Issues of scale in individual-based models:

applications in fungal and plant community dynamics

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Abstract

The central question addressed in this thesis is whether descriptions of the dynamics of ecological systems at one scale may be effectively used as descriptions of the dynamics of ecological systems at larger scales. This question is addressed in the context of the dynamics of fungal communities. A simple experimental system and complementary theoretical approach, in the form of an individual-based (cellular automaton) model, is presented. Experimental results derived from small-scale systems are used to quantify parameters of the model; results from large-scale experimental systems serve to test the model. The theoretical analyses clearly demonstrate that the dynamics observed are a result of both local and non-local features of the experimental system. In cases such as this the immediate extrapolation of results derived from experiments conducted out of the context of the community to represent system scale behaviour is not possible. In response to this observation a generic framework is developed to allow the consideration of effects at a range of scales through contextual parameterisation of localised dynamics. The framework is directed toward plant systems where a large body of experimental data exists, and may be parameterised by that experimental data. It represents the essential features of individual interactions in terms of competition for space and resource, and the behaviour of a given plant is described in terms of functional traits. Model runs demonstrate complex community patterns suggestive of a known biological phenomena, succession, that arises as a consequence of the coupling between the community and environment. This coupling may allow the long-term coexistence of species through some particular balance in individual function (traits) across the community. A search mechanism is determined to allow combinations of trait values at the scale of the individual to be assessed for a particular community-scale phenomenon. Initial results demonstrate that this mechanism may identify and converge on combinations of trait values that give rise to, in this case, a simple measure of diversity. The manner in which the generic framework developed may be applied to further the investigation into fungal community dynamics is addressed.

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Chapter 1 Introduction

1.1 Towards modelling ecological systems

1.1.1 The nature of ecological systems

Ecology is the study of natural systems; that is systems comprising assemblages of abiotic (nonliving) and biotic (living) elements (Ricklefs, 1993). The abiotic components range from basic inorganic elements and organic compounds to climatic features such as wind, rainfall and sunlight and will hereafter be referred to as the environment. The biotic elements, categorised into animals, plants, fungi, protozoa and bacteria, interact within this environmental context with energy as the unit of currency for such interactions. The biotic assemblage will hereafter be referred to as the community. (The notion of community is given more treatment below.) A given union of community and environment constitutes an ecological system, or ecosystem. Given the variety of possible community and environment compilations and combinations ecosystems can be both complex and diverse.

However, the definition of a specific ecosystem is often unclear since the boundaries of such a system are often not readily delineated (Mackenzie *et al.*, 1998). These boundaries are typically acknowledged where a marked change in composition, either community or environment, occurs. Such compositional changes are often a consequence of differences in natural spatial features such as an island or by vegetation change such as a forest (Dickinson and Murphy, 1998). This compositional change serves to partition some large ecosystem into a series of more addressable sub-ecosystems. Further, whilst extensive exchange of resources may exist within some sub-ecosystems, such territorial boundaries prohibit extensive exchange of resources between neighbouring ecosystems (Kormondy, 1984). However, some exchange may occur and thus ecosystems must be considered open.

Further, the delineation of an ecosystem is not always a consequence of differences in natural features. Ecosystems may also be defined in terms of artificial boundaries or laboratory systems (Dickinson and Murphy, 1998). The term ecosystem is a conceptual tool for simplifying the complex natural world into (artificial) manageable portions, and hence the interpretation of this term is varied. Ecosystems exist at a wide range of scales from microscopic microbial ecosystems to the macroscopic global ecosystem with many intermediate ecosystems.

Both the inherent complexity and the problematic definition of ecosystems make the study of such systems difficult. This difficulty is compounded by the dynamic nature of those ecosystems in terms of both environmental and community compositions. The source of such dynamics is twofold. Firstly, the open nature of ecosystems means that such systems are subject to fluctuations in the community and environmental compositions, as exportation and importation of genetic material in the case of communities, and substances or resources in the case of the environment, through (loose) connections with other ecosystems.

Secondly, the environment and community are intimately coupled. The community actively impacts upon the environment utilising energies, or resources, through the processes of growth, storage and reproduction, and replenishing resources through the process of recycling following death. This activity causes fluctuations in the amounts of various resources (energy sources) in the environment. Thus, the community of an ecosystem influences the composition of the environment. Further, the subsequent activities of the community are affected by the existing environmental composition. The processes of growth, reproduction, storage and recycling following death determine the composition of the community. Those processes are not independent of the environmental composition; indeed, they are modified, or parameterised, by that composition. Thus, the environment of an ecosystem influences the composition of the community. Hence, future community compositions are driven by not only the existing community but also by the existing environmental composition. Likewise, future environment compositions are dependent on both the existing environmental and community components of the ecosystem.

Clearly ecosystems are complex dynamic systems, open and evolving. The field of ecological study strives to understand such dynamics in terms of a set of generalised rules or laws as present in other sciences. Whilst much effort has been invested in identifying such a rule set, progress has been slow (Judson, 1994). One barrier to this theoretical progression is the difficulty encountered in attempting to describe properties associated with ecological systems. This difficulty is argued (below) to be a consequence of the spatial and temporal structure inherent in natural systems, and the range of spatio-temporal scales present in that system (Levin *et al.*, 1997).

1.1.2 Characterising ecosystems: the issue of scale

1.1.2.1 Describing ecosystems

The nature and content of the description of any system is dependent on the perspective from which that system is viewed. A single appropriate perspective from which to view ecosystems is not readily apparent. Ecosystems may be viewed at various levels of organisation ranging from the genes comprising organisms through intermediate levels up to the community itself. Further, those levels of organisation may be considered at or indeed over various spatial and temporal scales. Each combination of organisational level, spatial scale and temporal scale provides a different set of characteristic scales for that system, i.e. the set of scales useful in analyses, and thus gives rise to a different form of description for any given ecosystem. A number of levels of community organisation immediately present themselves as identifiable characterisations, and there are different properties and measures associated with each level of organisation, or perspective resolution, in any ecosystem. Here, a range of such characterisations is considered briefly, and the difficulties encountered when ascribing appropriate spatial and temporal scales are addressed.

1.1.2.2 Organisational levels

Arguably, the gene may be considered the most fundamental unit of ecology. Particular active genes, or combinations of genes, give rise to particular characteristics in an organism. Thus the genetic composition of an organism, termed the genotype, gives rise to the form of an organism, termed the phenotype. Further, changes in this genotype may manifest themselves as changes in the phenotype. However, the relationship between the genotype and phenotype is complex. Firstly, the phenotype is not solely determined by the genotype, but also by the environment. Secondly, and perhaps more importantly here, the mapping of (gene) sequence to function is not well understood in detail. Whilst the sequences of genes may be identified accurately through genome investigations, the role of those genes in the ecophysiological development of organisms is difficult to identify with much certainty. Given that the function of the genotype remains, in part, elusive many ecologists choose the phenotype – the organism – as the fundamental unit of study.

In many ecological studies the organism is discrete in space (Ricklefs, 1993) and is thus an individual component of a community with limited spatial and temporal extent – the organism is determinate in space and time in the sense that it has definite limits in these dimensions (Rayner, 1996). Such an individual interacts with its environment over time in terms of processing localised environmental resources to facilitate its (energy-driven) life cycle – resource uptake, resource storage, resource utilisation through growth and reproduction and resource recycling following (eventual) death. The levels of various resources as perceived by the organism will impact upon that life cycle. Indeed, a typical approach to identify the resource-based mechanisms present within an individual organism is to investigate the effect that varying the levels of resource has on particular aspects of the life cycle of individual organisms such as root extent (in plants) or reproductive capability (generally) (Silvertown *et al.*, 1992; Tilman, 1994a; Winkler *et al.*,1999). These studies, and many other investigations, demonstrate that individual organisms are sensitive to the surrounding environment. Individual organisms respond to limitations in resource in terms of inhibited development manifested through (detrimental) changes in the processes of growth, reproduction and death. Resource limitation may be the result of inherently low levels of resource and/ or competition from other organisms for that resource. Thus individuals interact with other individuals via the local environment, and many such localised interactions yield the non-local (spatially distributed) dynamics present in the community. Consideration of the organism and its mechanistic interactions with the environment represents an important scale of study in ecology.

This fine-scale study is made difficult when dealing with a class of organisms without definite limits in space and time, and such organisms are termed indeterminate. In such cases the very term individual may be inappropriate. Fungi, the subject of the initial and final parts of this thesis, are a class of organism that are indeterminate in that they grow and survive over potentially infinite areas for a potentially infinite period of time. In terms of physical structure, fungi are by nature filamentous and the individual filaments are termed hyphae. A fungal organism extends itself through its environment by extending these hyphae (from the tip) and by branching an individual hypha to form new hyphae. The network of individual hyphae resulting from these growth and branch processes, is termed the mycelium.

Whilst an hypha might be considered a determinate individual, this hypha is in fact merely a part of the larger interconnected mycelium. It is the mycelium – a colony of hyphae – that should be the focus of study, and since it comprises many hyphae of undetermined number and size it is spatially indeterminate (Rayner, 1996; Boddy *et al.*, 1999). The mycelium is able to relocate resource commodities around the network and so any individual hypha is in communication with other hyphae. Further, the mycelium has the ability to relocate through the colonisation and de-colonisation of regions of space. In this relocation the investment of the organism into hyphae in resource rich areas is extended and the investment in hyphae in resource poor areas is reduced, and this relocation strategy assists the fungal organism to exist potentially indefinitely. Fungal colonies employ a range of strategies to address environmental constraints (Boddy *et al.*, 1999) and are able to reproduce both sexually and asexually. In an attempt to characterise fungi measures of the mycelia including biomass – biological material, hyphal extent and fractal indices (Ritz and Crawford, 1990; Bolton and Boddy, 1993; Boddy *et al.*, 1999) – a measure of space filling properties – are employed. Whilst each of these measures is revealing, none aid in ascribing characteristic scales within which to study the dynamics of a fungal organism. This indeterminate nature makes fungal organisms both challenging and intriguing systems to study.

Considering a community of organisms within a single ecosystem as a single dynamical unit is clearly the coarsest resolution possible. Other resolutions of perspective (e.g. the gene, the organism) have associated processes and measures. Similarly, this holistic perspective community level of organisation has its set of pertinent processes and measures. For example, the notions of trophic level (defined below), food web (defined below) and diversity descriptions are available at this level of resolution, and brief treatments of each serve to illustrate the concept of community level descriptions. In each description the community is considered in terms of species rather than organisms. The selection of species as the descriptive unit of communities over the organism is a result of the intractable magnitude of detail arising from an organism-centred description. It is therefore usually assumed that all organisms within a species are sufficiently similar so as to remove the need to include the detailed intraspecific differences.

A trophic level description structures a community, in terms of its species, into an energy-dynamics hierarchy and was introduced by Lindeman (1942). In this scheme, species are ranked in terms of the distance of their energy supply from the fundamental environmental resources, for example inorganic compounds and sunlight. Autotrophs (producers) are organisms that directly use the fundamental resources available, thus translating the energy present in inorganic elements and external energy supplies (for example, sunlight) into organic elements. Heterotrophs (consumers) are organisms that use those organic elements as their source of energy. Thus, autotrophs lie below heterotrophs in the trophic hierarchy. Heterotrophs may be further sub-categorised into herbivores and carnivores, for example, where carnivores clearly have an energy supply that is more distant from the fundamental resources than herbivores. Such a categorisation serves to highlight similarities between species and so the complexities present in multi-species communities are ignored (Putman, 1994).

Food web descriptions take place at a finer resolution of biological detail than trophic level descriptions, as food web descriptions contain species-level information (Ricklefs, 1993). Food webs capture the interdependencies among species in terms of feeding relationships. This form of description is amenable to theoretical investigations into community dynamics where the topology of the food web is suggestive of the nature of those dynamics. While the details of such investigations are beyond the scope of this work, the food web description serves to illustrate one of many forms of characterising ecosystems at the scale of the community.

A further community level description is that of community diversity. The structure of a community is affected by both the relationships among species, as characterised by food webs for example, and the community composition itself. One approach to characterise community composition is to consider species abundance – the number of organisms of that species. It has been noted that the abundance of species within communities assumes some regular distribution. More precisely, a few species typically attain high abundance and a large number of species typically attain low abundance in any community. This distribution, typically shaped as a 'reverse J' (Ricklefs, 1993), is called lognormal – the y axis represents species abundance and the x axis comprises species ranked in decreasing abundance. Further, this species abundance distribution may be different for different communities and hence provides a community scale means to consider groups of communities (Putman and Wratten, 1984; Putman, 1994; Hastings, 1997).

1.1.2.3 The importance of scale in space and time

The above measures consider processes at the scale of the organism and the community. Huston *et al.* (1988) observe that any study of communities above the scale of the organism is at an intermediate scale arrived at by assuming some (simplifying) level of organisation. Indeed, studies between the scales of the organism (determinate or indeterminate) and the community are levelled at some recognised pattern or process introduced to simplify the study of the system as a whole. Two such intermediate scales of study are that of the population and the patch.

Organisms within a community may be grouped together into a population, and this grouping is normally based on species classification. The population is commonly considered in terms of the number, spatial extent and temporal extent of those grouped organisms. Unlike determinate organisms that have finite temporal and spatial extent – life span and size – populations are, like indeterminate organisms, potentially infinite in these dimensions, and pose many problems relating to analysis similar to that of indeterminate organisms. Whilst (determinate) organisms in populations have restricted temporal extent, populations have the potential to persist, in the form of different organisms, for an infinitely long period of time. The population size (number of organisms) will tend to fluctuate over time because of births, deaths and exchange (import and export) of organisms in a community. Populations are therefore dynamic in time. The properties of the population will also vary across space, and this distribution may be characterised by parameters describing spatial extent, density and spatial correlation. These properties can also affect the processes associated with a given population. For example, the rate of increase in population size has been demonstrated to be dependent on the density of that population (Putman, 1994; Hastings, 1997).

In some analyses many organisms within a particular spatial region may be conveniently grouped together into a patch. This intermediate scale considers sub-assemblages of a community, where divisions may be a result of some environmental features. Where this approach is adopted it is assumed that the dynamics of the community differs over its spatial extent and that these differences are structured in that space. Thus, the dynamics may be viewed in terms of fragmented, but coupled, patches. Here measures of the dynamics of these sub-divisions are of greater interest than the coarse community measures (above). Community-scale measures may, of course, be applied to each sub-community independently to usefully describe the system. For example, population level studies within the identified patches may reveal (localised) dynamics that differ among patches, and this may be a consequence of regional environmental differences. Thus, investigations into the response of a community to different environmental characteristics may be undertaken based on this detailed community description. However, this division of space will result in a divided, and more complex, description of the community that may be difficult to interpret. Given that both the population level descriptions and the patch divisions both serve as simplifying aids the appropriate (beneficial) use of each is dependent on context.

Studying ecological processes and identifying patterns resulting from those processes represents a central approach in ecology (Wu and Levin, 1994), as exemplified above. Importantly, each of the forms of analysis that links pattern and process is dependent on the treatment of both time and space within that analysis. The characteristic time-scale of a system is the time-scale over which significant dynamical change takes place, and this time-scale depends on the nature of the underlying system. In determinate systems the generation time-scale often plays an important part in the dynamics and this scale may inform the choice of time-scale. In indeterminate systems, however, there is no single characteristic time-scale, and the selection of a time-scale is generally related to the duration of ecological study.

Ascribing characteristic spatial scales to processes is more problematic. Each of the ecosystem characterisations above, e.g. population level and species abundance, assumes some particular spatial region. At the scale of the individual organism the spatial region that is immediately apparent is that of the individual itself, and this is most clear in determinate organisms. However, organisms interact with neighbours in terms of competition for resource and space (Tilman, 1994a).

Thus, the processes occurring at the scale of any individual organism are parameterised by organisms in the surrounding spatial region, or context. That context clearly has a spatial scale beyond the individual organism under consideration. Further, those processes occurring at the individual scale impact on that context at a range of scales. Processes resulting in resource competition take place in some localised neighbourhood above the scale of the individual. Processes resulting in spatial competition take place in both local and non-local regions (through dispersal for example). In the terminology of Wu and Levin (1994), process modifies pattern; pattern modifies process. It has been clearly demonstrated both experimentally and theoretically that the degree to which organisms are spatially mixed greatly influences the dynamics of the system. Thus, consideration of space and spatial heterogeneity is central to the understanding of ecosystems (Tilman and Kareiva, 1997; Levin *et al.*, 1997).

Measures above the organisational scale of the organism are also dependent on spatial scale. For example, the species abundance approach has been criticised as unrevealing, in part (Putman, 1994) since the process of identification of the number and abundance of species is clearly dependent on the size of the sampled area. Clearly, both the number of species identified and the probability of identifying a rare species will increase as the sample area increases. Further, the size of the sample area likely to encompass rare large mammals is radically different to the size of the area likely to encompass rare micro-organisms. Thus, it is difficult to obtain adequate measures of diversity at one spatial scale alone, and the ranges in scale required to measure diversity will vary across systems. This difficulty has resulted in studies into the dependencies between identified diversity and spatial scale, expressed through species area curves (Ricklefs, 1993). Further, Levin and Pacala (1997) argue that "*evolution has shaped the characteristics of species in ways that result in scale displacement: each species experiences the environment at its own unique set of spatial and temporal* scales" and stress that the proper treatment of space is imperative to understanding ecosystem community dynamics.

Clearly ecosystems have characteristic processes that are both attributed to one spatial scale and manifest themselves at one or more spatial scales. The following section initially describes the process of modelling systems in general, and then considers the use of models in ecological systems. The manner in which space is treated is given particular attention since models must address the relation between scales as indicated above.

1.2 Approaches to modelling ecological systems

1.2.1 Modelling: the process and its purpose

The real world poses many problems, and models of reality have been used for centuries to address those problems. A model is a construct designed to simplify the study of a particular real-world system or phenomenon. Physical models are commonly used to address difficult real world problems. An example of one such physical modelling approach is the building of scale-models prior to the construction of the real system. This approach has been employed in the designing of housing estates, where scale models of the new buildings are placed in the context of the (scaled) surrounding region to assess the impact of the new estate on that region. Another physical modelling approach is that of building a model that reflects only a subset of the aspects of the system under consideration, i.e. only those relevant to the given problem. For example, during the development of a new car a combination of a wind tunnel and a clay model of that car are used to identify and subsequently correct areas of excessive wind resistance. A clay model contains the essential detail since, in the case of wind resistance, only the profile of the car is of interest.

Mathematical models are a (non-physical) conceptual representation of a real world system or part thereof. The mathematical model serves the same purpose as the physical model – to represent a simplified viewpoint of the real system. The trend towards mathematical modelling is at least enhanced by, if not driven by, the development of methodologies directed at studying systems and system-orientated processes within the field of mathematics generally and computing particularly.

The widespread access to computers and the increase in computer literacy further support this trend. The mathematical modelling paradigm requires a quantitative description of the real world system under consideration. Further, any real world problem is typically complex and a complete description of the system is both involved and intractable (Murthy *et al.*, 1989; Giordano *et al.*, 1997). As noted in the consideration of physical models, in many cases only a subset of all possible aspects of a system are relevant to the modelling exercise at hand. Thus, the modelling process considers a partial representation of the system and is therefore, in part, a process of simplification. However the simplification process must be addressed with caution as it is non-trivial. Maynard Smith (1974) notes that a good model must operate with as little detail from the real system as possible whilst preserving sufficient detail from that real system to capture the behaviour appropriately. This abstract description (the system characterisation) typically yields both the remit of the system (its environment) and a number of identifiable objects within that system. An object is a physical entity with a range of characteristic attributes, termed parameters. Objects interact with other objects within that system and the effects of those interactions are described in terms of variables associated with each object. Parameters define the form of the objects; variables detail that form.

Given a system characterisation it is possible to build a model incorporating the objects, parameters, variables and relations of that characterisation. Where a simple characterisation exists, this model may be expressed in terms of mathematical equations, typically via systems of differential equations (Giordano *et al.*, 1997). In cases such as these, the model is amenable to mathematical reasoning and robust statements may be made regarding its properties. In simple systems the differential equations are linear and may be solved analytically – an algebraic expression thus relates the (small number of) parameters.

However, there exists a large number of systems for which analytical solution is impossible and it is necessary to resort to another form of solution – numerical – and, due to the amount of detail incorporated, is typically described with the aid of a computer (Giordano *et al.*, 1997). In a numerical solution many parameter values are considered and the expression relating the parameters takes the form of the solution for all those values. This solution is normally reached with the aid of an automated computer package – a differential equation solver.

Where the systems of differential equations are difficult to identify, perhaps because only qualitative rules can be found, a different kind of computer-based description is often employed. Here computer models may be used to represent the identified laws and relationships identified in terms of simple algorithmic rules and components that have an associated variable state. Such models are broadly termed cellular automata (Ermentrout and Edelstein-Keshet, 1993). Cellular automata are mathematical systems constructed from many identical – or similar – components, where each component is simple in isolation, and capable of exhibiting complex behaviour (Packard and Wolfram, 1985). Cellular automata are explicit and discrete in space and time and lend themselves readily to representing complex systems that comprise many individual elements that are structured in space and dynamic in both space and time. Cellular automata have received much attention in addressing problems of a physical nature, where individual (simple) elements interact in accordance to simple rules and result in complex dynamics at a larger scale. For example, Bak (1997) uses cellular automata models to investigate the phenomenon of self-organised criticality (Kauffman, 1993) in sand piles and its relation to power-law distributions.

Whilst different forms of solution exist – analytical and computer-based – the purpose of a particular model is independent of the form of the solution. Models are used for two purposes: purely for prediction, termed empirical models, or as a platform to understand underlying processes in the system, termed investigative models (Bak, 1997). Empirical models are based solely on experimental observations, and are derived through exercises in fitting functions to data (Prosser, 1994). The empirical approach is of use in the predictive sense, where determining the future response of a system in some detail from a given set of conditions (within an acceptable degree of accuracy) is of interest. The empirical model provides no understanding of the underlying processes present in the system. Further, any empirical model is necessarily highly coupled to the specific system in question. Therefore its utility is found only in studies of that system.

Generalities – the essential step towards revealing underlying processes – may be drawn across related empirical models, of course, but that is not the principle aim.

Investigative models are used where the principle aim is to identify the processes driving the dynamics of the system. Those processes are expressed through a series of assumptions defining the objects, and their variables, and the relationships among objects, i.e. their characterisation. When considering complex systems it is not possible to characterise the system in its fullest detail so, in addition to representing processes, these assumptions serve to simplify that characterisation. Given a characterisation, a process-based model may be used to generate predictions. Prosser (1994) notes that such predictions may be compared with experimental results and close fits support the assumptions made regarding the underlying processes. Process-based models are thus investigative and lend themselves more readily to generalisations than empirical models since they are not tightly coupled with any particular system.

1.2.2 Deterministic and stochastic models

The process of constructing mathematical models of real systems necessarily introduces simplifications in the representation of those real systems. As noted above, where the real systems considered are complex the constructed mathematical model represents only a subset of all system aspects. This subset comprises the smallest set of aspects deemed sufficient to represent the behaviour of that system. The remaining aspects not encompassed by the characterisation are either sufficiently unimportant so as not to require explicit consideration, or not measurable (or identifiable). Further, real systems tend not to be wholly isolated and lie within a wider context. Again, if this wider context is not explicitly represented – through some parameter set – then the model assumes that this context is sufficiently unimportant (with respect to the elements of the system that are represented).

The process of simplification, therefore, clearly introduces uncertainty into the behaviour of systems by ignoring the effects of parts of the system, immeasurable or otherwise, and the context, perhaps in part, in which that system finds itself. Uncertainty is also introduced where measurements of some system properties are taken, since the parameters used in models may only be estimates of the true system values. These uncertainties may be ignored, as in the case of deterministic models, or treated explicitly, as in the case of stochastic models (defined below).

Models of systems are described as deterministic when given a particular set of input values there is a single set of output values, i.e. that one solution (output) exists for any given problem (input). Deterministic models benefit from being generally mathematically more straightforward than stochastic models (see below), although by ignoring the uncertainties introduced through the process of simplification, deterministic models provide a characterisation of the system only in some average sense.

A stochastic model explicitly represents the uncertainty of a system in terms of probabilities. The uncertain elements or processes are represented by probabilistic components and the form of those components is often identified by considering a range of observed results (Giordano *et al.*, 1997). Thus stochastic models do not offer a single output from a single input. Rather, a range of outputs is possible from one such input. Moreover, this range of outputs is in the form of a (probability) distribution of outputs within the domain of all possible outputs.

Further, stochastic models have been viewed, by many, as compensating for the ignorance relating to the impact of one or more aspects of the system on its dynamics (Ulanowicz, 1997). Assuming stochastic elements do indeed represent ignorance of system elements, it follows from that if this ignorance could be addressed one may resume a deterministic study of the system, since the non-quantifiable would now be quantifiable. Thus, all systems may be ultimately characterised and modelled with certainty. However, Ulanowicz (1997) notes that contemporary views of complex systems, and in particular physical systems, indicate that such systems are inherently uncertain, or indeterminate, and so a wholly deterministic perspective for real systems is unattainable.

1.2.3 Models of ecological systems: the treatment of space and the community

The process of modelling in ecology has been driven by the desire to identify some general properties fundamental to all ecological systems (Maynard Smith, 1974; Judson, 1994). Therefore, ecological models strive for the appropriate level of detail so as to be sufficiently de-coupled from the particulars of any system, whilst preserving sufficient behavioural characteristics, to represent adequately that system. This selection of an appropriate level of detail is further constrained by the desire to express ecosystem behaviour in terms of analytically tractable systems but, as noted above, complex representations of systems – those including much detail – are not generally tractable. There exist a number of approaches to modelling ecosystems, each incorporating different levels of detail and each addressing the trade-off between (unrealistic) simplification and (realistic) complexity in a different manner.

Many models in ecology consider the community in terms of population sizes, i.e. the number of individuals of different species (Levin and Pacala, 1997). Here, the community is assumed to be unstructured in space in the sense that any single individual organism interacts with some averaged measure of the community in terms of those population sizes. Such models are termed non-spatial as a result of this averaging process. Space is ignored in these models since each individual organism is assumed to interact equally with all organisms in the community, independent of the physical distances among those organisms. Thus, all organisms are assumed to experience the same well-mixed, homogeneous, non-spatial habitat (Tilman, 1994a). Traditional models are usually implemented in terms of simple differential equations and are thus amenable to analytical solution. This tractability comes at the expense of realism.

In real ecosystems, a given organism is more likely to interact with organisms that are physically close to that organism and this is particularly true of sessile (non-mobile) organisms (Tilman, 1994a). Further, the assumption of a well-mixed organism composition is unrealistic at the scale of the community, since variation in environment will lead to patches of differing organisms in the community (Wu and Levin, 1994). Thus, by ignoring space for simplicity, the realism or complexity, of localised interactions is lost. It should be noted that , many traditional models refer to population densities but here space is treated only in an implicit sense. The community is considered to be of finite spatial extent and the densities relate population sizes to that spatial extent. No internal structuring of space exists, however. As a step towards realism, whilst avoiding the complexities of space, populations are sometimes divided into sub-classes in terms of age and/ or size (Hastings, 1997). Judson (1994) notes that whilst this step improves performance, in terms of realistic dynamics, these models begin to lose generality. Other models recognise that space is fundamental to the dynamics of the system. Whilst a range of model categories exist where space is explicitly considered, and in each the treatment of space is addressed in a different manner, attention to two categories in particular serves here, namely meta-population and individual-based models.

The meta-population approach assumes that the environment is spatially structured in terms of discrete patches that dynamically vary in both size and spatial position (Hanksi, 1997) – sub-divisions of the whole. The dynamics of each patch are considered independently (locally), although some (non-local) coupling exists between those patches. Thus, different patches may have different organism compositions, although homogeneous mixing is assumed within the patch (Levin and Pacala, 1997). Such an approach offers an intermediate scale of analysis, since mixing is accounted for below the scale of the community, and this intermediate scale is sufficiently free from complexity so as to be amenable to numerical analysis. However, this simplification is, again, at the expense of realism since there remains an (artificial) characteristic spatial scale below which the system is assumed to be well-mixed.

In the last few years there has been a considerable growth in the use of individual-based models (Ermentrout and Edelstein-Keshet, 1993; Winkler *et al.*, 1999). The increased interest in this category of model is, in part, a result of increased computational power (Judson, 1994). Communities comprise many individual organisms and the individual-based approach to modelling ecosystems considers that ecosystem in terms of the individual organisms within the community. This approach is inherently computationally intensive and implementations of this form of model have only recently become feasible. This interest is also a response to the acknowledgement that many interacting components, no matter how simple, may give rise to complex behaviour patterns expressed through patterns in the spatial domain (Bak, 1997). Further, the system is primarily expressed in terms of the response of individual organisms to interactions with other (local) organisms through a set of localised rules and some assumptions relating to the spatial extent of those interactions. This localised information processing is compatible with the modelling approach of cellular automata (Hogeweg and Hesper; 1990) – see Chapter 2 for a fuller description of cellular automata. In the cellular automaton approach space is explicitly represented in terms of a lattice of sites where individuals occupy those sites. Interactions between a given individual and other organisms take place within delineated neighbourhoods – only sites within a certain distance of the site containing the particular individual are considered. Thus, no assumptions are made regarding the well-mixed nature of the community in space, although the assumptions relating to the localised rules and neighbourhood clearly affect the dynamics of the system. Any model that assumes the individual as the basic unit of characterisation may also admit the explicit representation of individual variation. Such representation is clearly precluded in any mean-field (averaging) approach (Bown *et al.*, 1999).

The complexity of individual-based models in general, and of cellular automata in particular, allows a representation of space, and the interactions in that space, to be represented in a manner which more closely approximates the real system than other approaches (above). The model's assumptions and parameters may be measured directly and justified from experiment (Roughgarden, 1997). Indeed a great amount of detail may be included readily relating to both the states represented and the rules for translating states in time. Further, the form of this detail is most plastic in nature, facilitating an ideal platform for investigative studies (Laszlo and Silman, 1993), in the sense that the implementation of different forms of detail, or strategies, is straightforward. However, the inclusion of such detailed spatial information makes the results of individual-based models extremely difficult to interpret since no rigorous methods exist for the mathematical analysis of those results.

Roughgarden (1997) and Levin and Pacala (1997) note both the usefulness of individual-based models and the difficulty in deriving analytical results from these models, and both offer (very different) simplifications as a solution to this problem. Roughgarden (1997) suggests the use of spatially explicit individual-based models to describe a system, and converting that spatially explicit description into a spatially implicit formulation through spatial averaging – a mean-field approach in a sense. However, this is a mean-field approach beginning from an explicit description. This formulation is amenable to mathematical analysis and Roughgarden (1997) notes that whilst the aggregated properties that arise from this measure may lose important spatial detail, in some circumstances the importance of that spatial detail may be less than the utility obtained from a mathematically tractable model. Thus, Roughgarden (1997) argues that in those circumstances when space is important but broad-scale features are more so, space may be treated implicitly and the resulting (approximated) description suffices for detail.

Levin and Pacala (1997) note that there are a range of processes operating at a range of spatial (and temporal) scales in any ecosystem, and processes present at one scale may manifest themselves at higher scales. Those processes create patterns at the higher scales and such patterns may modify processes at lower scales. The authors argue that the identification of relationships between processes at different scales, or scaling laws, will allow the (related) descriptions of systems at different spatial scales. Thus, intractable individual-based models may be accurately described at some higher spatial scale, by integrating through these scaling laws to reach some scale-dependent description, and those integrated descriptions may be mathematically analysed.

Modelling must, therefore, begin to address the relation between these scales – the scaling laws – and it follows that any model must be capable of capturing features at all scales. Rand (1999) commented on the appropriateness of the general class of cellular automata to reflect properties of systems at both microscopic and macroscopic levels. By microscopic Rand means working at the level of an individual organism in a system that comprises a very large number of individuals. By macroscopic Rand means working at the level of some collection of individuals, which may be interpreted here as patches, sub-communities or the whole community. Hence, in spite of the difficulties encountered when interpreting the results of such models, they are argued to be useful in investigating issues of scale in ecology.

1.3 Scope of the work

The models presented within this thesis are all individual-based in form. A significant advantage of such models, as noted (Roughgarden, 1997), is that they lend themselves to parameterisation by measurements taken through experimentation. These experimental measures are generally, for convenience, undertaken in some simplified field study or more commonly in laboratory conditions, and the results of these measures are used to reflect behaviour in the ecosystems in question. Thus, such experimental systems are of a smaller spatial scale than the system being considered and as a consequence measures lack the contextual properties of that considered system.

This thesis considers the issue of scale-dependent behaviour in ecosystem modelling. The central question addressed is whether descriptions of the dynamics of systems at one scale may be effectively used as descriptions of the dynamics of systems at a different, generally larger scale. This question is addressed in the context of the dynamics of fungal communities. The nature of the treatment of this question here reflects the author's opinion that the inclusion of real biological data is fundamental to ecosystem studies and that the proper treatment of that data, generally taken out of context of the studied system, is crucial to the success of those studies.

The initial motivation for undertaking this investigation arose from preservation works being carried out on the Frigate Unicorn (White *et al.*, 1996). Currently, fungal communities are damaging the timbers in the boat; however, the fungal community responsible for the damage is not well understood. This project, together with an associated experimental project (Sturrock, in prep.), was undertaken to further the existing knowledge of this system in particular, and fungal systems in general. Whilst many fungal species are present in this community the study presented here, for simplicity, addresses only interactions between two of those species. The long-term aim of this project was to develop a predictive model of fungal community dynamics and this thesis details the first steps toward such a predictive model in terms of a series of investigative approaches.

Chapter 2 presents a simple experimental system and complementary theoretical approach, in the form of an individual-based (cellular automaton) model, developed to initiate this investigation. The experimental system described in Chapter 2, and described in some detail in White *et al.* (1998) allows the implementation and analysis of greatly simplified (with respect to the real world) and carefully designed experiments within sterile microcosms. This system permits a homogeneous resource base, or environment, ensuring that the observed dynamics are a consequence of the community composition and structure, and are not driven by resource structure. Experimental results derived from small-scale systems are used to identify parameters to be incorporated into the cellular automaton. Of note is the variation in possible outcomes between the simple replicated systems used for parameterisation. To encapsulate this variation a stochastic model is developed where the likelihood of any given outcome is derived from all small-scale experiments. A series of large-scale experimental systems serves to test the theoretical model, each differing in spatial arrangement.

The theoretical analyses of these experimental systems clearly demonstrate that the dynamics observed in these simple fungal communities are a result of both local and non-local features of the experimental system. In cases such as this the immediate extrapolation of results derived from experiments conducted out of the context of the community – i.e. at a scale less than that of the community – to represent system scale behaviour is not possible.

In order to progress beyond the scaling difficulties encountered in this system an approach is developed to allow the consideration of effects at a range of scales, both local and non-local. Chapter 3 details a generic conceptual framework that admits the contextual parameterisation of the local rule set to allow for the influence of non-local effects on the localised dynamics. Clearly, the nature of the contextual parameterisation is specific to the application area. In the case of the fungal studies the existing experimental system was not amenable to this theoretical approach and, given the desire to use experimental data within the theoretical approach, significant changes were needed in that experimental system.

However, before committing to an extensive revision of the experimental programme the framework is developed in the application area of plant systems where a large body of experimental data already exists. This plant-based application represents the essential features of individual interactions in terms of competition for space and resource. In the model presented individual plants consume resources within the environment and may consume space within that environment through the production of offspring. The behaviour of a given plant is described in terms of parsimonious traits and the development, in terms of progression through some life cycle, of that plant is modified according to the surrounding environment. Thus, both local (resource competition) and non-local (spatial competition) features drive the dynamics of the community. Moreover, both the resource substrate properties and the community interacting over that resource substrate, since different community compositions make different resource demands on the system, drive the dynamics of the environment.

