Determinants of *Betula* spp. Invasion of Lowland Heath

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Thesis submitted for the degree of Doctor of Philosophy of the
University of Liverpool.

September 2002

THE UNIVERSITY
of LIVERPOOL

Declaration of Authorship

The work contained within this thesis is entirely my own:

....

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September 2002.

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Acknowledgements

I would like to begin by thanking my supervisors Phil Putwain and Nigel Webb for their continued support and help throughout my PhD research. I would also like to thank *all* the staff at CEH Dorset, who provided me with so much assistance over the years. There are too many people to thank everyone in person but I would like to give special mention to James Bullock, Rob Rose and Karsten Schönrogge.

Thanks also go to NERC, who funded the research, The University of Liverpool, Horsell Common Preservation Society, Forest Enterprise, English China Clays and the RSPB.

I would finally like to thank all the people who have supported (and tolerated) me on a personal level over the last few years. Again there are too many to list (you know who you are anyway) but I would particularly like to thank Annette Manning and Liz Hale to whom this thesis is jointly dedicated.

Pete Manning
September 2002.

Abstract

1. The invasion of *Betula* spp. (*B.pendula* and *B.pubescens*) triggers a phase transition between lowland heath and scrub vegetation states. Transition to scrub is currently the most serious threat to the conservation of UK lowland heath; it has been found to correlate with soil phosphorus sorption capacity (PSC) at the landscape scale.
2. It was hypothesised that *Betula* invasion of Lowland heath was limited by numerous factors that may be subdivided into safe-site and seed limitation and that phosphorus availability was a key axis in the determination of a *Betula* safe-site.
3. An implicit assumption of earlier research was that PSC affected the P available to invading plants. An approach combining observation, statistical modelling and experimentation found that PSC affected the retention and availability of phosphorus in heathland soils. Synthesis of these findings with the published literature suggests that the direct effect of PSC on P-availability is small compared to indirect effects on organic matter (SOM) accumulation and vegetation cycling.
4. These findings allowed the hypothesis that P-availability affects the likelihood of invasion to be tested within an experimental framework. P-availability, seed rain and disturbance were experimentally manipulated in a multifactorial field experiment on a wet heath ecosystem in a stable, uninvaded heath area. *Betula* seedling densities and numerous covariates were also measured. It was assumed throughout this research that *Betula* seedling densities were indicative of the likelihood of heath-scrub transition.
5. Analysis of deviance found that all three treatments had significant effects on *Betula* seedling densities with seed availability proving to be the single greatest limitation at the site. Conversion of the experimental treatment factors into a continuous form allowed for a more detailed description of the phase transitional area within the site. The most significant descriptors of seedling densities were seed-rain, various plant neighbour variables and P-availability.
6. Replication of this experiment with fewer treatment levels and replicates at two additional sites found that the identity of the factors controlling *Betula* seedling densities was broadly similar, (e.g. vegetation and seed availability factors played a role at all sites) but that their relative contributions to within-site heterogeneity varied widely.
7. A single statistical model was fitted to data collected from three experimental sites. The model, which explained 59.8% of the deviance in seedling densities, describes *Betula* colonisation as a function of biomass density, necromass density, vegetation height, seed bank density, phosphorus availability, and to a lesser extent, soil water content. The form of the fitted relationships was complex with numerous interaction and polynomial terms. If the model is applicable to a wider range of conditions then it may be concluded that it

is heathlands close to seed sources and in the degenerate state, and possibly those subjected to severe burns, that are the most likely to shift to the *Betula* scrub state. At larger scales these conditions are probably most common in low management intensity, high phosphorus sorption capacity (PSC) regions.

8. Validification of the combined-site model was attempted using data that was equivalent to that used in the fitting of the model and which was collected over two 5ha grids of 130 sampling points and covering a wider range of heathland environments. Low predicted and actual seedling densities prevented formal testing of the models accuracy but predictions were qualitatively accurate, despite extrapolation.
9. Exploration of spatial heterogeneity in the determinant factors using the aforementioned spatial grid data, was achieved with geostatistics. This revealed that seed bank densities and edaphic factors displayed small-scale patchiness of around 50m while vegetation factors possessed longer ranging autocorrelation resulting in single across-site gradients. The proportion of spatially structured variance in the variables, within the studied range (17.6-150m), was low for many factors. The pattern of these factors is discussed with reference to the exclusion of *Betula* colonists and management recommendations are proposed.
10. It is concluded that the combined-site model provides a coarse but fairly accurate definition of the phase-transitional area between lowland heath and *Betula* scrub ecosystem states and that the determinant factors are at larger scales governed by landscape-scale processes (e.g. soil (PSC), climate and management regimes). These factors may explain regional differences in the scale and extent of scrub transition.

Glossary

Within the thesis are a number of ecological terms with differing semantic connotations. To avoid confusion a glossary is provided below. The majority of the definitions are either directly cited or derived from those given in Calow (1998) and are credited as such. The definitions without credits are my own.

COLONISATION

The process of arrival of a species (as adults, juveniles or propagules) in an unoccupied patch of habitat. Establishment does not necessarily follow colonisation as most colonists die without establishing a self-replacing population (Crawley, in Calow 1998)

DISPERSAL

Movement of individuals away from where they were produced (Smith, in Calow 1998)

ECOTONE

Defined by di Castri *et al.* (1988) as "the zone of transition between (different) adjacent ecological systems with characteristics uniquely defined by time and space and the strength of the interaction between the adjacent ecological systems". In contrast to an ecocline an ecotone is usually used to describe abrupt transitional gradients (Ferry & Thompson, in Calow 1998). "Ecotones occur where there are threshold or non-linear responses to gradual gradients in the physical environment that cause long-term changes in ecosystem dynamics and the distribution of dominant species" (Gosz 1992; Risse 1995). "A system poised between two or more phases (see below) is an ecotone" (Loehle *et al.* 1996).

ESTABLISHMENT

A particularly confusing term. In population dynamics, the formation of a local breeding population (Crawley, in Calow 1998), but in plant ecology the term is more commonly used to describe the process of development and survival of individuals from seed to reproductive maturity. The intended meaning of this word should be clear within this thesis.

FACILITATION

Facilitation (of succession) occurs when the chance or speed of establishment of a given species is increased by the prior occupation of the site by another species (Grime, in Calow 1998).

