept of the SDI would need rethinking to include the possibility of cohorts of shade tolerant species regenerating underneath fully-stocked cohorts of shade intolerant species. Even without additional species it is probably worth investigating differences in self-thinning behaviour between pine and birch (as reported by Hynynen, 1993). However, even a change as small as making the thinning constant (T) species-dependent would require reasonably major reworking of the multi-cohort self-thinning algorithm.

Density-independent mortality

Compared to the density-dependent mortality module, the density-independent mortality module is simplistic. However, it may be noted that it is no less simplistic than the equivalent mortality sub-model used in JABOWA and subsequent gap models (see Botkin, 1993). One simple modification that perhaps should be made would be to make longevity dependent on growth rate, since slow growing trees live longer than fast growing ones (Rackham, 1990). Further improvements to this aspect of the model will require better data on mortality in semi-natural woodlands than are currently available.

7.2.3 Wind sub-model

Wind speed generation module

The strength of the wind speed generation module lies in its derivation from the general wind climate model DAMS, which has been tested and found to be a good predictor of the effects of topography on wind speeds (Suárez *et al*., 1999). However, the sensitivity of the landscape response to wind parameters *Ua* and *k* indicates the importance of this module to prediction of landscape structure. Thus, evaluation of the GALDR module must be directed at (a) the EDAMS method of estimating windiness for particular wind directions and (b) application of Quine's (2000) methods of predicting extreme wind speeds to EDAMS.

The collection of wind speed data from mast-mounted anemometers in three sites of varying topography in Glen Affric may help to validate the EDAMS model. Preliminary analysis of these data suggest that EDAMS is a better predictor of wind speeds than DAMS for wind directions differing from the prevailing. Furthermore, the data seem to support the hypothesis that directional effects for winds of a single direction will be higher than those used in DAMS.

However, the difficulties encountered using the heightened direction factors of EDAMS indicate that the methods for estimating extreme wind speeds for individual wind direction sectors may need reviewing. Even with attenuation factors set to unity, the aggregated extreme wind speeds predicted by EDAMS do not quite match with those of DAMS, but in this case the differences are not great. It is considered that despite limitations of the extreme wind speed generation method, use of EDAMS is still preferable to the default option of using DAMS unmodified. This is because using unmodified DAMS would tend to produce the same patterns of disturbance every timestep, which, over time, would lead to an unrealistic representation of landscape structure.

Stability module

In the most part the validity of the stability model rests on the use of ForestGALES (Dunham *et al*., 2000) to predict stability of semi-natural stands. From the point of view of stability, semi-natural stands differ from even-aged plantations in that they may be: (a) uneven aged; (b) multi-storied; (c) mixed-species; and (d) variable in stem density, both within and between stands. Furthermore, the tree-pulling data on which ForestGALES is based covers stand ages only as far as one hundred years. Semi-natural stands *may* be structurally similar to plantation stands, particularly where the disturbance regime tends towards stand replacement, but equally they may be considerably different.

Nonetheless, Quine (2003) accepted all of these limitations in using ForestGALES to characterize wind disturbance regimes in Glen Affric. In reference to the question of extrapolation of stand ages, it was noted that, at the end of the range covered by ForestGALES, threshold wind speeds change little with increasing age.

7.2.4 Seed production and dispersal sub-model

Seed production module

Limitations associated with the seed production module may be summarized as follows.

1. Values of baseline production are arbitrarily chosen.
2. Initiation of seed production might be more accurately based on minimum tree size.
3. The altitude-germinability factor relies on a single study at a single site.
4. The stand density factor may misrepresent production in stands of two or more cohorts with widely differing heights.
5. The effect of limitation of pollination in low density stands is not simulated.

Of these, points 2 and 5 are probably most easily addressed, although it is questionable as to whether such refinements are likely to affect appreciably the performance of the model as a whole. Point 4 may be a more fundamental defect of the model, but the modelling effort required to rectify the problem is significantly higher.

Limitations associated with the seed dispersal model may be summarized as follows.

1. Vertical profile of wind speed distribution is not considered.
2. Vertical components of wind speed are not accounted for.
3. No differentiation in wind speed is made between open and wooded ground.
4. Effects of topographic variation on vertical displacement of falling seeds are not considered.
5. The wind speed distribution of the source cell is assumed to act on falling seeds over their entire trajectory of fall.
6. The factor of non-random abscission should be a function of average wind speed rather than a constant.
7. Directional effects of dispersal are not simulated.
8. Long distance dispersal is not simulated.