This coupling between community and environment is demonstrated through the inclusion of sample model runs. Further, the runs indicate that the model gives rise to complex community patterns and the distributions were suggestive of known biological phenomena. In particular, succession is seen to arise as a consequence of this coupling between community composition and environmental conditions. The community and environment co-evolve in time and space through these runs, each driving the dynamics of the other.

Chapter 4 suggests that this coupling may, in a restricted set of circumstances, give rise to some form of long-term coexistence of species through some particular balance in individual function (traits) across the community according to environmental conditions. A simple framework for investigating this concept is developed. An appropriate search mechanism is determined to allow combinations of trait values at the scale of the individual to be assessed for a particular community-scale phenomenon. Initial results demonstrate that this search mechanism is able to identify and enhance (through variation) combinations of trait values that give rise to, in this case, a simple measure of diversity: population levels above a threshold. However, the solutions – the combinations of trait values – as identified by the search mechanism are complex data sets and to date no approach has been developed to interpret properly these data sets. Certainly the work indicates the value of considering system properties at the scale of the community.

Chapter 5 provides a summary of the work addressed and details further developments intended for the plant-based model and associated search mechanism presented in Chapters 3 and 4. The problems encountered in Chapter 2 are returned to. In particular the manner in which the generic framework developed may be applied to further the investigation into fungal community dynamics is addressed. Fungal species may be represented in terms of traits, and those traits may be parameterised by contextual information. Complementary experimental and theoretical systems are suggested as a means to identify both the context-free values of the traits for species measured in small-scale systems, and the impact of context on those traits at a range of spatial scales. The experimental system will be used to generate spatio-temporal data at different scales, and the theoretical system will be used to identify corrective adjustments, through searches to fit data observed at one scale to data observed at another. This process will identify the dependencies between scale and behaviour as observed in the approach described in Chapter 2. This revised approach to studying fungal community dynamics will investigate the relationship between scale and behaviour in an endeavour to identify behavioural scaling laws.

1.4 Notes on the work presented

This thesis details a range of theoretical approaches aimed toward addressing the issues of scaling as noted above. In the descriptions of these approaches attention is given to the need for and purpose of each approach. The results and associated commentary of the models used to support each approach are also provided. The central chapters are presented with the scientific investigation at the forefront, and with the intention of clearly demonstrating the development of a series of models that maintains a consistent focus throughout, that of relating spatial scales. Indeed, to serve best the clarity of this document, no specific detail is provided regarding the (computer) implementation of the supporting models. However, the implementation of these models represented a substantial investment of time and as such requires mention here.

The cellular automaton model presented in Chapter 2 was an extension to existing work. Familiarisation with this existing work was necessary so that required extensions could be made. The major extensions were the incorporation of varying spatial arrangements, the expression of the neighbourhood rules that enabled the parameter search detailed in Chapter 2 and the algorithms for spatial analyses – for example, patch size evaluation and state transition analysis (White *et al.*, 1998). An important element of the work was the undertaking of experimental design. Spatial arrangements of various designs were developed by the author as a means to investigate the fungal system, most notably those large-scale experiments described here and in Bown *et al.* (1999). The identification of useful experiments required a working knowledge of the experimental system used.

The model presented in Chapter 3 is the product of substantial software development. Much time was spent in discussions with the biological collaborators analysing the system under study, resulting in the identification of the processes and states necessary to implement a model of this complexity. These discussions gave rise to the schematics presented in Figures 12, 13, 15 and 16 below. The schematics, and supporting notes, served as a design for the implementation detailing the functions and data required. During implementation, each function was tested both in isolation and in context. Where extensions and revisions were necessary, re-testing was undertaken.

The model presented represents the final version, and many intermediate versions were employed to reach this stage. Indeed, early prototypes – partial implementations – were used to identify the processes and states required. These prototypes, with the supporting graphical outputs (spatial maps) were used to support the necessary inter-disciplinary communication. A graphical user interface, developed to the specifications of the author, has also been attached to this model for demonstration purposes.

The search mechanism developed in Chapter 4 required familiarisation with search algorithms in general and genetic algorithms in particular. A number of early prototypes addressing generic search problems – here searching parameter space to maximise and minimise function values – were developed to facilitate the understanding of the genetic operators used in this search approach. As in the implementation of Chapter 3, any modules developed were tested fully.

Chapter 2 A study of scaling effects in fungal community dynamics

2.1 Background

2.1.1 Context of the work

Previous work (White *et al.*, 1998) described an experimental system capable of providing detailed quantitative spatio-temporal data from two- and three-species interactions over a range of scales. The system allows for the design of fungal communities within a tessellated agar microcosm, where communities are defined in terms of the number of species considered, the scale of the system (number of tiles) and the initial spatial pattern (a distribution of species over the tiles). The evolution of the system may be monitored, through destructive analysis of replicates, in terms of occupancy of tiles.

This system contrasts with more typical experimental approaches which either qualitatively assess communities *in situ* or quantitatively assess very simple systems, for example confrontational measures at small scales, e.g. Halley *et al.*, 1996. The first approach necessarily trades measurement detail against the complexity of the underlying system. More fully, the underlying system is natural and thus extremely complex. It is not reasonable to assess such a system quantitatively since many parameters are available on which assessment may be made and such assessment compromises the natural state of the system. Conversely, the second approach trades complexity of the system against measurement detail. Simple systems are amenable to experimental frameworks, typified by laboratory studies, making quantitative studies possible. However, the simplicity of these systems compromise the important effects of spatial heterogeneity and scale which are known to be important in the understanding of community dynamics (Silvertown *et al.*, 1992; Tilman, 1994b; Wu and Levin, 1994; Levin *et al.*, 1997). The system described by White *et al.* (1998) and summarised in Section 2.2.2 attempts to combine elements of complexity, i.e. spatial scales and patterns in a uniform substrate, and quantitative measures. Thus, the experimental system under consideration allows some elements of the complexity known to be important without relaxing the constraint of quantitative measures.

2.1.2 Difficulties particular to fungal colonies

2.1.2.1 Contextual behaviour

The experimental system admits only a restricted set of complexity parameters, i.e. spatial scale and pattern. Whilst the system does not preclude the incorporation of substrate spatial heterogeneity per se, this additional layer of complexity is not addressed here. Importantly, the system also removes any elements of 'biological noise' – the systems are maintained in sterile environments and interactions take place at a constant temperature. A suite of small-scale experiments designed to investigate the effect of temperature was undertaken by Sturrock (in prep.) and demonstrated that when simple two-species interaction systems are considered over a range of temperatures the interaction outcomes are very much a function of the particular temperature imposed. More precisely, the identity of the successful fungus was dependent on temperature regime.

The work by White *et al.* (1998) clearly demonstrated that the initial spatial configuration of fungal communities, in terms of scale and pattern, affects community development in addition to the community composition, in terms of species. This work further notes that the complex and co-operative behaviour of fungi may have notable impact on community dynamics. Thus, any successful theoretical model must have some representation of spatial pattern and scale, and admit some form of co-operation parameter as a function of the contextual spatial pattern and scale. Interestingly, co-operative strategies are typically ignored in even the most advanced models of fungal community dynamics, for example Halley *et al.* (1996). This is almost certainly a response to the difficulties associated with capturing those strategies, rather than any deliberate statement on the lack of importance attached to such co-operation.

A secondary, but important issue arising from this study is the need to replicate a given experiment. Fungal interactions observed previously (White *et al.*, 1998) have not been wholly deterministic. As noted in White *et al.* (1998), a degree of stochasticity was observed and that this stochastic element was more significant in smaller scale experiments as larger scale experiments typically average over that stochasticity (since the number of interactions is larger). This feature has important implications for the investigative framework outlined below. It also imposes a high cost on any single community configuration, as multiple instances of that community require some combined interpretation.

2.1.2.2 Indeterminacy

When spatially discrete models are applied to communities of individuals, a cell typically maps onto one such individual or more commonly the space which one individual is able to occupy. This mapping process is tractable when ecological systems are based on determinate organisms, as is generally the case. In such cases, the size of the individual and/ or its mobility can be used to define the extent of the automata's spatial representation and the granularity of the cells within that spatial representation. Hence, determinate organisms have characteristic neighbourhood scales that can be used in theoretical analyses.

As discussed above, fungal colonies are indeterminate in nature. Thus, the definition of a characteristic scale is made difficult since significant interactions, i.e. interactions determining survival, can occur over a range of spatial scales. In other words, the characteristic spatial scale of indeterminate organisms, and in particular fungi, may be considered as approaching continuous in nature and thus is not amenable to the process of spatial discretisation; this process is clearly a requisite in discrete spatial models. Hence, the modelling process required an, albeit arbitrary, choice of scale. This choice of scale, as discussed below, was driven by experimental constraints.

In the only previous attempt to model multi-species fungal communities, Halley *et al.* (1996) assume that the individual growth units, or hyphae, are independent and support this assumption through a qualitative comparison with data. Previously, Ritz and Crawford (1990) demonstrated that the presence of spatial correlations in the distribution of hyphae argues against spatial independence, and, like Halley *et al.* (1996), support this (conflicting) assumption qualitatively. Clearly, the question of whether the dynamics of fungal communities are addressable by considering independent interactions is still open and is addressed in this work and in Bown *et al.* (1999).

2.2 Investigative framework

2.2.1 Overview

The initial aim of this work was to test the assumption that information derived from small-scale fungal interactions provides a sufficient behavioural characterisation to be useful in predicting interaction outcomes within the context of larger-scale systems. If such prediction is possible then some understanding of the biological processes driving the dynamics of the system has been gained. At best, the mechanisms governing fungal interactions are identified, and the roles of scaling and context – which are, of course, related – understood. At worst, some intuitive feel for the nature and outcome of interactions is gained, which can be used to drive further experimental and theoretical investigations. Further, if a system is understood to some degree then it is possible to manage that system (to an extent governed by that degree to which the system is understood). Here, such system knowledge might be used to identify suitable bio-control strategies for use in the Frigate Unicorn. More concisely, the work has three fundamental premises that must be considered:

1. Simple (two-species) small-scale experiments may be used to predict, and therefore understand, simple (two species) larger-scale experiments. Thus, the relation between small-scale and simple larger-scale systems is identified.
2. Given 1, this relation holds for n-species systems where n>2, i.e. complex communities.
3. Given 2, management of complex communities is possible, allowing bio-control principles to create stable environments as appropriate for the application area, i.e. the identification of conditions which favour the growth of organisms which do not decay timber at the expense of wood decaying organisms.

Thus, a framework that allows the relation between small-scale interaction properties and larger-scale interaction properties to be investigated has been developed. Given these premises, and the first premise in particular, the form of the experimental and complementary theoretical systems used required the representation of fungal interactions at a small scale, whilst encompassing the dynamics of larger-scale experiments. Further, the systems were sufficiently general to allow n-species interactions to be modelled. While a detailed description of the experimental system used, and a justification of its appropriateness to the above constraints, is not within the scope of this project, it is useful to provide an outline of that system. Such an outline serves to place the theoretical work in context. An explanation of the relevant biological system, explaining the mechanisms for generating the data used in the theoretical study is given in the following section.

The theoretical system comprised a number of components: a set of data derived from small-scale interactions, a set of data derived from larger-scale interactions and a computer model that served to relate these data sets. The small-scale interaction outcome data served to parameterise the model; the computer model had, therefore, a rule set which was used to determine the outcomes of interactions within larger-scale systems. The larger-scale interaction outcome data served as targets for the model. The modelling process itself involved imposing a series of assumptions regarding the manner in which the parameterising data set was used to define the outcomes of theoretical larger-scale systems. These outcomes were explicitly spatial in nature, in the form of a lattice of sites. Clearly, each assumption had an impact on the interaction outcomes predicted by the model, and so each assumption was assessed in terms of the nature of that impact – be it improved predictions or otherwise.

Importantly, any assumptions imposed during the modelling process should have an associated biological interpretation within the context of the system considered. Without this interpretation, those assumptions lead to only a predictive model of a form that offers nothing in terms of a systematic understanding of the process under consideration – an empirical model. Further, the assumptions selected should be as simple and generic in nature as possible, implying as simple and generic a biological interpretation as possible. This is particularly important when combinations of assumptions are required to obtain an appropriate model, since the understanding gained is initially expressed in terms of that combination. The meaning of that combination is best addressed, however, in terms of its composite parts. To this end, the models considered and assessed here are indeed as simplistic as possible, and each assumption made within those models has an associated interpretation. Thus, those successful models readily yield insight into the underlying processes present in the system.

Of final consideration is the notion of a successful model. Here, success is thought of in terms of the degree to which the biological results match the suggestions made by the theoretical system. There are a number of properties associated with the results provided by each system that may be used to assess this degree. The selected manner in which interaction outcomes of the larger-scale systems are compared with interaction outcomes suggested by the model was introduced in White *et al.* (1998), and is termed 'state transition analysis.' Other measures include the proportion of each species, the patchiness (the number of intra-species interfaces) of the system and the mixed nature (the number of inter-species interfaces) of the system. The single measure of state transition analysis has been observed to give a good measure of the activity of the system (White *et al.*, 1998; Bown *et al.*, 1999).

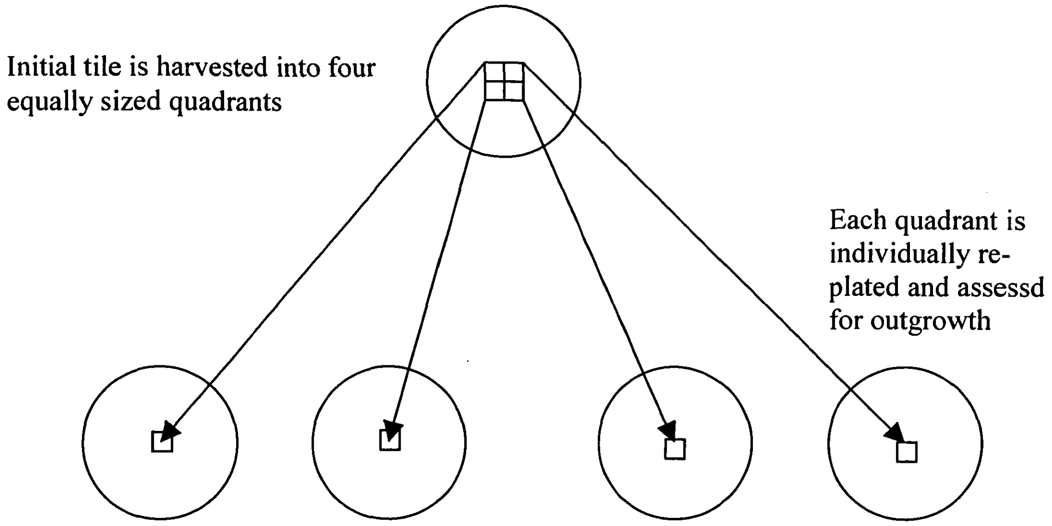
To address state transition analysis it is necessary to consider the output from both the experimental and theoretical systems. As noted above, the experimental system provides interaction outcome data in the form of occupancy of tile quarters, post-assessment, at given time points. Also noted earlier, the theoretical system provides simulated interaction outcome data in the form of a lattice of sites (cells), over a series of discretised time points. Thus, each system provides a spatio-temporal measure of the community dynamics, and whilst the exact mapping of tiles and/ or tile quarters to lattice cells is addressed in the following section the notion of state transition analysis is explained here. In short, each spatial outcome was characterised in terms of the changes in state that had occurred relative to the initial arrangement.

More fully, each system began in the same position, and each system evolved from that position to a new position over a given period of time. Quarter tiles that were in an occupancy species, or state, α must have evolved into a finite range of species mixtures, or states: α, β, or $\alpha\beta$. Similarly, model cells that were once in a state β must have evolved into a finite range of states: α, β, or $\alpha\beta$. Thus, this measure gives a representation of the nature of the changes, in terms of occupancy, that have taken place within state transition classifications, i.e. $\alpha\rightarrow\alpha$, $\alpha\rightarrow\beta$, $\alpha\rightarrow\alpha\beta$, $\beta\rightarrow\alpha$, $\beta\rightarrow\beta$ and $\beta\rightarrow\alpha\beta$ in two-species interactions. By comparing the number of state transitions in each classification occurring in each of the experimental and theoretical systems, it is thus possible to assess the degree to which the systems are similar.

2.2.2 Experimental system

The biological system used in all experiments was based on that described by Ritz (1995) and is fully detailed in White *et al.* (1998). In general, square tiles (10mm x 10mm x 3mm) of nutrient (2% malt extract agar) were arranged in a prescribed configuration in sterile Petri dishes. In order to prevent significant movement of extra-cellular diffusables that may complicate the interpretation of observed spatial effects, 2mm gaps were introduced between the tiles. There was no apparent effect of these gaps on the fungal outgrowth over neighbouring tiles (K Ritz, personal communication). The centre of the tiles were then individually inoculated with a core of the fungal species under investigation in accordance with an imposed spatial arrangement. The Petri dishes containing the tiles were incubated at a controlled (constant) temperature for a range of incubation periods. Over time, the fungal mycelia within the core typically grow to colonise initially the host tile and then interact with other fungal mycelia outgrowing from neighbouring tiles.

After a given incubation period the species occupancy of individual tiles was assessed by dividing each tile into four equally sized quadrants and placing each of these onto fresh agar plates. The new tiles were inspected for outgrowth of fungal species after three to four days and the presence of specific species confirmed by visual observation. This isolation process, whilst destructive, offers a methodical objective procedure rather than an *in situ* observation which is clearly subjective. Figure 1 illustrates the tile assessment procedure described above.



Initial tile is harvested into four equally sized quadrants

Each quadrant is individually re-plated and assessd for outgrowth

Figure 1: Tile assessment procedure, taken from Sturrock (in prep.) with amendments

In general, the interaction outcome data for two species α and β obtained from tiles in this manner were compiled into two categories: those tiles which were initially inoculated with species α; and those tiles which were initially inoculated with species β. The results of experiments under this system were expressed as the proportion of quadrants containing either a single fungal species or a mixture of the two species. Within this system it was not possible for quadrants to be empty as sufficient nutrient was made available to prevent starvation over the assessment periods (White *et al.*, 1998). Thus, each community configuration, regardless of scale or pattern was expressed uniformly as the number of quarter tiles resulting in one of three states (α, β or αβ) with respect to an initial state (α or β) as defined by the spatial configuration considered. This information may be captured at any assessment point, thus providing detailed spatio-temporal measures of the community dynamic.

Figure 2 and Table 1, below, illustrate the process of translating an example interaction outcome between a (different) sample pair of species used in a previous investigation, *Poria placenta* and *Coniophora marmorata* – see White *et al.* (1998) – (α and β respectively as noted in the orientation) at a particular time point into the proportional results indicated above. Illustrated are ten replicate experiments of the simple binary pairing and it is worth drawing attention to the considerable variability in outcome demonstrated here.

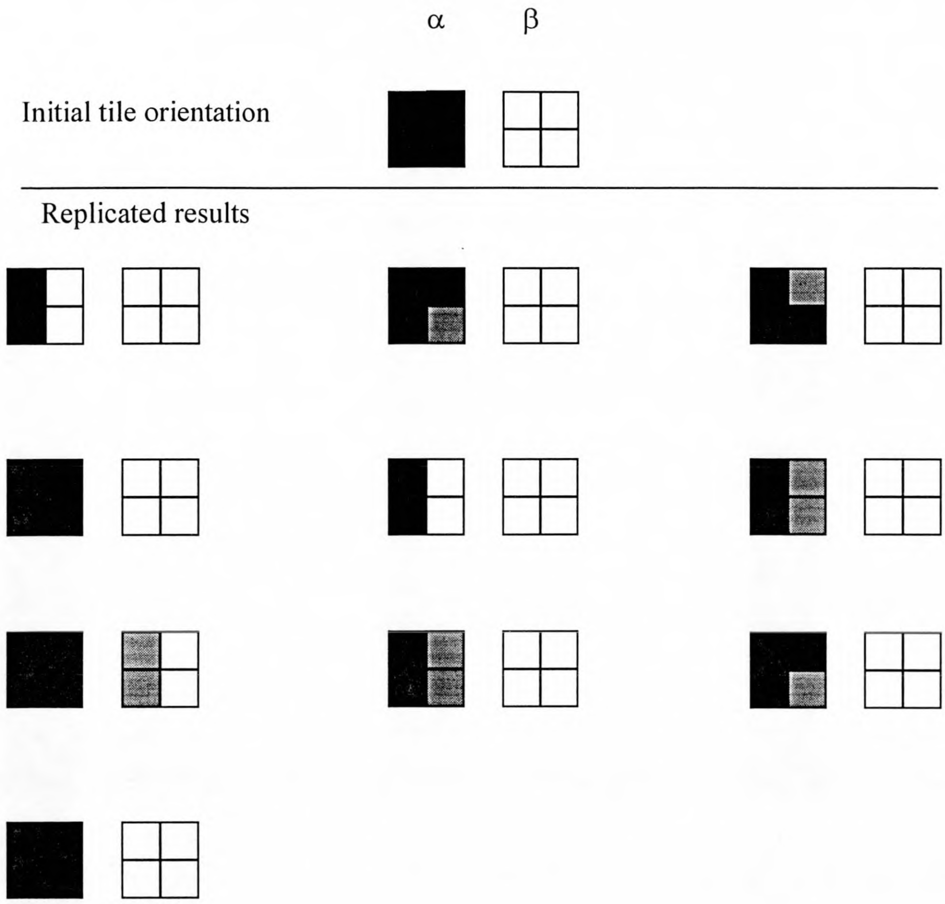


Figure 2: A schematic indicating the initial orientation of ten replicated 'binary' interactions and their associated results between a pair of species, α and β, indicating the final tile quadrant occupancy, when assessed after a period of time where ▨ represents a mixed population containing both α and β (biomass is not measured).

Table 1 Interaction Outcome Categorisation

Initial Species present in tile	*Number of quadrants containing β*	*Number of quadrants containing α*	*Number of quadrants containing α & β*
Species β	38	0	2
Species α	4	29	7

The outcomes indicated in Figure 2 are summarised numerically as a 2x3 transition matrix (Table 1) with quadrants that were initially Species α sub-categorised into those that remained Species α, those that resulted in Species β and those that resulted in a species mixture (labelled αβ). The initial Species β tiles were also differentiated in this manner.

The pair of species used in the theoretical analysis here are implicated in wood decay, and were isolated from the Frigate Unicorn (White *et al.,* 1996). They have been identified as *Coniophora marmorata* – a cord forming basidiomycete, and a *Paeciliomyces variotti* strain. These species are subsequently referred to as species Cm and species Pv respectively, with associated transitions being Cm→Cm, Cm→Pv, Cm→CmPv, Pv→Pv, Pv→Cm and Pv→CmPv.

2.2.3 Modelling considerations

As noted in Chapter 1, this work considers the application of individual-based models, discrete in space and time, to problems of an ecological nature. The general modelling paradigms of cellular automata, introduced in Chapter 1, are particularly well suited to the experimental system described above.

Cellular automata comprise individual cells that are usually arranged in a regular lattice, representing a discretised approximation to the spatial domain considered. Individual cells assume a state, from a finite range of states, in an initial (spatial) configuration. Rules are chosen which determine the temporal evolution, through discrete time points, of a cell as a function of its neighbourhood and, in general, this neighbourhood may be defined in accordance with the underlying system. Further, the function governing the state of a cell in terms of that neighbourhood need not be constant over time. In models of sessile species, the neighbourhood is typically defined as one of two forms identified by von Neumann (1966): a five-cell neighbourhood and a nine-cell neighbourhood, as illustrated in Figure 3. Such neighbourhoods are considered appropriate since often an individual organism is more likely to interact with its immediate neighbours than with others (Tilman, 1994b).

Figure 3: von Neumann neighbourhoods of five-cell and nine-cell definitions.

The individual cells inherent in cellular automata, which serve to discretise space, correspond well to the (agar) based tile implementation of the experimental system, although the exact nature of this correspondence is addressed later. As noted, in a cellular automaton each cell has an associated state, within a finite range of states. In general, for two-species interactions (assuming no empty cells – see above, Section 2.2.2) there are three possible states: state α, i.e. the cell contains only species α; state β, i.e. the cell contains only species β; and state $\alpha\beta$, i.e. the cell contains a mixture of the two species). These assumed states permit the expression of both an initial imposed spatial pattern and a measure of the spatial dynamics as they occur through time – the state transition analysis (White *et al.*, 1998).

The five-cell neighbourhood was used here since the interaction between tiles in the biological system occurred, in the large part, at the edges of the those tiles. Indeed, a series of experiments were undertaken to assess the implications of this assumption, and it was apparent that no significant interaction took place over corner-to-corner interfaces. Thus, the cellular automaton used had a five-cell neighbourhood in two dimensions – the assessment method in the experimental system ignores the third dimension of height (approximating to biomass) of the species, since outgrowth on fresh agar acknowledges only viability of each species, and hence biomass is not reflected in this measure. The rule defining the state at time t+1, of a given cell (i,j), termed the subject-cell, in the two-dimensional lattice a at a (previous) time t, as given by Packard and Wolfram (1985) is:

$$a_{t+1}(i,j) = \phi_t[a_t(i,j), a_t(i,j+1), a_t(i,j-1), a_t(i+1,j), a_t(i-1,j)]$$

The function ϕ is defined in terms of the parameterising data set comprising interaction outcomes derived from small-scale experiments. This function is therefore required to be stochastic and temporal in nature, since the data set that it represents has inherent stochastic and temporal features. Those stochastic properties arise from the need to replicate the experiments for a given time point due to contextual sensitivity; the temporal properties arise from the multiple instances in time at which the system is sampled.

The manner in which the data set is translated into parameters for the model, and the use of those parameters in determining interaction outcomes in larger-scale systems, is addressed in Section 2.2.4 below. Here, a more fundamental issue is addressed: the treatment of space for which, as noted in Chapter 1, proper consideration is essential.

As discussed previously, fungal colonies are indeterminate in nature, and thus lack characteristic scales upon which to perform theoretical analyses. Here, the form of the experimental system imposed constraints on the characteristic scales that may be considered. These scales are, of course, artificial in the sense that there is no reason to assume that interactions below that scale are any less important than those above that scale; they are simply symptomatic of the experimental procedure. The experimental system expressed two spatial scales through its design: that of the tile and the quarter-tile. The tile is the unit of initialisation, and is limited by the surrounding air gaps, although these air gaps appear to have no effect on the dynamics (see above). The quarter-tile is the unit of assessment, as noted previously in Section 2.2.2. The choice of scale is arbitrary in the sense that no scale of study is more appropriate than any other. To examine the influence of the choice of scale on the predictions of the dynamics of the system three combinations of scales were considered:

1. The model was parameterised, run and compared against the larger-scale experiments at the scale of the tile. This assumes that the detail measured below the scale of the tile was unimportant to the dynamics of the system.
2. The model was parameterised, run and compared against the larger-scale experiments at the scale of the quarter-tile. This assumes that the detail measured below the scale of the tile was important to the dynamics of the system.
3. The model was parameterised and run at the scale of the quarter-tile whilst compared against the larger-scale experiments at the scale of the tile. This assumes that the detail measured below the scale of the tile was important to the dynamics of the system and that the experimentally measured larger-scale interaction outcomes were noisy.

In combinations where whole tile resolution is used for any element (parameterising, running or comparing model output), all information below the scale of the tile is lost. The quarter-tile assessment data serves only to identify the occupancy, or state, of the tile as a whole. Thus a form of spatial averaging takes place when relating quarter-tile data to whole tiles. The spatial information relating to the relative location of the different quarter-tile occupancy states is ignored. Thus, a tile is in a single species state if all quarter-tiles are in a single species state; the tile is in a mixed species state if at least one quarter-tile is in the mixed state or if at least two quarter-tiles are in a different state.

Of the three proposed combinations, only the third combination, under any of the models described in the following section, produced results that were consistent with the observed behaviour. This suggests that the interactions below the scale of the tile are important, but that for comparative purposes the output must be spatially averaged.

This, in hindsight seems almost intuitive. In the absence of an obvious scale, it seems reasonable to work with the finest resolution of data available, this being the quarter-tile scale. In the experiments used to parameterise the model only two tiles were used – the choice of spatially averaging eight interaction outcomes (four quarters per tile) into two interaction outcomes does not seem sensible since much information is lost. Thus, parameterising data should be in quarter-tile form. If, therefore, the most reasonable course of action is to parameterise in terms of quarter-tiles then the interaction rules derived from that data set will be expressed in terms of conditional probabilities associated with quarter-tiles. Thus, the model should compute interactions in terms of quarter-tiles, and hence a cell must map to a quarter-tile. The requirement to average spatially the experimental and theoretical outputs to obtain an agreement also makes sense. Previous studies indicated that five replicates of each larger-scale experimental system were sufficient to capture the necessary interaction details. Indeed, as may be observed later, the theoretical model produced outcomes that well encompass the 'typical' experimental responses. (This typical response being the mean number of state transitions, occurring at the cell level, for each system at each time point.)

Whilst each of the combinations was investigated, only the results from work with the third combination are presented below. The models presented in the next section all assume this (intuitive) spatial scaling assumption.

2.2.4 Modelling approach

2.2.4.1 Forms of model

The model comprises a lattice of cells that undergo a number of state transitions through time. This temporal evolution of the system was governed by state transition probabilities, $p(x \mid \alpha, \beta, t)$, defined to be the probability of obtaining state *x* given a subject cell in state α is challenged by a neighbouring cell in state β for a time, *t*. The values of the probabilities were derived from the pair-wise challenges in the following way. The tiles belonging to all replicates corresponding to a particular time point were quartered and the state of each quarter was individually assessed. The value of $p(x \mid \alpha, \beta, t)$ was set equal to the fraction of quarters that changed from state α to state x during the time interval *t*. Since the experiments are necessarily snapshots at the sampled time points (4, 6, 7, 8, 10 and 12 days), linear interpolation was used to provide values at intervening times (i.e. for days 5, 9 and 11). The selection of these time points was assisted by previous experimental investigations into interactions between these species. (Likewise, the selection of the two time points used in the larger-scale experiments was also assisted by experimental investigations.) These values for $p(x \mid \alpha, \beta, t)$ are used in the automaton where each cell represents a quarter-tile in the real system. The model is thus able to simulate the dynamics of the system in time and space.

To test the hypothesis that information derived from small-scale fungal interactions provides a sufficient behavioural characterisation to be useful in predicting interaction outcomes within the context of larger-scale systems, various assumptions were made about the way in which the set of $p(x \mid \alpha, \beta, t)$ are implicated in the dynamics of the microcosm community. The first and simplest assumption, subsequently referred to as Case A, is that the nearest-neighbour challenges (cells within the neighbourhood) are independent. Therefore if a cell simultaneously contains two species, each one interacts as if the other were not present. For example the probability that a cell containing species α changes to containing species β when challenged by n neighbourhood cells containing species β for a time, t is:

$$1-(1-p(\beta \mid \alpha,\beta,t))^{n}. \qquad (1)$$

The next simplest assumption, subsequently referred to as Case B, is that the outcome of a 5-neighbourhood challenge can be expressed as a weighted sum of the probabilities of the pair-wise challenges. Thus, $p(x \mid f_{\alpha},f_{\beta},t)$ was defined to be the probability of outcome x after time t in a 5-cell neighbourhood where the subject cell is in state α, and f_{α} and f_{β} are the frequencies of the states α and β in the neighbourhood respectively. In the evaluation of neighbourhood frequencies it is assumed that cells containing both species are treated as if each species in the cell is independent of the other; i.e. each behaves as if the other were not there, and the result of each interaction in that cell combined. Under this assumption, the summed frequencies of species α and β may exceed the number of cells in the neighbourhood. Figure 4 illustrates both the calculation of f_{α} and f_{β}, and the shared cell assumption made in the calculation.

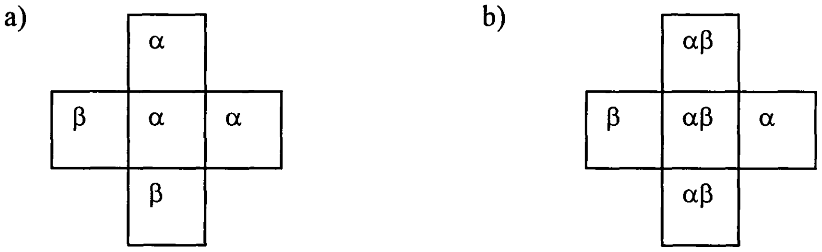


Figure 4: a) The calculation of frequencies f_{α} and f_{β} in the case of no shared cells. Here, $f_{\alpha} = 3$ and $f_{\beta} = 2$. b) The calculation of frequencies f_{α} and f_{β} in the case of shared cells. Here, $f_{\alpha} = 4$ and $f_{\beta} = 4$. Note the total of f_{α} and f_{β} exceeds the number of cells in the neighbourhood, i.e. $f_{\alpha} + f_{\beta} > 5$.

The general form of the relation between $p(x \mid f_{\alpha},f_{\beta},t)$ and $p(x \mid \alpha,\beta,t)$ is given by:

$$p(x \mid f_\alpha, f_\beta, t) = \frac{(f_\alpha - \delta)^v p(x \mid \alpha, \alpha, t) + f_\beta{}^w p(x \mid \alpha, \beta, t)}{(f_\alpha - \delta)^v + f_\beta{}^w} \tag{2}$$

where *v*, *w* and δ are constants (and real numbers). The parameter *v* represents the weighting applied to the frequency of the species α, f_α, within the neighbourhood of a subject cell of species α. The parameter *w* represents the weighting applied to the frequency of the species β, f_β, within the neighbourhood of a subject cell of species α. If the subject cell is ignored in the weighting then $\delta = 1$. However, for the purpose of subsequent analysis δ remains a parameter since varying the value of δ (between 0 and 1, inclusive, as described below) changes the nature of the species interactions. In cases where δ is less than 1, the strength of challenge made by the challenging species relative to the subject species is effectively weakened since the relative frequency of subject species in the neighbourhood increases. For example, if $v = 1$, $w = 0$ and $\delta = 1$ then the values of f_α and f_β in the neighbourhood depicted in Figure 4 a) above are 2, i.e. (3 α cells - $1)^1$, and 1, i.e. (2 β $\text{cells})^0$ – respectively.

2.2.4.2 Spatial arrangements

As noted previously, the work by White *et al.* (1998) clearly demonstrated that the initial spatial configuration of fungal communities, in terms of scale and pattern, affects community development. Here three systems of two-species interactions with different initial patterns are considered; the spatial scale is constant across these systems. Thus, the three systems together may be used to assess the impact of scaling, between the small- and large-scale tessellations, by comparing the similarities present in successful models. The impact of spatial pattern may then be independently assessed, across the large-scale tessellations, by contrasting the differences present in successful models.

Figure 5 a, b, c shows the 6x6 layouts (termed 'Tessellation 1', 'Tessellation 2' and 'Tessellation 3' respectively) used in the large-scale experiments. These arrangements were specifically designed to investigate the influence of initial large-scale patterning in the distribution of species on the dynamics of the community. The size of the same-species patches progressively decreases from Tessellation 1 to Tessellation 3, and therefore the number of inter-species interfaces progressively increases.