INHIBITION

Inhibition (of succession) occurs when earlier invading species reduce the chance (or mean rate) of establishment of another (Grime, in Calow 1998)

INVASION

The colonisation and establishment of what is perceived as an unwanted or detrimental species often with an expanding geographical range. Invasion of exotic species is often seen as a separate process to invasion in succession but it is often controlled by the similar processes e.g. competition, resource availability and seed limitation (Pickett *et al.* 1987; Burke & Grime 1996; Crawley 1987). Invasion will be viewed as the net result of colonisation and establishment in this thesis. Invasion must be considered scale dependent, at the local scale a species has invaded where there is the presence of an adult, invasion at the patch scale is signified by the presence of a viable breeding population while at the landscape scale invasion is usually viewed as successful when a persistent breeding population has established.

PERSISTENCE

A measure of the stability of a system. Persistence is formally defined as "How long a variable lasts before it is changed to a new value. Systems that often change could be described as having a high turnover, so turnover would be the reciprocal of persistence. Persistence is measured as time" (Pimm 1991).

PHASE

"A state of a macroscopic system that is qualitatively different in its characteristics from other states of the same system" (Uzumov 1993).

PHASE TRANSITION

Phase transition is an interdisciplinary scientific term used to describe the transfer of a system from one qualitatively different phase or state to another. The nature of the systems phase depends upon a transition switch or critical point in which a state variable reaches a threshold and the transition from one state to another occurs. In this study the critical point in the phase transition from heath to scrub is *Betula* colonisation, a factor that depends upon a multivariate threshold in state variables (see Loehle *et al.* 1996 for a more detailed description).

POSITIVE FEEDBACK SWITCH

A process in which a community modifies the environment making it more suitable for that community (Wilson & Agnew 1992).

SAFE-SITE.

Sites suitable for the germination and establishment of seedlings.

SEEDBANK

A repository of dormant seeds found within the soil

SORPTION

P adsorption is defined as “any process in which phosphate ions in solution react with atoms on the surface of soil particles” (Barrow 1978). The retention of P is, however, a continuum between surface reactions and precipitation as after a certain amount of time physically adsorbed P is transferred to chemisorbed P; the surface bond is desorbable but the chemisorbed P is not (White 1980; Frossard *et al.* 1995). The combination of the physically and chemically sorbed pools is termed sorbed P. Sorption will be the term used in this thesis except when discussing the work of others who specifically state adsorption.

STABLE STATE

A stable state is represented by a point in the multidimensional state space of an ecosystem at which the state of the system remains constant (derived from Doebli, in Calow 1998). As most natural ecosystems are subject to continuous change and fluctuation the term 'stable state' is technically inaccurate but has by convention been retained over the more technically correct 'dynamic regime'. It has been proposed that assemblages must persist for at least one generational turnover to be classified as a state (Connell & Sousa 1983).

SUCCESSION

Directional change in community composition (Grime in Calow 1998)

A note on nomenclature

In keeping with the tradition of heathland ecology:

Betula or birch = both *Betula pendula* (Roth) & *B.pubescens* (Erhh.) unless stated specifically.

Calluna = *Calluna vulgaris* (L.) Hull

Bracken = *Pteridium aquilinium* (L.) Kuhn

Molinia = *Molinia caerulea* (L.) Moench

In all other respects nomenclature follows Stace (1997).

Chapter 1: Impacts and determinants of birch (*Betula* spp.) invasion on heathland ecosystems.

Introduction to Ecological State shifts

"Ecological dynamics are organised by more than one stable state, with abrupt shifts between stability domains being common" (Holling 1992). These changes are in many ways analogous to the 'phase transitions' identified by landscape ecologists studying the behaviour of ecotones in that critical points or thresholds in environmental conditions distinguish between the systems attraction to qualitatively different states (Scheffer *et al.* 2001; Loehle *et al.* 1996; Milne *et al.* 1996). A review of these processes reveals that transitions to alternate states, which are usually defined by the dominant plant species or functional group (e.g. *grass*land, *wood*land, *heath*land etc.), are usually initiated by the invasion of 'foundation species', typically the dominant (Petraitis & Latham 1999). These species typically modify the environment making it more suitable for their and/or their offspring's' survival (Peterson 1984; Wilson & Agnew 1992) and causing changes in the environment that generate successional patterns (Chapin *et al.* 1997) thus reinforcing the widespread changes in both community composition and ecosystem properties.

It has long been observed that small changes in biota or environment trigger switches between alternate states and it would seem both plausible and likely that phase transition occurs when there is a change in dominance caused by the alteration of conditions which affect the recruitment success of the 'foundation' species. Disturbances often generate the changed conditions in which critical thresholds are reached (Petraitis & Latham 1999) but the condition of a system may also shift endogenously towards an unstable point or be moved gradually towards them by external forces e.g. climate changes. What is common to these processes is that the conditions and mechanisms apparently causing the switch appear to represent biophysical factors relating to the recruitment of the foundation species. These are likely to form a complex, multidimensional critical point or phase transitional area in phase space; i.e. the threshold conditions represent the edges of the invading species niche space.

In this thesis I present the results of an attempt to identify and describe the phase transitional area of the state shift between lowland heath and *Betula* spp. dominated scrub and woodland ecosystems. It is widely acknowledged that the invasion of *Betula* spp. generates a new, altered ecosystem state (e.g. Mitchell *et al.* 1999) and so this study focuses on *Betula* seedling establishment as the key moment of transition. Research is presented and discussed with respect to both the ecological understanding of phase transitions between alternate ecosystem states and the conservation and management of lowland heath ecosystems, where *Betula* invasion is a major problem.

Heathland Ecosystems

Lowland heaths are semi-natural ecosystems occurring on infertile soils at altitudes of less than 250m. They are generally restricted to temperate regions with mild winters and relatively long spring and autumn periods. The specificity of these conditions limits lowland heath to the oceanic regions of Western Europe (Gimingham, *et al.* 1979). Lowland heath is characterised by its ericaceous dwarf shrub community, with species composition organised upon a moisture gradient. Dry heath, e.g. the H2 and H3 communities of the National Vegetation Classification (Rodwell 1992), is dominated by *Calluna vulgaris* but may also contain *Erica cinerea, Ulex minor* or *U.galii* and scrub species (e.g. *Ulex europaeus*, *Pinus sylvestris* and *Betula* spp). *Calluna* persists in damper, wet heath sites e.g. the M16 community but *E.cinerea* and the *Ulex* species are lost from the community which, with waterlogging, becomes increasingly dominated by *Molinia caerulea*, *Erica tetralix* and *Sphagnum* spp. These communities form the transitional type between wet heathland and the mires and peatlands (Chapman *et al.* 1989c). Although lowland heaths often support similar vegetation to upland heaths, or moorlands, as they are more commonly known, they differ from them by having higher temperatures, lower rainfall and lower nutrient status (Chapman & Clarke 1980). Lowland heath may develop naturally on sandy deposits but most heaths are believed to have arisen from forest vegetation where tree felling and grazing on freely draining soils has resulted in podsolisation (see below). After formation, the heathland ecosystem state is traditionally maintained by a host of utilitarian management methods including the burning and grazing of *Calluna* shoots, the use of *Pteridium aquilinum* for animal bedding and the utilisation of *Ulex* spp. for fuel, thatching and fodder (Webb 1986).