The most consequential of these in terms of overall model behaviour will almost certainly be point 8. Over short timescales the inclusion of long distance dispersal events has little impact on results, but in the long term the consequences can be profound (Higgins and Richardson, 1999). The major difficulty to be overcome in the production of such a model is the parameterization, since the mechanisms of long distance dispersal are poorly understood. Greene and Johnson (1995) present a ‘background model’ of long distance dispersal which acts at the landscape scale (i.e. deposition probabilities are constant over the whole landscape). This model may be easily adapted to be used in GALDR but as yet, this has not been attempted.

To address points 1,2,6 and 7 would necessitate augmentation and reworking of the mathematics presented in Section 4.3.4, as well as additional parameter estimation. Rectification of points 3, 4 and 5, however, would probably require substantial model restructure. Furthermore, it is likely that the resulting reconceived model would be very costly in processor time. In the current model, calculation of the seed dispersal algorithms already accounts for c. 90% of the processing time; therefore, any increase in processor usage in the seed dispersal model will have a major effect on overall model run times.

If costs in development time and increased processor usage were thought to be justified, a reformulated seed dispersal model might use a random walk type algorithm. Such a model should require less sophisticated mathematics than the equivalent reworking of the present model to incorporate improvements to points 1,2 and 7 (point 6 is independent of the dispersal algorithm used). Furthermore, if the model were to consider extreme values of the distribution of vertical components of wind speed, especially in relation to topography, such a model could form the basis of an effective simulation of long distance seed dispersal.

7.2.5 Seedling establishment sub-model

The establishment model represents a major generalization of the processes outlined in Section 4.4.2. Such generalization is considered unavoidable in a study of this scope for the following reasons.

1. There are a large number of factors involved (e.g. predation by at least ten animal species).
2. Quantitative data on individual factors considered in isolation are very scarce.
3. Relationships between factors affecting establishment are frequent and complex.
4. The scale at which establishment factors operate is often much smaller than the scale of the model.
5. Collection of spatial data to support models of individual processes would be challenging.

In the absence of a process-oriented model of establishment, the most desirable alternative would be an empirical model based on appropriate studies of regeneration using variables that may be easily incorporated into the simulation model.

The factor of canopy density at least has some basis in quantitative field assessment (Cameron and Ives, 1997; Vickers and Palmer, 2000). However, it must be noted that the quantifications of canopy openness or cover used in these studies cannot be directly related to those of stand density used by GALDR. Developing relationships between canopy cover and GALDR stand variables (i.e. height, age and stocking density) need not be an onerous undertaking and could significantly improve the accuracy of this element of the model. Nonetheless, it is expected that even without such refinements, the broad behaviour exhibited by the model should be realistic.

The situation regarding site suitability is less clear. The current model is highly arbitrary in both design and parameterization because of the scarcity of suitable data. The ESC concepts are likely to prove useful, since they provide standardized classifications for basing studies. However, as ESC has only recently become a standard tool in British forestry, few studies have been made relating ESC to natural regeneration (but see Thompson and Milner, 2001). The principal limitation of the use of ESC to predict regeneration is that it is designed to predict growth of trees rather than establishment of seedlings. In view of this, ESC may be expected to be useful in predicting where regeneration will not occur, as well as providing some indication of early mortality, since Miles and Kinnaird (1979a) observe that seedling survival is heavily dependent upon growth rate. However, the number of seedlings that establish is likely to be more dependent upon the availability of suitable microsites, which in turn will probably be contingent on the vegetation type and structure. This latter point provides an argument for the use of NVC communities instead of, or addition to, that of ESC. This was not undertaken because: (a) only part of the study area is covered by NVC survey and (b) in the long term, vegetation communities may be expected to be more changeable than soil characteristics.

The issue of long-term change in site conditions is one that is not addressed in the current model. A more well-appointed model might include field vegetation sub-models that would influence soil conditions over time. A useful application of such a model would be to investigate the effects of climate change, particularly in relation to peat formation and changes of moisture regime in mires. Such sophistication is beyond the scope of the present study.