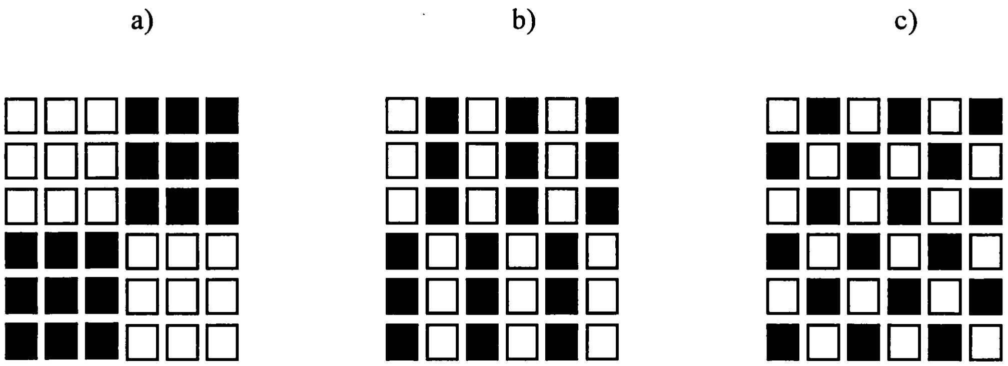


Figure 5: a) The arrangement of tiles in Tessellation 1; b) the arrangement of tiles in Tessellation 2 and c) the arrangement of tiles in Tessellation 3. Arrangement a) has a patch size of 9 with 12 Cm/Pv interfaces; arrangement b) has a patch size of 3 with 36 Cm/Pv interfaces; arrangement c) has a patch size of 1 with 60 Cm/Pv interfaces

2.3 Model results

Biological interactions were analysed for the 6x6 tessellations, 1, 2 and 3 (Figure 5 a, b, c). The experimental systems were harvested at days 8 and 12, as noted above. The observed state transition data for these experiments, expressed as means of the replicates, are shown in Tables 2, 3 and 4 below. Note that the transitions Cm→Pv and Cm→CmPv were never observed which implies zero frequency, and hence are assumed to have zero probability. The transition Cm→Cm was always observed which implies unitary probability. These trivial transitions are omitted from the tables for the sake of clarity. The computer models were run and the outcomes observed at 8 (simulated) days and 12 (simulated) days for the three 6x6 configurations (Tessellations 1, 2 and 3) using the calibration data from the 2x1 experiments. One thousand runs of each tessellation, providing sufficient output for testing the model against the biological data at the 5% significance level (Marriott, 1979) were undertaken and ranked. The means and central 95% confidence intervals for each state-transition category are also shown in Tables 2, 3 and 4 (Case B assuming $v = 1$ and $w = 0$; see below for these assumptions). Whilst only the data from the final investigation are presented, other results were assessed in a similar manner.

The models were run for each of the three tessellations under Case A assumptions. The predicted outcomes disagreed with the results of the biological experiments for all tessellations, i.e. not all the observed state transition data were within the central 95% confidence intervals. This demonstrates the important result that the dynamics of these fungal communities do not result from independent challenges from nearest neighbours (Bown *et al.*, 1999).

Models were also run for each of the three tessellations under Case B assumptions. An exploratory investigation indicated that the optimal values for v and w would be found within the range 0 to 2. In a more focused investigation the constants v and w were allowed to vary independently from 0 to 2 in increments of 0.1 with δ fixed at 1 (the subject cell is therefore not included in the weighting of $p(x \mid \alpha, \alpha, t)$). Models having non-zero values for w were inconsistent with the experimental results, i.e. not all the observed state transition data were within the central 95% confidence intervals. Models with parameter values $v = 1$ and $w = 0$ performed best, in terms of the number of observed state transition data within the central 95% confidence intervals, in all tessellations. In particular a good agreement with the results of Tessellation 1 was obtained, in the sense that all observed state transition data were within the central 95% confidence intervals.

In order to understand the poorer agreement with the experiments conducted in Tessellation 2 and Tessellation 3, the effect of large-scale patterning on the local interactions was considered. This was investigated by modifying the value of the parameter δ in equation (2). Values of δ less than 1 effectively weaken the challenge of Cm on Pv (generally α on β) relative to the situation encountered in Tessellation 1. In this search δ was allowed to vary from 0 to 1 in increments of 0.05. It was found that the optimal value of δ (i.e. the value such that all the observed state transition data lay within the 95% confidence interval and were closest to the observed mean) depended on the nature of the large scale patterning in the tessellations. For Tessellation 1 the optimum δ value was 0.9; for Tessellation 2 the optimum δ value was 0.15; for Tessellation 3 the optimum δ value was 0. For comparative purposes the means and central 95% confidence intervals for each tessellation for each of the three δ values noted are provided in Tables 2, 3 and 4.

Table 2: Results of the comparison between model output and the experimental microcosm for tessellation 1. The Table shows the observed transition data corresponding to the number of each type of transition averaged over the five replicate experiments at day 8 and day 12. For comparison, the number of transitions of each type averaged over 1000 realisations of the Case B simulation are shown for values of δ =0, 0.15, 0.9 (see text). Numbers in brackets represent the central 95% confidence interval derived from the simulations, and the emboldened transition data denote the optimal fit to the observed data.

State Transition Categories			Pv→Pv	Pv→Cm	Pv→CmPv
Observed State Transition Data		Day 8	8.6	0	9.4
		Day 12	0.4	14	3.6
Mean and Central 95% Confidence Interval of Predicted State Transition Data: (Lower, Upper)	δ=0	Day 8	9.37 (7, 13)	0.09 (0, 1)	8.06 (5, 11)
		Day 12	2.79 (0, 4)	7.13 (4, 12)	8.07 (4, 11)
	δ=0.15	Day8	9.69 (7, 12)	0.11 (0, 1)	8.2 (5, 11)
		Day 12	2.43 (0, 6)	8.03 (3,11)	7.54 (4, 12)
	δ=0.9	Day 8	**8.86 (6,12)**	**0.26 (0, 2)**	**8.88 (6, 12)**
		Day 12	**1.33 (0, 4)**	**11.4 (7, 16)**	**5.24 (2, 9)**

(The values of v and w were constant for each run: $v = 1$; $w = 0$.)

Table 3: Results of the comparison between model output and the experimental microcosm for tessellation 2 under the assumptions of Case B. See caption to Table 2 for details.

State Transition Categories			Pv→Pv	Pv→Cm	Pv→CmPv
Observed State Transition Data		Day 8	0.4	9.2	8.4
		Day 12	0	16.58	1.42
Mean and Central 95% Confidence Interval of Predicted State Transition Data: (Lower, Upper)	$\delta=0$	Day 8	0.34 (0,2)	6.22 (3, 11)	11.43 (7, 15)
		Day 12	0 (0, 0)	17.16 (15, 18)	0.83 (0, 3)
	$\delta=0.15$	Day8	**0.23 (0,1)**	**7.35 (3, 12)**	**10.42 (6, 15)**
		Day 12	**0 (0,0)**	**17.5 (16, 18)**	**0.5 (0,2)**
	$\delta=0.9$	Day 8	0.08 (0, 1)	12.18 (8, 16)	5.79 (2,10)
		Day 12	0 (0, 0)	17.98 (18, 18)	0.02 (0, 0)

(The values of v and w were constant for each run: $v = 1$; $w = 0$.)

Table 4: Results of the comparison between model output and the experimental microcosm for tessellation 3 under the assumptions of Case B. See caption to Table 2 for details.

State Transition Categories			Pv→Pv	Pv→Cm	Pv→CmPv
Observed State Transition Data		Day 8	0.2	1	16.8
		Day 12	0	15.8	2.2
Mean and Central 95% Confidence Interval of Predicted State Transition Data: (Lower, Upper)	$\delta=0$	Day 8	**0.88 (0, 3)**	**0.69 (0, 3)**	**16.42 (14, 18)**
		Day 12	**0 (0, 0)**	**15.57 (14, 18)**	**2.43 (0, 5)**
	$\delta=0.15$	Day8	0.67 (0, 3)	0.94 (0,3)	16.39 (14, 18)
		Day 12	0 (0, 0)	16.64 (14, 18)	1.36 (0, 4)
	$\delta=0.9$	Day 8	0.33 (0, 2)	2.67 (0, 6)	15 (12, 18)
		Day 12	0 (0, 0)	17.92 (17, 18)	0.07 (0, 1)

(The values of v and w were constant for each run: $v = 1$; $w = 0$.)

2.4 Conclusions

2.4.1 The effect of scale: emergent behaviour

The simplest model assumes that the dynamics of the communities is a result of independent challenges from species in a predefined local neighbourhood. Comparison with the results from the experimental microcosms showed we could exclude this hypothesis at the 5% significance level (Bown *et al.*, 1999).

The next simplest model assumes that the challenges are not independent, and that the probability of a change in state of the subject can be written as a weighted sum of the probabilities relating to the independent challenges. The weightings relate to the assumption that the strength of the challenge from an individual cell in the neighbourhood depends on the number and species types in the rest of the local (five-cell) neighbourhood. Two weighting factors, v and w, and an additional value δ parameterise this model. The values for these parameters are determined by comparison with experiment and yield insight into the nature and scales of interaction between individuals in the microcosm community.

The parameter w represents the weighting applied to the frequency of the species β within the neighbourhood of a subject cell of species α. Comparison with the experimental results from the microcosm show that the optimal models for all tessellations require $w = 0$. This value for w indicates that the number of β in the immediate neighbourhood is not important – i.e. that species β does not co-operate with its neighbours. Thus, only the presence or absence of species β in the neighbourhood is of significance for the dynamics.

The parameter v represents the weighting applied to the frequency of the species α within the neighbourhood of a subject cell of species α. Comparison with the microcosm results shows that the optimal models for all tessellations require $v = 1$. This value for v indicates that the number of α in the immediate neighbourhood is important – i.e. that species α does co-operate with its neighbours. Thus, the number of subject species cells in the neighbourhood is important for the dynamics.

Whilst the values of v and w are consistent with the experimental results for all tessellations, δ varies across tessellations. Furthermore, this variation reveals a relation between the value of δ and the large-scale spatial arrangement of species in the corresponding tessellation. More precisely, as the patch size of individual species increases, the value of δ increases. As noted earlier, species Cm readily forms cords across mycelia suggesting that initially isolated mycelia may undergo a process of anastomosis or hyphal networking (Rayner *et al.*, 1994; Rayner ,1996), effectively resulting in a scale change in its mycelia. The trend of an increase in the value of δ with an increase in the degree of patchiness represents a strengthening of the combative nature of species Cm in large patches.

Since the large-scale patterning of the community changes with time, it might be expected that δ would also be time-dependent. The experimental data are not inconsistent with this, but it was not possible to detect a statistically significant time-dependency. The fact that we were able to model the dynamics using a constant value for δ, that depends only on the initial state of the microcosm, may reflect the relatively slow rate at which the system loses 'memory' of previous states.

From these results we can conclude that the community-scale dynamics of the microcosm is a consequence of dependent local interactions, and that the community-scale features of the system modify the nature of these interactions. This behaviour may be a consequence of anastomosis leading to translocation of resources from sites of low combative stress to interaction fronts where antagonistic or defence responses increase metabolic demand. This combination of "scale effects" greatly complicates understanding of the large-scale behaviour of microcosms, and precludes the extrapolation of results from experiments conducted on individual mycelia without reference to the spatial context within a community.

2.4.2 The need to link fine-scale measurements to broad-scale behaviour

The work carried out by White *et al.* (1998) demonstrated the influence that co-ordinated behaviour may have on community dynamics. The subsequent theoretical analyses carried out by Bown *et al.* (1999) and described above further demonstrate that community dynamics are a consequence of both local and non-local effects. Thus, a coupling between fine and broad scales exist. More fully, it is clear that the interactions among organisms that occur at local scales govern the patterns that emerge at non-local scales. For instance the invasion of one fungal species into another, as observed in the above experimental system, is a consequence of a localised interaction between the mycelia surrounding the interaction front. However, the rate and direction (i.e. which species invades which) of that invasion may be augmented by contextual features. The above system certainly demonstrates that the rate of invasion of one species into another is modified by the patchiness of the system as a whole – i.e. the propensity of the system to coalesce affects the rate of local interactions. As notes earlier, a related study (Sturrock, in prep.) has demonstrated that particular temperature regimes can also significantly affect the nature of system dynamics. In that study, the interactions between two species were studied under different experimental temperatures. At one range of temperatures one of the two species was observed as being invasive; at another range of temperatures that same species was readily invaded by its paired species. Clearly a range of contextual factors may have an impact on the dynamics of fungal communities.

Chapter 3 of this thesis describes the development of a conceptual framework that serves as a platform for investigations into the linkage between the scales of fine-scale processes, intermediate-scale patch dynamics – local communities – and broad-scale dynamics – global communities. Crucially this model must, like the cellular automaton model described above, be capable of capturing features at all these scales. As discussed in Chapter 1, Rand (1999) notes the appropriateness of the general class of cellular automata to reflect properties of systems at both microscopic and macroscopic levels.

The modelling approach for investigating fungal microcosms described above, and cellular automata in general, is inherently 'bottom-up' in the sense that global behaviour is generated from a local set of rules. Further, that local set of rules is either qualified or quantified by out of context experiments and/ or observations – here small-scale systems comprising paired tiles of fungal species quantify the rule set. Such modelling approaches can never address the impact of context on localised elements of a system. Indeed, the results of the above study strongly suggest that most progress will be made by studying the dynamics at both local and non-local levels, acknowledging the influence on the dynamics of emergent behaviour resulting from co-operative (and competitive) strategies amongst small-scale elements (Bown *et al.*, 1999).

Conversely, the approach outlined in Chapter 3 considers the dynamics in a 'top-down' sense. Such an approach will be demonstrated to facilitate the coupled relationship between process and pattern, or fine-scale and broad-scale properties. The model, as noted, must be able to express features at both the microscopic and macroscopic levels. To maintain the strong link between experiment and theory central to this study the complementary experimental system must also express features at those scales. Further, the scope and depth of the conceptual framework to be addressed allows investigation into a range of process-oriented and pattern-oriented properties. To reference these theoretical studies with an experimental system requires the development of a novel experimental system more sophisticated than that considered above. In particular spatial heterogeneity, well known to be important in ecosystem dynamics (Silvertown *et al.*, 1992; Tilman, 1994a; Wu and Levin 1994; Ziv 1998, Oborny *et al.*, 1999) must be incorporated.

Further, it is undesirable to destructively assess complex fungal communities (or even simple ones!) for two reasons. Firstly, the configuration and harvesting procedures used to initialise and subsequently identify the occupancy of the fungal microcosms requires is costly in terms of time. This cost limits both the number of replicate experiments and the number of time points considered, since one experiment is required for each replicate at each time point. Secondly, there is no allowance for continuity under this scheme. No individual replicate may be measured at two different time points, and so the significance of observed variations at a given time point on the subsequent dynamics of the microcosm cannot be addressed.

Hence, a range of experimental approaches and techniques has been and is currently being investigated by the experimentalist within the group associated with this study. These approaches include the incorporation of 'Green Fluorescent Proteins (GFPs)' into fungal species to allow the precise mapping of community components in space, the development of soil-based heterogeneous environments and assessment measures to allow the profiling of fungal species characteristics in time and space. Chapter 5 provides a synopsis of experimental and theoretical advances to further studies into fungal community dynamics. However, the time required to develop such novel approaches is significant and rather than wait for experimental data the theoretical approaches were developed in a manner independent to the particulars of any suitable experimental system. Thus, the underlying philosophy of the framework and its components are inherently generic.

To assess the viability of the theoretical techniques addressed in that framework before the substantial investment of a complementary experimental system this framework was applied to a more readily accessible application area, that of plant community dynamics. This application area is supported by a wealth of experimental and theoretical literature, and importantly a particular set of data relating to three grassland species and the spatial patterns of those co-existing grasses in field contexts. Thus, an instance of the application of this generic framework to plant population dynamics is described.

Chapter 3 A conceptual framework to address general issues of scale

3.1 The generic framework

3.1.1 Underlying philosophy

The 'bottom-up' approach noted in Chapter 2 is dependent on the notion that a set of local rules, derived from observations out of context, can adequately represent community level behaviour. However, given that mechanisms defined at one scale can be augmented by features of a system at different scales, context cannot be ignored. Of course, in theory the 'bottom-up' approach is viable since the set of local rules can be derived from a suite of observations that take into account all possible contexts. Thus, context is inherent in the (exhaustive) local rule set. Modelling, however, strives to find the simplest set of rules that describe the behaviour and to understand the processes present. Rather than use an exhaustive rule set it is often more useful to seek patterns in the results derived from a smaller set of contextual experiments using and building upon existing behavioural knowledge. Such pattern seeking is facilitated by a 'top-down' approach.

In assuming a 'top-down' approach individual organisms within a community are expressed as a part of that community, having a set of process-based behavioural characteristics that are parameterised by their context. Thus, they have a rule set that is modified by contextual properties. In admitting contextual parameterisation to the local rule set, the important coupling between fine-scale mechanisms and broad-scale properties, such as spatial distribution of organisms and heterogeneity of any resource, is represented. The nature of this contextual inclusion is clearly specific to the application, and is exemplified here in the application to plant community dynamics described here. In general, however, the individual organisms of a community have a definition that has rigid upper and lower bounds in its form, reflecting the extremities of physiologically possible contexts – here resource absence and resource saturation –, combined with much plasticity within those bounds, reflecting the range of contexts present between those extremes – here intermediate resource levels.

The processes represented are generic in nature and take the form of algorithmic descriptions. Differences in individual organisms manifest themselves through the expression of functional traits (behavioural characteristics), which act as parameters to the algorithmic representation of process. Traits therefore reflect ecophysiological strategies governing the interaction between that individual organism and its environment (Wardle *et al.*, 1998). An individual organism is thus expressed as a collection of functional traits that define the manner in which it interacts with its surroundings.

An important consequence of considering an ecological system at the community level is that the use of species as a classification tool in the identification of community system role is not immediately obvious. Species are defined in terms of sexual compatibility – organisms of the same species can mate and produce viable offspring. However, this definition is only firm in higher organisms; in lower organisms such as fungi and some plant forms it is a less definite concept. In this work, the individual organisms within a given community are expressed in terms of function, and are then most clearly considered in terms of their functional role within the whole community. Further, this modelling approach is individualistic in nature, and each individual organism may then have its own unique set of traits and thus its own unique role in the community. Any individual organism may then be thought of as a (functional) type within the community.

Of course, there is a relationship between type and species, in that a given species has a finite number of functional types under its scope. In a sense, the classification of species sets limits on the range of types, i.e. any given trait value is constrained by some species-specific limits. However, these ranges are not necessarily exclusive; indeed overlap between ranges will occur. Further, many species may perform the same, or similar, roles and the relationship between genetic content – the genotype –, paramount to the notion of species, and the expression of functions – the phenotype –, crucial to this modelling approach, is not clear (as noted in Chapter 1).

In a given community there will be a large number of types. Indeed, if all individual organisms are unique there will be one type per organism in the absence of functional groupings. For initial analyses however, a small number of types are considered, with many instances, or clones, of those types. Each individual within a type may be different as the development and behaviour of each individual organism is a function of its context. Further, we assume any offspring reproduced are clones of the parent – there exists no genetic coupling between plant types. Thus individual organisms are classified in terms of constant types, since no diversity occurs through genetic coupling. This functional classification is also applied in the work described in Chapter 4.

Throughout this thesis the importance of a strong link between experiment and theory has been maintained, and this (more conceptual) modelling approach is no exception. Experimental parameterisation with contextual inclusion is more tractable in 'top-down' approaches, since it is the relationship between process and context that is being identified, rather than a series of mappings between a rule and an associated context as required by the 'bottom-up' approach. This relationship may be identified by setting the upper and lower limits, i.e. best and worst possible contexts, and assessing some intermediate points. Chapter 5 considers related work that addresses the issues of experimentally parameterising this framework. The aim of this chapter is to introduce the important concepts within this modelling paradigm in a very general sense, followed by a sample application of this framework to plant community dynamics and associated examples.

3.1.2 Framework components

If a model is to be generic in nature, applicable to real systems and to be amenable to experimental parameterisation it must incorporate a number of features. The fundamental unit of exchange between individual organisms of a community should be based on resource to allow the expression of quantitative competition. Many existing models employ a hierarchical rule structure to express inter-species competition, in either an explicit or implicit manner. For example, in their studies of fungal community dynamics, Halley *et al.* (1996) use an explicit hierarchical rule structure to govern spatial displacements by one (fungal) species over another, based on some 'competition rule' – A displaces B according to a competition table – derived from (pairwise) small-scale experiments amongst four species. Winkler *et al.* (1999), in their model of clonal plant competitiveness, consider interactions between two species and introduce a competitiveness rating which, although modified by non-local abundance, serves as an implicit hierarchical rule applied to those species. When addressing the issues of context, hierarchical rules are inappropriate unless they include contextual information, which is not easy to express. Indeed, hierarchical rules suffer from the same inherent problems associated with 'bottom-up' rules in general when considering context.

A resource-level driven approach allows the expression of spatio-temporal heterogeneity in resource substrate, and permits that substrate to impose conditions on the individual organisms within that substrate. Consequently, individual organisms should be defined as interacting with that resource substrate through physiologically based processes, parameterised by the individual's traits, for example uptake and allocation. Thus, the competition experienced by a given individual organism becomes a property of both that organism's traits and the available resource and space. Such rules therefore incorporate contextual information, since the context in the form of resource substrate and localised individual organisms is expressed in terms of resource and space availability.

For the model to be generic, the incorporation of a wide range of strategies associated with each functional trait must be possible. In other words, the process-based mechanism must be both generic and flexible to diversity in parameter values, allowing a wide range of types to be incorporated. Further, each individual organism has its individual set of traits, allowing the expression of unique strategies. Those strategies are to be (potentially) dynamic as the organism develops; for example small structures require less resource than large structures and so any uptake strategy must acknowledge this feature.

The requirement for a wide range of strategies which are temporally dynamic has important implications for any modelling implementation. The form of cellular automaton defined for the fungal community analyses considered a single form of rule applied to a fixed neighbourhood, and that rule was parameterised by a temporal component. In the modelling approach described here the type of organism occupying that site governs the rules that are applied to a single site. Rules may vary in the extent of interaction with the resource substrate and may vary in the processes that they invoke. The appropriate rules are defined by the nature of the individual organism's traits.

Since the aim of this framework is to provide assessment at a range of scales it is important that features present at those scales are explicitly expressed. The model, therefore, should produce spatio-temporal output in a form that allows features of the community to be analysed at that range of scales in space and time.

There is a tension created by the requirement that the model should be as generic as possible while the number of traits should be as small as possible. Clearly the model should be as simple as possible for ease of interpretation. Further to this interpretative constraint the need to keep the number of traits small is supported by the desire to search an n-dimensional state space, where n is the number of traits. The search process aims to relate combinations of fine-scale, individual processes and specific broad-scale, community properties and is addressed in Chapter 4. Thus, the traits themselves must be carefully selected.

This set of requirements leads to a modelling approach with a number of components. A representation of an individual organism of a community in terms of functional trait definitions; a representation of an underlying resource substrate; an algorithmic description of the key process-based mechanisms identified within the application area and a spatio-temporal output and associated classification.

The following sections consider an instance of the framework as applied to plant based systems. The assumptions relating to the nature of the important processes in plant development and interaction are given below. This set of processes aims to be as simple and as generic as possible, without oversimplification. The underlying resource substrate is also described. Given this platform of processes and resource base, the algorithmic description is addressed. Where appropriate, the functional traits are introduced within this description.

The spatio-temporal classification is not addressed here, although examples of the spatio-temporal output are given in the form of demonstrative examples. This classification is considered in Chapter 5.

3.2 Application to plant community dynamics

3.2.1 Related work

Within the last decade many authors have raised the importance of relating processes at different scales. The most important of those contributions are discussed here and some recent modelling approaches that address scaling effects are described. The general terminology used in ecological discussion is pattern and process, and the exact interpretation of these terms is scale-dependent. Pattern refers to the (explicit) spatial arrangement of patches (as in Chapter 1), or clumps, of individual plants at the level of the community, or the spatial arrangement of individual plants within a patch at the level of the (spatially divided) sub-community. Process may refer to a) the ecophysiological processes that are present within the individual plant; b) properties associated with a patch such as frequency, density and aggregation within some classification scheme, species or otherwise; or c) dispersal and exchange of individual-based properties, for example traits, at the community level (between patches). The importance of an explicitly spatial, individual-based approach to ecological modelling, as noted in Chapter 1, is apparent from this terminology.

Silvertown *et al.* (1992) give consideration of the effect of pattern on process. In particular they consider the spatial arrangement on individual plants, i.e. the importance of the neighbourhood (at some scale) on the individual. The plants in that model interacted through rules derived from experimental studies carried out by Thorallsdottir (1990) and Marshall (1990), where small numbers of competing species were grown in different spatial patterns, and those plants were subsequently analysed in terms of physiological properties. The results suggested that the spatial arrangement of competing species had an impact on individual plant performance. Silvertown *et al.* (1992) note that whilst many (plant) competition models include space in some averaged sense, through measures of frequencies and densities of competitors, they do not consider the effect of aggregation of species. Indeed they conclude that spatial distribution of competitors is as important as the frequencies and densities of those competitors in determining system dynamics. Clearly individual-based models with an explicit treatment of space can be used to investigate this relationship.

Wu and Levin (1994) in their comments on modelling ecosystems in terms of explicitly spatial patches and their associated dynamics, and considering plant based systems in particular, frame the same issues: "process modifies existing pattern and creates new pattern; pattern enhances or constrains ecological processes". Also, they note that such patch patterns occur across a range of spatial scales and that the relationship between process and pattern is central to ecology. They further comment that many investigations classify systems at the characteristic scales of the individual, population and community levels without considering the relation among those scales, although such classification provides a useful starting point. A spatial patch dynamics model is presented where the functional unit is a patch – a patch is a mixing of species that occupies space. Intra-patch dynamics take the form of plant competition and reproduction, and are considered in terms of density-dependent mechanisms. Thus processes within the patch are affected by the pattern intrinsic to that patch. Inter-patch dynamics take the form of seed dispersal. This model is used to demonstrate the spatio-temporal dynamics of populations of two species on the local (patch) and landscape (community) scales. They show, amongst other properties, that the local dynamics of patches substantially contribute to the landscape level pattern. The work clearly illustrates the importance of considering the coupling across scales.

Ziv (1998) describes this coupling between pattern and process as occurring over a continuous range in spatial scale. Further, the notion of spatial heterogeneity is linked to the scale at which that pattern is assessed. Ziv cites Ricklefs's study (1987) of species diversity, which demonstrated that this diversity is affected by different ecological processes at different scales. As a consequence of these observations, Ziv states that the "understanding of large-scale species diversity patterns and processes cannot be simply deduced from the understanding of local-scale patterns and processes. We need to explore large-scale species diversity patterns in the context of their occurrence, given the relevant multi-scale processes and the heterogeneity of the environment in question."

The suggested approach to addressing this complex exploration is in the form of a multi-species patch-based model. This model is, in a general sense, like that presented by Wu and Levin (1994). Ziv's model differs in its treatment of processes which are both more sophisticated and, importantly, parameterised by results from empirical studies. Patches comprise cells of varying levels of a single resource type, and are spatially arranged. Local-scale processes occur within the patches governing population growth and sustainability in the underlying habitat, each implemented through a number of processes. Global-scale processes occur between patches through dispersal and extinction where extinction is a density-independent effect applied to the whole community due to some environmental feature such as extreme cold weather. Species are assumed to have a probabilistic resistance to such events, and so extinction events may reduce or eradicate the presence of a population within a patch. The model allows the investigation of the effect of spatial arrangement of habitats on community-scale pattern. Important here is that the work focuses on the need to consider processes and patterns at a range of scales.

The importance of characterising individuals in terms of traits is noted by Wardle *et al.* (1998). The authors note that the importance of individuals, rather than species, on ecosystems is becoming increasingly apparent, and to make progress in understanding that significance it is necessary to define the relationship between an individual and its environment. Wardle *et al.* (1998) study a range of species out of context and characterise each in terms of ecophysiological traits. The results show that large differences in trait measurements are observed among the species when all traits are considered, although many inter-species similarities exist within a single trait measurement. They also note a relationship between some traits, including a clear link between fast growth rate, limited overall growth and early flowering. This co-variation between traits may provide a link between processes at the plant and community scales (Reich *et al.*, 1992). In a study by Köhler and Huth (1998) the classification of species into functional groups is argued to make a more apparent link between the ecological properties of the system and the physiological properties of the individual plants than a speciated classification.

Oborny *et al.* (1999) describe a competition model for vegetative clonal plants. Such plants reproduce by developing modules that are semi-autonomous. In some species an integrated network of modules is formed, allowing the sharing of resources between modules, much like the anastomosis process observed in one fungal species in Chapter 2. Other species do not form such modules. These different strategies were implemented in a simple process-based approach. Using an explicitly spatial model, the authors investigate the impact of habitat substrate on the effectiveness of these strategies. By imposing different habitat properties on a community of these two functional forms the authors were able to demonstrate exclusion of the integrating form, exclusion of the non-integrating form, and coexistence of both forms. They emphasise the importance of habitat pattern on process sustainability and the use of individual-based spatially explicit models.

Preliminary studies into regional pollen dispersal from oilseed rape situated in the Carse of Gowrie, Scotland, UK have raised issues relating to the impact of non-local context on local behaviour, although this impact is of a different form to that previously discussed. Squire *et al.* (1999) describe a model of pollen dispersal parameterised by measurements derived from a transect of sample points at a range of distances from a single field. This transect provides a pollen dispersal profile which parameterises a source-diffusion process. The model aims to predict the dispersal of pollen at a regional scale, roughly 20 km^2, under the assumption that the transect used to identify the pollen profile is isolated from other pollen sources. Thus, the pollen dispersal model is based on purely local assumptions.

However, subsequent analyses of the observed and simulated data sets reveals an inconsistency. In particular, pollen levels at the sample points are higher in the simulation than in the observed system. This suggests that the transect is subject to contextual noise from surrounding, yet relatively distant fields, and was therefore showing significantly higher levels of pollen than would be obtained from the field in true isolation. Again, the dynamics of the system are a consequence of both local – pollen from the most immediate field – and non-local – pollen from surrounding fields – effects. The coupling between scales is once more evident, since the regional pollen is governed by local sources, and those local processes are influenced by non-local effects, for example the augmentation of pollen dispersal from other fields and interference by geographical features. The authors intend fitting the model and its associated pollen dispersal profile to the observed data set, and then contrasting the fitted pollen dispersal profile to the observed transect data as a first step in understanding the impact of contextual noise in this system.

The model described in this thesis provides a platform to allow investigation of the main issues in the examples addressed above. The coupling across scales noted by Wu and Levin (1994), Ziv (1998), Oborny *et al.* (1999) and Squire *et al.* (1999) is addressable in the context of a spatially explicit individual-based model (Silvertown *et al.*, 1992; Oborny *et al.*, 1999), where a combination of the functional traits (Wardle *et al.*, 1998) present in those individuals and the environmental context of those individuals govern the dynamics of the system. Köhler and Huth (1998) support the classification of type, i.e. functional rôle, used here. In acknowledgement of the potential link between co-variant traits and ecosystem scale processes noted by Reich *et al.* (1992) and supported by Wardle *et al.* (1998), Chapter 4 provides an initial study into this co-variation property.

The above plant community models offer insight into the dynamics of natural communities and each approach has an associated number of simplifications. Wu and Levin (1994) only consider communities of two species. Likewise, Oborny *et al.* (1999) incorporate two forms of the same species into their model – those that form integrative structures and those that do not. Silvertown *et al.* (1992) include five species representations in their theoretical model. However, all these approaches rely on qualitative rules leading to a hierarchical expression of competitiveness, and suffer from inherent limitations in the diversity of function that may be represented. This work offers the potential to include quantitative experimental data in a genuinely individualistic model – in this work all individuals may be different. Thus species or type need not be inherent in this model, but may serve as simplification tools (as in natural community studies).

Ziv (1998) offers a multi-species model with some quantitative details. Processes are incorporated that act at species, population and community levels. In ecosystems, processes originate at the individual level, at that individual's characteristic scales, although the manifestations of these processes – patterns – may be present at higher scales. Therefore, the expression of processes directly coupled at the species (or other) level, for example birth rate, represents a simplification of reality. This simplification may compromise the transparency of the relationship between fine-scale detail and broad-scale features. This relationship is at the heart of the work presented here and so no such intermediate processes are represented.

3.2.2 Physiological processes represented in the model

The model of plant community dynamics must represent the essential features of competitive interactions in space and time. It is rarely practical to incorporate all features of these interactions in a model. Firstly many aspects of the plant life cycle are not fully understood. Secondly, the impact of context on that life cycle is not clear – hence the motivation for this work. Finally, such a model would have prohibitive associative developmental and computational time-scales. Therefore, assumptions to make the modelling process addressable are made. The most fundamental of these assumptions is that there exists a single resource type, structured in a two-dimensional lattice. This resource represents some combination of all types of resource available. As will be seen below, a multi-resource system increases the number of traits required to represent an individual plant since many traits are parameterised by the resource availability, i.e. the contextual inclusion. An increase in the number of traits greatly complicates both the interpretation of the model and the search element of the work addressed in Chapter 4.

The plant forms and the biological processes represented are general, with the aim of representing the main features of any form of plant through combinations of wide ranging traits values. The model incorporates four general biological processes associated with the life cycle of a plant: uptake of resource, allocation of resource, reproduction and development. The general features of these processes are summarised before the computational details of the model's algorithm are provided. The assumptions and representation of the biological processes were taken from personal communications with Dr G. Squire of the Scottish Crop Research Institute, Dundee.

A plant is characterised in the model by traits that determine its performance under the conditions imposed by the resource substrate with limits in this characterisation set by maximum and minimum resource availability. The model simulates development in time by allowing each plant to pass through a series of (discrete) stages, where each stage has an associated set of trait values.

Thus, the trait values are not a single set but a list of sets, where this list contains as many sets of values as there are development stages. Transitions between the stages are predominantly regulated by the acquisition of resource and its subsequent accumulation. This accumulation is assessed in terms of developmental thresholds – an individual must accumulate a certain amount of resource to progress to the next developmental stage. Not all traits are considered in resource terms. Where appropriate traits are expressed purely in terms of time. Combinations of resource-regulated and time-regulated development and behaviour can clearly represent a wide range of plant forms.

The resource uptake strategy of an individual may be considered in terms of extent, in two-dimensional space, from some centre (or resource capture area) and activity as a function of distance from that centre (or resource capture amount). The area occupied and the distribution of activity within this area, though two-dimensional, may be combined in different ways to mimic three-dimensional structures. For example, a young plant may have a very localised resource capture area, as shown in Figure 6 a). This reflects a small resource capture area and little activity, due to the small size of the plant, within that area. As the plant develops it may expand that area in a radial form as in 6 b) indicating a large resource capture area with little activity relative to the area covered. It may invest more into the immediate area as in 6 c) indicating a small resource capture area and with great activity relative to the area covered. It may equally develop some structure between these extremes as depicted in 6 d) where an intermediately sized resource capture area is coupled with varying activity, here little towards the boundary of the capture area and greater activity towards the centre of the structure.