The biological diversity of most heathlands is low but they support a number of species that are effectively restricted to the heathland habitat. The better known of these species act as flagships for heathland conservation and include the Dartford Warbler (*Sylvia undata*), Woodlark (*Lullula arborea*), Nightjar (*Caprimulgus europaeus*), Sand Lizard (*Lacerta agilis*), Smooth Snake (*Coronella austrica*), Dorset Heath (*Erica ciliaris)* and Marsh Gentian

(*Gentiana pneumonanthe*). The survival of these species is highly dependent upon the persistence of the heathland habitat, e.g. *Sylvia undata* avoids woodland areas (Van den Berg *et al.* 2001), and so the existence of heathland areas increases the overall biodiversity of the landscape.

The unique combination of species in the heathland community coupled with the international scarcity of the habitat and the high proportion of European heath found in the UK means we have an international obligation to protect our heaths against further loss. This responsibility has been recognised and is currently served by the Site of Special Scientific Interest (SSSI), Special Protected Area (SPA) and Special Area of Conservation (SAC) status of most heathland areas.

The History of Heathland: Creation, Persistence and Decline

Although there is some evidence for anthropogenically induced heath formation dating back as far as 2500BC most heathland areas seem to have arisen in the Bronze and Iron ages when the oligotrophic brown earths of open woodlands were cleared. The process of podsolisation, which results in the formation of heathland ecosystems, is thought to be initiated by the removal of trees as bare soils are prone to erosion and nutrients are leached out the system. The establishment of ericaceous plant populations (e.g. *Calluna vulgaris*), either from newly colonists or the buried seedbanks of these depleted soils, is likely to be the second major process in the systems transformation. Willems (1988) observed recovery from the seed bank of *Calluna* heath after the felling of *Betula/Quercus* woodland which had established on heath c.50 years earlier. These species, once established, initiate a positive feedback mechanism (Wilson & Agnew 1992) that maintains the oligotrophic status of the heathland system. This mechanism operates through slow decomposition and nutrient release that in turn leads to low plant-available nutrient concentrations in the soil. The slow uptake and long residence time of the nutrients within the plant complete the cycle (Aerts & Chapin 2000). Concurrently, the high tannin and polyphenol contents of the ericaceous litter (which contribute to the low decomposition rates of the system) produce an acid mor humus that is inhospitable to earthworms and most plant species but tends to support mites, enchytraeid worms, springtails and a thriving fungal community (Killham 1995). *Calluna vulgaris* for instance, has been observed to acidify soils within 10 years (Miles 1985). Eventually, mineral soils become bleached from the leaching of humus and iron compounds that become redeposited lower in the profile forming a classic podsol soil type with a dark organic layer laying atop a pale mineral soil with a hardened iron pan. The podsolisation associated with woodland clearance is thought to have interacted with grazing and climatic deterioration to produce even stronger podsolisation and subsequently widespread heathland across lowland Britain (Gimingham *et al.* 1979, Webb & Haskins 1980).

Since their formation the lowland heaths of England have undergone numerous expansions and contractions but in the last century the trend was one of decline. From medieval times through to the onset of the industrial revolution heathland was utilised for multiple purposes including grazing and turf cutting (Webb 1998). This began to cease with the industrial revolution of the late 17th and early 18th centuries. Industrialisation brought about a decline in traditional management and a change in attitudes that led to the perception of heaths as wastelands. The corresponding changes in management practice and land use destroyed much of the characteristic biota of the heaths; fuel gathering on the Dorset heaths for example, declined from the mid 19th century when coal became available. This would have ended a direct check on scrub invasion that had persisted for centuries (Webb & Haskins 1980).

Estimates made in the early 1960s (Moore 1962) suggested that most of the UK's heathlands had lost at least 50% of their area since the early-19th century. The declining Dorset Heaths, which have seen an 80% reduction since the mid 18th century, are the best documented of these losses and have received a good deal of attention in the last 40 years (e.g. Moore 1962, Webb & Haskins 1980; Webb 1990; Rose *et al.* 1999). The single most important factor in the loss of the Dorset heaths has been the conversion of the nutrient- poor podsols into less acidic and more nutrient-rich agricultural land. The remainder of the direct losses is attributable to urban development, the establishment of coniferous plantations and to a lesser extent mineral extraction and the building of golf courses (Moore 1962). In recent years the formation of new plantations has waned but the general trend of destruction has continued with agricultural conversion accounting for 46% and urban/industrial development accounting for 37% of the heathland lost between 1978 and 1987 (Webb 1990). Direct heathland habitat losses in other regions of the UK (e.g. Breckland, Surrey and Hampshire) are also accounted for by the same principal reasons, although the relative importance of these factors varies from region to region (Moore 1962). In all cases, it is dry heathland that has suffered the greatest loss, mainly because of its undemanding conversion to other land uses.

As the conservation movement has developed there has been an acknowledgement by the public and legislators that both the heathland habitat and its associated species are endangered. The response to this has been to increase the status of legal protection on many heathland areas in the UK, safeguarding them against future developments. Despite the increase in legal protection, heathland area has continued to decline. In the last few decades the major threats to the heathland habitat and its biota have shifted from direct destruction to genetic and metapopulation problems associated with fragmentation and the natural colonisation of the heaths by woody invaders. The 100 remnant heaths observed in Dorset, 1960 for instance, were broken into 768 fragments by 1978; only 14 of these were greater than 100ha (Moore 1962, Webb & Haskins 1980). This fragmentation has been caused by a number of factors including the intersection of roads through the heaths and the formation of pockets of heath isolated by areas of scrub. Encroachment of scrub and woodland into lowland heath has been considerable and is widely thought to be a product of the cessation of traditional management methods, especially grazing and more recently burning. Webb (1990) for example, reports an extensive invasion of the Dorset heaths by Gorse (*Ulex* spp.), Birch and Pine (*Pinus* spp.) with the cover of these species increasing by 15% between 1978 and 1987. Widespread scrub invasion of the Dorset heaths is further evinced by the results of a remote sensing survey conducted by Veitch *et al.* (1995). This tentatively concluded that 9.98% of the heathlands found in the 19th century were now occupied by deciduous woodland. The encroachment covered 36.42km^{-2}, an area comparable with that of the remaining Dorset Heaths, 38.6km^{-2}.