The timing of regeneration is another critical issue. It is a noticeable feature of natural regeneration that it may not always occur on favourable sites even in good seed years. Population dynamics of damaging animals, field layer vegetation dynamics and climate variability may all play a part in determining the temporal pattern of regeneration. All of these above factors could be modelled alongside the rest of the GALDR model in an attempt to yield better predictions of regeneration timing. However, given the state of the knowledge on quantitative effects of these factors on regeneration, it is debatable whether such added models would be any less arbitrary than the blunt instrument currently utilized. The current version of the establishment model represents all sources of variation by one stochastic factor in which the probability of regeneration is dependent upon site suitability. This, like many of the other broad assumptions made in this sub-model, requires testing.

Parameter estimation in models such as the above, which may be considered indicative predictors of expected behaviour, is necessarily rather arbitrary. The default parameter set used here is consistent with a naively optimistic expectation of regeneration in the absence of browsing and grazing. It also gives rise to a null model with respect to differences in establishment between pine and birch, since the tenfold difference in baseline establishment ratio (E_i) exactly compensates for the tenfold difference in baseline seed production (Q_i^*). In terms of average numbers of establishing seedlings this may well be reasonable, but it is also fair to expect that the nature of the variability will be rather different for the two species. For instance, when a good seed year is followed by climatic conditions conducive to germination and early growth, birch may have the potential to produce much more prolific regeneration than pine. Such an advantage may also give rise to longer effective dispersal distances. However, such combinations of mast years with suitable climate may be infrequent, leading to spatial synchrony in regeneration at the scale of decades despite relatively even seed production at the same temporal resolution.

7.2.6 Browsing sub-model

The browsing sub-model is the most simplistic of all the sub-models representing dynamic landscape processes; in fact, the degree to which the process is *modelled* at all is quite minimal. Given the importance of browsing in determining woodland structure and dynamics, this lack places a major limitation on the confidence that may be placed in model predictions. However it is considered that the major impediment to realistic representation of the effects of browsing on woodland dynamics is a dearth of scientific data and knowledge on herbivore behaviour and impacts.

7.3 Identification of knowledge gaps

The principal long-term objective to which the development of GALDR is directed is the provision of predictive tools for forest managers and restoration ecologists (see Newton *et al*., 2001). However, in the course of model development it may be noted that certain observable effects may lack satisfactory explanatory mechanisms or that certain processes may be so poorly understood that representation is very difficult. In such cases the model serves to identify gaps in the scientific understanding of the system under study. This by-product of the modelling process may be considered almost as important as the end-product model. In the course of the GALDR model development process the following subjects have been identified as lacking in appropriate ecological theory:

1. Self-thinning in multi cohort stands
2. Stability of stands of mixed species and varying structure
3. The mechanisms and effects of long distance seed dispersal
4. Spatial and temporal variation in natural regeneration
5. Spatial impacts of herbivores on woodland regeneration

Some of these problems may be pertinent to other fields of interest and thus solutions may become available. For example, subjects 1 and 2 are likely to be pertinent to the development of continuous cover forestry systems and therefore may receive attention in the near future (Page *et al*., 2001; Mason, 2002). To examine the effects of human disturbance on red deer, Sibbald *et al*. (2001) have demonstrated a method of tracking deer with GPS (global positioning system) collars that may prove crucial in gathering understanding of deer habitat use.

7.4 Quality of initial and static state data

Subcompartment database

Use of the Forest Enterprise subcompartment database alone to define the distribution of species and ages classes is less than ideal because:

- areas of heterogeneous vegetation (i.e. at the 50m grid cell level) are represented as homogeneous;

- where birch (as well as other broadleaved species) occurs as a minor component of stands it is often shown as absent;
- age classes have often been estimated on little evidence.

Nevertheless, the data do give a broad impression of the overall distribution of pine and birch in Glen Affric, and the forester's estimation of stand ages are better than no spatial age information at all. The acquisition of accurate, spatially explicit data on cohort ages is certainly not possible at present without a massive program of tree coring.

In some situations, it can be assumed that height provides an indicator of tree age for the younger age-classes (although it provides no indication of tree age at all for older age-classes). It is hoped that fine resolution tree height data will shortly become available from the Glen Affric Radar Project (GARP; Cloude *et al.*, 2001) for a large part of the GALDR study area. Spatially explicit height data would be invaluable for initializing the height raster as well as providing a check for yield class estimation.

It may be possible to use remote sensing techniques (e.g. classification of spectral signatures using LANDSAT Thematic Mapper) to add detail of the spatial distribution of tree species. Determination of species composition at 30m resolution has been successfully achieved for Strathfarrar and Abernethy native pinewoods under the Earth Observation for Natura 2000 project (Anon., 2000).