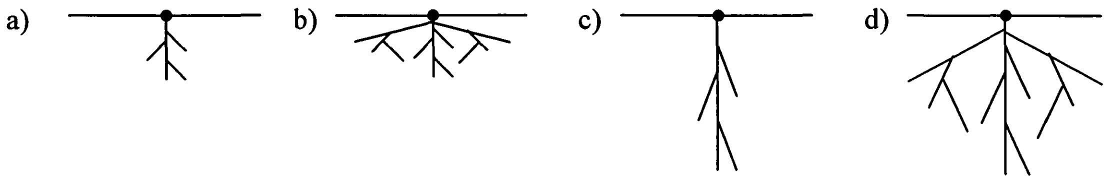


Figure 6: Schematic of different resource acquisition strategies

Distance from the origin of the plant is discretised into bands (see 3.2.3) and uniformity within a band is assumed for simplicity. The form of the model does not prohibit the expression of irregular shapes, which may be adaptive to an underlying heterogeneity in resource.

Having acquired resource it is necessary to allocate that resource within the plant. A plant is assumed to partition resource over three compartments: its non-reproductive structure, its reproductive structure and some surplus resource pool. When considering the total amount of uptake a plant achieves, some margin of excess is included (i.e. an amount above the plant's requirement for optimal conditions). Acquired resource above this amount is stored in the surplus pool; acquired resource below this threshold is stored in the structural compartments of the plant. A portion of this structural store is allocated to reproductive structure, and the remainder to non-reproductive structure. A portion of the uptake may also be allocated to reflect offtake, perhaps by grazing. As with resource acquisition, when appropriately parameterised, a wide range of resource allocation strategies may be represented via modifications to the partitioning process. The surplus store may be used for both reproductive investment and for offsetting resource shortfalls (see below).

Reproduction may be regulated temporally, as when controlled by global signals such as temperature, photoperiod or other seasonal features. Reproduction may also be resource-regulated, and may be initiated when the individual has reached a certain level of resource. Acquiring this threshold of resource implies a particular developmental stage, since developmental increase is resource-regulated as indicated above. These regulators are not mutually exclusive, and so a wide range of reproductive strategies may be expressed in terms of a combination of temporally-regulated and developmentally-regulated events.

Once a reproductive event is invoked a simple function relates the uptake amenable to reproductive investment (i.e. the reproductive store and surplus store as described above) to the number of offspring, or propagules, produced. Altering the form of that relationship may effect different strategies of translating accumulated (reproductive and surplus) store to offspring. An example range of such relationships is given in the description of the algorithm below.

The produced offspring are dispersed in a range of spatial patterns, as defined by an individual's trait. The propagules carry the parent's reproductive resource with them divided evenly across all propagules, and transfer it to the location of each propagule during the dispersal process. Thus, resource is both conserved and redistributed within the resource substrate during dispersal.

Encapsulated in the process of development, where an individual's accumulated resource is assessed to determine development stage, is the notion of survival – i.e. the issue of whether an individual has accumulated enough resource to survive is addressed. Plants are therefore characterised by the way they respond to low levels of resource, be that through environmental shortfalls or competition for available resource. This allows comparison between differing functional types in their ability to compete and survive. An individual plant experiencing a low level of resource may temporarily offset that shortfall by drawing on its surplus store. Continued shortfall may result in the death of the plant and individual parameterisation allows the representation of different tolerances to shortfall. Again, a wide range of strategies may be implemented here.

3.2.3 Representing the environment: resource substrate definition

The underlying resource substrate is represented as a spatially discrete lattice of sites where each site has a number of associated characteristics, expressed in units of a single, unspecified resource. The characteristics describing a site define the existing level of resource, a maximum level of resource reflecting saturation, a time-dependent resource release rate, and a time-dependent resource replenishment rate. This fine-scale resolution of substrate characteristics allows the representation of a wide range of resource substrates, in terms of levels and spatial arrangements. The resource substrate may be configured so individual sites may carry a wide range of resource levels, allowing resource poor, intermediate and rich sites. These sites can be arranged to provide substrates including homogeneous, resource patched and resource sloped patterns. In addition, the release and replenishment rates can be varied in time to investigate the effects of resource accumulation or degradation.

The resource substrate facilitates interaction at local and non-local scales. Local interactions are expressed through competition for resource: individual plants with overlapping resource capture areas clearly draw on the same resource site, although perhaps to differing degrees. Non-local interactions are instantiated by propagule dispersal, where resource relocation occurs. Resource is removed from the parent representing structural loss in the form of that propagule, and is added to the resource level of the site wherein the seed is deposited. In the implementation described here, only seeds that land on empty sites are considered viable. If viable, seeds immediately germinate and the subsequent survival of the new plant depends on both its traits and the resources available. Regardless of the viability of the seed, the resource within the propagule is always transferred to the site in which it lands. This simplification and the measures required to improve the representation of seed are detailed in Chapter 5.

3.2.4 Representing the physiological processes: computational aspects and traits

3.2.4.1 Overview

The biological process described above is represented in terms of a computational algorithm and a set of associated functional traits. This algorithm describes the four general biological processes associated with the life cycle of a plant: uptake of resource, allocation of resource, reproduction and development. These four general processes lead to the high-level schematic shown in Figure 7.

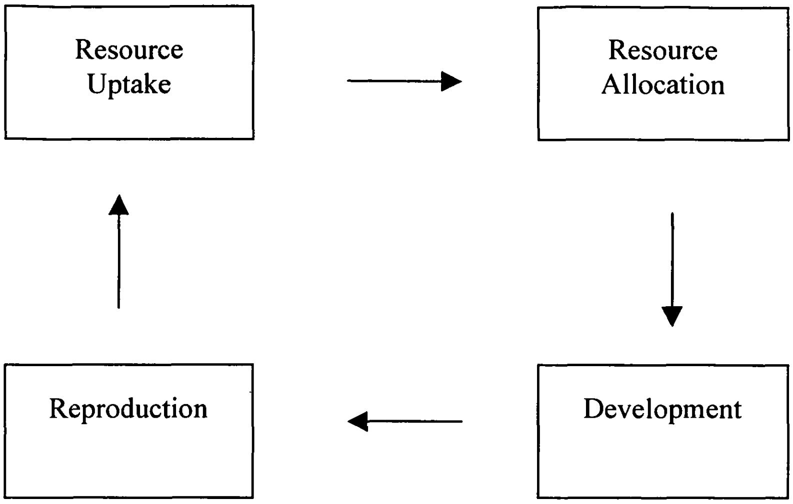


Figure 7: High-level schematic of the representation of the four biological processes

3.2.4.2 Resource uptake

The uptake mechanism is considered in terms of the extent and activity of a resource capture area, and is characterised by two developmentally varying traits: 'requested uptake' and 'distance-proportioned uptake'. 'Requested uptake' is a trait that is independent of the current environment or degree of competition, and it may be considered as the maximum uptake possible by a plant in a single time step. 'Requested uptake' defines the absolute activity of the whole resource capture area, and is expressed as the amount, in units of the resource substrate, to be drawn from that substrate. Figure 8 illustrates three different phenotypic forms which indicate that plants more advanced in development are capable of more uptake. However, this need not be the case for all plant forms. For example, a form of uptake that increases to a maximum, and then falls (within limits) after that maximum may simulate senescence.

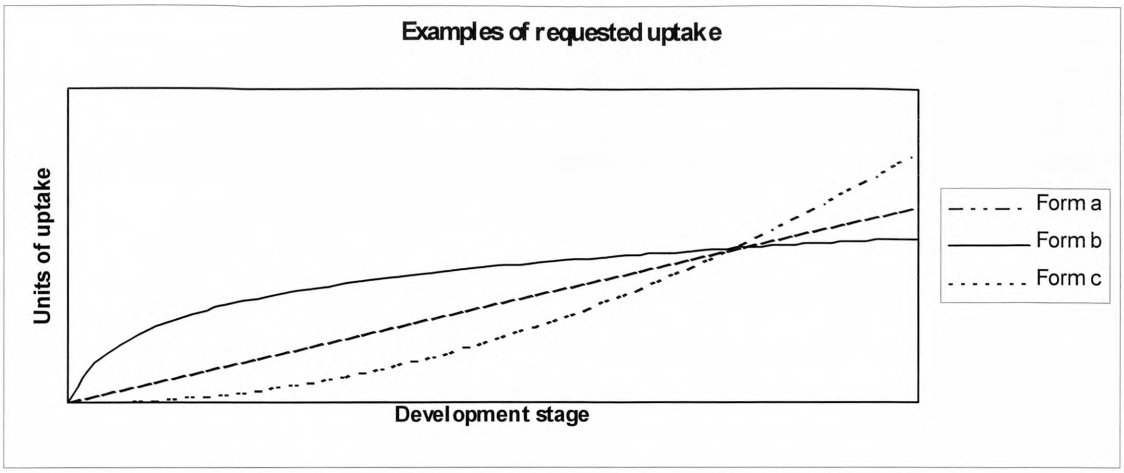


Figure 8: Forms of absolute uptake as a function of development stage

‘Distance-proportioned uptake’ defines the shape of the resource capture area in terms of extent over the resource base and the relative (proportional) activity at the various, discrete distances from the origin, where the origin is the single site in the lattice in which the individual plant is centred. Discrete distances away from the origin are defined in terms of bands from the origin: the first band is the cell at the origin; the second band by the eight cells surrounding the origin; the third band by the sixteen cells surrounding those eight; and so on. This ‘banding’ scheme offers a computationally simple approach whilst supporting a wide range of strategies. Other strategies are, of course, possible including a perhaps more realistic circular discretisation. Regardless of the nature of the discretisation, allowing adaptation in the bands where each cell in the band may request differing amounts depending on previous uptakes could further enhance the representation. However, the biological collaborators considered this rectangular representation sufficient at this stage of development. Figure 9 illustrates the discretisation of distance for uptake purposes.

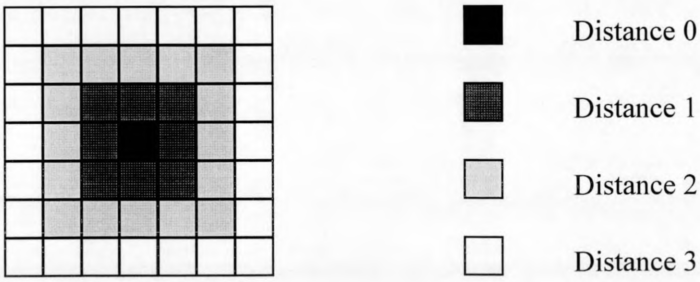


Figure 9: The discretisation of distance for the resource uptake process

Figure 10 shows an illustration of the manner in which 'distance-proportioned uptake' may vary across development stages. The example shows an early stage x, an intermediate stage y and a later stage z. When small in structure, at stage x, the individual is only able to access more immediate sources of resource and so a large proportion of its nutrient uptake is gained from very close by. As it develops and expands the resource capture area, through stages y and z, it may access more distant sites of resource placing less (proportional) emphasis on the immediate area. 'Distance-proportioned uptake' is expressed as vector per development stage of the form [distance 0; distance 1; distance 2; distance 3; ...]. Such a form allows the representation of a great number of strategies.

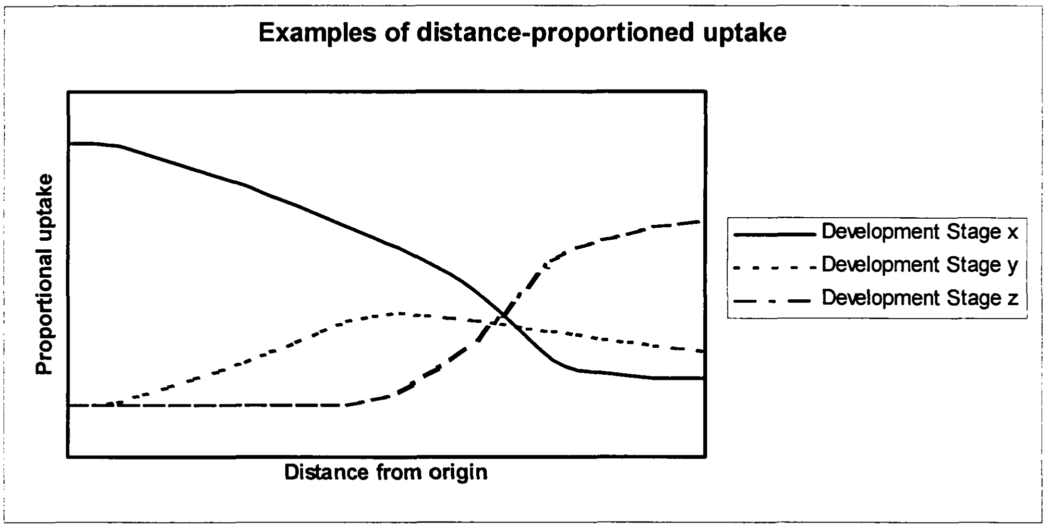


Figure 10: Relative uptake as a function of distance for three separate stages of development

The algorithmic relationship between the underlying resource substrate and the traits 'requested uptake' and 'distance-proportioned uptake' is best explained by example. Consider a plant with 'requested uptake' of 10 units of resource, and with 'distance-proportioned uptake' of [0.2,0.8], i.e. 20% uptake from the origin, or distance 0, and 80% uptake from the next band, or distance 1. In a non-limiting substrate the plant will acquire 2 units from the distance 0 cell and 1 unit from each of the distance 1 cells. If the substrate were limited in terms of the amount of resource available at all sites, say 1 unit, and assuming no transportation of resources through dispersal, the plant then acquires 1 unit from the distance 0 cell and 1 unit from each of the distance 1 cells, totalling 9 units – a loss of 1 unit due to limitation.

As noted above, resource competition occurs when the resource capture area of plants overlaps. In the simplest case this overlap presents itself in a single site, on the extremity of the resource capture area of two neighbouring plants. The algorithm used to reflect such competition is again well expressed by example. Consider two plants A and B which have 'requested uptake' values of 16 and 10 units respectively, and have 'distance-proportioned uptakes' of [0.2, 0.3, 0.5] and [0.2, 0.8] respectively. Again the substrate is limited in the same manner, by applying the constraint that only 1 unit of resource is available at all sites. Figure 11 illustrates the spatial arrangement of the two plants and the resulting single site of competition.

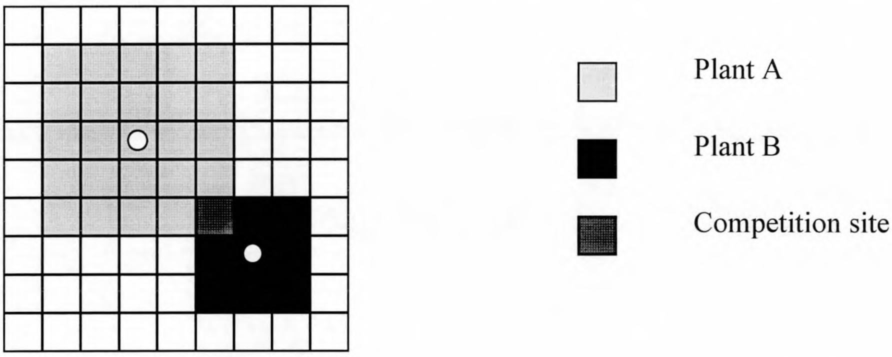


Figure 11: The spatial arrangement of two plants, A and B with a single site of competition. The white circles indicate the origins of the plants.

The amount of uptake demanded by each plant on a given resource site is defined to be the product of the 'requested uptake' value and the appropriate 'distance-proportioned uptake' vector entry, divided by the total number of sites at that distance. When considering the competition site, plant A demands (16 * 0.5 / 16 =) 0.5 unit and plant B demands (10*0.8/8=) 1 unit. Therefore the total demand on the competition site is 1.5 units of resource, which exceeds the resource available at that site (1 unit). The model assumes the resource is shared between the two plants in proportion to the demand, reflecting uptake in accordance with investment of resource capturing activity. In general, a given plant receives the product of its demand and the release rate of the site, divided by the total demand made on that site. Here, plant A receives (0.5*1/1.5=) 1/3 unit, and plant B receives (1*1/1.5=) 2/3 unit. Both demands total the 1 unit available. Clearly, this implementation of resource competition is independent of the number of plants and shared sites involved.

Figure 12 shows a schematic of the relationship between the sub-processes of the resource uptake process. This schematic outlines the main components and substrate of the algorithmic description of resource uptake. Note that elliptical entries represent traits, rectangular entries represent sub-processes and open boxes denote computational stores. Lines represent the flow of the algorithm, and heavy lines indicate computational store updates.

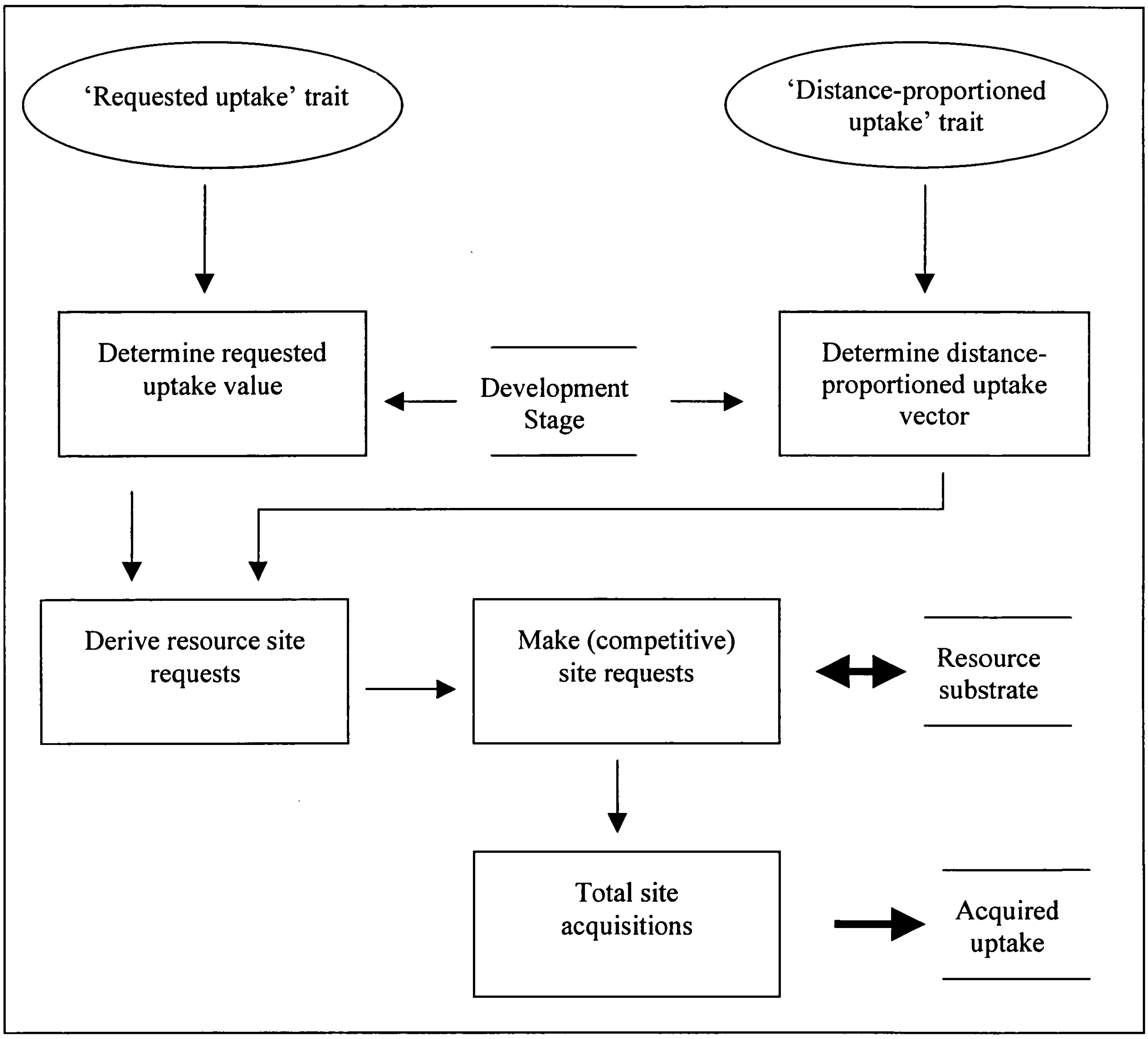


Figure 12: Schematic of the Resource Uptake Process

The schematic shown in Figure 12 is applied to every member of the community (plant) in turn. The first steps are to determine the values of the traits of 'requested uptake' and 'distance-proportioned uptake' by considering the form of the trait and the development stage currently held by the plant. Given those trait values, it is then possible to identify the requests that plant will make to its surrounding resource substrate sites. Those requests are then made on the resource substrate, and once all requests from all individuals have been evaluated, and competition and limitation effects considered, the individual site acquisitions are totalled. This total is recorded in the computation store Aquired Uptake. This store is the coupling between this and the following sub-process: resource allocation.

In the implementation of the algorithm the process of assessing site requests, competition and limitation is computed on a (resource) site by site basis. Each site assesses the surrounding individuals for potential requests. Those requests are totalled, limitation and competition effects applied, and the resulting resource acquisition passed to the individual plants as appropriate. This approach was taken for computational efficiency, and great care was taken to ensure logical equivalence with the above schematic. Within this sub-process the resource substrate is replenished and assessed for saturation as the requests on each site are processed.

3.2.4.3 Resource allocation

Plants allocate resource to build and maintain structure and to accumulate stores for later use in terms of shortfall or reproduction. In the previous section, the trait 'requested uptake' defined the maximum amount of resource units a given plant may acquire in a single cycle. A second, and associated trait, 'required uptake', defines the minimum amount of resource units a given plant may acquire in a single cycle and still develop at an optimal rate. The difference between the 'required uptake' and the 'requested uptake' represents the temporary store of surplus resource, termed surplus store. Therefore a plant that continually acquires the 'required uptake' value will develop at the same rate as a plant that continually acquires the 'requested uptake' value. However, acquiring only the 'required uptake' value will result in no surplus store.

Resource uptake equal to and below the level of the 'required uptake' is allocated to less mobile pools. This uptake is partitioned into three stores: non-reproductive, reproductive and offtake. The non-reproductive store represents the structure of the plant that is invested into resource capture which cannot be converted into reproductive vegetation. Conversely, the reproductive store represents the structure of the plant that can be converted into reproductive vegetation. The offtake store represents loss from the plant; it is termed a store since the model tracks this offtake to ensure resource is conserved.

A series of traits govern the allocation strategies. The 'offtake proportion' trait defines a proportion that is lost through environmental effects. The 'reproductive proportion' trait defines the proportion of the remaining uptake that is placed in the mobile structural store, i.e. the store that may be mobilised for reproduction. The remainder of the uptake is allocated to the – vegetative only – immobile store. Individuals having a large value for the 'reproductive proportion' trait might reflect plants with annual reproductive strategies, whilst those with a small value for this trait might reflect the perennial strategy. It is possible that a plant type is not able to re-mobilise the total resource held within the reproductive store within a single reproductive event, and this potential limitation is addressed in section 3.4.2.4 below.

If a given individual acquires the 'required uptake' amount only then it accumulates no store, although no other functions are affected. If, however, that individual acquires less than that value then the uptake may be augmented by any available surplus store. This augmentation may be subject to limitations within a single cycle, governed by a 'surplus store release rate' trait. Figure 13 shows a schematic of the relationship between the sub-processes of the resource allocation process. This schematic outlines the main components and structure of the algorithmic description of resource allocation. The notation is as in Figure 12.

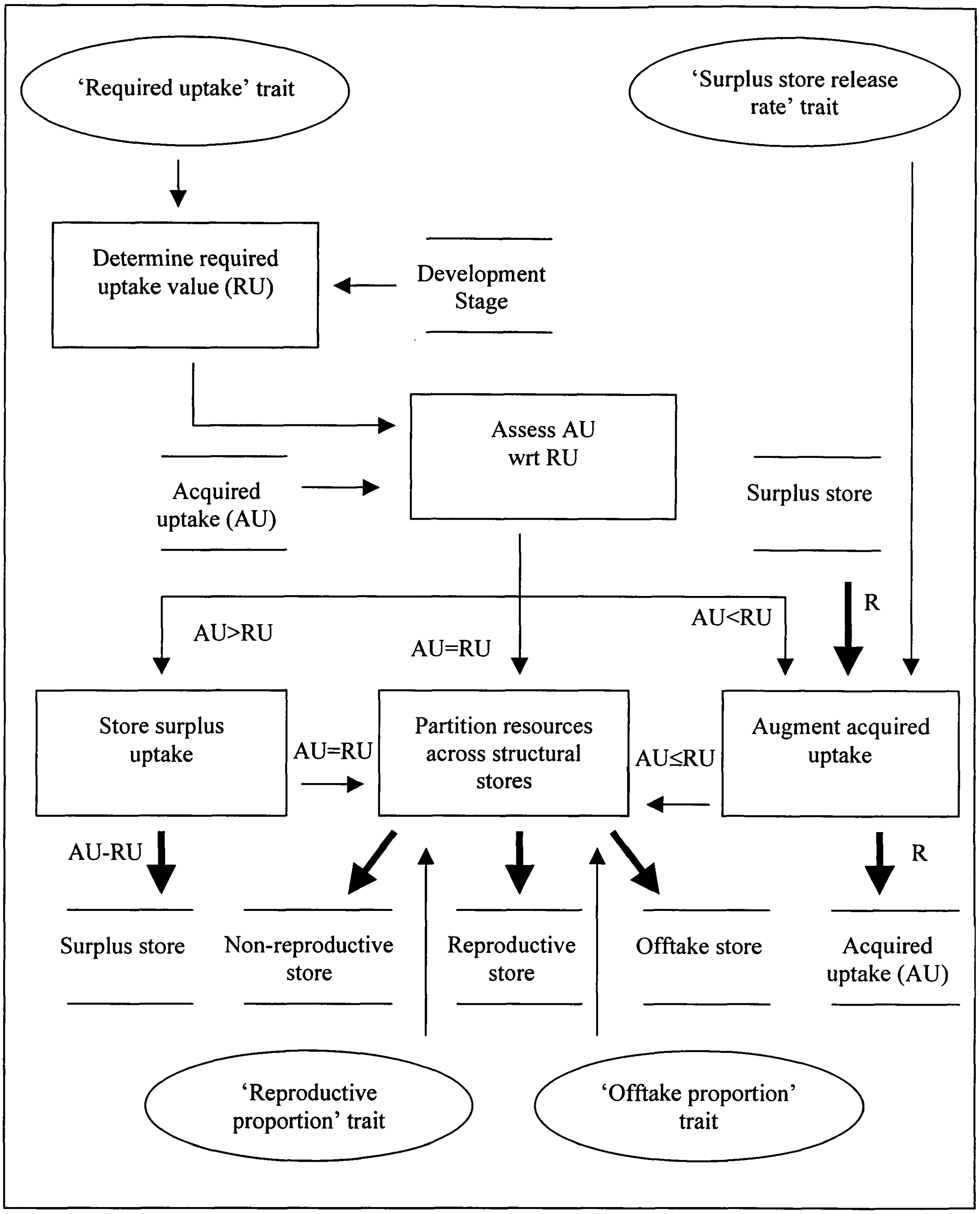


Figure 13: Schematic of the Resource Allocation Process

The first step in the above schematic is to determine the 'required uptake' value by considering both the form of the trait and the development stage currently held by the individual. This 'required uptake' value, termed RU in the schematic, is compared with the 'acquired uptake' value for that current cycle, noted as AU. A comparison between these two values must result in one of three possible outcomes, AU>RU, AU<RU and AU=RU. The case of AU>RU reflects the uptake of an excess of store, limited by the 'requested uptake' value. This excess is placed in the surplus store and the remaining acquired uptake, now equal to the 'required uptake' value (AU=RU), is partitioned across the structural stores. The case of AU<RU reflects a shortfall in uptake, and in this case the individual has the opportunity to augment the acquired uptake by drawing on the surplus store. The amount that may be mobilised from this store to top-up the shortfall is governed by the 'surplus store release rate' trait. The schematic indicates the transferral of resource from the surplus store to the acquired uptake value by the notation R. The resulting amount of acquired uptake, which may by less than or equal to the 'required uptake' value (AU≤RU), is partitioned across the stores. The traits 'reproductive proportion' and 'offtake proportion' as indicated govern this partitioning.

3.2.4.4 Reproduction

The reproductive characteristics of a given individual are expressed in terms of episodic reproduction phases, the number of offspring produced at such a phase and the dispersal pattern of the offspring produced. The reproduction phases may be regulated according to development stage, representing the need to acquire a certain level of resource before reproductive processes may be invoked, or in terms of time, representing some form of global signal. A pair of traits in the form of vectors, 'development dependent fecundity' and time dependent fecundity', are able to reflect strategies associated with each regulation form. The 'development dependent vector' comprises a list of development stages, and once the individual reaches a specific point corresponding to any of these development stages the reproduction phase is initiated. The 'temporal dependent vector' comprises a list of time steps, and once the global clock (measured in time steps) matches any of the organisms within the vector the reproduction phase is also initiated. Since the development-regulated and time-regulated strategies are expressed in separate traits it is possible to combine both strategies within a single individual.

Once the reproduction phase is initiated the individual is assessed for the available storage that may be used for reproduction. Only the reproductive and the surplus stores determine this level of storage. It is possible that a plant type is not able to re-mobilise the total resource held within the reproductive store within a single reproductive event, and this potential limitation is represented by a 'reproductive store release rate' trait. The value of this trait sets an upper limit on re-mobilisation, which may allow some or all of the reproductive store to be re-mobilised as defined. Thus, the reproductive store, subject to any release rate constraint, and the surplus store determine the storage available for reproduction.

The number of offspring produced at any reproductive phase is determined by the ratio of that assessed storage and the maximum storage capacity of the individual, and is governed by a trait termed the 'fecundity storage relation'. The maximum storage capacity is defined to be the cumulative 'requested uptake' values through all development stages, and the ratio of assessed storage and this maximum is a reflection of the long-term environment of the individual. The form of the ratio is assumed to be sigmoid, and Figure 14 illustrates two phenotypic forms of the fecundity storage relation. Each form has some threshold of the storage ratio below which a minimum number of offspring are produced, and a further threshold above which a maximum number of offspring are produced. 'Form a' shows a requirement for a high ratio to produce offspring and indicates a maximum number of offspring; 'form b' shows a requirement for a low ratio to produce offspring and indicates the same maximum number of offspring. Thus individuals with 'form b' as the 'fecundity storage relation' trait are able to reproduce under resource-poor conditions whereas individuals with 'form a' need resource-rich conditions to reproduce. Different degrees of reproduction limitation due to resource levels may be effected by altering this function in terms of its minimum and maximum values, as well as the gradient and position of the transition between those values.

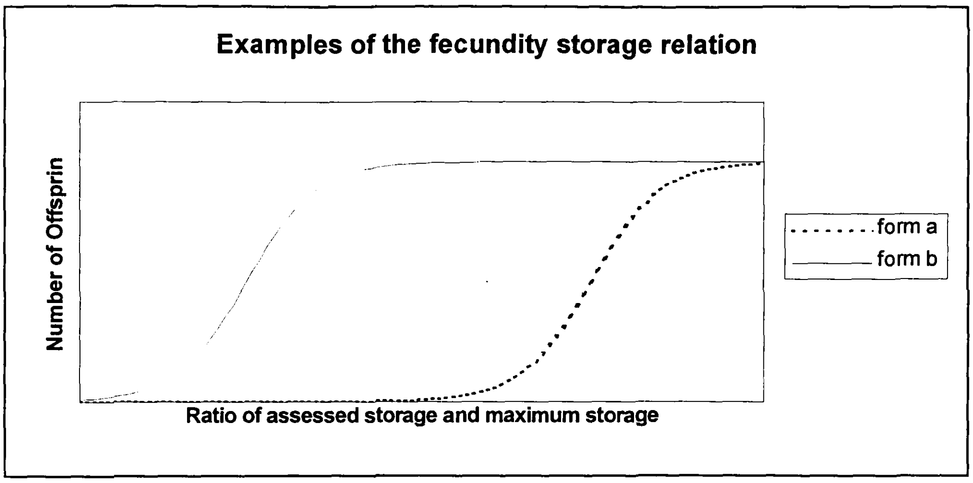


Figure 14: Two examples of the 'fecundity storage relation' trait.

A 'seed dispersal trait' defines the way in which offspring are dispersed over the resource substrate. Clearly this trait may represent complex distance dependent distribution functions, although for simplicity in this first implementation the trait determines an interval, in terms of a minimum and maximum distances (in terms of squares) from the parent plant, within which seed may fall with uniform probability.

Figure 15 shows a schematic of the relationship between the sub-processes of the reproduction process. This schematic outlines the main components and structure of the algorithmic description of reproduction. The notation is as in Figures 12 and 13.

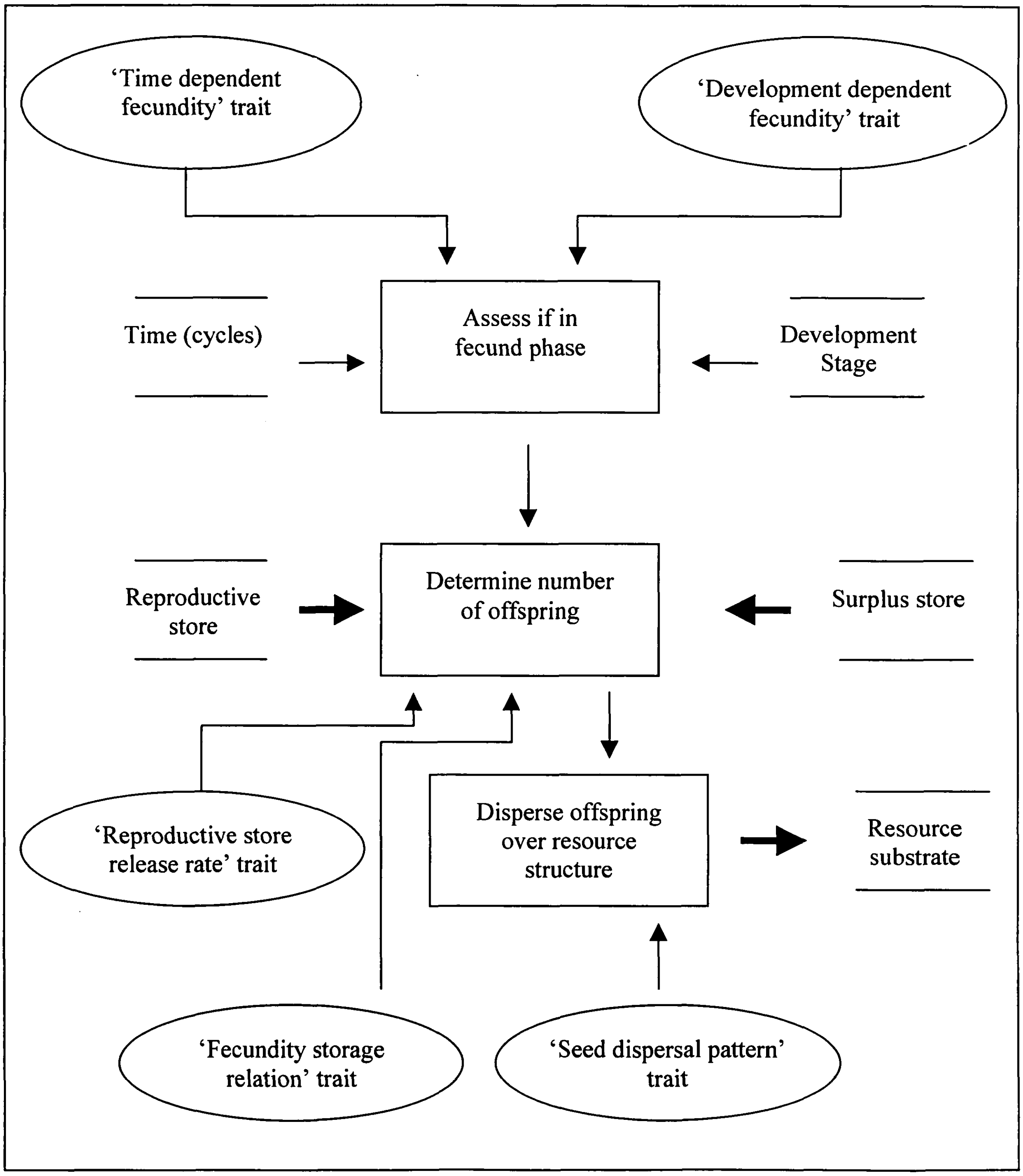


Figure 15: Schematic of the Reproduction Process

Each individual is assessed at each time step as to whether that individual is to enter a reproduction phase or not. This assessment considers the traits 'time dependent fecundity' and 'development dependent fecundity', together with the associated respective computational states time and development stage. Clearly, most assessments will result in an individual not entering a reproductive phase. However, when this phase does occur the algorithm evaluates the number of offspring produced and this number is governed by the available storage, in terms of the surplus store and the reproductive store (limited by the 'reproductive store release rate') and the 'fecundity storage relation' trait. Finally, that number of offspring are dispersed over the resource substrate in a manner determined by the 'seed dispersal pattern' trait.