The concurrent processes of fragmentation and successional change are thought to be interactive because fragmentation increases the likelihood of edge interactions with other habitat types (Webb & Vermaat 1990; Webb & Hopkins 1984; Nolan 2000). As the regions surrounding heathlands may contain higher densities of woody species, dispersal of these species into uninvaded areas may become increasingly frequent. Fragmentation could therefore accelerate the rate of invasion by woody species, in turn leading to greater habitat loss and further fragmentation.

Recent years have seen an increase in the intensity of conservation management on the Dorset heaths but woody invaders have continued to spread at a rate of 1.7% per year. This invasion is almost certainly a major contributor to a decrease in heathland area of 552ha from the 7925ha recorded in 1987 a loss that is, in contrast to the past, predominantly wet heath. This 'drying out' may be caused by the greater transpiration losses of the taller dwarf shrub vegetation and the now-widespread scrub and woodland vegetation types (Rose *et al.* 1999).

Other areas of the UK heathlands have undergone similar losses to Dorset, but it is the Surrey Heaths that have seen the most rapid decline with heathland area being reduced from an estimated 20,020 ha in 1863 to 3060ha in 1985 (Farrell 1993). Surveys combining the quality and resolution of the Dorset Heathland Database have not been executed in Surrey but anecdotal evidence indicates that the major cause of heathland loss has been successional change. This viewpoint is supported by numerous accounts describing tree invasion (Chapman *et al.* 1975; Chapman *et al.* 1989b) and a lack of evidence documenting widespread conversion to farmland. From the early 19th Century onwards "nearly a sixth of the whole of Surrey turned spontaneously into woodland, mainly in the mid-nineteenth century. In the 1790s Surrey had been about 20% heath and 4% woodland. It is now according to the Ordnance Survey 3.2% heath and 15.6% trees" (Rackham 1986). The rate of pine and birch encroachment was thought to have been particularly rapid in the 1950s (Farrell 1993) and land use maps of the region support this view by showing that many small heaths present in 1932 were totally covered in woodland by 1959 (Harrison 1976). Birch invasion has also been described as problematic on the larger heaths of Thursley and Hankley commons (Harding 1981). The main causes of this rapid and widespread invasion of the Surrey heaths are thought to be linked to changes in management practice, namely the cessation of grazing and the spread of pines that were introduced into the area for forestry purposes around 1830. Other factors such as high phosphorus availability (see below) and declines in Rabbit grazing at the time of the myxomatosis outbreak may have also played a role in this rapid encroachment.

The Impact of *Betula* Invasion on Heathland Ecosystems

A number of species are responsible for dwarf-shrub to scrub succession on lowland heath. These include *Rhododendron ponticum*, *Pinus sylvestris*, *Ulex europaeus*, *Pteridium aquilinum*, *Salix* spp. and *Betula* spp. Although all induce changes in the soil and plant communities it is *Betula* spp. that are thought to have the most dramatic and irreversible impacts on the heathland environment (Mitchell *et al.* 1997; 1998; 1999).

The reputation of *Betula* as a soil improver and transformer of community structure is a long established one and there is little doubt over its ability to generate phase-transitions between alternate ecosystem states. In a correlational study based upon the examination of different aged sites Dimbleby (1952) observed that the growth of *Betula* stands on *Calluna* moors caused a gradual increase in pH, the formation of a mull horizon and the slow disintegration of the iron pan. From the accumulated evidence he estimated that *Betula* would convert the raw humus of the moorland to a mull within 60-100 years of invasion. Miles & Young (1980) found a similar pattern of change when observing upland heaths. Here *Betula* was found to transmute the mor humus to a mull type and increase the pH, base status and rates of N mineralisation and cellulose decomposition. These changes were simultaneous with the death of the *Calluna* and replacement by *Deschampsia flexuosa* and *Vaccinium myrtillus* and the appearance of woodland species including *Agrostis* species, *Oxalis acetosella* and *Hypericum pulchrum* alongside corresponding changes in the soil seedbank. In contrast to this Satchell (1980a,b), who compared experimentally generated *Betula* woods with neighbouring *Calluna* moorland, found relatively little change in the supporting podsols 30 years after colonisation. Although there were increases in pH, K, Ca, Mg, P, N, earthworm populations and a transition to a *D.flexuosa* dominated community, the soil profile under *Betula* remained as a fully differentiated podsol. Miles (1981) helped elucidate this apparent contradiction in another study of moorland. He concluded that soil change was minimal under *Betula* in low nutrient soils but that it brought about many changes in more fertile soils. These included a blurring of the soil horizons, increases in pH, exchangeable Ca and total P and decreases in C:N, C:P and C:K ratios.

Mitchell *et al.* (1997) observed concurrent changes to both soil and vegetation during the phase transition between *Calluna* heath and *Betula* scrub. In this study *Betula* invaded sites known previously to be heathland were compared with adjacent uninvaded sites. It was assumed that successional sites were similar to open heath sites before the invasion occurred. *Betula* was found to bring about a full phase transition from heath to scrub eliminating virtually all heathland species and presumably facilitating the co-invasion of several other species of which *Agrostis capillaris*, *Pteridium aquilinium*, *Pseudoscleropodium purum* and *Rubus glanduosa* were the most common. Changes in the soil were also substantial; extractable Ca, extractable P and extractable ammonium concentrations displayed dramatic increases as did pH which was >5 in some of the *Betula* stands but only 3.5-4 in the heaths. Further evidence of *Betula* induced environmental change is provided by the work of Rode (1995), who found that German heaths displayed higher transmitted PAR and a lower turnover of nutrients via litter fall than the neighbouring *Betula-Pinus* woodland (formerly heathland) resulting in a larger pool of plant-available nutrients.

In the long term, changes to the environment may be even more drastic than those described above. *Betula* is a pioneer species which may, but rarely, form self replacing woodlands in the lowlands so it is likely that *Betula* scrub represents one equilibrium point on a long-term successional trajectory to a very different stable state. Likely positions on this long-term trajectory are the NVC W16 *Quercus-Betula-Deschampsia flexuosa* woodland, the W10 *Quercus robur-Pteridium aquilinium-Rubus fruticosus* woodland, the W15 *Fagus sylvatica-Deschampsia flexuosa* woodland and, on wetter sites, the W4c *Betula pubescens-Molinia caerulea-Sphagnum* woodland (Rodwell 1991). Kuiters and Simm (2002) describe *Betula-quercus* and *Fagus-Quercus* communities as post-heath states in the Netherlands but the eventual community states and the temporal scale of transition are unknown because no detailed scientific studies have been made as to exactly what the ultimate post-*Betula* invasion communities may be.