ESC analysis

Determination of site suitability and yield class for species is another area where the model is data-limited. Ideally, the ESC variables would be determined from detailed soil surveys of the whole area. Use of the Native Woodland Model (Hester *et al.*, 2003) is a circuitous (though not circular) method of arriving at ESC type. Use of NVC survey map data may help to define soil quality variables more accurately, though some fine tuning using a wetness map (WIM) may be necessary to resolve the fine scaled community mosaics, of which much of the vegetation description consists. Further survey of the study area would be beneficial as the current survey is restricted to the main areas of native woodlands and adjacent open ground communities only. In areas where trees have been planted, field based ESC analysis (see Pyatt *et al*., 2001) could be used to detect spatial variation in soil variables that may not be picked up by NVC.

7.5 Sources of uncertainty

Uncertainty is an unavoidable element in any form of prediction but it may be worthwhile to attempt to identify some of the types and sources of uncertainty. Sources of uncertainty may be split into those that are intrinsic to the system being modelled and those that arise as part of the abstraction process. Uncertainty intrinsic to the system may arise as a result of chaotic behaviour or the unpredictable behaviour of individual animals. Where such effects are important to the model application they may be simulated as stochastic processes. An example of this from the GALDR model is the random nature of individual wind disturbance events; this process may be considered intrinsically unpredictable because the weather system that drives it is chaotic. Stochastic processes may also be used to represent behaviour which may be theoretically predictable given sufficient data but where the relevant controlling processes operate at a scale below the organizational resolution (for definition see Section 2.1.1) of the model. For example, uncertainty in tree regeneration at the site (cell) level might be reduced if data were available to describe microsite characteristics in detail; however, the benefits of uncertainty reduction would be likely to be outweighed by the increase in model complexity.

Uncertainty in model and data abstraction occurs in (a) estimation of model parameters, (b) acquisition of initial state data, and (c) specification of model behaviour. Systematic analysis of the effects of uncertainty on model results is practical in the case of (a) only since variation of each parameter occurs in one dimension only, whereas in (b) and (c) the scope for variation occurs in many more ways. (For uncertainty analysis of model parameters, see Chapter 5.)

Against the obvious benefits of reducing uncertainty must be set the time and cost of obtaining the necessary data to do so. For example, consider the relative benefits of (1) setting up experimental plots to provide data for better models of self-thinning in uneven-aged stands, versus (2) conducting a survey of the present distribution of Bryoria furcellata in Glen Affric. These measures would address uncertainty of types (c) and (b) respectively; thus, quantification of the effects of these sources of uncertainty is difficult. Nonetheless, one may reasonably conjecture that (2) will reduce uncertainty in GALAM output by a greater margin than (1); and, with more confidence, predict that (1) will involve significantly more time, effort and expense. It therefore seems reasonable to undertake measure (2) as part of a programme of improvement of the GALAM, but to defer (1) until data might be acquired opportunistically from some other programme of work. Other actions which might help to significantly reduce uncertainty for low costs include using LANDSAT data to improve the initial state and using NVC data to improve the landscape ESC assessments (see Section 7.4 for both).

7.6 Future application of GALDR

The potential for future development of GALDR is considered in terms of two directions in which the model may be further applied:

1. as a management tool;
2. as a more general FLDM.

GALDR as a management tool

Since the GALDR project represents the first effort at developing a FLDM for British woodland, the approach is necessarily exploratory and research-oriented. A framework for integrating a FLDM into a decision support system for ecosystem management is presented in Section 1.3.5. To realize such a system completely will require:

- refinement of model processes in collaboration with forest mangers and researchers;
- testing of model components, possibly as part of the above process;
- development of further SEPMs for a greater range of target species.
- development of a *management submodel* that might simulate the effects of various planting, thinning felling and deer management regimes.

Furthermore, if such a system were to be used in areas other than Glen Affric, a certain amount of generalization would be required. This is discussed under the next subheading.

Generalization of GALDR

In its first incarnation, GALDR is an area-specific model, developed for the purpose of simulating forest landscape dynamics in Glen Affric. However, apart from the methods used to generate the initial state, there is little in the model which could not be put to more general application. The level of modification that would be needed to generalize the model so that it may be used in other areas depends on how widely the modified model would be applied. For example, to be of use in managing restoration in Glen Strathfarrar, located two glens to the north of Affric, all that might be required would be the addition of oak to the species list. Application to the pinewoods of the eastern highlands might require the development of a fire submodel. However, if the aim were to present a model that could be applied generally to any temperate or boreal forest system (as in LANDIS) then major changes to the model structure would be required. One generalization that would require reasonably major modification to be carried out would be the inclusion of shade tolerant species (see Section 7.2.2). Application to landscapes with greater anthropogenic influences would create challenges of a different nature.