3.2.4.5 Development

The progression through development stages is resource-regulated, in that certain resource level thresholds must be met across the stores described above. These thresholds are in terms of accumulated resource, based on the 'required uptake' trait. Thus, those instances where the amount of uptake falls below the required level after augmentation will result in individuals that do not develop optimally, i.e. such individuals will develop more slowly than the equivalent functional type in an optimal context.

When assessing an individual for developmental increase the total structural resource (reproductive and non-reproductive) held by the individual is compared with the cumulative uptake of development stages up to the development stage above the current stage of the individual. If the total resource held by the individual exceeds that cumulative total, the individual progresses to that next development stage and assumes the trait values associated with that new development stage.

The process of reproduction clearly results in a loss of an individual's resource, in terms of some or all of the reproductive store. When an individual reproduces is it set back in terms of developmental stage to that stage corresponding to the stored resource. Thus, individuals that invest lightly in reproduction pay little cost developmentally; individuals that invest heavily in reproduction pay greater cost for that investment. This mechanism imposes a cycle for the reproduction process in general, and for the resource regulated form in particular. An individual may reach a particular stage, reproduce and be set back a number of stages. That individual re-develops to the reproductive phase with re-acquired storage and the cycle is repeated.

In very extreme cases the individual may get such a small amount of uptake that death will result, and the traits used to express the resilience of a type to such shortfalls are addressed here. Plants are therefore characterised by the way they respond to low levels of resource, be that through environmental shortfalls or competition for available resource. This characterisation takes the form of two traits, 'shortfall survival threshold' and 'shortfall survival period'. The 'shortfall survival threshold' trait defines the resilience of the plant to sustained low levels of resource. This threshold is expressed as a proportion of the 'required uptake' trait, and so is linked to developmental sequence only indirectly. This threshold is integrally assessed over a period of time, and the associated trait of 'shortfall survival period' defines that period. This trait is not developmentally linked in any form. (Of course, there is no fundamental problem with a direct link between these traits and developmental sequence.) This pair of traits effect a representation of survival as follows. The plant must take up at least the amount of resource, including resource top-ups from the surplus store, defined by the 'shortfall survival threshold' and 'required uptake' traits over the integrated period of time (steps) defined by the 'shortfall survival period' trait. Since the period and threshold traits are separate parameters a good range of tolerances in terms of both amounts and durations may be expressed.

Failure to meet the required threshold in terms of the integrated uptake over the defined period will result in death of that individual. The algorithm associated with the death event is both simple and conservative in terms of resource. When an individual dies, the total resource held by it (excluding offtake) is distributed in a prescribed pattern over the resource substrate in a single cycle. The pattern of distribution is in proportion to the resource capture area with the reasoning that the resource held by the plant represents its physical form, and the resource capture area reflects the distribution of that form over the substrate. One consequence of this approach is that a large resource deposit, precipitated by a death event, in a resource substrate may locally exceed the limited maximum capacity and this in turn may result in a loss of resource globally to the system. Modifications are feasible by, for example, introducing a time-released measure of the resource within a dead plant representing decay, although this is not implemented at this stage.

The Figure 16 shows a schematic of the relationship between the sub-processes of the survival and development process. This schematic outlines the main components and structure of the algorithmic description of survival and development. The notation is as in Figures 12, 13 and 15.

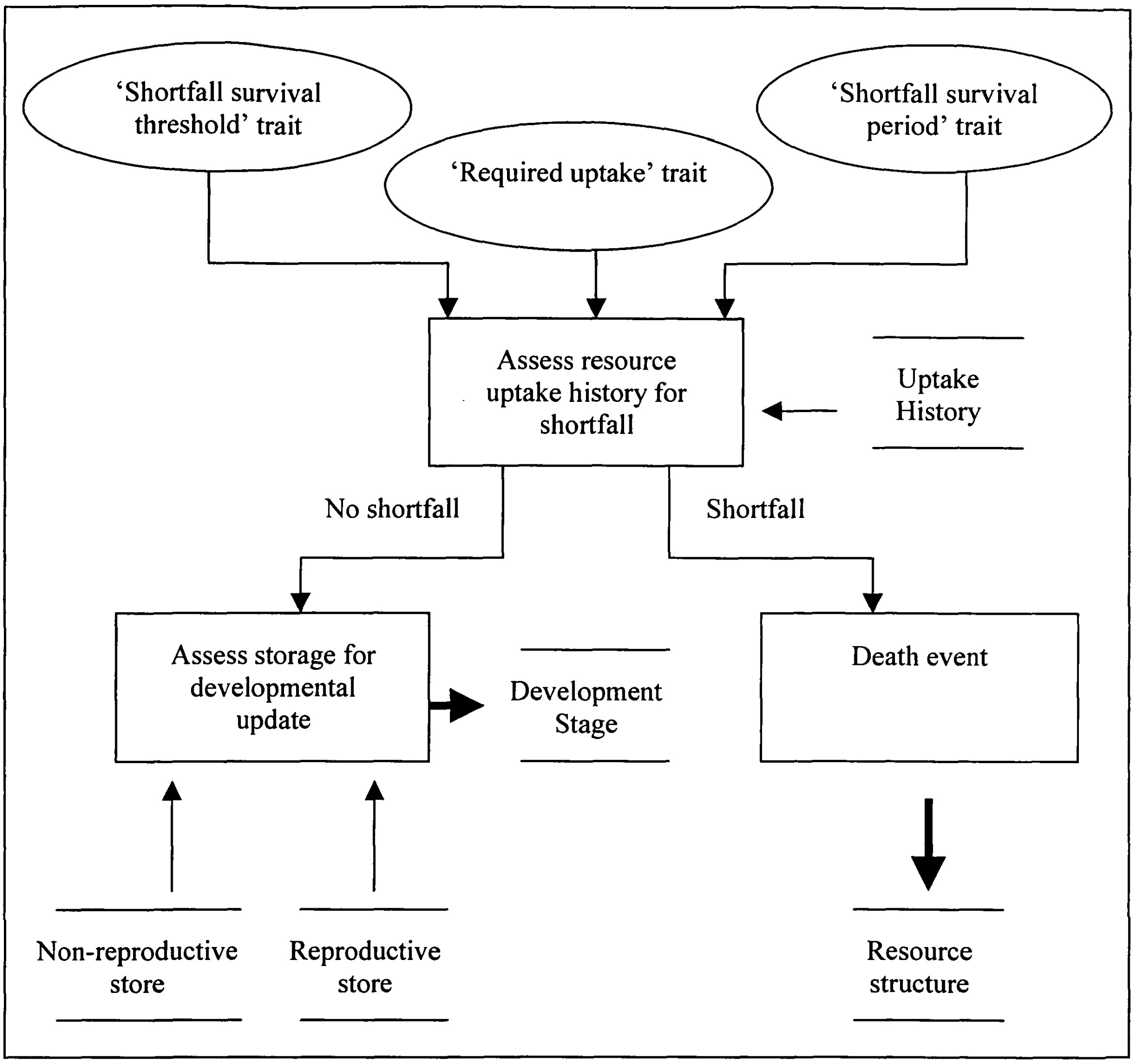


Figure 16: Schematic of the Development Process

When assessing an individual for development (and survival) the uptake of that individual is considered over a period of time. That period of time is defined by the 'shortfall survival period' trait, and the historical uptakes are recorded in the computational store 'uptake history'. The uptake is integrated over that time period and compared with the amount needed to survive, which is a function of the 'shortfall survival threshold' and 'required uptake' traits as noted earlier. This comparison results in one of two outcomes: the integrated uptake was sufficient for survival, in which case the individual is assessed for developmental update; the integrated uptake was insufficient for survival, in which case the individual dies and its structure is distributed over the resource substrate.

3.3 Demonstrative runs

3.3.1 Preliminary notes

The following demonstrative runs serve to illustrate some of the features of the described model. These runs are not present to indicate any particular property associated with the model or its components. The first sample run, 'A simple two type system', has been taken from an early prototype, and thus illustrates a simple community and associated resource substrate. This prototype served as a crucial communication and development tool during the phase of identifying, understanding and logicalising the above biological processes and subsequent algorithm and associated traits. The second and third runs are drawn from the fully developed model, hence the difference in style of output and size of lattice. A brief narrative accompanies each run to help explain the underlying concepts presented.

3.3.2 A simple two type system

This example demonstrates the impact of resource substrate patchiness on a very simple two type community. The aim of this example is to show the relationship between environmental and community composition. It considers a subset of all traits, and was used in an early model to ensure community response to environmental patterns. The resource substrate is on the whole poor, with one extremely rich patch, and is shown in Figure 17. The figure also shows heterogeneity on a site by site basis, more for an illustration of site by site parameterisation rather than for any analytical purpose.

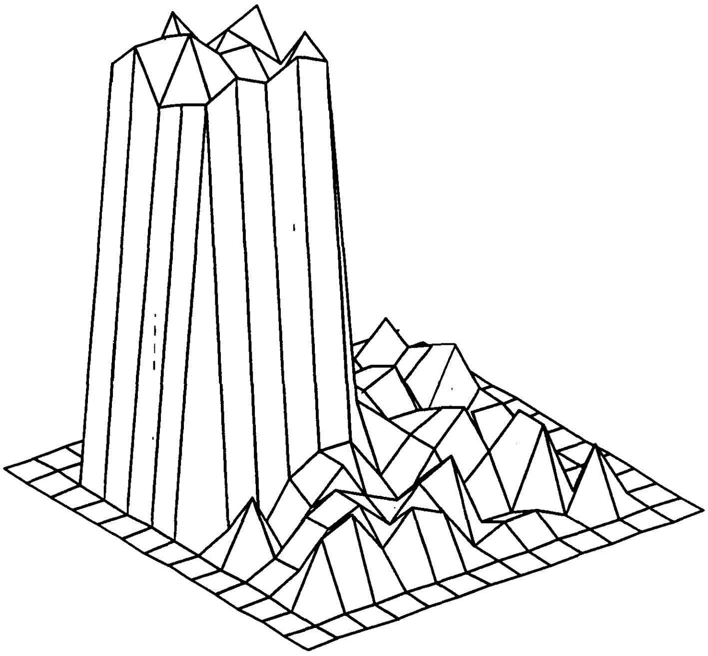


Figure 17: Resource substrate, largely poor with one very rich patch

Two (clonal) types were defined and twenty individuals of each type were distributed at random over this 100 site (10x10) substrate in initially equal proportions. The two types were identical except for the traits associated with resource uptake. Type A had an extensive resource capture area and a low required uptake relative to type B. The qualitative trait descriptions of each, categorised into Resource Capture Area and Required Uptake, are summarised in Table 5. The prototype model was run for 50 time steps, and over that period the occupancy and nature of the occupancy of each site was recorded. Figure 18 shows the length of time each site was occupied.

Type	Uptake per unit area	Reproductive capability
A	Low	Low
B	High	High

Table 5: Qualitative trait descriptions for types A and B

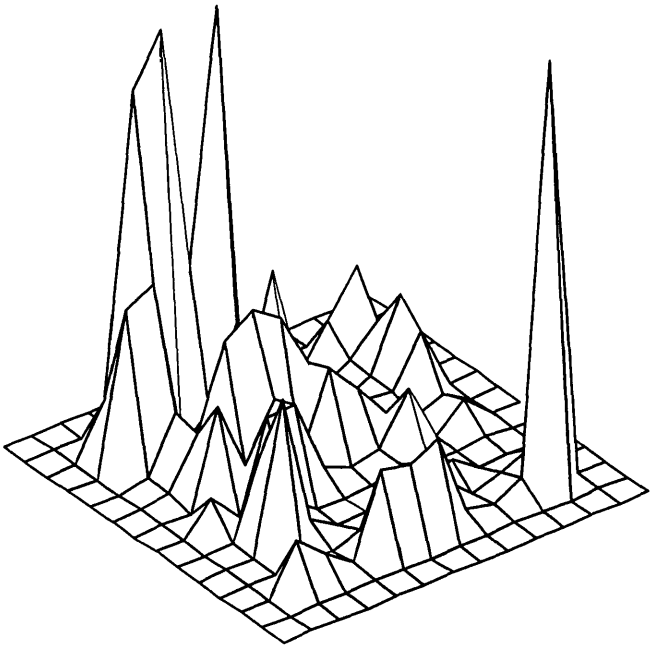


Figure 18: Length of occupation site by site

As one might expect, richer sites are occupied for a longer period of time with respect to the total number of time steps. The singular spike with high occupancy to the right of the picture cannot be explained unless the spatial patterning of each type is considered independently. Figures 19 and 20 illustrate the period of occupancy with respect to the total number of time steps for type A and B respectively.

From Figure 19 it is clear that type A is able to occupy most of the resource substrate. The singular spike is a group or series of individuals of type A. The high degree of occupancy of this region is a chance event, since type A is able to persist anywhere, independently of the distribution of resource levels in space. Of note is the limited occupancy by type A of the resource rich patch. Figure 20 shows the occupancy of sites by type B, and it is plain that this type is restricted to the rich area of the resource substrate.

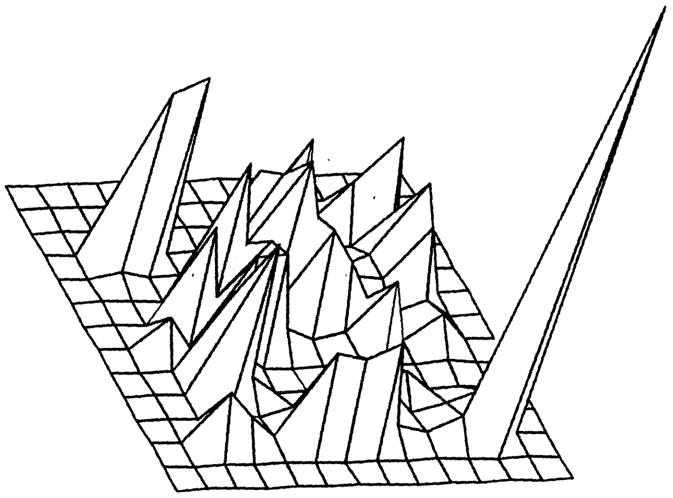


Figure 19: Spatial patterning of type A over the resource substrate

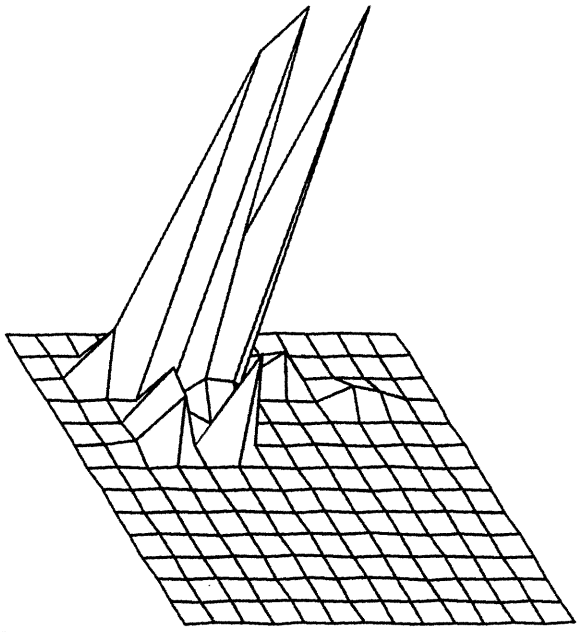


Figure 20: Spatial patterning of type B over the resource substrate

The main purpose of this demonstrative run is to indicate the impact that the underlying resource substrate has on the life cycle of the individual plants, and that this impact is dependent on the trait values associated with each individual. (All individuals share the same generic life cycle, parameterised by trait values). Type A is able to average over the heterogeneity of the resource substrate due to a low uptake per unit area. Type B is strongly dependent on the resource rich patch due to a high uptake per unit area. Of course, type A has sites in the resource rich sites, as it is not totally driven out by type B.

3.3.3 A more complex two type system

This second sample run demonstrates another pair of functional types, over a larger resource substrate. The resource substrate, comprising 50x50 cells, is on a continuous slope – it is richer towards the bottom and poorer towards the top of the picture. The types, termed Black and Grey differ in two ways. Firstly, as above one has a higher uptake requirement per unit area than the other; here type Black has a higher uptake requirement per unit area than type Grey. Secondly, type Black is more fecund, in terms of frequency of reproductive phases and number of offspring, than type Grey. Again many (200) clonal individuals of each type are distributed over the resource substrate in a randomised pattern. The model was run for 20,000 cycles (applications of the algorithm).

Figure 21 shows the spatial distribution of the types Black and Grey early on in the run (after 60 cycles). The very resource poor top quarter of the lattice is barely occupied, and occupied by type Grey exclusively. Clearly, there is not enough resource per site for type Black to survive in this region. The remaining three quarters of the lattice are occupied by a mixture of Grey and Black types, although it is clear that type Black is more prominent. This is due to its greater reproductive capability.

Figure 22 shows the spatial distribution of the types Black and Grey later in the same run (after 480 cycles). By this stage the upper half of the lattice has been almost entirely colonised by type Grey, and the lower half of the lattice has been colonised by a mixture of the types with Black being greatly predominant. In short, type Black has reached its limit with respect to survival in the poorer region of the lattice. During the course of the run, Black repeatedly dispersed offspring into the poorer region. These offspring survived whilst small but died off due to resource limitation during development. Type Grey, in contrast, takes a more passive role in the dynamics of the system. Throughout the lattice type Grey has taken residence where space permits – the regions unsuitable for Black occupancy in the upper half of the lattice and space through chance (see below) in the lower half of the lattice.

Figure 23 indicates the population levels of each type over the duration of the model run. Types Black and Grey are represented by the top and bottom lines respectively. The spikes along each type population level reflect reproduction events, and are most frequent and larger in the type Black profile. Note the very large peak near the start of the run for both types as the resource substrate had initially very high levels in the rich sites reflecting an abundance of resource; these levels rapidly decayed to more stable values as the system evolved. Thus, the peaks take on a more regular form. Note, the horizontal axis represents not cycles but sample points, where each sample point reflects the dynamics of 20 cycles.

The figure clearly shows some form of coexistence over the model run. The spatial partitioning observed at the second sample point is observed throughout the run, and fluctuations within the well mixed lower region of the upper half are common. This is due to resource levels rising during predominantly empty and type Grey occupancy, which allow colonisation of that resource substrate by type Black. The resource levels subsequently fall as a consequence of type Black occupancy, freeing space for empty and type Grey sites; thus, the cycle repeats. It is likely that pockets of low resource levels arise in the lower half of the substrate and these are poached by type Grey on some occurrences.

It is worth noting, however, that this run was hand crafted in terms of traits and resource substrate levels for such behaviour. A typical two type run does not demonstrate sustained coexistence, and occasionally results in extinction of both types. Here, a very delicate balance between competitive strategies is shown, where type Black is a superior spatial competitor and type Grey is the superior resource competitor. As will be demonstrated in Chapter 4, multiple separate runs of a given set of parameters produce the same general trends – the behaviour observed is repeatable.

Figure 21: Spatial distribution of type Grey and Black after 60 cycles. The resource gradient is applied vertically, where the lower regions are richer and the higher regions poorer.

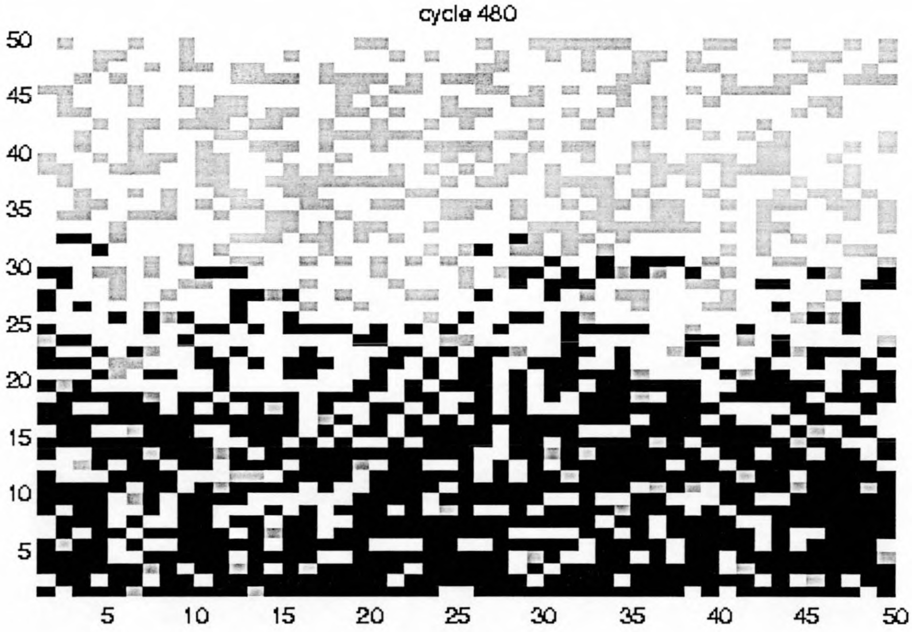


Figure 22: Spatial distribution of type Grey and Black after 480 cycles. The resource gradient is applied vertically, where the lower regions are richer and the higher regions poorer.

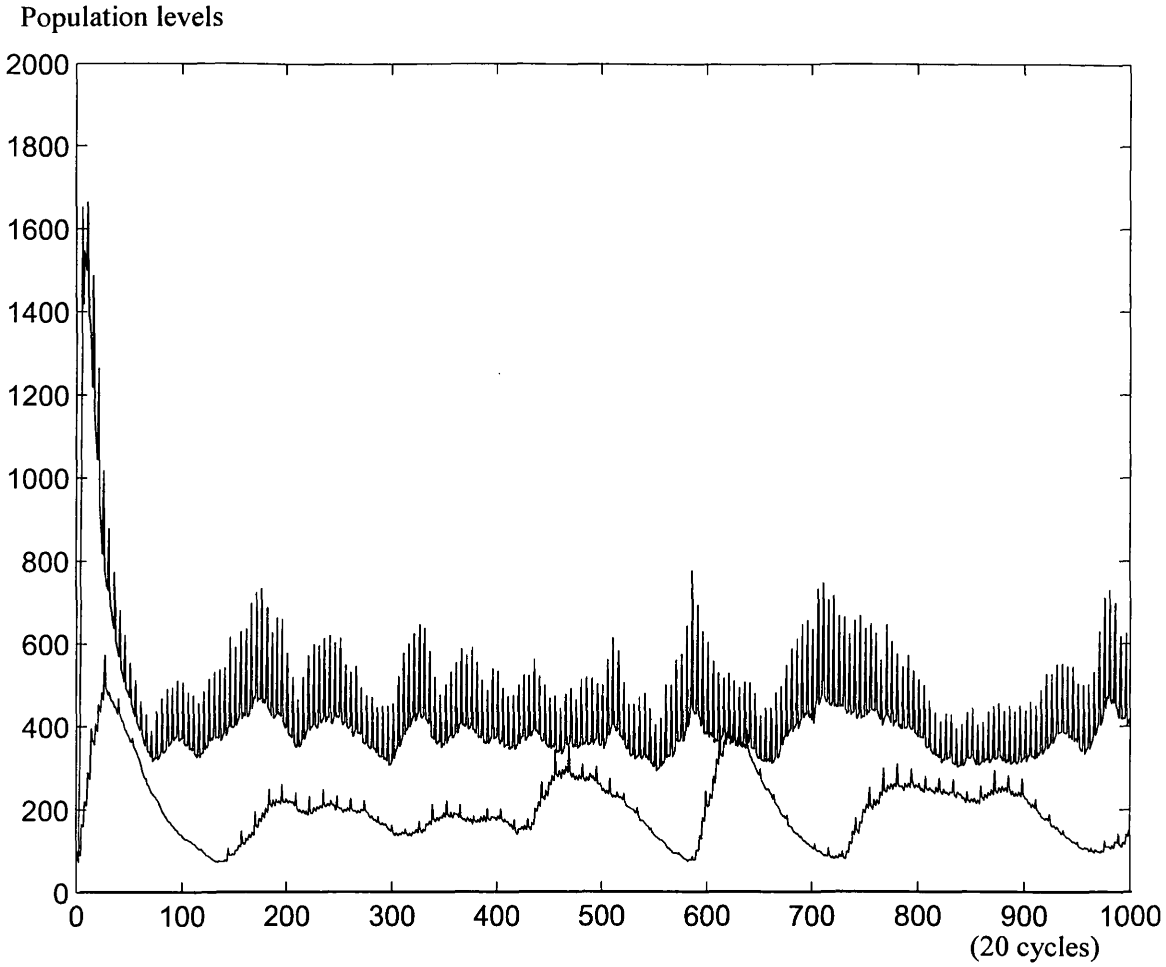


Figure 24: Population levels, indicated on the vertical axis, of types Black (top line) and Grey (bottom line) over 20000 cycles. Note the horizontal axis represents sample points equating to 20 cycles of dynamics.

3.3.4 A four type system

The final sample run presented here demonstrates a four type community interacting within a heterogeneous resource substrate of 100x100 sites. This resource substrate comprises four distinct and equally sized patches, of 25x100 cells, of varying levels of resource. Each site within a given patch has the same initial characteristics. Figure 25 qualitatively illustrates the resource levels (the specific values are not important here), and it is worth noting that this resource substrate is different in nature to that described in the previous section. This resource substrate is not a smooth slope from poor to rich as it only contains four levels of resource, rather than the fifty levels in the smoother slope above. This four patched substrate generates different dynamics in each patch as can be seen below.

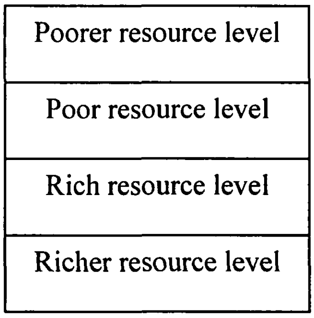


Figure 25: Qualitative illustration of patches and associated resource levels

Four types were defined, Red, Blue, Green and Yellow, and one hundred instances of each type – four hundred plants in total – were distributed over the resource substrate in six evenly spaced distribution areas. Figure 26 indicates the spatial distribution of those distribution areas with respect to the resource patches. The individuals were distributed randomly between the six distribution areas.

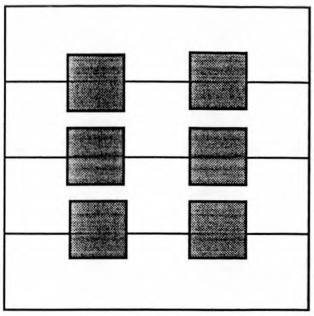


Figure 26: The six distribution areas (shaded) with respect to the four resource patches. The distribution areas were placed to straddle each interface between patches.

Types again principally differed in the traits defining uptake per unit area and reproductive capability, describing both the reproductive phase frequency and the fecundity storage relation. The qualitative trait descriptions of each, categorised into Uptake per unit area and Reproductive capability, are summarised in Table 6.

Type	Uptake per unit area	Reproductive capability
Red	Low	Low
Blue	High	High
Green	Intermediate	Intermediate
Yellow	High	Low

Table 6: Qualitative trait descriptions for types Red, Blue, Green and Yellow

The model was run for 5,000 cycles and Figures 27, 28, 29, 30, 31 and 32 show the spatial distributions of those clonal individuals at 100, 300, 700, 1500, 2500 and 4000 cycles respectively.

Figure 27 shows the spatial distribution of typed clonal individuals after 100 time steps. The immediate observation on inspection of this distribution is that the lower region of the lattice is notably more occupied than the upper region. This density difference occurs as a result of two responses by individual plants to the underlying resource levels. Firstly, those plants that have a high uptake per unit area will struggle to survive in poorer regions. Secondly, the community has had an opportunity to enter into a number of reproductive phases and, since the amount of offspring an individual reproduces is a function of its store, individuals tended to produce more offspring than individuals of the same type in the upper region. This density difference is observed in all spatial distributions, and further narration will constrain itself to the discussing the type occupation of the whole lattice and of each patch as appropriate.

As indicated in Figure 27 types Blue and Green have begun to dominate due to their higher reproductive capability. Type Yellow and type Red indicate much lower population levels. Type Yellow has not survived in the poorest region of the lattice due to a high uptake per unit area and low reproductive phase frequency. Type Red has survived throughout the lattice as little resource is required by individuals of this type.

Figure 28 shows the spatial distribution after 300 cycles. Here, it is clear that the high reproductive capability of type Blue has allowed it to dominate in all regions except the poorest regions, and this domination is most apparent in the lower regions of the lattice. Where space permits, and in particular in the richer of the two poor sites, type Green also has a strong presence. Again types Yellow and Red are low in number, and occupy similar space to the previous spatial distribution. Of note is the 'gap' present between patches. This empty space is a result of the sharp drop in the resource level from a relatively rich patch to a relatively poor patch. The richer patch supports a density of individuals that the poorer patch could not support. The uptake area of this denser patch of individuals encroaches the poorer patch, making the immediate area between the two patches (on the poorer patches side) extremely poor indeed.

Figure 29 shows the spatial distribution after 700 cycles. In the previous distribution type Blue had most space, whereas here type Green has rapidly increased in number. Type Blue still dominates the richest patch. The system has gone through the process of succession, driven by resource substrate depletion. The resource has been consumed by the community and is held within the individual organisms. All patches, excluding the richest, have suffered a drop in resource levels due to dense occupation by type Blue. The successor, type Green, is the type best suited to occupying the lower resource areas. Again types Yellow and Red are low in number, and occupy similar space to the previous spatial distribution.

Figure 30 shows the spatial distribution of types after 1500 cycles. Here, the process of succession driven by resource depletion continues. Type Green dominates in the lower half of the lattice. Of interest is the lower (richer) patch of the upper (poorer) region of the lattice. Here, type Green has collapsed the substrate further, the density of this type has dropped and the successor is type Red – the most suited to occupying areas with very low levels of resource.

Figures 31and 32 show a continuation of this trend, with Green replacing Blue followed by Red replacing Green, at 2500 and 4000 cycles respectively. Clearly this process is a property of both the trait values and the resource substrate. If, say, the resource substrate were modified so that the replenishment rate exceeded the release rate of each site then resource levels would never deplete and different dynamics would occur.

Figure 33 indicates the population levels of each type over the duration of the model run. The spikes along each type population level reflect reproduction events, and are most frequent in type Blue and larger in the type Green profiles, indicative of the higher reproductive capabilities of these types, albeit through different strategies. The population levels demonstrate the succession process, and if left long enough the lowest resource user would dominate (given a set of traits that do not lead to early extinction). This is not in conflict with existing theoretical models (Tilman, 1994a), where the lowest resource user is predicted to displace other competitors in a resource limited system. Note, the horizontal axis of this figure represents not cycles but sample points, where each sample point reflects the dynamics of 20 cycles.