Mechanisms controlling post invasion ecosystem state shifts

The physical and biological mechanisms, which regulate the community change following *Betula* colonisation, were studied experimentally on Scottish moorland sites by Hester (1989) and Hester *et al.* (1991a,b,c.). In the early stages of invasion the reduced light penetration of the *Betula* canopy may cause etiolation in *Calluna* thus increasing its vulnerability to winter damage. It was also found that the lower light and higher nutrient conditions created by the *Betula* canopy reduced the competitive strength of dwarf shrubs when grown with graminoids like *Agrostis capillaris* and its common precursor in post *Betula* colonisation, *Deschampsia flexuosa.* These species came to dominate the understorey as the *Betula* canopy developed, forcing the ericoids out of the community. Grazing under established birch hastened this species replacement. The exact mechanisms that raise nutrient availability in the soil of *Betula* scrub are unknown but the change is usually attributed to its greater relative P content and high litter decomposability (Mitchell *et al.* 2000). *Betula* may also acquire nutrients that were previously unavailable to the heathland flora from deep within the soil profile.

Suggestion that nutrient enrichment is an important mechanism in phase transitions away from heathland systems is supported by numerous studies of Dutch heaths. These demonstrate that increased nitrogen deposition, and therefore the nutrient status of heathland soils, consistently triggers a community shift from the dominance of ericaceous shrubs to that of more competitive grasses (Aerts & Berendse 1988; Aerts 1989; Berendse *et al.* 1994). This work is anecdotally supported by that of Angold (1997) who observed a *Calluna* to *Molinia* shift at the sides of roads in the Hampshire heaths, areas where high nitrogen deposition would be expected. These grasses, of which *Molinia caerulea*, *Deschampsia flexuosa* and *Agrostis capillaris* are the most important, are also capable of transforming the system. *Molinia* for instance, interacts with a variety of soil components to form a more rapidly cycling system (Aerts & Chapin 2000) characterised by, amongst other properties, the breakdown of the heathland podsol and an increased rate of nitrogen mineralisation (Berendse 1990).

The successional transitions associated with grass and scrub invasions of heathlands share common properties that, when coupled with descriptions of heathland formation, fit well within the theoretical framework of positive feedback switches (Wilson & Agnew 1992) and phase transitions (Loehle *et al.* 1996) between alternate ecosystem states (Scheffer *et al.* 2001; May 1977). The transformation of heathlands to scrub, woodland and grassland systems can be viewed as being a shift between two systems which are stabilised by a positive feedback mechanism in a symmetric switch in which "both community states modify the same factors but in different directions" (Wilson & Agnew 1992). This multidimensional switch, which controls both nutrients, light, pH and the faunal community, is mediated by the establishment of the foundation species (e.g. *Betula, Molinia, Calluna*) which triggers a phase transition shifting the system through an ecotone between evergreen, low productivity, slowly cycling systems to those dominated by species with higher productivity and faster nutrient cycling. The first state is characterised by the process of podsolisation described above. The other, depodsolised, state is characterised by the frequent release and rapid decomposition of plant litter nutrients resulting in higher inorganic nutrient concentrations in the soil and the rapid uptake and short residence time of soil nutrients (Berendse *et al.* 1989; Aerts & Chapin 2000). The change in the plant community is towards species with high growth rates and high nutrient losses e.g. Grimes C strategy, from the low growth rate and low nutrient loss heathland species, which are generally classified as belonging to Grimes S strategy (Berendse 1994). The key determinant of this switch and therefore the nature of the system is the invasion of the foundation species into the heathland community; a critical point determined by a species-specific multivariate threshold (see below).

Extent and management of *Betula* invasion.

The loss of heathland to urban development and its conversion to intensive agricultural or forestry use is an issue that is largely within the jurisdiction of planners and landowners. The prevention of successional change, however, is a problem whose solution is within the scope of conservation management. Like all conservation resources those of heathland managers are limited, necessitating the use of cost-effective management methods in heathland conservation and restoration. Birch species are particularly problematic to managers; evidence suggests that once *Betula* woodland has reached maturity it is remarkably resilient to restoration management as the altered soil status and understorey community prove difficult to displace (Mitchell *et al.* 1999).

Successful control methods for *Betula* do exist (Marrs 1984; 1985; 1987a,b) but these are often labour intensive as the tree resprouts readily from cut stumps (Marrs 1984; 1987a) and it is associated with understorey species that are more competitive than those of heathlands on the enriched soil it generates. Because it can resprout from cut stumps *Betula* must be treated with herbicide to avoid regeneration. This may cause short-term detriment to the dwarf shrub community or may allow other species, e.g. *Pteridium aquilinium,* to become dominant (Marrs 1984; 1987a). Another problem in the restoration of *Betula* invaded heathlands is the cost. The clearance of 1ha of *Betula* scrub takes 4 people approximately 35 hours at a cost of £1507 (in 1992), making it one of the most expensive forms of heathland management (Auld *et al.* 1992).

Table 1. The area (ha) of *Betula* dominated land found within and around the dry heaths of Dorset.

Area (ha).	**1978**	**1987**	**1996**
Dry Heath	2551.7	2012.8	2056.7
Humid Heath	1474.7	1627.7	1765.6
Betula Carr	98.7	103.8	51.98
Betula Scrub	110.58	186.5	237.59
Betula Woodland	209.3	260.5	301.71
Total *Betula*	418.58	550.8	591.28

Further understanding of the severity of the birch invasion problem is gained when the evidence of ecological state shifts presented above is combined with information on the scale of *Betula* invasion. Of the species invading the heaths of Southern England *Betula* spp. covers perhaps more former heathland than any other invasive species. The net increase of *Betula* in the Dorset region has been calculated from CEH's Dorset heathland database using the data collected from the 1978, 1987 and 1996 Heathland surveys (Chapman *et al.* 1989c; Rose *et al.* 1999). The data relate to a repeated survey that has recorded virtually all the heathland in the Dorset area on a 200m x 200m basis. All land within each of these squares was categorised for its vegetation type, topography, management regime and several additional attributes. Although the vegetation was recorded on two nested 1-3 scales an algorithm has been devised to convert these values into percentage covers and therefore areas (Chapman *et al.* 1989c). The figures in Table 1. represent the estimated areas of *Betula* dominated vegetation found within and around the 2551.7ha of dry heath recorded in 1978. The overall increase is from 418.6ha to 591.3ha between 1978 and 1996. It must be noted however, that this analysis was complicated by the inclusion of managed areas, therefore underestimating gross *Betula* invasion.

In other regions of the country (e.g. Surrey and North Hampshire) the scale of *Betula* invasion is even greater but unfortunately data on the area covered by and increase of, *Betula* is not at present, available. Anecdotal evidence however, suggests that the values given for Dorset represent the low end of the scale (see above).

What determines *Betula* invasion?