7.7 Preliminary management recommendations

The recommendations made in this section are presented with the following caveats:

- both GALDR and GALAM are at early stages of development;
- many sources of uncertainty are present in the models, parameters and data used;
- the project here documented was not designed to answer management decisions at this stage.

Nonetheless, since FLDMs tend to remain as works in progress throughout their working lives, the following tentative suggestions may be made regarding management of the Glen Affric woodlands based on the modelling work presented in earlier chapters. The major implication of the lichen modelling results (see Chapter 6) is that special care should be taken in areas that might act as long term refugia for light demanding lichens. These areas may be characterized as being of marginal suitability for tree growth, thus tending never to develop into closed-canopy stands. Such areas may often exist on the edge of bogs where the soils are often too wet to favour pine and too nutrient deficient to favour birch. Management in such areas should be strictly minimum intervention; the only active management should be mitigation of artificial negative influences – e.g. removal of self-seeding exotic tree or shrub species. In the wider landscape, the most critical factor is likely to be the management of grazing. It appears that tree regeneration is currently sufficiently widespread to secure future generations of woodland in the glen. However, a possible danger might be that grazing levels could be reduced to lower than natural levels and regeneration could be *too prolific*. This could result in a widespread reduction of suitable habitat for light demanding lichens and thus endanger some of the scarcer taxa.

An attempt has not been made here to produce a complete set of guidelines for management for *Bryoria furcellata*. However, the development of the models GALDR and GALAM has created an avenue of opportunity for supporting management decisions that may affect lichen biodiversity in Glen Affric. It is envisaged that the process of informing management by these means will involve extensive collaboration with the Forest Enterprise staff who manage the forest and, as such, will form a further phase of the GALDR project.

7.8 Closing remarks

In its present condition, landscape ecology has little to offer those wishing to plan and manage the landscape of the future.

Hobbs (1997, p.6)
in 'Future landscapes and the future of landscape ecology'.

Hobbs' statement carries a strong challenge to those wishing to apply theories of landscape ecology to forest management and the practicalities of ecological restoration. This quotation is reproduced in the concluding chapter of Mladenoff and Baker's (1999a) book 'Spatial modelling of forest change' in which the authors claim that spatial modelling techniques, and FLDMs in particular, offer significant potential in bridging the gap between theory and practice. However, even in North America, where the technology is most mature and progressing most rapidly, much development is required before landscape models can become everyday tools for forest management. In the UK, such a position appears still more distant, since the discipline is truly in its infancy here. For the time being at least, it seems likely that the majority of work on forest landscape modelling in the UK will follow the lead of work taking place in North America.

Nevertheless, wherever modelling takes place, a major issue governing development of landscape models as management tools is confidence in the accuracy and realism of the predictions. Experience so far with the development of the GALDR model suggests that the principal limiting factors to accuracy and realism are (a) the acquisition of good quality baseline data at landscape scales and (b) thorough understanding of the relevant ecological processes. Even if it is possible to build models that are accurate and realistic enough to use as a management tool with current data and ecological knowledge, generating confidence in the models will be dependent on adequately rigorous model validation. This presents a further problem since the validation would ideally operate at the same spatial and temporal scale as the model. Given the limitations on the availability of historic spatial data, the best that may be hoped for is that spatial data collected recently and in the near future might be useful for model validation in the more distant future.

However, it is worth recollecting that many benefits arise as a result of the modelling *process* rather than the model as a *product*. The discipline of modelling forces the modeller to identify the most important processes of the system under study, and formalise hypotheses about how they operate and interact. This process may highlight gaps in our understanding of the system or priorities for data collection. Where the system under study is an entire ecosystem, as in an FLDM, the process also necessitates the synthesis of theories and models from various sources and disciplines. The bringing together of seemingly disparate theories, which may have been developed separately, affords an overview of their relative places in our conception of the system as a whole. Some sets of hypotheses may work together in concert to engender emergent properties in the system as a whole; other sets may contradict or conflict with each other when combined. In either case, the results are interesting. In time, as the project develops, GALDR may be able to feedback insights to the theories upon which it is founded as a result of their integration in a single structure.

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