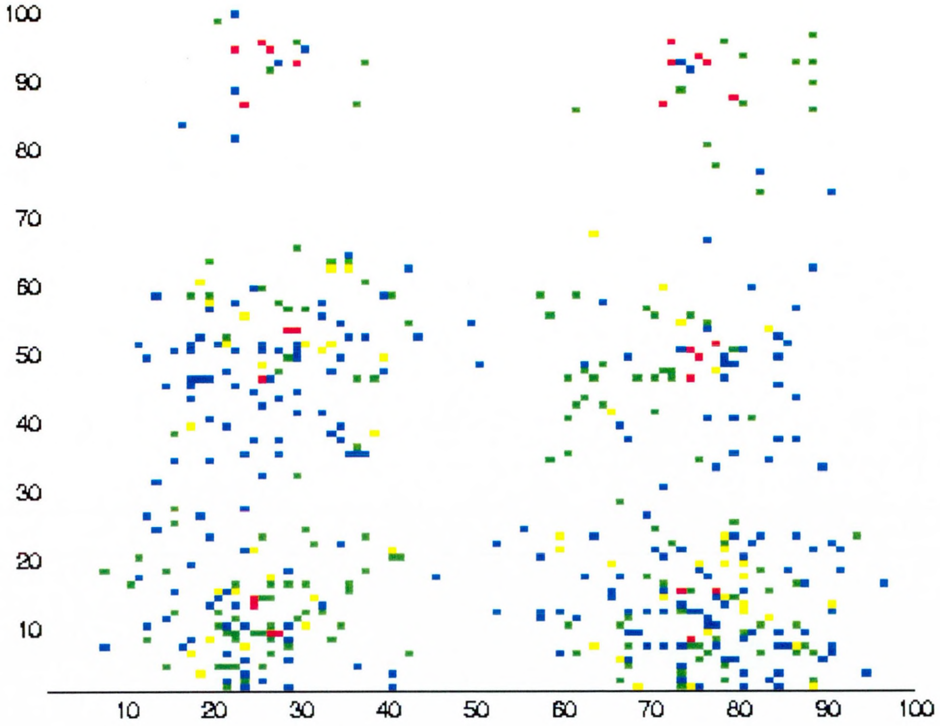


Figure 27: Spatial distribution of individuals after 100 cycles

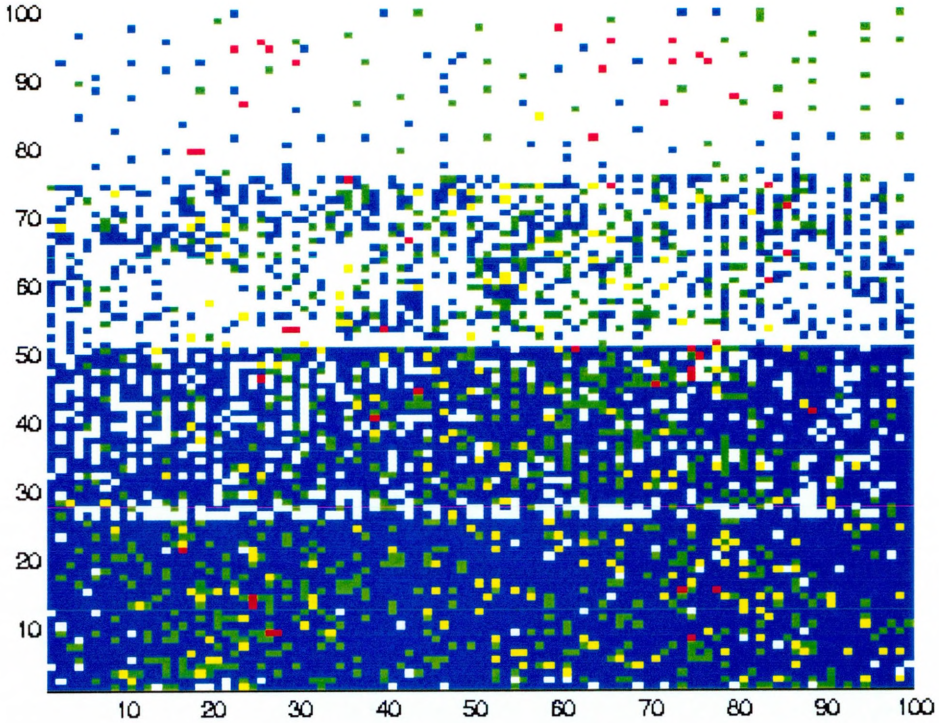


Figure 28: Spatial distribution of individuals after 300 cycles

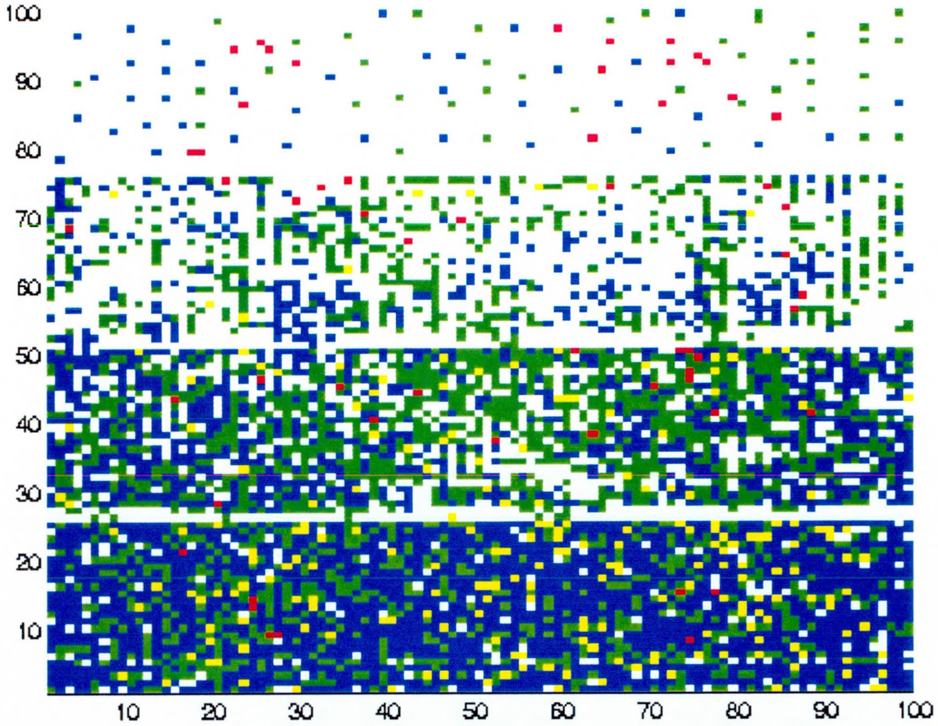


Figure 29: Spatial distribution of individuals after 700 cycles

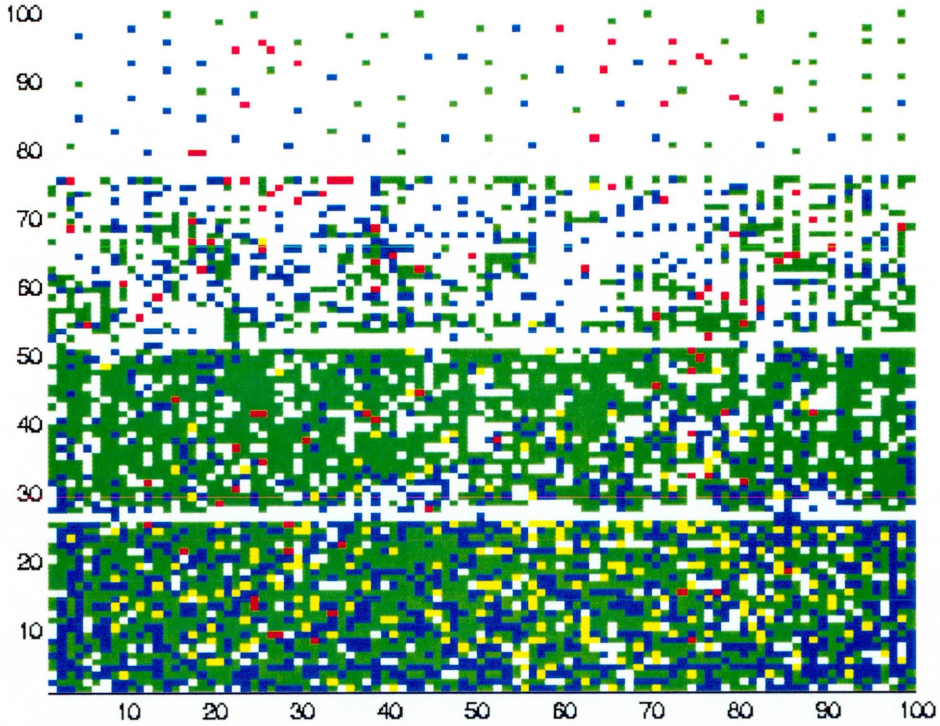


Figure 30: Spatial distribution of individuals after 1500 cycles

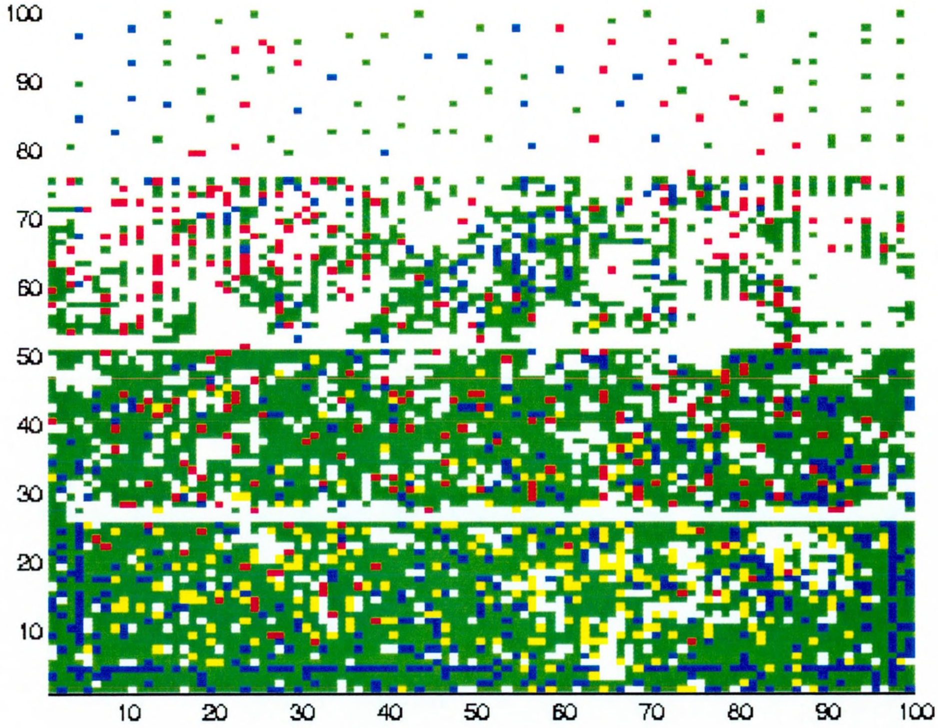


Figure 31: Spatial distribution of individuals after 2500 cycles

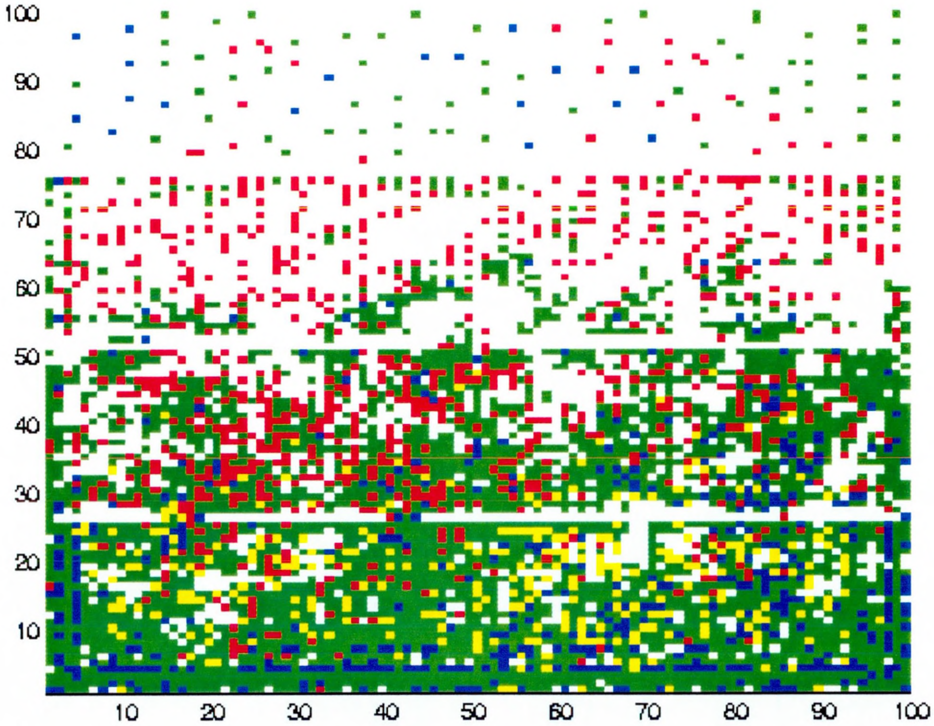


Figure 32: Spatial distribution of individuals after 4000 cycles

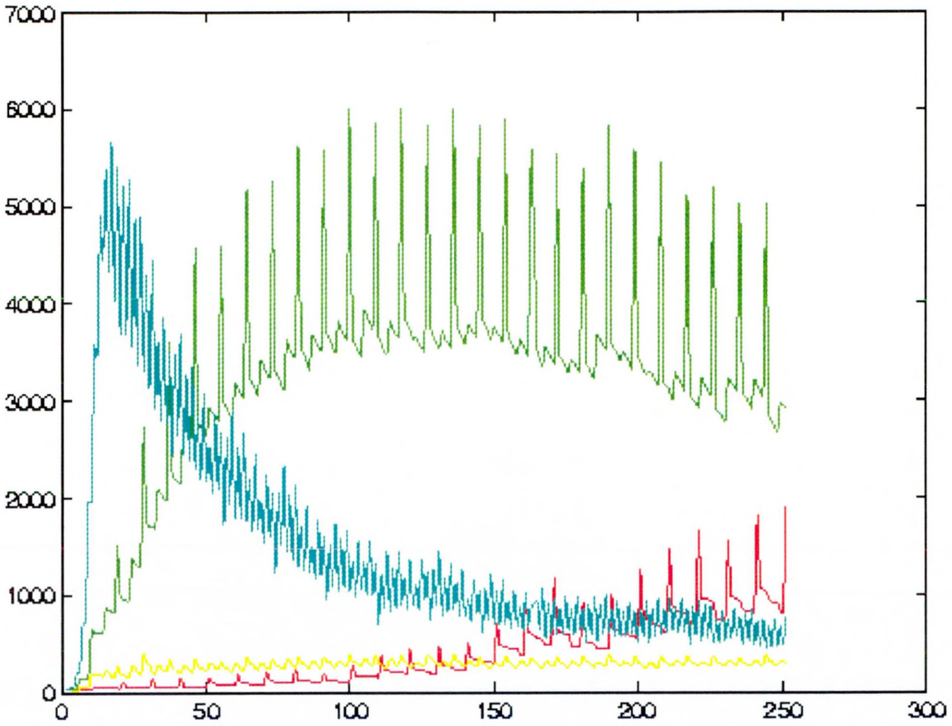


Figure 33: Population levels, indicated on the vertical axis, of types Red, Blue, Green and Yellow over 5000 cycles. Note the horizontal axis represents sample points equating to 20 cycles of dynamics.

3.4 Discussion

3.4.1 Summary

The model described assumes a 'top-down' approach, and in this approach the behaviour of individual plants is not fixed. The behaviour of a given plant is explicitly described, through functional trait values, assuming that plant experiences optimal environmental conditions. This behaviour is then modified by contextual information. Figure 27 clearly illustrates this feature: the number of offspring produced by a plant towards the top of the lattice is reduced from an optimal amount due to resource limitations; reproduction at, or approaching, an optimal level may be seen towards the bottom of this lattice, where little resource limitation occurs.

Whilst a suite of functional traits describes all plants, different plant forms, or types, may be characterised by attributing different values to those traits. Combinations of traits with particular values may be used to represent a wide range of strategies. The flexibility of such combinations is illustrated in Figure 6 above, where the traits 'requested uptake' and 'distance-proportioned uptake' are shown to represent three dimensional structures. Further, this trait-based approach may be used to characterise individual plants uniquely, i.e. each plant may have its own trait values. The model is, therefore, genuinely individual-based. Here, clonal 'type' specification and reproduction is imposed for simplicity.

The importance of considering genetic coupling between plants is acknowledged, as is the impact of influx of (new) genetic material. However, this is the first stage in a long-term research strategy. This long-term strategy will ultimately result in a plant community dynamics model capable of admitting quantitative parameterisation derived from individual plants in natural contexts. These experimental data will be used to construct species distributions of trait values. The developed model is to include genetic influx, realistic breeding and an improved representation of seeding strategies all derived from experimental systems. Chapter 5 acknowledges development work undertaken to incorporate distributions of trait values attributed to particular species. Thus, the relationship between type, or functional role, and species, or taxonomic classification, is addressed in this work. The representation of seeding strategies is also detailed in Chapter 5. The work presented here represents the first stage in this development. The main achievement is the implementation of the process-based algorithm, developed in conjunction with biologists.

This process-based algorithm relates the community of individuals and the underlying resource substrate. Whilst this algorithm is simple and generic in nature, it is shown to generate patterns in community structure with complex spatio-temporal dynamics. Work by a colleague, Elizaveta Pachepsky, at the Scottish Crop Research Institute has demonstrated that this model produces results that, when analysed and summarised, conform to the accepted species-area relations noted in Chapter 1. Further work to facilitate more rigorous testing is also detailed in Chapter 5.

3.4.2 Succession, biodiversity and coexistence

The demonstrative runs shown in sections 3.3.3 and 3.3.4 provide examples of the ecological pattern termed succession. The two type system shown in section 3.3.3 demonstrates a form of coexistence, in that both functional types persist for the duration of the model run. The nature of that coexistence is not static – the central region of the resource substrate is variable in occupancy. Indeed, the type occupancy of this region may be seen as cyclic, as described above. The cyclic pattern is driven by levels in the underlying resource substrate: when resource levels are high, type Black is seen to dominate the region; when resource levels are low, type Grey is seen to dominate the region. The transition from resource rich to resource poor levels is a consequence of high occupancy of type Black; the transition from resource poor to resource rich levels is a consequence of high occupancy of type Grey.

This suggests that some balance between the competitive abilities, in terms of resource and space, for this pair of functional types gives rise to persistence of both forms, i.e. a maintenance of biodiversity. The more complex four type system shows another example of succession. If the population levels of each type shown in Figure 33 were extrapolated, as might be tempting, it would be reasonable to expect dominance of type Red over all other types. In fact types Yellow, Blue and (eventually) Green would be expected to become extinct. However, such extrapolation is based on the assumption that the property of the system driving its current behaviour, i.e. resource levels, remains constant. Given type Red has an extremely low uptake per unit area, resource levels may be seen to rise as a result of increased Red occupancy. Here, the replenishment rate of an occupied site may be higher than the demands on that site. This may make the resource substrate more amenable to types Blue and Green in time, resulting in an increased occupancy of these two types ... until the resource substrate level begins to again deteriorate. Of course, given the handcrafted parameters of this run this may or may not happen. The important issue is that it may happen – the succession observed in this run, and to a lesser extent in the two type system of Section 3.3.3, may give rise to sustained biodiversity.

Chapter 4 considers the ecological patterns of succession and maintained biodiversity, the link between them, and how they may be a consequence of particular combinations of functional forms and spatial structures. The conceptual framework presented here is extended to allow the investigation into the relationship between functional forms that demonstrate coexistence in spatially structured ecosystems. This investigation takes the form of a search for combinations of functional forms that give rise to coexistence in particular resource substrates.

Chapter 4 Searching for coexistence

4.1 Coexistence in ecological systems

4.1.1 Succession and biodiversity

Ecological succession may be considered as a directed change in the composition of a community. This directed change is driven by a large number of small changes in composition over a period of time so that the "community develops a new emphasis" (Putman, 1994). As described in Chapter 3, the development of organisms, here plants, is governed by the environmental conditions experienced by those organisms. A change in those environmental conditions, for whatever reason, may result in a change in the development of those organisms experiencing the change. This change in development may be beneficial or costly to any given organism as a given set of environmental conditions will favour some functional types over others, in that some types will be well adapted to that set of conditions in terms of their function. Changes to that set of environmental conditions may lead to a corresponding change in favoured functional types. This change of favour may lead to an increase in the newly favoured types over the formerly favoured, i.e. a change of emphasis. Thus, succession comes about through changes in the environmental conditions.

The dynamics associated with the set of environmental conditions may be driven by external events, such as annual variation and by community composition. The presence of a community in an environment modifies that environment and so a continual adaptation between community composition and environmental conditions emerges. More fully, the individuals within a community impacts upon the development of the environment; the environment impacts upon the development of the community composition (Tilman, 1990). This is a coupling between the scales; a link between process and pattern (Wu and Levin, 1994).

In any static environment the favoured functional types will become greatly amplified, possibly resulting in a loss of biodiversity. Indeed, this is observed in arable systems where a regime of herbicide treatments is repeatedly applied to the weed population. This regime has the effect of dampening change in the environment since it dampens change in the community resulting in an overall depletion and loss of biodiversity in the weed community. Those weed types best adapted to the (now nearly static) environment out-compete all other weed types (Squire *et al.*, 1999).

By allowing the environment and community to adapt dynamically in tandem some measure of biodiversity, in the form of coexisting types, may arise. In situations of coexistence no functional types should dominate for a period of time long enough to exclude other types. The domination of particular types will modify the environment, which may in turn reduce the dominating effect of those types, allowing other types to become dominant – for a period of time, until the environment gradually imposes a new set of constraints. In other words, the dominance of any one type, or group of similar types, may fluctuate in line with environmental fluctuations caused by that very domination. To make progress in understanding the property of coexistence, both the environment and the community must be considered simultaneously. Central to the consideration of the relationship between environment and community are the balance of function within a community and the manner in which that community is distributed in space over the environment.

4.1.2 Functional trade-offs

A number of empirical studies have identified some co-variation in traits. For example, in studies of plant resource allocation patterns, Tilman and Wedin (1991) and Gleeson and Tilman (1994) observe a clear co-variation in root and seed allocation patterns. These studies demonstrate that those plants that allocate much resource to root structure necessarily have to allocate little resource to seed structure. Thus, those plants that are superior competitors in resource acquisition are inferior competitors in seed production and dispersal. Likewise, those plants that invest more in seed production tend to invest less in root production. Wardle *et al.* (1998) note that plants observed to grow slowly were also observed to grow less and flower earlier than fast growing plants, which were observed to grow quickly and flower late.

This co-variation in traits demonstrates that for a fixed resource level an increased allocation in one trait results in a decreased allocation in another trait. Thus, a given plant faces necessary trade-offs in function due to an internal resource limit. Any plant, therefore, has a trait trade-off strategy suited to a (small) range of the possible environmental conditions. Such a plant, and those of similar form, will thrive in that environment. In other environments, that same plant may not be so competitive.

The trade-offs between traits imply that the success of a plant type is coupled with its experienced environmental conditions. In the continued adaptation of community and environment described above it is therefore possible to have a range of types coexisting, given an appropriate dynamic, balance across the community in those traits. Coexistence may occur within an environment that is both homogeneous in resource and is well mixed in terms of type occupancy. In this case, the coupling between community and environment is homogeneous in space. When such a homogeneous coupling occurs, coexistence of a number of types is possible within the limits set by that environment. However, when the environment is spatially structured, or partitioned, in some way the limits of coexistence may be relaxed, leading to an increase in potential biodiversity, since different environmental conditions may be experienced in different spatial locations (Tilman, 1994a).

4.1.3 Space and spatially structured resource

Plant competition for resource takes place within localised neighbourhoods. Within a local neighbourhood dominance will occur, and change, as described above. In a spatially homogeneous community, i.e. one that is well mixed in terms of type occupancy in space, a single type, or group of types, will dominate throughout the environment – those types best suited to that particular environment. However, when considering a spatially heterogeneous community, i.e. one that is not well mixed in terms of type occupancy in space, it is not necessarily the case that a single type, or group of types, will dominate (Tilman, 1994b).

Tilman (1994a) illustrates this idea with an example. If a trade-off exists between the ability of a plant to compete in a local neighbourhood and its ability to disperse seed, under a given set of conditions, then many types may be absent from local neighbourhoods even though they may be potentially superior competitors because they are limited by dispersal. It then follows that less superior competitors dominate in the absence of more adapted competitors. Thus, biodiversity is increased as a consequence of space and/ or habitat diversity.

Given biodiversity is increased as a result of spatial heterogeneity in the community itself, it follows that spatial heterogeneity in the underlying resource substrate will also increase biodiversity (Wilson and Chakraborty, 1998). Plants in different areas of the system will experience different resource availability, and this will result in different forms of community at those different areas. For example, an area rich in some resource will attract the best competitors for that resource; the community will be dominated by the type(s) best adapted to that (high) level of resource. An area poor in that resource will attract a different strategist – one with a low uptake per unit area perhaps; that community will be dominated by the type(s) best adapted to that (low) level of resource. Tilman (1994b) argues that if a habitat (here resource substrate) were spatially heterogeneous then this heterogeneity could allow a large number of species to coexist. Tilman further notes that the number of species coexisting in a given environment should be a function of the spatial heterogeneity of that environment, i.e. a highly heterogeneous resource substrate should support high biodiversity.

Indeed, heterogeneity in a spatially structured resource will arise as a consequence of the space itself. As noted above, spatial heterogeneity in the community will arise from trade-offs between resource competition and dispersal. That community will therefore make different demands on the underlying resource substrate, which must lead to spatial heterogeneity in the resource. Likewise, that modified resource substrate will impose spatially heterogeneous constraints on the community, which must lead to further spatial heterogeneity in the community. Thus, the coupled continual adaptation of community composition and resource substrate is adaptive in both time and space.

The second demonstrative run in Chapter 3 provides a simple example of the notion of functional trade-offs in a (special case of a) spatially heterogeneous resource base – a gradient of resource. One type, Black, trades off high reproductive capability against a high resource uptake requirement. The other type, Grey, operates the opposite strategy: a low reproductive capability is traded off against a low uptake requirement. Clearly, in resource rich environments type Black will out-compete type Grey. In resource poor environments type Grey will out-compete type black. As the community and environment continually adapt through time and space an oscillation in community composition is apparent in Figure 24. When type Black increases in number, type Grey decreases. This dynamic is followed by a decrease in type Black, due to environmental change, and in increase in type Grey follows as a consequence of that change. This oscillation is most pronounced in the region of intermediate resource, the level of which is largely regulated by type occupancy rather than resource substrate properties.

4.1.4 Coexisting communities

Under a given set of initial environmental conditions some communities will persist and some will not; some communities will retain diversity and some will reduce to one type, or a group of similar types. Those communities that persist in a given environment must have some particular attributes associated with their composite individual members. It follows from the above discussion that a persistent community must have a range of values in each trait suited to the fluctuations arising in environmental conditions. Whilst the frequency of each value may alter in accordance with changes in the environment, a particular trait value will be optimal in an environment until that environment changes. Subsequent to this change another value will succeed as optimal in response to that change. Hence, the robustness of the community to persist through change is a property of the breadth of trait values present.

Tilman and Downing (1994) demonstrate this property in an eleven-year study of grassland dynamics. In this study, they imposed different environmental conditions on grassland communities varying in (species) composition, and noted that compositions high in biodiversity were more resilient to fluctuations in environmental conditions than those low in biodiversity. Vitousek and Hooper (1994) assert that there exists a relation between diversity and stability (persistence), i.e. coexisting systems have a high degree of diversity in terms of ecophysiological function.

The remainder of this chapter describes a (brief) investigation into coexisting communities (the definition of coexistence used here is addressed below). This investigation takes the form of a search through the state space of all possible (represented) trait values, in an attempt to identify particular combinations of traits – shapes of trait spaces – that give rise to coexistence. The following section addresses some more general issues relating to the representation and searching of this space of trait values. A first investigation into the coexistence of functional forms is then presented.

4.2 Framing the search

4.2.1 Trait space

The model described in Chapter 3 represents the characteristics of an individual plant in terms of a set of functional traits. Each individual in the community has identical traits, and differences among individuals are expressed through values attributed to those traits. Individuals with similar trait values may be thought of as closer in their behaviour, or strategy, than individuals with very different trait values. The magnitude of difference between individuals may be considered in terms of distance in a trait space. This trait space is an n-dimensional state space, where n is the number of traits. Each dimension in that space represents a trait, and the axis associated with that dimension has all possible (considered) values of that trait. An individual occupies a single point in that trait space, and individuals with similar trait values, or strategies, will be close in this trait space; individuals with dissimilar trait values will be distant in that same trait space.

A community of individuals may be considered as a cloud, or clouds, in trait space. The functional properties of that community may then be considered in terms of the position, size and shape of that cloud(s). As an illustrative example consider a two dimensional trait space – such spaces are easier to visualise than the more general n-dimensional spaces. Consider the traits ‘uptake per unit area’ and ‘reproduction capability’, as introduced in section 3.3.4. These are, of course, composites of the traits used in the model of Chapter 3. This trait space is illustrated in Figure 34.

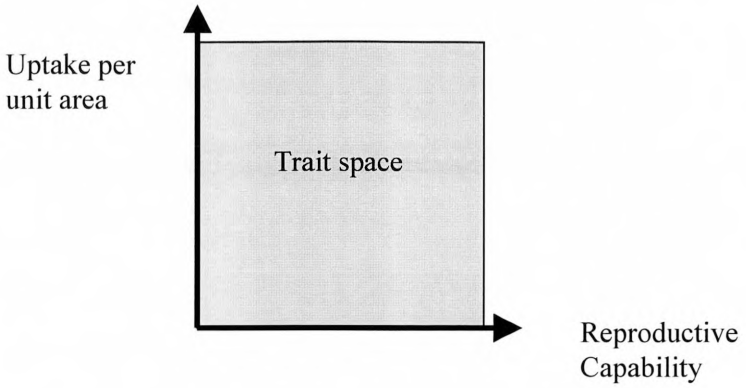


Figure 34: An illustration of two dimensional trait space

Clearly, all possible combinations of these trait values are encompassed in this trait space. Different communities will occupy different portions of that trait space, and the extent and position of the particular portion occupied confers properties relating to that community. For example, Figures 35 and 36 illustrate two communities that differ in trait space, in terms of extent and position. Figure 35 shows a community occupying small proportion of the total trait space. Individuals within this community are all similar, at least in the traits considered here. Conversely, Figure 36 shows a community occupying a large proportion of the total trait space. Individuals within this community may be very diverse.

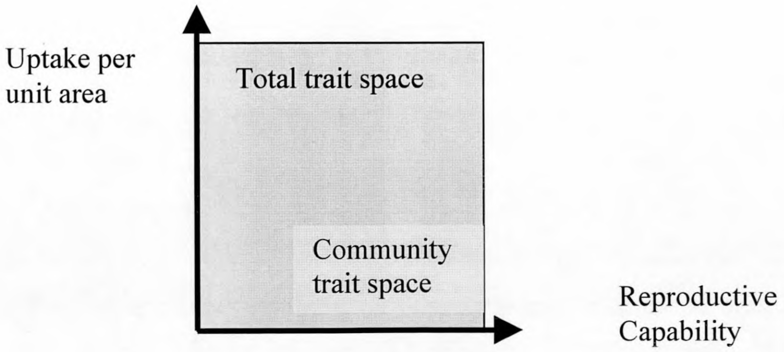


Figure 35: A community occupying a small portion of two dimensional trait space

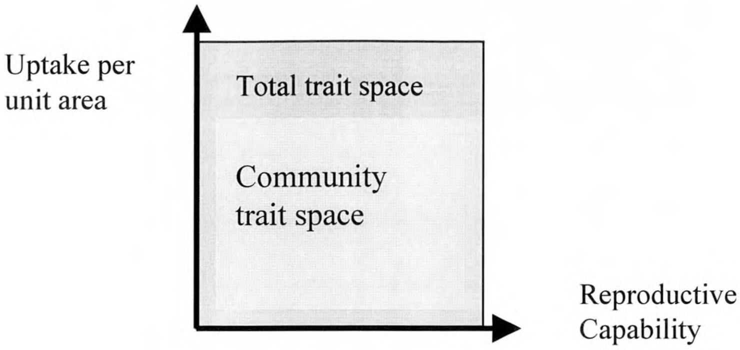


Figure 36: A community occupying a large portion of two dimensional trait space

The occupied trait spaces of each community allow certain properties associated with the coupling between the environment and the community composition to be identified. For example, consider two communities C1 and C2 that have initially identical trait spaces and two dissimilar environments E1 and E2. Community C1 is placed within the environment E1; community C2 is placed within the environment E2. Assume that the communities C1 and C2 are distributed identically over the environments E1 and E2 respectively. Over time, the trait space of C1 evolves to that shown in Figure 35; the trait space of C2 evolves to that shown in Figure 36. Clearly, the combination of C1 and E1 supports a much less diverse community, in terms of the range of trait values present, than the combination of C2 and E2.

Given C1 and C2 were initially identical in trait space and spatial distribution, the reason for this difference may lie in the characteristics of the environments E1 and E2. A suggested reason for E1 supporting a less diverse range of trait values than E2 may be that E1 was more homogeneous than E2. This suggestion could, of course, be investigated by analysing the spatial pattern of resources. Equally, in other circumstances, the higher levels of resulting diversity in trait values attributed to the C2 E2 combination may be a consequence of a difference in initial trait spaces between C1 and C2 in identical environments E1 and E2.

In the more general case C1, C2, E1 and E2 are likely to differ, and a particular trait space reflects a particular coupling between the community composition and environment. The extent of the trait space occupied reflects the degree of coupling; the position reflects the nature of that coupling. Small trait spaces indicate a tight coupling between community and environment; i.e. to survive in a given environment, individuals must be of a particular optimal functional form, or forms similar to that optimum. Large trait spaces indicate a loose coupling; i.e. to survive in a given environment, individuals may adopt a wide variety of strategies, although clearly some strategies may be better than others. The position of that trait space indicates the nature of the functional forms that exist within the community. Here, Figure 35 shows only those forms that have a low uptake per unit area and a high reproductive capability exist, suggestive of a harsh environment.

The concept of trait space may also serve to illustrate trait trade-offs. As noted, Tilman (1990) and Wardle *et al.* (1998) suggest, trade-offs among traits are the necessary result of organisms having limited internal resource. These trade-offs will restrict the available trait space as indicated in Figure 37. Here, those individuals that invest in reproductive capability do so at a cost to uptake per unit area (where low values represent a large investment in resource capture area).

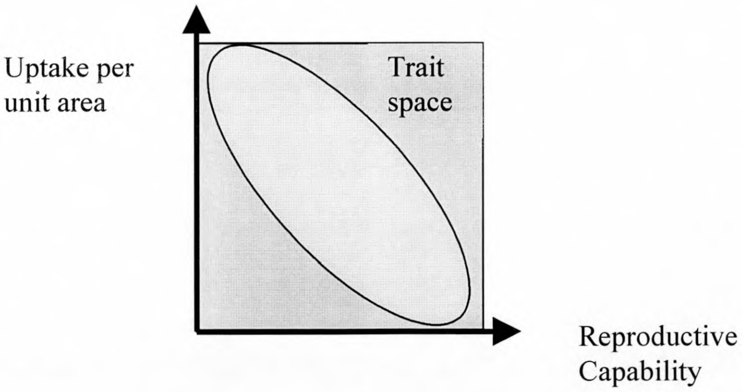


Figure 37: The two dimensional trait space is restricted by inherent trade-offs, as shown by the lightly shaded area which represents the space that individual plants may occupy.

In the model described in Chapter 3, the community comprises a few functional types, where individual plants are clones of one of those types. This approach was taken as a necessary simplification, with ramifications on the nature of the trait space occupied by a community. This simplified model occupies a number of points in space – the number of points being the number of types represented. The number of types defines the density of the cloud of states in trait space. When the number of types (points in space) is large the community is a dense cloud(s) of trait space; when the number of types is small the community is a very sparse cloud indeed.

4.2.2 Searching trait space

The hypothesis addressed here is that the community scale property of coexistence in a given environment arises as a consequence of the functional traits comprising that community. The trait space described above may be searched to identify combinations of trait values that give rise to coexistence. This search takes the approach of identifying a possible combination of types, thought of as points in trait space, in some initial state, and observing properties of the resulting community composition as the system dynamics progress. The suitability of each combination of points in trait space must be assessed in terms of meeting the search target, i.e. demonstrating coexistence. This search must take place in an n-dimensional space, where n is the number of traits.

Searching large state spaces poses conceptual and computational problems. A state space of one, two or three dimensions is relatively easy to visualise, in terms of lines (along the plane of that line), areas and volumes respectively. A fourth dimension may be seen as an intensity associated with each point in a three dimensional trait space. State spaces of more than four dimensions are impossible to visualise in their full dimensionality, which makes results from such multi-dimensional searches difficult to interpret. Suggestions are made, however, as to how to interpret those, and similar, results towards the end of this chapter.

With regard to the computational aspect, the problem is a result of the size of the state space. A wide range of trait values together with a large number of trait axes generates a state space of substantial size. An efficient search mechanism used to traverse this space must take the state space size consideration. In any exhaustive search mechanism, each position, or point, in the state space is independently assessed, through an evaluation function, for suitability in terms of meeting the search target. Further, the search space is assumed to be wholly unstructured, i.e. there exists no correlation among the values of the evaluation function of those points in space (Thornton and Du Boulay, 1992). An exhaustive search mechanism is sure to identify the best possible solution to the search problem, as all possible solutions are assessed. In the case of this multi-dimensional state space an exhaustive search is not desirable due to the extensive search times associated with such searches.

Many problems have a state space that is structured in some way, where structure implies a state space contains some (spatial) correlation between the evaluation function values of suitable points (Dean *et al.*, 1995). In a structured state space it is assumed that good solutions to problems (points with a high evaluation function value) lie near other good (perhaps better) solutions to a problem, and that poor solutions to problems (points with a low evaluation function value) lie near other poor solutions. If a particular point is assessed as being a good solution, the search effort should concentrate on the surrounding state space; if that point is assessed as being a poor solution, the search effort should address a distant area of state space. (Note, the qualitative terms 'surrounding' and 'distant' are clearly context specific.) Search strategies that assume structure in the state space and make use of results of assessed search points are termed heuristic (Dean *et al.*, 1995).

The way in which assessed parts of state space are used differs according to the search mechanism used. One approach is to consider the structure of state space in terms of gradients from poor solutions to good solutions. Here, a 'hill climbing' approach is useful, where the search travels from low (poor) regions 'uphill' to high (good) regions. A single (possibly randomly selected) point may be assessed for suitability. Further, its neighbouring points may be assessed in a similar manner. The relative suitability of each of these points will give an indication as to where in state space the search mechanism should next assess. In hill climbing the search mechanism will direct the search to the first neighbouring point better than the current point. In a variation of hill climbing, steepest ascent, the search mechanism will move from its identified point in the direction of the best solution found in the surrounding area, on the assumption that travelling up the steepest hill will lead to the best solution. When a search space is known to have a single, global, optimum value such searches are effective in finding that value. However, when the state space is large it may contain a number of local optima, i.e. an optimal solution within the (restricted) area of the total state space currently being searched. Hill-climbing strategies will find the (local) optimal solution nearest to the initial starting point. Further, when the state space is sparse in optima, hill climbing may take a long time to identify any optimum value. Conversely, when the state space is dense in optima, hill climbing will very quickly find a local optimum.