When the information presented above is synthesised it reveals that a major component of the long-term persistence (*sensu* Pimm 1991) and conservation of heathland communities is a function of *Betula* invasion success. Of key importance to heathland conservation, therefore, is an accurate understanding of the processes that regulate this invasion.

Initial observations reveal that some heaths undergo a rapid colonisation by *Betula* but that others remain uninvaded for several decades. In the majority of cases regular grazing and burning are the believed causes of this stability but some heaths remain scrub free in the absence of management (Chapman *et al.* 1975; Chapman *et al.* 1989b) and the causal mechanisms through which management promotes heath stability are only partially understood. Meanwhile, at the patch scale, invasion occurs in both homogeneous and patchy fashions often with stands comprising of even aged individuals (Atkinson 1992). Although these phenomena suggest that there are inherent differences in the invasibility of heath the underlying determinants of these differences remain largely speculative.

The central question in this instance, as in many ecological studies (e.g. Eriksson & Ehrlén 1992; Shurin 2000; Rand 2000; Maron & Gardner 2000), is whether recruitment failure of the invader is primarily governed by local conditions, often defined in plant ecology as the number of safe-sites, or seed limitation. A number of studies suggest that local conditions play an important role in recruitment limitation of *Betula* (e.g. Gong & Gimingham 1984; Kinnaird 1974; Chapman *et al.* 1989b). Other studies (e.g. Nolan 2000 & Aradóttir *et al.*

1997) have suggested seed limitation as an important factor but such studies are fewer in number. This is probably due to the species' long distance dispersal capabilities, prolific seed production (Atkinson 1992) and the general underestimation of seed limitation by ecologists in the past.

The review given below describes the ecology of *Betula* spp, their dispersal capabilities and synthesises current knowledge on the determinants of 'safe sites' in heathland vegetation.

The Ecology of *Betula* spp.

Betula spp. are amongst the most common trees in the UK where they are successful colonists of a wide range of sites including spoil heaps, grasslands and heathlands. The two main *Betula* species in the UK are *B. pendula* (Roth) and *B. pubescens* (Ehrh.) a pair of ecologically similar species that share a wide geographic distribution and hybridise when *B.pubescens* is the male parent (Atkinson 1992; Holm 1994a,b). In comparison with most deciduous trees, *B. pendula* and *B.pubescens* would be classified as r-selected (*sensu* McArthur). This is justified by their short lifespan (60-70yrs), production of many (up to 43,000m^{-2} on the ground) light (0.12-0.17mg) widely dispersed seeds and the onset of reproductive maturity at an early age (5-10years) (Harding 1981; Atkinson 1992). The r-strategy of *Betula* is further evinced by its shade intolerance, a high seedling mortality of around 80-100% in the first year (e.g. Miles 1972) and the potentially rapid growth rate of both individual trees (Seedling RGR 0.5-0.9week^{-1}) (Grime *et al.* 1988) and population size. This life history strategy enables *Betula* to become a pioneer species of a wide range of sites previously uncolonised by deciduous trees (e.g. lowland heaths).

A review of the (extensive) literature on *Betula* spp. would suggest that the two major species in the UK overlap considerably in their habitat requirements and so in many habitats the distribution of the species is more easily accounted for by colonisation patterns than environment (Grime *et al.* 1988). The major ecological distinction between the two species is evinced by their habitat preferences; *B.pendula* is found more abundantly in warm and dry habitats, often growing on coarse-grained soils while *B.pubescens* is biased towards organic, mesic to moist soils with a more humid local climate (Holm 1994a;b). This leads me to believe that a major ecological difference between the two species is their organisation upon a water use and availability gradient.

Seed limitation

SEED PRODUCTION, DISPERSAL & PERSISTENCE

Betula is a prolific producer of seed; a single tree can produce as many as 9-10 million seeds per year. (Arnborg 1946 in Holm 1994a). This seed has a highly variable viability (0-100%) (Holm 1994a), as *Betula* produces seed, regardless of pollination (Atkinson 1992). Inconsistency in seed production is further influenced by climatic conditions, resource availability and predation (mainly by gall midges of the genus *Sumudobia*) (Holm 1994a). Although most *Betula* seeds fall within 40-50m of their source (Atkinson 1992) distances of up to 445m have been reported (Harding 1981) suggesting that the species are capable of colonising relatively remote areas.

Although *Betula* spp. are classified as having a transient or short-term persistent seed bank (Thompson *et al.* 1997) seed persistence is habitat specific. Stoglund & Verwijst (1989) for instance, found that seed half lives ranged from <1 year in wet meadows to >13years in forest soils. The latter figure may however, be an exaggeration as it was obtained using artificial burial methods and inaccurate assumptions of the seed's initial viability. A review of records given in the Northwest European Seedbank Database (Thompson *et al.* 1997) reveals a wide range of values for *Betula* seed longevity that may be summarised by stating that most studies find seed longevity to be short (<1 year) but potentially >2 years for both species. The combination of wide-ranging dispersion of *Betula* spp. and their long shedding period (June-April) means that although the seeds are usually short lived they form a virtually continuous presence in the seed banks of many heathland soils. Mitchell *et al.* (1998), for instance, found that the seeds of *Betula* spp. were present in the soils of many uninvaded heathlands although densities were <800m^{-2}, substantially lower than those of its principal heathland competitor *Calluna vulgaris* (2000-2800m^{-2}). On sites invaded by *Betula* its seed bank ranged between 400 and 8000m^{-2}.

Evidence of seed limitation in *Betula* can be seen in studies at both patch and landscape scales. On eroded Icelandic lava fields Aradóttir *et al.* (1997) found the colonisation patterns of *B. pubescens* to be affected by wind direction at distances >4m from an extant population. This suggested that despite a generally effective dispersal capacity, seed limitation begins to play a role in recruitment limitation at short distances from the parent tree. At the landscape scale, Nolan (2000) found that increases in the area of scrub on contiguous patches of the 4ha squares of the Dorset Heathland Database could be predicted by both the density of dwarf shrub species and the area of invasive species in a patch. A result that suggests that heath-scrub transition shares properties with contagious epidemics. The low fit of the models (r^2 typically = <40 %) suggest, however, that a number of other factors may also control the degree of scrub invasion.

Safe-site limitation

Following dispersal there are numerous factors including predation, competition, and physical stresses that control *Betula* establishment, a complexity that requires any formal definition of a safe-site to be multidimensional. The roles of these many factors, although interactive, are described separately below.

GERMINATION

There is considerable evidence to suggest that the successful establishment of *Betula* seedlings requires open and disturbed ground (Harding 1981; Satchell 1980a; Grime *et al.* 1988). This idea is supported by the germination requirements of the seed in which dormancy is broken by a light treatment. Black & Wareing (1954), for example, found (at 15°C) that *B.pubescens'* germination rose from 40% in the dark to 90% after 16h exposure to red light. Scarification or chilling treatments have been found to remove this light requirement enabling germination to occur where temperatures are >20°C (Atkinson 1992).

SUBSTRATE

In the post-germination phase, *Betula* seedling establishment is thought by many to be confined to bare mineral and humus soils (Atkinson 1992). This is attributable to the low seed reserves of *Betula*; only a short radicle is produced and this is unable to penetrate deep leaf litter or tolerate its fluctuating microclimate. In a study of both upland *Betula* woodland and *Calluna* moorland, Kinnaird (1974) found that *Betula* seedling densities were highest on cushion *Sphagnum* (430m^{-2}) followed by bare mineral soil (130m^{-2}) and bare humus soil (117m^{-2}). Densities were substantially lower on litter substrates (7m^{-2}). Furthermore, the litter supporting *Betula* seedlings was significantly shallower (mean 13mm) than the uncolonised litter (mean 32mm).

COMPETITIVE INTERACTIONS:

1. LIGHT & SPACE

Once the seedling has germinated it must compete with neighbouring plants for light and nutrients. As seedling stage *Betula* has a high light requirement it is rare for seedlings to survive canopy closure, which occurs in the building and mature phases of the *Calluna* cycle (e.g. Satchell 1980a). These observations support beliefs that the species' establishment is gap dependent, requiring an area of 25cm^2 when grown with *Calluna* (Miles 1974). An experimental study on Scottish heaths found that the establishment of *Betula* was most successful in the recently burnt and pioneer stages of the *Calluna* cycle; the degenerate phase also permitted the establishment of some seedlings. Mature and building phase *Calluna* restricted the establishment of virtually all *Betula* seedlings (Gong & Gimingham 1984). This requirement for low competition gaps is further evinced by the observation that *Betula* spp. frequently colonises and eventually replaces degenerating *Ulex europaeus* bushes (Grime *et al.* 1988).

2. PHOSPHORUS

Although the supply of virtually all plant nutrients in lowland heath is limited (Chapman 1967; 1970) phosphorus is particularly scarce with acetic acid extractable P being typically 0.05-50µg P g^{-1} (Chapman *et al.* 1989b). When this scarcity is considered alongside the renowned growth-response flexibility of *Betula* to phosphorus (Harrison & Helliwell 1979) it would seem likely that variation in phosphorus availability plays an important role in the establishment of *Betula* upon heathland soils.

In comparison with *Calluna* and *Erica* spp. *Betula* spp. are thought to have a high nutrient demand (Atkinson 1992; Gimingham 1961; Bannister 1966). As both dwarf shrub and *Betula* species concentrate their roots in the organic matter of heath soils it is possible that they compete directly for nutrients and that their relative competitive strength depends upon both nutrient availability and the proportions of those nutrients contained within a number of soil pools. Soil phosphorus sorption characteristics, which can be thought to represent the capacity of the soil to retain the nutrient, were predicted to influence both the soil and vegetation dynamics of the heathland system (Chapman *et al.* 1989a). A nation-wide survey of 50 heathland sites allowed for the classification of the UK's Southern lowland heath soils into three phosphorus adsorption types, each of which relates to a distinct geographic area. They are:

1. The New Forest type (phosphorus sorption capacity (PSC) (originally presented as P adsorption maxima (*Pmax*) typically c.1500μg P g^{-1})
2. The Dartmoor type (PSC typically >2000μg P g^{-1})
3. The Dorset Type (PSC typically <100μg P g^{-1}).

Although the isotopically exchangeable P of the soils was found to correlate with the likelihood of the surrounding area being encroached upon by scrub PSC displayed a closer relationship (Chapman *et al.* 1989b). This finding led to the conclusion that in sites lacking in traditional management, where the PSC was <70μg P g^{-1} invasion was unlikely to occur, where values ranged from 70-700μg P g^{-1} invasion by *Ulex europaeus* was probable and where PSC exceeded 700μg P g^{-1} the colonisation of *Betula* and *Pinus* spp. was a distinct possibility. In sites that had received sustained grazing management invasion did not appear to occur, regardless of the phosphate sorption capacity of the soil. The accuracy of these conclusions does however, remain to be seen as the soils from the invaded areas were taken from remaining heathland patches, which may not be representative of the previously invaded soils. The same landscape gradient patterns that correlate birch invasion with P sorption capacities may also correlate with a number of other variables including the time of traditional management cessation, the regional abundance of *Betula* and the intensity of amenity use.

Perhaps the strongest direct evidence for nutrient limitation of *Betula* recruitment on heathland comes from studies of tree establishment in experimentally cleared and fertilised soils of various types in the North East of Scotland. The study, conducted by Miles (1974) found that nutrient enrichment boosted the growth and survivorship of *B.pubescens* on peaty and humus-iron podsols. Virtually no *Betula* establishment (both species) occurred without the addition of fertilisers.

INTERACTIONS BETWEEN PHOSPHORUS, DISTURBANCE AND COMPETITION

Although the total extractable P of heathland soils generally declines with depth (Pywell *et al.* 1994) the B -horizons of soils are thought to have higher PSC than those of the surface (Chapman *et al.* 1989b) as a result of the greater concentrations of iron and aluminium lower in the profile (S. Chapman, Personal communication.). Removal of the upper horizons or mixing of the soil may therefore bring seedlings into contact with a greater P availability than would normally be expected. Although findings of Allen *et al.* (1969), Traynor (1995) and Pywell *et al.* (1994) have all found the upper, organic layer of podsol to have the highest concentration of extractable P amounts of truly 'available' P may also depend on the location of more strongly sorbed P and its availability to the plant. The nature and vigour of the surrounding plant community is also likely to play are role in the availability of plant nutrients e.g. nutrient availability may be reduced during the active growth, high nutrient demand, phases of the *Calluna* cycle.