A hill climbing search strategy takes small steps through state space as directed by the gradient. Another extension to this hill-climbing strategy, termed simulated annealing, allows the taking of large steps in that direction of gradient, or in another direction (Dean *et al.*, 1995). Simulate annealing, inspired by a technique used in the production of metals with a high degree of malleability, makes use of a 'temperature' parameter. This (temperature) parameter serves to admit some randomised element into the search. The randomised element reduces in effect as the search approaches a region of good solutions. Thus, large steps are taken when in regions of poor solutions; small steps are taken when in regions of good solutions. In terms of the temperature analogy: when in a region of poor solutions in state space the temperature parameter is high (and jumps may be large); when in a region of good solutions in state space the temperature parameter is low (and jumps may be small). The optimal solution is, therefore, approached from some initial point in a series of ever-decreasing steps. If the search mechanism makes jumps, or steps, of large size through state space in the direction of the gradient then the optimal solution closest to the initial starting point will be found. Thus, simulated annealing will find a local optimal, which may not necessarily be the global optimal solution. However, the direction of the step does not necessarily have to be in the direction of the localised gradient. It may be in a randomised direction, allowing some opportunity to avoid local optima.

Simulated annealing suffers from the same problems as hills climbing in state spaces which are sparse or dense in local optima, although simulated annealing offers a means to avoid local optima in state spaces sparse in optima. It is assumed that the trait space to be searched here has some structure. This assumption is based on the exercises undertaken to generate the demonstrative runs of Chapter 3. However, it is not possible to characterise the nature of that trait space in terms of the distribution of optima. Indeed, optima may not even exist in this search space, due to an inappropriate assessment of solutions (evaluation function) or even an inappropriate trait space itself.

The investigation into trait space is therefore full of uncertainty. The following section describes a search mechanism that traverses a state space in terms of a number of initially randomised parallel searches (see below), and uses information derived from each of those searches to guide the next parallel search. This search mechanism hopes to limit the impact of this uncertainty (Mitchell, 1996).

4.2.3 Genetic algorithms

A genetic algorithm is a search mechanism which draws on the mechanisms evolution is understood to use – natural selection and (sexual) reproduction in terms of genetic combination. In natural selection, individuals compete for the opportunity to reproduce, and that reproduction is in the form of an exchange of genetic information. Only those individuals that are sufficiently fit to reproduce have that opportunity – natural selection. The reproduction process produces new individuals with characteristics derived from each parent. These new individuals then undergo the pressures of natural selection, reproduce given the opportunity and the cycle repeats.

Genetic algorithms, developed by Holland (1975), consider individuals within a population. Each individual is a candidate solution to a given problem and represents a state space point. Thus, the (genetic algorithm) population is a collection of candidate solutions, i.e. a collection of state space points that may be the solution to the problem. Each individual is assessed in terms of the quality of solution that arises from that candidate, termed the fitness of the individual. The most fit individuals – the best solutions – are recombined (see below) in the hope that the resulting population – the next generation, comprising a mixture of individuals of the preceding generation – has an overall increase in fitness, and that certain members of the population are fitter than the fittest members of the previous generation of individuals. Thus, the search mechanism begins with an initial population, consisting of a number of candidate solutions, and adapts that population across a series of generations as directed by the fitness of individual candidate solutions at the preceding generation.

A candidate solution, or individual, is represented as a coded string, where each code, or group of codes, maps onto a particular state space value. The string is typically of finite length, and the code is drawn from some finite alphabet so there are a finite number of state space values. The string is often termed the chromosome; an element of the chromosome is termed an allele, in line with genetic terminology. Thus, an individual chromosome is defined in terms of its allele. The translation from state space value to the coded form, the encoding process, is an important step: this process determines the resolution of the search. The traditional approach in genetic algorithms is to encode state space values in terms of two states; the allele is then 1 or 0. Thus, a state space axis with six values requires a code of three bi-state alleles, since 2^3 allows up to eight combinations (2^2 allows only four). A state space of three such axes (of six values) then requires nine alleles to represent (encode) each individual chromosome (3 axes x 3 alleles). An alternate encoding may use more characters than are in the binary alphabet (0, 1). If the alphabet comprised six symbols, then each state space axis in the example above may be represented by a single allele, resulting in a chromosome of length three. The genetic operators, described below, perform at the level of the allele. Operations on a short chromosome will therefore have more impact than an operation on a long chromosome; in other words, long chromosomes are more resilient to the genetic operators.

This property of long chromosomes clearly has advantages, in that a good region of state space may be carefully (slowly) explored; it has disadvantages, in that a good region of state space may take a long time to find. (The opposite is true of short chromosome representations.) No general framework exists to aid in deciding search resolution and alphabet choice – the performance of a genetic algorithm is very much application specific (Mitchell, 1996).

Each chromosome is one individual in a population of chromosomes. An initial population is generated at random, within the alphabet of the coding. Thus, the search starts at a number of points in an n-dimensional state space simultaneously – one point per chromosome. The number of individuals within the search population is another important issue in the design of a genetic algorithm. A small number of individuals in a population will allow a fast turnover of generations (parallel steps in the search process), since only a few areas of state space are being assessed in parallel. A large number of individuals in a population will allow an extensive search of state space per generation, although a generation may take a long time to be evaluated. As with the coding strategy, the optimal population size is very much a property of the nature of the state space being searched. Grefenstette (1986) and Schaffer *et al.* (1989) performed independent, extensive searches on a range of problems, and noted that optimal population sizes lie within the range of twenty to thirty. Mitchell (1996) sensibly notes that the optimal population size is likely to change during the search – initial populations should be large for breadth; later population sizes should be small for performance.

Once encoded, individual chromosomes within that population are assessed for fitness, and an application specific fitness value is attributed to each chromosome, depending on the extent to which that individual solves the application problem. Goldberg (1989) describes a simple example of the use of a genetic algorithm. This example, with some adaptations, serves to illustrate the encoding process, the building of the population of individuals and the attribution of fitness. This example also allows the introduction of two of the genetic operators used in this search process, namely reproduction and crossover (or combination).

Consider a black box with five input switches. For every setting of the five switches there is an associated output. Assuming the switches are bi-state (on, off), an encoding of (0, 1) will suffice. If the switches were tri-state (high, medium, low), encodings of (0, 1, 2) or (00, 01, 10) may be appropriate. Each switch generates a signal on its associated output when on (1), and the goal of the search is identify the combination of switch settings that leads to the largest signal (the most signals present). (Clearly this is all switches on.)

Each individual chromosome is five alleles (0,1) in length, since there are five switches. The population of individuals in a genetic algorithm is typically generated at random in the first instance. Table 7 shows a population of size four generated at random:

Individual number	Chromosome
1	01101
2	11000
3	01000
4	10011

Table 7: A sample population, generated at random

A very simple fitness function suited to this application problem would be arithmetic summation. The alleles in the chromosome are added together to derive a measure of fitness. In evolution, natural selection dictates that, on the whole, the most fit individuals are typically the most likely to reproduce – the genetic algorithm has a reproduction operator based on this observation. The implementation of the reproduction operator is most easily explained in terms of a biased roulette wheel (Goldberg, 1989), where each individual has a number of slots equal to its fitness, and the wheel has a total number of slots equal to the summed fitness of all individuals. A spinning of the roulette wheel randomly selects an individual, based on the fitness of that individual. Of course, as in nature, individuals of limited fitness have the (limited) opportunity to be selected for reproduction. Table 8 shows each chromosome and its attributed fitness, with the roulette wheel slots as allocated by fitness (the number of slots totals the summed fitness of all chromosomes).

Individual number	Chromosome	Fitness	Roulette wheel slot
1	01101	3	1, 2, 3
2	11000	2	4, 5
3	01000	1	6
4	10011	3	7, 8, 9

Table 8: The sample population of Table 7 with an attributed fitness and roulette wheel slots.

The least fit population member is the third, since only one input switch is on. The most fit population members are the first and last, since three of the five switches are on. The least fit chromosome only has one roulette slot, and is thus three times less likely to be selected by the fittest chromosomes (with three wheel slots).

The reproduction operator selects pairs of individuals to act as parents. Each pair of parents generates two offspring. In the example presented here, two pairs of parents are selected at random, with probability of parent fitness divided by the total fitness (roulette wheel slots) to produce four offspring. Generally sufficient parent pairs are selected to maintain the population size across generations. Table 9 shows the selection of two pairs of parents at random from Table 8. In general, the selection of the same parent twice is permissible, although some implementations prohibit this (see below). This case is not shown here.

Parent pair	Associated allele
1 and 2	01101 and 11000
1 and 4	01101 and 10011

Table 9: Parent pairs and associated alleles

The alleles of the four resulting offspring are determined by the crossover operator. This operator randomly selects a position, *p*, along a chromosome of length *l*, i.e. a location within the range [1, (*l*-1)], and generates two new chromosomes by swapping alleles between (*p*+1) and *l* inclusively. Here, consider the first randomly generated location to be 1, and the second randomly generated location 3. The first parent pair swap all but the first allele; the second parent pair swap the last two alleles. Parent pair 1 and 2, with alleles 01101 and 11000, thus produce offspring 01000 and 11101; likewise, parent pair 1 and 3, with alleles 01101 and 10011 produce offspring 01111 and 10001. Table 10 shows the resulting offspring, i.e. the next generation, and the attributed fitness of each individual.

Individual number	Chromosome	Fitness
1	01000	1
2	11101	4
3	01111	4
4	10001	2

Table 10: The next generation chromosomes and their attributed fitness

The next generation is fitter than the previous population in terms of both the average fitness and the mean fitness. Poor chromosomes are possible of course, as in population member 1 above. Clearly, in this trivial example, the optimal solution is reachable based on the (contrived) crossovers that occurred. In many searches it is desirable to have some complete memory of the previous searched space. To achieve this, the crossover operator is applied with a probability of slightly less than 1, typically 0.75 – 0.95 (Greffenstette, 1986; Schaffer *et al.*, 1989). This complete memory allows some backtracking in case of (unlucky) re-combinations resulting in a population of very unfit individuals.

However, this is not always the case. Even with a parallel search, genetic algorithms are prone to sticking at local optima. A restricted case of a search remaining at a local optimum occurs when one individual may be greatly fitter than all other individuals in the population. This single individual will be the likely source of all new offspring, i.e. both parents, since the general reproduction operator does not prohibit clonal reproduction. A number of approaches are available to assist in this situation. The reproduction algorithm may be extended to prohibit such clonal reproduction, forcing the selection of unfit mates for the fit individual. The fitness function may be amended to express relative rather than absolute values for fitness. Such a ranking approach will limit the domination of super-fit individuals in the population. Mitchell (1996) suggests the use of relative ranking in the early phases, and absolute ranking when the search becomes more focused.

The more general problem of remaining at local optima can be addressed in two ways, both of which incorporate new 'genetic material' into the chromosomes comprising the population. The first approach addresses the problem at the individual level: a small number of randomly generated individuals are introduced to the population at each generation, replacing the potential offspring of one parent pair. This allows the search to consider a fresh area of state space without losing the progress in terms of previously searched state space. This previous search information is still encapsulated within the larger portion of the population derived in the reproductive manner. The second approach is that of the final genetic operator, mutation. The mutation operator potentially affects all alleles involved in the crossover process, although it is rarely applied. The mutation operator changes the allele symbol from its present state to another state in the alphabet. This has the effect of adding a small amount of new material, which modifies the position of the chromosome in state space in one dimension per mutation event. The probability of a mutation event is typically small, usually 0.005 – 0.01 (Greffenstette, 1986; Schaffer *et al.*, 1989).

Genetic algorithms offer an inherently parallel search mechanism, with a structured yet randomised information exchange between a given set of individual state space points to generate a new set of state space points. The search mechanism models evolution, and the search process has often been envisioned as a walk over a 'fitness landscape' (Niklas; 1997; Kauffman, 1993), since the plot of fitness values in state space can form hills and valleys. The adaptive search traverses this fitness landscape looking for optima. The search traverses this landscape from a number of starting points, and in general will find more than one optimum. As with hill climbing and simulated annealing, the optima found may not contain the global optimal. However, by finding a range of optima the identification of the global optima is more likely. The notion of a fitness landscape is used to support the interpretation of preliminary searches outlined below.

For the purpose of this investigation, genetic algorithms are an appropriate search mechanism. This preliminary study is most interested in whether any optima exist at all, global or otherwise, in this unstudied trait space. The following section details a first investigation into that trait space. A simple genetic algorithm is specified, and the search parameters are set based on the above discussion. A simple fitness function is also specified. The results of three searches are described.

4.3 First searches

4.3.1 Algorithm particulars

As noted, the principle aim of this first investigation is to identify whether or not the genetic algorithm search mechanism can identify combinations of trait values that lead to coexistence (see below for working definition). This search is to be undertaken in a large state space, where the structure of that state space is unknown. In order to simplify the search process in this first investigation a number of simplifying steps are taken including limiting the number of traits, trait combinations and trait values considered at any one time, thus reducing the dimensionality and the size of the state space considered.

To reduce the number of trait combinations represented by any one candidate solution – a chromosome in the population – only communities comprising ten functional types are considered where many individual plants of each type (clones) exist in that community. Each type is defined in terms of the traits detailed in Chapter 3, and the search takes place in a multi-dimensional state space, where one state space dimension is required for each trait considered. In general, each individual plant corresponds to a single point in trait (state) space – its position in trait space is determined by the values of its traits. Under the assumption that all individuals of a given type are clonal, the communities considered here comprise one point in trait space per type (and individual). Thus the communities are expressed as ten points in trait space.

The defined types are used to parameterise the plant community dynamics model detailed in Chapter 3. A given community comprises an initially equal number (500) of clonal individuals of each of ten types distributed randomly over an initially uniform resource substrate of 100x100 sites, resulting in an initial community of 5000 individuals. The dynamics of this community and environment are evaluated as described in Chapter 3.

Clearly, performing a search on a small number of functional types, say two, greatly reduces the complexity of the search. However, such a small number of types will not give insight into the balance of trait values required to maintain coexistence (defined below) – to investigate properties associated with a high degree of biodiversity, a complex community must be considered. That noted, a community of ten types is arguably too simple.

Each community – a candidate solution for coexistence – is expressed as an individual chromosome within the context of the genetic algorithm in the form of the trait values defining each of the ten types present in that community. The genetic algorithm operates with a population size of 20 individual chromosomes – 20 instances of a community composition. This population size is within the limits suggested by the literature, 20 – 30 above, for a general search. Although this search size is towards the lower end of this limit, multiple (separate) runs are undertaken. Here, three such searches are described; thus, sixty different starting points are considered.

The trait values for each population in a first generation are produced at random. As noted above, restrictions to the trait space may be imposed to reflect inter-type functional trade-offs, due to internal resource limitations. However, in this first investigation no such restrictions are imposed. Indeed, it is anticipated that in the longer term such functional trade-offs should emerge in coexisting communities, as a consequence of the need to balance functional traits both within types and across communities.

The translation from trait values to the coded form – the encoding process – allows a simplification to be introduced into the search. The encoding process sets the resolution of the search, as discussed previously. Here, the 13 plant traits identified and described in Chapter 3 are collapsed (unevenly) into 6 'composite traits', with each composite trait having an identifiable interpretation, as illustrated in Table 11 below. Those traits that seemed to be most important in the development of the demonstrative runs of Chapter 3 are combined to a lesser extent than those traits that seemed to be least important. (The subjectivity and lack of rigour in this decision is acknowledged. Section 4.4 indicates measures to compensate for this convenient simplification as the search process progresses.) This measure reduces the dimensionality of the trait space from 13 to 6. Similarly the definition of a functional type (and an individual plant) is reduced from 13 traits to 6 composite traits. Thus, 6 'code alphabet' characters, one character per trait represent each of the 10 defined types, where the particular character represents the value of that trait. Each chromosome is therefore 60 'code alphabet' characters in length – 6 traits per type; 10 types. Without the trait dimensionality simplifications outlined above, this chromosome would be more than twice as long – one allele per original (Chapter 3) trait.

The traits 'requested uptake' and 'distance-proportioned uptake' are seen to be very important, and these traits are not combined. Thus two of the composite traits map directly to the original trait set. The five traits 'required uptake', 'offtake proportion', 'reproductive proportion', 'surplus store release rate' and 'reproductive store release rate' relate to storage potential and mobility and are grouped thus. The traits relating to shortfall survival, 'shortfall survival period' and 'shortfall survival threshold', are combined for a fourth composite trait, a reflection on shortfall resilience. The traits 'time development fecundity' and 'development dependent fecundity' are combined to provide a fifth composite trait, providing some representation of time to reproduction. 'Fecundity storage relation' and 'seed dispersal pattern' are combined into the final trait defining the reproduction characteristics of a plant.

Original traits	Composite traits
Requested uptake	Requested uptake
Distance-proportioned uptake	Distance-proportioned uptake
Required uptake	Storage potential and mobility
Offtake proportion	
Reproductive proportion	
Surplus store release rate	
Reproductive store release rate	
Shortfall survival period	Shortfall resilience
Shortfall survival threshold	
Time dependent fecundity vector	Time to reproduction
Development dependent fecundity vector	
Fecundity storage relation	Reproduction characteristics
Seed dispersal pattern	

Table 11: The 13 original plant traits are collapsed into 6 composite traits to reduce the dimensionality of the search space. The composite traits are shown in the order they appear in the chromosome.

In the search process, each of these 6 traits assumes 16 possible values, again limited for simplicity. This simplification means that the trait space is structured so that each of the 6 axes (dimensions) has 16 values on an interval scale. For notational ease, an alphabetic character in the range a-p represents each code. Alleles may of course assume more than 16 values by extending the coded representation, for example a-z, and associated trait values. However, the inclusion of more allele (and thus trait) values further increases the complexity of the search. The codes of the composite traits express different combinations of values of the traits within that composite.

The chromosomes comprise a list of codes for trait values, C. This list is for ten types, A-J, with six traits, 1-6, per type. The traits are expressed in the order 'requested uptake', 'distance-proportioned uptake', 'storage potential and mobility', 'shortfall resilience', 'time to reproduction' and 'reproduction characteristics'. The chromosomes are of the form:

$$C_{A1}\,C_{A2}\,C_{A3}\,C_{A4}\,C_{A5}\,C_{A6}\quad C_{B1}\,C_{B2}\,C_{B3}\,C_{B4}\,C_{B5}\,C_{B6}\quad\ldots\quad C_{J1}\,C_{J2}\,C_{J3}\,C_{J4}\,C_{J5}\,C_{J6}$$

where C_{A1} represents the trait 'requested uptake' for type 1 of trait value (strategy) A. In spite of the many simplifications detailed here the chromosomes are still lengthy and not intuitive. Example chromosomes, taken from one search are:

pijfpc hnfjbk ngkhnp jilhog ijhepd ehechm miedhk acmhjj gkpdic adfgck

and ifmkci amaadk jkonel kcnola kjmplg fnpnkd bjlign fbamnc pmblag bmngfi

and have been included to illustrate the complexities of this search problem.

Each of these chromosomes – the representation of a community – is assessed for fitness using a simple fitness function in which a measure of coexistence was specified. The community initially comprised 500 (clonal) individuals of each of the 10 specified types. The model described in Chapter 3 is parameterised with the specified types, and the fitness of a given community was assessed in terms of the length of time – model cycles – all functional types remained above a threshold in number in that community. This threshold was (arbitrarily) set at 100. Thus, each community was monitored through time, up to an upper limit of 1000 model cycles. When the number of individuals of any type within that community fell below 100 the model run was stopped. The fitness of each individual chromosome was, therefore, an integer between 1 and 1000: the number of cycles that coexistence was sustained.

The reproduction operator considered fitness values in terms of absolute values. Selection was based on the weighted roulette wheel approach described above. No new 'genetic material' through novel chromosomes is introduced to population at any generation. The mechanisms of adaptation in the algorithm were crossover and mutation only. The probabilities associated with these genetic operators were 0.95 and 0.05 for the crossover and mutation processes respectively. These values were selected according to the literature. The population passed through 10 generations – 10 iterations of an initial population – in each run.

The general architecture of the search process used is shown below in the form of an algorithmic description. Here, an initial population is randomly generated. Each chromosome – a representation of a community – is assessed for fitness through the fitness function. The fitness function parameterises the plant community model with the trait values encapsulated in the chromosome and each parameter set is assessed in terms of the length of time coexistence is sustained. This assessment ascribes a fitness value to each chromosome in that population. The population, with the associated fitness values, is then genetically re-combined to produce the next generation of chromosomes using the genetic operators as detailed above.

```
for each run (1 to 3 searches)
    generate initial population(random)
    for each generation (1 to 10 generations)
        for each chromosome in the population (1 to 20 candidate solutions)
            assess fitness (1 to 1000 model cycles)
                parameterise model with trait values in chromosome
                set fitness to length of time coexistence is sustained
                    until any number of type < 100 or until 1000
```

produce next generation through genetic operators

4.3.2 Preliminary results

As noted, the results of three searches are described. Each search considers 20 chromosomes, passing through 10 generations. Thus, up to 600 (20x3x10) chromosomes in state space are assessed for fitness. The number of chromosomes assessed is typically less than this maximum number as a result of duplicate chromosomes. These duplicate chromosomes are the result of convergence on a local optimum. (Of course, the search algorithm may be amended to prohibit such duplicates, as noted above, although this is not done here for reasons addressed below.)

Central to the description of search results are the summary graphs shown in Figures 38, 39 and 40. The graphs show the progression of both the maximum fitness and the average (mean) fitness values through successive generations. The maximum fitness indicates the current optimal chromosome in the population of chromosomes; the mean fitness gives a measure of the fitness of all chromosomes in that population. The standard deviation in fitness values across all chromosomes is also shown on the mean fitness plot although, as will be discussed, the interpretation of the magnitude of the standard deviation is not immediately clear. The figures indicate properties relating to the nature of the search space under consideration, and these properties are exemplified with reference to particular search results.

In general, the maximum fitness plot lies well above the mean fitness plot, indicating a wide range of fitness values in the population. This suggests that the fitness landscape associated with the trait space is uneven, in the sense that this landscape contains a number of hills and valleys. Identical values for the maximum and mean fitness of chromosomes in a number of populations indicate a perfectly flat fitness landscape. Searches giving rise to maximum and mean fitness values that are similar suggest a smooth landscape, containing only slight inclines and few peaks.

The difference between maximum fitness and mean fitness is particularly marked in the search illustrated by Figure 38. Here, the first assessment of trait space combinations indicates no fit chromosomes. In the first generation – the first offspring from the initial parent set – a very fit chromosome is identified, with fitness of 861 cycles (from a maximum 1000 cycles). This causes the maximum fitness value to be well above the mean fitness in that generation. For reasons discussed below the mean fitness value is slower to rise. Thus, a single point in assessed trait space rises well above others; the fitness landscape is not smooth.

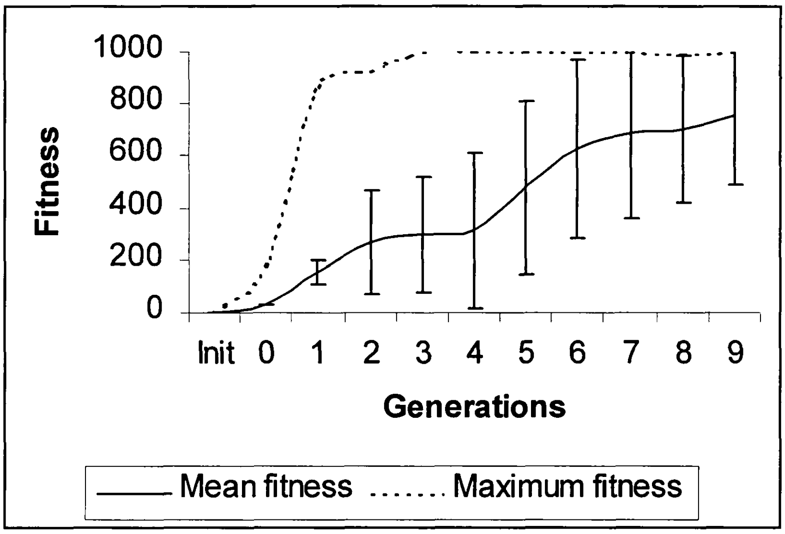


Figure 38: A search illustrating the early identification of a very fit chromosome, as shown in the Maximum Fitness plot. The Mean Fitness plot is slower to respond to that identification. The error bars indicate the standard deviation in fitness values at each generation.

The values of the maximum fitness in a given population increase in the initial phase in all searches (the first two or three generations), indicating that better solutions may be found from recombining initially poor solutions. Further, the rate of subsequent improvement in maximum fitness is shown to slow over generations, see Figures 39 and 40, with the exception of Figure 38 which identifies an optimal chromosome early on, and remains fixed at this optimal level. This slowing of fitness improvement suggests that the searches identify many local optima of intermediate fitness. Further, those local optima are close to each other in trait space, since many trait codes are shared.

Thus, the fitness landscape of the searches in Figures 39 and 40 may be seen as having clusters of many hills of intermediate height.

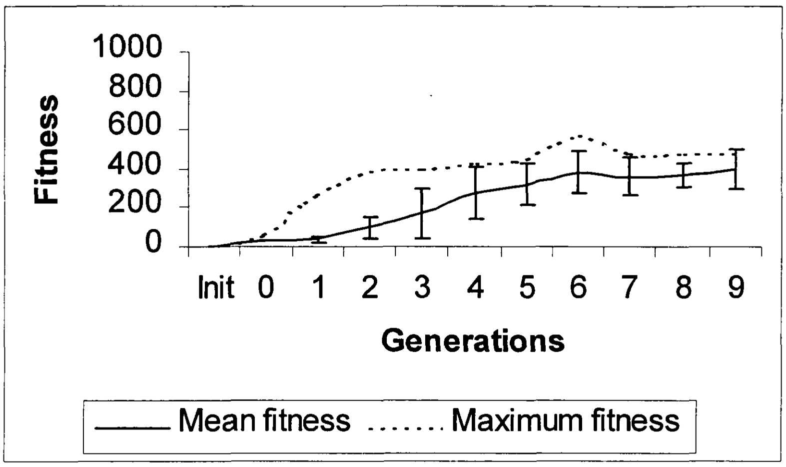


Figure 39: A search illustrating initial improvement in fitness, and the sticking at a local optima. The plot of Maximum Fitness shows a loss in the fitness of the optimal solution at generation 6 that is never regained (see below). The error bars indicate the standard deviation in fitness values at each generation.

The search represented by Figure 39 has an initial population with no fit chromosomes. After the first generation, a chromosome with a fitness value of 262 cycles (the maximum) is identified. Re-combinations of other chromosomes with that fit chromosome result in an immediate increase in the maximum fitness value, from 262 to 392 cycles in the second generation. Subsequent improvement is slower: 392 cycles in the second generation rises to 427 and 547 cycles in the third and fourth generation generations respectively.

The corresponding values of mean fitness are notably lower than the maximum fitness values in the first few generations, indicating that those better chromosomes, although reachable, are not common. The rate of improvement in mean fitness assumes a steadier rate, and across generations, the mean fitness approaches the maximum (1000). This is due to convergence around the optimal chromosomes identified by the searches. This convergence is achieved by way of the natural selection mechanisms, as poor combinations are removed from the population over generations.

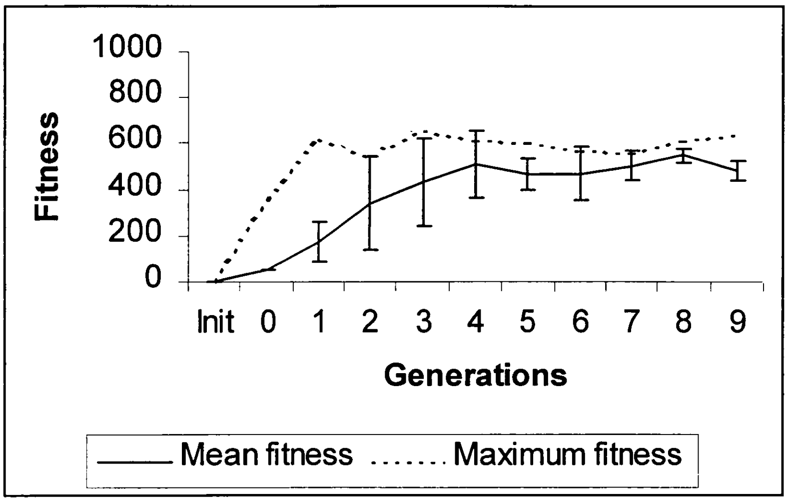


Figure 40: A search indicating convergence to a local optima. This optima is robust to small changes in the chromosome, as indicated by the small standard deviation (error bars) in fitness values.

Convergence towards local optima occurs across the population. However, the process of recombination, allowing the assessment of new areas of trait space which are related to already assessed areas, is seen to result occasionally in a decrease in fitness of the optimal solution. This may be observed in Figures 39 and 40. The fitness of the optimal solution may be decreased as a result of recombination with another solution, or a mutation event – either event may increase or decrease the fitness of the optimal solution. The plots of maximum fitness suggest that whilst loss occurs, resulting in a drop in fitness for the optimal solution, that loss is temporary. Both figures indicate rises in maximum fitness occurring after falls.

The mean fitness value of the population is observed to rise in general across generations. However, this mean value is also observed to fall, see Figures 39 and 40. Indeed, the fluctuations in mean fitness occur independently of the fluctuations in maximum fitness, for example, Figure

40. Again, this is due to the recombination and mutation events that in general allow the search to find better solutions, but often results in a loss of fitness for individual solutions in the next generation. This loss in fitness may be small or large as is shown below.

An example evolution (in the sense of the search algorithm) of related chromosomes serves to illustrate the above points. These chromosome lists are not themselves informative – their inclusion is to aid in the explanation of the refining nature of the search and reinforce the difficulties encountered in interpreting the results. The refining nature is not always beneficial, as illustrated below. Some attempt to attribute biological meaning is provided in the latter part of this section.

The search illustrated by Figure 39 identified a better chromosome in the first generation. This chromosome was of the form:

bnkain gkjblg pgigjm dofmel nmghif kldobg pggcda mmodka kdpbib lcjmll, fitness 262.

This chromosome was the product of the crossover of parents (p=5, l=60 in notion of Section 4.2.3) with lower fitness (redundant material italicised):

bnkai*m loclng ejaend mlmboc ghhdin pmjjio hcoiab fhkeoc cbknkd pdaloo*, fitness 21

and

*gpafp*n gkjblg pgigjm dofmel nmghif kldobg pggcda mmodka kdpbib lcjmll, fitness 41.

Incidentally, the complementary offspring derived from this parent pair had a fitness of 17. Thus parents of fitness 21 and 41 recombined to give offspring of fitness 262 and 17 in the first generation. In the next generation offspring are more likely to be parented by the fitter of the current generation offspring. This fit chromosome of the first generation is combined with other material through the recombination and mutation operators to produce chromosomes that are both more fit and less fit. For example, the second generation contained the following chromosomes (new material italicised):

bnkain gkjblg pgigjm dofmel nmghif kldobg pggcda mmod*gj idlmgf hjoall*, fitness 392,

and

*iglnke mphbcd ihj*gjm dofmel nmghif kldobg pggcda mmodka kdpbib lcjmll, fitness 370.

Some variations on this initial chromosome in that second generation were not as fit as the source. For example, the second generation contained the chromosome (new material italicised):

bnkain gkjblg pgigjm dofmel nmghif kl*nbai hgpnoa gkemgj idlmgf hjoall*, fitness 159.

Subsequent generations introduce new material, resulting in a general increase in overall fitness, as the strings become more and more similar. A maximum fitness increase is observed, as some offspring are better than their parents. This maximum fitness is not always retained, as illustrated in the passing from generation 6 to generation 7 in Figure 39. Two chromosomes are developed in generation six with fitness values of 567 and 552. Subsequent chromosomes incorporated elements of these chromosomes, but no new chromosome had fitness exceeding those generation 6 chromosomes. Neither chromosome was retained or regenerated in subsequent generations. The resulting maximum fitness at the end of the search was, in this case, less than the maximum within the whole search, a fitness value of 481.

An issue arising from attributing fitness values to individual chromosomes is that of consistency. The attributed fitness may be a product of stochastic elements in the underlying model, here initial configuration and dispersal patterns. To identify the extent to which the attributed fitness is a product of the trait values represented by the chromosome, and not the spatial patterns arising in the model by chance, a series of fitness attributions to a single chromosome is necessary. Note, the spatial patterns will differ in each model run. Fortunately, the search algorithm provides this as a side effect of the search process itself, through duplicate chromosomes.

Figure 40 illustrates a search that has a small standard deviation in the later generations. In this case this small standard deviation is a result of a population concentrated on a single (duplicated) chromosome with a small number of variations. This single chromosome is readily identified by examining the population of chromosomes, and is repeatedly attributed similar fitness values with many identical fitness values. This indicates that fitness is largely a function of the codes in the chromosome, with some noise introduced by the stochastic elements in the model. (It is acknowledged that this is not a statistically robust statement.)

As noted, Figure 39 shows a small standard deviation around the mean. In general this, on examination of the population chromosomes, may be a result of convergence around a single optimum. This convergence will lead to a population of many identical chromosomes with identical (or similar) fitness. However, small standard deviations may also be created by a population of very diverse chromosomes with similar fitness values. Thus, a small standard deviation reveals nothing of the dispersal of peaks within a fitness landscape. It may be a landscape of one peak and all chromosomes cluster round that peak. It may be a smooth landscape where all points have similar fitness. It may be a landscape of many similar sized peaks, and each chromosome, or group of chromosomes, clusters around one such peak.

A small standard deviation does, however, give an indication of the sharpness of the inclines of those peaks. The genetic operators in the algorithm make small changes to the populations of chromosomes in terms of new material. A population with a small standard deviation is suggestive of a population that occupies peaks with shallow inclines, since small changes in chromosomes result in small changes in fitness. For example, the population of the search of Figure 39 contains a number of identical chromosomes of the following code:

mboanc pnockk kdhpmc ealpec cojijk helfip hekfhh baceig khnjmg djmcem, fitness 482.

This code, which is present from an early generation, has a number of variations including:

mboanc pnockk kdhpmc ealpec cojijk helfip hekfhh baceig khn*cab nfilhm*, fitness 512.

and

mboanc pnockk kdhpmc ealpec cojijk helfip hekfhh baceig khn*cab nfilhg*, fitness 531.

In contrast, the search illustrated in Figure 38 has a large standard deviation across generations. A large standard deviation may be caused by either a population comprising very diverse chromosomes, or a population clustering around a peak with very sharp inclines. In the first case, some chromosomes will be in very fit positions and some chromosomes will be in very poor positions, and each chromosome, or group of chromosomes, will have a very diverse code. Examination of the codes for the search of Figure 38 reveals that this is not the case. All chromosome codes cluster around two optima in this case, and a small change in a fit chromosome may result in a large change in its fitness. For example, in the later generations of this search, the population contains two similar codes:

hpaebg iphlbk iomgcp gjaock gcmjcn ggenkl elnmnc pbmlag bmngfi, fitness 861,
and ↕
hpaebg iphl*p*k iomgcp gjaock gcmjcn ggenkl elnmnc pbmlag bmngfi, fitness 41.

Another example shows a less extreme case:

hpaebg iphlba iomgcp jgkemi gjhkjo nagice lhkoig jbobae bnnaeg bmnfgi, fitness 789,
↕ and ↕
*i*paebg iphlba iomgcp jgkemi gjhkjo nagice lhkoig jbobae *pbmlkd* bmnfgi, fitness 89.

This indicates a landscape containing optima with sharp inclines, meaning that any move away from that optimal point may result in a large loss of fitness. Both of the preceding examples illustrate dramatic changes as a result of small changes in the chromosome. In the first example, the second type has a trait change of one allele resulting in a drop in fitness of 820. This drop is a consequence of the difference in the fifth trait of this type, defining the time to reproduction. Trait code 'b' represents a frequent time to reproduction (every 10 cycles); trait code 'p' represents an infrequent time to reproduction (every 150 cycles). Clearly the survival of this type is dependent on a frequent reproductive cycle.

The second example illustrates more change – one complete type and one trait of another type – with a similar drop in fitness (700). The biological interpretation of this case is more difficult since more traits are changed. One approach, suggested in more general terms in the following section, is to investigate the cause of this drop in fitness in a much more systematic manner, perhaps by exhaustively identifying the effects of all changes to these traits. This will lead to the same level of knowledge as is present in the first example – detail relating fitness changes to individual trait changes.

However, even if such a process were undertaken it would not reveal the whole picture. Indeed, the biological interpretation in the first of these two examples is a little misleading. The statement 'the survival of this type is dependent on a frequent reproductive cycle' should be extended to 'the survival of this type is dependent on a frequent reproductive cycle in the context of both the environment and community in which this type exists'. The complex inter-relationships between traits must be explored to address properly this problem.

4.4 Discussion

The work detailed above describes the development of concepts and a search algorithm to support a brief investigation into the properties of coexisting communities. This first study identifies the forum of investigation, in terms of functional trade-offs and spatial structure, and necessarily makes a number of assumptions and simplifications within that forum, as indicated above. Thus, it is important to acknowledge that results from this model are informative only within the remit of these assumptions and simplifications. The work does, of course, provide a basis for subsequent study.

The demonstrative searches presented here indicate that under the fitness function, and imposing trait value and trait dimensional simplifications, some combinations of trait values lead to coexistence. Most combinations, however, do not lead to such coexistence suggesting that optima in the trait space may be sparse. The most immediate progression is to undertake many more searches of the form described above to find more optima. The optimal solution(s) from each search may be used to construct a super-population of chromosomes. This super-population may be used as a platform for further searches under more stringent fitness functions. Improvements in the fitness function may take the form of an increase in the period over which all types are to remain above a threshold and/ or the modification of that threshold.

Such extended searches may allow the identification of areas of trait space that contain optimal solutions. The trait space dimensionality may be expanded around these 'hot-spots' in trait space to more fully investigate the inter-relationships between traits in coexisting communities. Those solutions identified as coexisting seem sensitive to small changes, and by expanding the dimensions of trait space, investigations into the reasons for that sensitivity may take place, and the need for inter-type trade-offs, providing functional balance at the community level, may be identified.

Having profiled the trait space more thoroughly, consideration will be given to more suitable search mechanisms. More fully, if the topology of the state space may be coarsely mapped by the parallel genetic algorithm search technique, a more focused exhaustive search mechanism to be applied in areas of interest may be more appropriate. At this stage, the trait space is still very much unknown, and no other search approach may be sensibly adopted.

The importance of spatial heterogeneity in the resource substrate was acknowledged in section 4.1.3. This additional, yet (probably) crucial complexity has not been addressed here. As noted earlier, a heterogeneous resource is likely to support a wider range of communities than a homogeneous resource. Certainly, the trade-offs in a community coupled with a heterogeneous environment will be of a different form to the trade-offs in a community coupled with a homogeneous environment. Thus, it is important to introduce spatial heterogeneity into the search framework at an early stage. However, this introduction has associated difficulties.

Consideration has been given to the consistency of fitness values for a given chromosome. In the current scheme, plant types are initially distributed in a randomised manner over an initially homogeneous resource, and seeds are dispersed likewise over that same resource. If the resource were spatially structured, the impact of the stochastic processes is likely to be amplified. Thus, more careful consideration must be given to consistency.

The fitness function employed above is trivial, and useful only in a spatially unstructured context. In a spatially structured resource, a small well defined region may be well occupied by a particular type for a long period of time. However, the small area may not support that type in numbers sufficient to meet the (arbitrary) threshold set by the fitness function. Chapter 3 has shown that different patches of resource exhibit very different dynamics, and it will be important to incorporate this feature in any fitness assessment. Chapter 5 introduces a novel method for classifying the dynamics of spatio-temporal systems that will be useful in both identifying the persistent properties of type as required here, and more general community scale properties required in analyses of fungal and plant communities alike. This method is an extension to the state transition analysis introduced in Chapter 2, and additionally incorporates a measure of the patchiness of the system.

Chapter 5 Summary and future work

5.1 Associated work

5.1.1 An application to vegetative communities

The model presented in Chapter 3 is generic in nature in that it allows the description of the developmental behaviour of individual plants in general terms, and this developmental behaviour is represented by attributing values to functional traits. Any trait may assume a wide range of values, and thus the model is flexible in terms of the forms of plant represented. The model incorporates time, in terms of discrete time steps, and the algorithm representing the life-cycle of the plant is applied each time step. This section describes the use of the model within the context of vegetative communities. The model is parameterised by data derived from experimental studies in grassland plant physiology, and both the form of the plants considered, i.e. the values attributed to traits, and the time-scale used are derived from these experimental data.

The Macaulay Land Use Research Institute, Aberdeen, generated the experimental data utilised here. Both this data generation and the subsequent model parameterisation were carried out within the context of a Scottish Executive funded investigation into Vegetation Dynamics (SERAD Project 816/95). The work described below has been undertaken jointly with a colleague at the Scottish Crop Research Institute, Elizaveta Pachepsky. It is included here as it both reflects a significant investment of collaborative time on the part of the author, and serves to illustrate the applicability of the model to studies outwith those carried out here.

The experiments considered three grassland species: *Rumex acetosa*, *Agrostis capillaris* and *Festuca rubra*. From hundreds of plants isolated from two different regions in Scotland, the Macaulay Land Use Research Institute randomly selected twenty of each species for detailed physiological study. Ten plants were taken from a site in Cleish, a lowland site in Fife, and ten from a site in Kirkton, an upland grassland site near Crianlarich. These sites were selected for their different topologies: Cleish is flat; Kirkton is highly sloped, dry at the top and moist at the bottom. The impact of this heterogeneity in environment on the measured characteristics of the plants (see below) is currently under investigation by other colleagues. It is anticipated that the results of this study will support the theoretical investigation into the coupling between community composition and environment, as outlined in Chapter 4.

The twenty plants were vegetatively propagated (cloned) to allow (destructive) assessments at seven time points over a nine-month period, January to September. Measurements were made to identify resource uptake, allocation and storage. Resource uptake was assessed by measuring the difference between the levels of nitrogen and carbon present at two successive time points, i.e. the increase in nitrogen and carbon levels at the second time point with respect to the first indicating the amount of uptake. When assessing resource allocation the plant was compartmentalised – leaves, reproductive parts and roots – and the amount of nitrogen and carbon allocated to each compartment was assessed in the same manner as resource uptake. Resource storage was assessed by examining the amounts of nitrogen and carbon retained from a pre-assessment period. (The retained resources, applied at a previous study period, were distinguishable from those applied within the assessment period.)

To date, the measurements from one species, *R. acetosa*, have been used to quantify most of the traits used in Chapter 3. The remaining traits, for example seed dispersal pattern, have been quantified using existing literature. The quantification of traits, as derived from measurements on twenty plants, take the form of a distribution of values. For example, consider the trait 'time-dependent fecundity'. This trait is quantified by considering the dry weight of the reproductive parts over time. The dry weights at the seven harvest points are plotted and a (lognormal) curve is fitted to identify the estimated maximum weight of reproductive parts. Reproduction is assumed to occur when the plot of measured weight falls (beyond the maximum). Figure 41 illustrates the number of plants that reproduced at each of those times. Excluding the three extreme values, the Ryan-Joiner test (Ryan and Joiner, 1976) was used to determine if these data were drawn from a normal population. Figure 42 shows the sample data close to the straight line consistent with a normal distribution. This is confirmed by an R-value of 0.9749 and the p-value greater than 0.10. This normal distribution may represent a large population *of R. acetosa* plants.

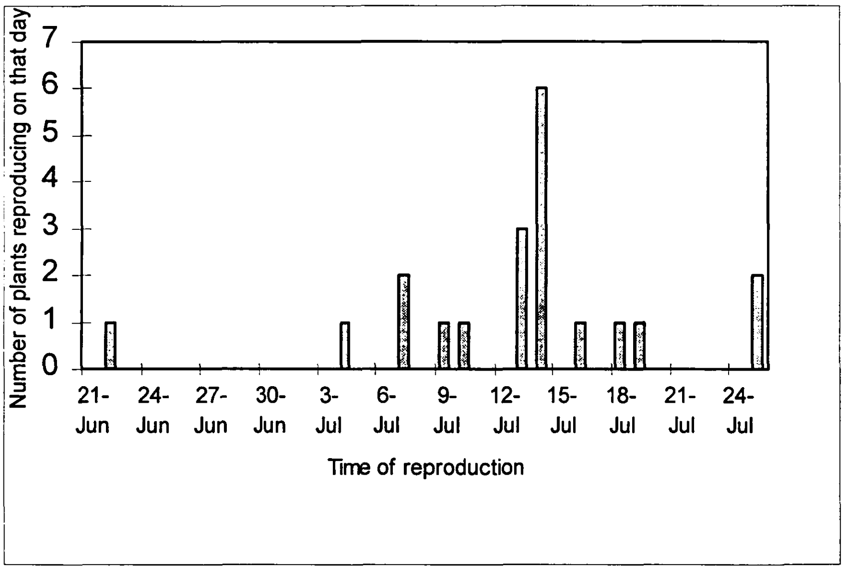


Figure 41: Frequency distribution of the maximised dry weight of reproductive parts

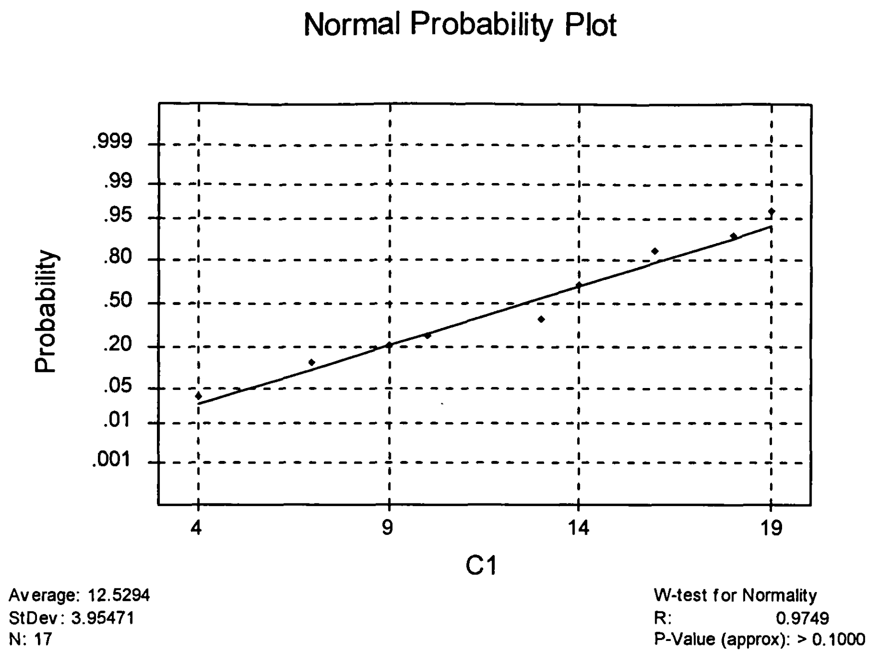


Figure 42: The Ryan-Joiner normality plot, indicating data consistent with being drawn from a normal population.

Each trait is parameterised in a similar manner, and is therefore characterised by a distribution of values. In the case of 'time-dependent fecundity' the trait distribution is independent of the development stage of a plant. Where traits are linked to development stage, separate trait distributions are present for each stage. The original measurements were made at seven points during the development of the plants. These points equate to stages, and linear interpolation was employed to generate parameter values for intermediate development stages as required. As the measured stages map to a definite period of time, it is possible to approximate a period of time to the model time step.

The *R. acetosa* species, and in general any species, is thus represented by a suite of trait distributions, one per trait per development stage (where applicable). In the (vegetation dynamics) model, an individual plant is assigned a trait value drawn at random from the relevant trait distribution, as defined by its species. Thus, an individual plant may be considered an instance of its species, derived from all possible (represented) forms of that species. In the terminology of

Chapter 3, an individual is a plant type, with duplicate plants (plants with the same traits) being of the same type. The notion of species, i.e. a suite of trait distributions, sets limits to the range of values assumed by types and, as noted earlier, species may have overlapping trait value distributions.

The dynamics of *R. acetosa* plants, and other species when parameterised, may be modelled. The form of search introduced in Chapter 4 will be incorporated into this application as a mechanism to investigate the dynamics of such *R. acetosa* populations within the context of other populations (other trait distributions). *R. acetosa* exists with many other plant forms – too many to measure without causing disturbance to the community. The theoretical investigations, detailed below, may be used to understand vegetation system dynamics in a range of contexts (populations). This understanding may be used to direct and thus limit necessary field studies.

The genetic algorithm will be encoded with indices to trait distributions, where the search string will define all other (non-*R. acetosa*) plant types in a community. Initially, this will be one or two other populations (species). Figure 43 illustrates the concept of a *R. acetosa* population in a community of another population, all other plants. This second population may be varied according to a genetic algorithm search, where a particular broad-scale property is considered the goal; for example coexistence with the observed *R. acetosa* distribution, as in Chapter 4, or a well mixed spatial pattern of the two populations.

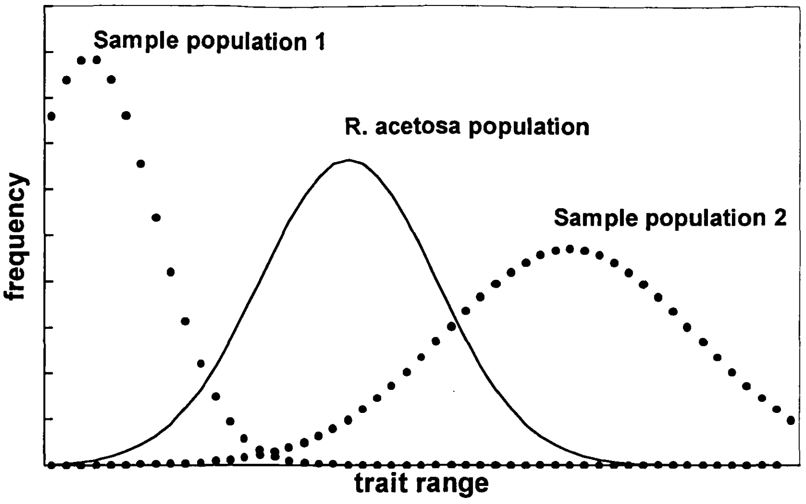


Figure 43: A population of *R. acetosa* (solid line) within a community of other plant types, represented by the sample populations (dotted lines) shown.

5.1.2 The incorporation of seedbank

The model described in Chapter 3 admits a number of assumptions for simplicity. Perhaps the most unreasonable of these assumptions is the treatment of buried seed. A seed, when dispersed, is only considered viable when it lands on an empty lattice site. If the site is occupied by a plant, the seed is simply absorbed into the resource substrate (for resource conservation). It may be imagined that in certain ecosystems, where both strong competition and no cultivation occurs, this is an acceptable assumption. New seed is unlikely to displace existing plants, and existing plants are unlikely to be removed through cultivation or other means. However, in the more general case, this assumption is less likely to be acceptable.

The dynamics of arable systems offer a case where large amounts of seeds are produced yearly and removing the crop increases the chance of new seeds developing into plants as existing competition is removed. Such arable systems are of increasing experimental and theoretical interest, and particular attention is given to the persistence of genetic material in arable communities. Persistence of genetic material, represented here as the conservation of functional types, occurs in such intensely managed systems as a consequence of the banks of seeds. Thus, the system has a potentially diverse memory of both its previous occupancy and previous contexts, in terms of neighbouring communities. This memory can extend beyond ten years, and can come from external sources hundreds of metres away (Squire *et al.*, 1999).

Thus, it is important to consider the memory, or seedbank, in any generic model. Rather than dissolve a seed on an occupied site into the resource substrate, as is currently assumed, it is necessary to store that seed at that location for subsequent (potential) germination. Multiple seeds may be present at a single location, and this too must be incorporated. Further, seed germination currently occurs on a 'first-come-first-served' basis. The incorporation of memory into the model allows for a better representation of this process. This work assumes the context of arable systems, since support in the form of experimental data is immediately available from long-term work at the Scottish Crop Research Institute. However, the representation of the seedbank developed within this project will be generic in nature.

5.1.3 Improving spatio-temporal classifications

The analysis of spatio-temporal patterns in fungal communities described in Chapter 2 took place in terms of state transitions. The initial configuration of the system was remembered and subsequent spatial outcomes were contrasted with this initial configuration. The system was therefore characterised in terms of distance from the original arrangement. For the simple (6x6) spatial arrangements this measure was sufficient a characterisation for the purpose of demonstrating the presence of processes at a range of scales. However, for more complex configurations, either in plant systems (described above) or fungal systems (described below), a more detailed characterisation will be required.

Work undertaken by a colleague at Biomathematics and Statistics Scotland, Scottish Crop Research Institute, and described in Augustin *et al.* (1999), provides an extended classification scheme for state transition analysis. In this scheme, transitions are initially categorised as described in Chapter 2 and in White *et al.* (1998), and then further sub-categorised to provide detailed information relating to the patchiness of the system. More fully, each spatial location is categorised initially in terms of a current state with respect to a previous state. Each spatial location is then further categorised in terms of its neighbourhood, and is attributed a neighbourhood score between 1 and 5. The score is a measure of the position of a given location within a patch of locations of the same state. A score of 1 indicates that the given location has no neighbours of the same state. A score of 2 indicates that the given location has some same state neighbours and some differing state neighbours, i.e. that the location is at the edge of a patch. A score of 3 indicates that the nearest 8 neighbours all have the same state, i.e. that the location is within a patch. Scores of 4 and 5 indicate 24 and 48 same state neighbours respectively, i.e. that the location is within large patches. Such a classification scheme therefore gives temporal measures of proportion of states and patch dynamics, in terms of the size and position of those patches.

The classification scheme has been applied to field-scale studies of semi-natural vegetation, where data are derived from aerial photographs over a period of thirty years. The scheme is demonstrated to provide a useful measure of this spatio-temporal data set. Whilst the scales, both space and time, are very different in systems considered here, it is suggested that such a classification scheme may be employed to characterise better the spatio-temporal data observed in both experimental and theoretical systems. This characterisation, of course, applies equally to fungal and plant studies.

5.2 Applying the trait-based approach to the study of fungal community dynamics

5.2.1 Overview

The study detailed in Chapter 2 clearly demonstrated that fungal community dynamics are a consequence of both local and non-local effects. This prohibits the use of behaviour observed at small-scale systems to predict the behaviour of larger-scale systems. Moreover, the general approach of 'bottom-up' modelling is shown to be inappropriate for this fungal system. This section outlines the use of a 'top-down' modelling approach, as described in Chapter 3, to investigate such systems. Fungal species are characterised in terms of traits, and those traits are parameterised by contextual information.

A fundamental aspect of the work described in Chapter 2 was the tile-based experimental system, that allowed the design of simple experiments in spatio-temporally homogeneous environmental conditions in terms of resource abundance, constant temperature and isolation (via sterile petri dishes). Further, this system imposed discrete spatial scales as a consequence of the method of analysis. Such an experimental system readily lends itself to spatially discrete modelling, typified by cellular automata, allowing the investigation into complex issues of scale in highly simplified contexts. However, it is acknowledged that this system lacks immediate applicability to real systems. Here, complementary experimental and theoretical systems based on the conceptual framework developed in Chapter 3 are outlined. Notably, those systems no longer consider (agar) tiles and use soil as the medium of interaction. The systems acknowledge the complexity of that medium in the form of the measured traits.

5.2.2 Theoretical approach

The transition from a spatially discrete (tile-based) agar system to a spatially continuous (no tiles) soil system introduces additional aspects of complexity. The spatially discrete agar system allowed the profiling of fungal species behaviour in terms of expanse over space (tiles at the resolution of the quarter tile) in time. This expanse, by one species, was always into space already occupied by the other species. Encapsulated in this profile are properties relating to growth rate and space filling - measures of extent and density or activity in space - and combativeness, and these properties are likely to be resource dependent. With the simplifications present in the agar system, including no empty tiles, no resource limits (within the duration of the experiment) and uniformity in the agar itself, it is unnecessary to identify these properties independently. Growth rate and combativeness are clearly coupled in systems with no empty tiles, since growth must include invasion in fully occupied systems. Resource dependencies are not required to be addressed in a resource unlimited system. Space filling properties need not be considered since the agar is homogeneous in spatial structure and so density or activity of the fungal mycelia is not subject to variability in properties of the resource base (up to the inherent variability of fungal expansion). Sporulation was not considered in the agar system for simplicity, although clearly this process may impact on the colonisation of the tiles non-locally.

Soil is heterogeneously structured in space, in that features attributed to (natural) soil, including bulk density, degree of aggregation and moisture content, typically vary in space. That spatial structure is also continuous in nature; no artificial scales relating to tiles are present, although any experimental or theoretical treatment will necessarily impose scales in terms of an associated spatial resolution of that treatment (see below). Further, soil-based systems are typically only partially occupied in space by the fungal communities. Thus, many of the simplifications identified above are not appropriate in such a system.

The trait-based approach adopted in Chapter 3 provided a (localised) behavioural characterisation parameterised by contextual information, and it is anticipated that this approach will prove useful in such a soil-based system. The traits of fungal species may be profiled in suitably designed experimental systems, and these systems will admit a range of contexts in terms of measurable soil properties. This contextual parameterisation is to be extended to include the presence of other fungal species. Clearly, only a subset of all possible contexts may be investigated, although this subset should lead to a generalised mapping between behaviour and context. Such an approach will lead to the contextual parameterisation of those traits profiled. Currently the traits ‘growth rate’, ‘space filling’, ‘propensity to anastomosis’, ‘fecundity’ (via sporulation) and ‘combative ability’ are envisaged as being appropriate to characterise fungal species.

An experimental system has recently been developed which may allow the measurement of both 'growth rate' and 'space filling' traits in a range of contexts (other fungi and soil properties). Additional experimental systems that allow the profiling of other traits are not yet developed, and particular difficulty is anticipated when considering 'combative ability' since existing studies (White *et al.*, 1998) suggest this aspect is very sensitive to context. The experimental systems are anticipated to generate a range of values associated with each trait, via a series of replicated experiments, due to the inherent variation in fungal behaviour as indicated in Chapter 2. These stochastic outcomes may be represented as a distribution of trait values, as in the parameterised plant model described above. This trait distribution will be used to generate instances of trait values during the modelling of fungal species dynamics.

The experimental systems are developed to provide characterisations at the scale of the colony and accordingly attribute contextual properties at that scale. Currently it is not clear as to the range of scales over which context is important, as a range of scales exist up to the scale of the community. As an initial approach to this aspect, a larger-scale experimental system (relative to the characterising system scale) will be implemented and this system will be monitored in space and time (see below). A spatially explicit model will be developed allowing the representation of fungal species in terms of traits. This model will be drawn from the cellular automaton paradigm, although the selection of an appropriate neighbourhood and rule set may be driven by the state (occupancy) of the spatial location. Each species present in the theoretical system will be assigned characteristics as identified at the (smaller) scale of the characterising system. The theoretical system will be used to identify the evolution of the system (based on contextual properties derived at the scale of the characterising system).

Comparison between the experimental and theoretical systems will yield insight into the role of context. More fully, the differences between the dynamics of the experimental and theoretical systems may be overcome by introducing scale-dependent behavioural correction terms, i.e. terms that modify the behaviour (value) of a given feature (trait) at a range of scales, where scale determines the spatial extent over which context is considered. Searches will be conducted to fit the predicted outcomes to the observed outcomes, and this search will identify the form of the dependence between scale and behaviour (expressed in terms of a trait value). Thus colony-scale parameterisation will be extended to the scale of the community.

Initially, the investigations will take place in sterile soil, i.e. soil where only the fungal species are present. Given that the dependencies between scale and behaviour have been identified in such sterile environments, it should then be possible to predict the dynamics of large-scale systems in those sterile environments. However, for more general applicability non-sterile soil must be considered, where non-sterile soil contains an indigenous microbial community. It is anticipated that the non-sterile systems will alter the behaviour of the fungal species.

A theoretical approach may be employed to predict the outcome of non-sterile systems, based on trait values initially identified by colony-scale experiments and subsequently corrected for sterile soil systems at the community-scale. The trait values will be further corrected to admit the indigenous microbial community by (again) fitting predicted to observed outcomes – using the search mechanism – in those non-sterile systems. Different forms of community will require different forms of corrective adjustments, and the nature of those adjustments is related to the nature of the indigenous microbial community. Thus fungal species could be used as probes for categorising indigenous communities present in soil, where the response of the added fungal species acts as an indicator of the original community present.

5.3 Summary

The initial aim of the project was to develop a computer model to predict the dynamics of fungal communities. A simple experimental system and complementary theoretical approach were developed to initiate this investigation. The tile-based experimental system described in Chapter 2, and described in some detail in White *et al.* (1998) and Sturrock (in prep.) allowed the implementation of carefully designed experiments within sterile microcosms, and facilitated analysis of those experiments at a fine resolution. This system provided detailed spatio-temporal data relating to fungal interactions. These data were used to parameterise, through small-scale experiments, and validate, through large-scale experiments, a theoretical model.

The theoretical approach described in Chapter 2 clearly demonstrates that the dynamics observed in even simple fungal communities, here comprising two species in especially simplified systems, are a consequence of both local and non-local properties. Further, the form of the model used suggested the nature of those local properties, in terms of the parameters v and w, and those non-local properties, where the effective scale change of sub-communities via the process of anastomosis is encapsulated in the parameter δ. In cases such as this, where the dynamics of the system are driven by processes over a range of scales, the extrapolation of results derived from experiments conducted out of the context of the community to represent system behaviour is clearly precluded (Bown *et al.*, 1999). Others have noted the importance of scale-dependent behaviour and scale-related processes, i.e. processes that are apparent at only a subset of all spatial scales, for example Wu and Levin (1994), Ziv (1998).

In response to these issues a conceptual framework was introduced in Chapter 3. Fundamental to this framework is the consideration of community dynamics in a 'top-down' sense. Rather than assuming that global behaviour may be generated from a local set of rules (typically parameterised out of context) the 'top-down' approach described here assumes that global behaviour may be generated from a local set of rules (as the dynamics are, of course, driven by local elements) that are parameterised by contextual information. By admitting contextual parameterisation to the local rule set non-local effects are considered.

The nature of the contextual parameterisation is specific to the application area. In the case of the fungal studies the existing experimental system was specifically designed for 'bottom-up' analyses. The desire to maintain the strong coupling between experiment and theory in these fungal studies meant that a change in theoretical approach demanded a corresponding significant change in experimental system. Thus, the framework was developed in the application area of plants systems. This area is well supported by literature and, importantly, a wealth of data was readily available from a Scottish Executive Rural Affairs Department (SERAD) funded programme as noted above. Whilst the framework presented in Chapter 3 is presented in terms of a plant-based system, the fundamental concepts arising from this development are applicable to fungal and plant systems alike. Indeed, the previous section discussed the application of the conceptual framework to fungal communities in some detail.

This plant-based application represents the essential features of individual plants interacting in terms of competition for space and resource. The behaviour of a given plant is described in terms of functional trait values and it is assumed that the plant is in an optimal context (in terms of resource). The behaviour of that plant is modified according to detractions from those optimal resource conditions, and these detractions occur as a result of both local resource shortage and non-local competition for resource. Thus, the dynamics of individual plants is driven by both local and non-local features. Moreover, the dynamics of the underlying resource substrate is driven by both resource substrate properties (principally release and replenishment rates) and the community interacting over that resource substrate – different community compositions make different resource demands on the system. Hence, there is a coupling between the composition of the community and the spatially structured resource.

The demonstrative runs presented indicate that the model gives rise to patterns suggestive of known biological phenomena. In particular, succession arises as a consequence of this coupling between community composition and environmental conditions. The community and environment co-evolve in time and space, each driving the dynamics of the other. Chapter 4 suggested that this coupling may, in a restricted set of circumstances, give rise to some form of coexistence. More fully, the notion was considered that certain combinations of functional trait values – some balance in function, according to environmental conditions, when considered at the scale of the community – give rise to coexistence.

A simple framework for investigating this concept was developed. An appropriate search mechanism was determined and implemented, where this search mechanism assumed some structure in the search space, i.e. that good solutions lay close to other good solutions and that poor solutions lay close to other poor solutions in that state space. Initial results clearly demonstrated that this search mechanism was able to identify combinations of trait values in (state) trait space that gave rise to a particular phenomenon; in this case a simple measure of maintenance of function: the time population levels remained above a threshold. The search mechanism was also able to direct a search to such, albeit local, combinations of trait values. The solutions identified by the search each comprise sixty search-alphabet characters and are therefore complex data sets. Currently no approach has been developed to interpret properly these data sets, although measures including plotting values pairs of traits against each other, more focused searches and other search strategies are being considered. Certainly the work indicates the value of considering system properties at the scale of the community.

The previous section has indicated the way in which the framework developed in the context of plant systems may be applied to further the investigation into fungal community dynamics. Fungal species may be represented in terms of traits, where particular species have particular trait values. Further, as in the plant system, those traits may be parameterised by contextual information. Complementary experimental and theoretical systems may be used to identify both the values of the traits for species and the impact of context on those traits at a range of spatial scales. The experimental system will be used to generate spatio-temporal data at different scales, and the theoretical system will be used to identify corrective adjustments, through searches to fit data observed at one scale to data observed at another. This process, leading to the amendment of trait values for scale, will identify the dependencies between scale and behaviour. Such dependencies have been observed in the 'bottom-up' approach described in Chapter 2. This 'top-down' approach to studying fungal community dynamics aims to investigate more fully the relationship between scale and behaviour.

Clearly, the initial aim of a predictive model of general fungal community dynamics has not been met. Such a model would reflect an understanding of complex processes acting over a wide range of spatial and temporal scales. The approach has demonstrated the presence of both local and non-local processes, and suggested the nature of some of those processes. This observation has made apparent the need to consider approaches admitting a range of scales in this parameterising process, and such an approach is termed 'top-down' in this thesis. The 'top-down' mind-set was applied to the context of plant systems initially, with continuing consideration as to the applicability of the concepts arising from this effort to fungal community studies. The application of the 'top-down' approach is outlined in the preceding section.

Finally, it is important to note that in this chapter, and throughout the thesis, the importance of linking experiment and theory is maintained. This coupling has provided a sound platform for inter-disciplinary research that has been central to the progress of all studies described here. This collaboration has allowed the identification of detailed, quantitative, spatially explicit models to explore experimental and natural systems alike. It is the firm belief of the author that the continued (close) union of experiment and theory, where each drives the other, will eventually lead to an understanding of the nature of scale-dependent behaviour known to be present in both fungal and plant communities.

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Appendix 1: Model algorithms

A1.1 Fungal community dynamics model

A1.2 Plant community dynamics model

A1.1 Fungal community dynamics model

```
Begin main
For 100 replicates
    Initialise lattice with experimental layout
    For cycles = 1 → maxcycles
        For each cell
            Evaluate frequencies of subject species, $fs$, and challenger species, $fc$
        For each cell
            Evaluate outcome
        If cycle = sample point (8 or 12 days)
            Calculate and store state transitions
End main
```

```
Begin evaluate outcome
Determine probability vectors of outcomes from binary experiments (see Chapter 2 for notation)
$ps = [\ p(A|A,A,t), p(B|A,A,t), p(AB|A,A,t)\ ]$          (note ps = [1,0,0])
$pc = [\ p(A|B,A,t), p(B|B,A,t), p(AB|B,A,t)\ ]$
$ps = ps \times fs$, $pc = ps \times fc$
$poutcome = ps + pc$     (where + is vector addition)
normalise $poutcome$
$psubj = poutcome(1)$, $pchal = poutcome(1) + poutcome(2)$
generate random number, $R$
if ($R \le psubj$) cell outcome = subject species
else if ($R \le pchal$) cell outcome = challenger species
else cell outcome = mixed (both species)
end evaluate outcome
```

A1.2 Plant community dynamics model

(† indicates subsequent expansion)

```
Begin main
Configure environment:
    Initialise substrate (homogeneous, heterogeneous – patterns)
    Set individual's type values (from file or keyboard)
    Distribute individuals over substrate
For maxcycles:
    Process environment:
        Resource acquisition †
        Resource usage †
End main

Begin resource acquisition
For each site in substrate
    Assess resource demand †
    Process resource demand †
    Replenish site by amount specified in replenishment rate
End resource acquisition

Begin assess resource demand
For each site
    For each individual accessing that site
        Identify resource demand made by that individual
End assess resource demand

Begin process resource demand
```

```
Limit resource requests by resource availability (proportional to demand)
Distribute (limited) resource to individuals
Deplete site's current level by (limited) demand
End process resource demand


Begin resource usage
For each individual
        Allocate resource †
        Assess development †
        Produce offspring †
End resource usage algorithm


Begin allocate resource
If acquired resource > required resource
        Increase surplus store by (acquired resource – required resource)
        Acquired resource = required resource
If acquired resource < required resource
        Increase acquired resource by accessible store in surplus
        Decrease surplus store accordingly
Increase reproductive store by (acquired resource x reproductive proportion)
Increase non-reproductive store by (acquired resource x (1 - reproductive proportion))
End allocate resource process


Begin assess development
If uptake amount, integrated over assessment period < shortfall survival period
        Individual dies
If individual stores ≥ requirement for next development stage threshold
        Progress to next development stage
End assess development
```

```
Begin produce offspring
If in fecund phase (determined by time and development dependent fecundity vectors)
    Evaluate fecundity †
    Disperse offspring †
    Amend development stage †
End produce offspring

Begin evaluate fecundity
Determine total store for reproduction – repro. store limited by release rate + surplus store
Identify number of offspring from fecundity storage relation using total store for reproduction
Deplete stores by total store for reproduction, to represent structural loss
End evaluate fecundity

Begin disperse offspring
For each offspring
    Randomly place offspring on lattice (with limit set by seed dispersal pattern)
    If location is occupied
        Remove offspring
    Add resource amount carried by offspring to new site's current level
End disperse offspring

Begin amend development stage
Determine total store of individual (after reproductive losses)
For each development stage
    Identify development stage requirement
    If total store < development dependent stage requirement
        Assign current development stage to development stage of individual
End amend development stage
```

Appendix 2: Published work

Bown, J. L., Sturrock, C. J., Samson, W. B., Staines, H. J., Palfreyman, J. W., White, N. A., Ritz, K., and Crawford, J. W., 1999. Evidence for emergent behaviour in the community-scale dynamics of a fungal microcosm.

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As seen in *FEMS Microbiology Ecology,* **27**, 21-32.