NITROGEN

Nitrogen is the other major limiting plant nutrient in the soils of heathlands (Gimingham *et al.* 1979). Although there is little observed evidence to suggest that *Betula* invasion is nitrogen limited there is a considerable body of evidence relating to nitrogen limitation in the grass invasion of the Dutch heaths (e.g. Aerts & Berendse 1988; Aerts 1989; Berendse *et al.* 1994). This, like the ecosystem changes following grass invasion, has many parallels with scrub invasion in the UK. As mentioned earlier, raised nutrient availability, resulting from anthropogenically enhanced nitrogen deposition has shifted the competitive balance of the Dutch heaths in favour of more rapidly growing grasses like *Molinia caerulea* and *Deschampsia flexuosa*. However, examination of N deposition maps show that, with the exception of East Anglia, the areas with the worst birch problems have some of the lowest N deposits in the UK with N loads generally higher on the Western heaths than on those of Surrey (CLAG 1997). A relationship between *Betula* invasion and N deposition, if one exists, is therefore likely to be complex and interactive with other variables. It is likely, for instance, that naturally low nitrogen mineralisation rates typical of heathlands, particularly those with a low soil organic matter content (Berendse 1990), can prevent *Betula* establishment. *Betula* colonists may be released from this limitation where N-deposition is high. It is also possible that a history of nitrogen deposition has changed the balance of nutrient limitation on many lowland heaths placing greater emphasis on the role of phosphorus limitation. This is thought to have occurred on the wet heaths of the Netherlands where high N depositions mean that it is experimentally added P rather than N that causes an increase in the abundance of *Molinia caerulea* (Aerts & Berendse 1988).

MYCORRHIZA

Of key importance in the establishment of *Betula* spp. is the early formation of an ectomycorrhizal link, a relationship that is thought to be especially important where N & P is low (Bjorkman 1970). By utilising plant-unavailable sources of nutrients e.g. proteins, peptides and amino acids (Abuzinadah & Read 1989a,b; Perez-Moreno & Read 2000, 2001a,b) ectomycorrhizas may allow *Betula* to become established in soils that would otherwise be inhospitable. Mycorrhizas also benefit the plant by increasing root size and longevity, improving water relations, protecting the roots against pathogens and possibly sequestering aluminium (Killham 1995). Miles and Kinnaird (1979) observed the germination of 833 *Betula* seedlings, only the five that formed mycorrhiza survived beyond the first year.

In many heathlands there may be both propagule and safe-site limitation of this important group of symbionts, which suggests that in certain conditions a lack of suitable mycorrhizal partners may limit *Betula* invasion. Mycorrhizal development is thought to be slow on podsols & peats (Miles & Kinnaird 1979) and it has also been suggested that mycorrhiza are inhibited by fungitoxic compounds exuded by *Calluna* roots (Robinson 1971). Studies that have focussed on the succession of mycorrhizas on *Betula* roots conclude that 'early stage' species common to young individuals e.g. *Hebeloma spp.* are thought to disperse from fruiting bodies rather than inoculate through direct contact with extant mycelium (Deacon *et al.* 1983). These early stage species are believed to contrast with 'late stage' species like *Amanita muscaria* in their capacity to initiate colonisation of seedling roots. As the mycorrhizal environment of heathlands is predominantly ericoid, spore limitation of early stage mycorrhizas may occur. Terwilinger & Pastor (1999) have described a similar limitation of tree invasion by mycorrhizal absence where pine invasion onto beaver meadows was limited by the dispersal of mycorrhizal spores by small mammals. However, some ericoid mycorrhizal fungi also have ectomycorrhizal morphotypes (e.g. Vrålstad *et al.* 2000). The abundance of such types and their compatibility with *Betula* will greatly affect the degree of mycorrhizal dispersal limitation.

Mycorrhizal type may also affect the outcome of nutrient competition. The arbuscular mycorrhizal invasive grasses of Dutch heaths are thought to be superior competitors for inorganic nitrogen, in contrast to ericoids, which, it has been suggested, are superior competitors for organic N forms (Aerts & Chapin 2000). Similarly, ectomycorrhizas, as found on the roots of *Betula,* are thought to be less effective at obtaining organic P than ericoid mycorrhizas (Allen 1991) thus potentially placing a greater importance on the availability of inorganic P forms when *Betula* is growing in close competition with ericaceous plants.

OTHER FACTORS

Betula, like any organism, is subject to the bio-physical pressures of the environment with damping off, drought, frost heaving and flooding all being seen to equate with high *Betula* mortality (Atkinson 1992). The low pH of heathland soils is a physical constraint to many plant colonists that appears to be both created and favoured by the ericoids. Although *B.pendula* has a pH range of 4.0 to 6.8 and is most common on soils of pH <5 (Grime *et al.* 1988) root damage occurs at pH of 3.5 (Harding 1981) potentially limiting its growth and survival on some heaths. Direct allelopathy by *Calluna* has also been postulated (Robinson 1971).

The role of Disturbance

Disturbance, "a mechanism which limits plant biomass by causing its partial or total destruction" (Grime 1979), is an integral part of heathland ecosystem dynamics. Not only does it affect the endogenous dynamics of the dwarf shrub vegetation but also the interaction between dwarf shrubs and the species of alternate vegetation states such as scrub and grassland. Disturbance to heathlands is usually associated with anthropogenic activity and comes in a number of forms, many of which are traditional management techniques. The effects that these are thought to have on *Betula* establishment are described below.

GRAZING

Grazing, once a major use of heathlands declined throughout the twentieth century perhaps reaching its lowest levels around the myxomatosis outbreak that removed the last vestiges of grazing pressure on many of Britains lowland heaths (Chapman *et al.* 1989b). It has recently been re-introduced on many heathland reserves where it is generally believed to have a net positive effect on heathland persistence.

Traditional practices of grazing livestock on heathland are thought to have limited scrub invasion for many years. *Betula,* which is grazed by sheep, cattle, deer and rabbits amongst others, (Harding 1981) is sensitive to grazing (Kuiters & Simm 2002), with the risk of damage increasing greatly once it has risen above the field layer (personal observation). In the survey of Chapman *et al.* (1989b) sites grazed by domestic animals displayed little or no evidence of scrub invasion. Suppression of woody species by grazing animals is also documented by the work of Bullock & Pakeman (1997) who found strong but not significant trends for reduced scrub cover on a variety of heavily grazed lowland heath sites. Bokdam &

Gleichman (2000) found that *Betula* successfully colonised grazed sites but that cover was maintained at low levels by the grazing & browsing

In addition to direct damage, grazing animals affect *Betula* regeneration by effecting a suite of changes to the heathland environment that include the spatial redistribution of nutrients, alteration of physical vegetation structure, and the creation of disturbed soil microsites. The exact nature of these changes will undoubtedly depend greatly on the species and variety of the grazing animals, their stocking density and their temporal distribution e.g. free ranging or folding (Webb 1998).

BURNING

Betula colonists have a complex and ambivalent relationship with fire. Fires are seen as a necessary tool in heathland management as they halt the degeneration of the dwarf shrub vegetation and keep it competitive (Bullock & Webb 1995). In addition to the physical destruction of vegetation regular burning is believed to maintain the low nutrient status of the heaths by preventing the build up of organic matter and by encouraging leaching losses of nutrients e.g. phosphorus. The perceived result of these changes is that the competitive balance remains tipped in favour of the ericaceous shrubs (Chapman *et al.* 1989a; Aerts 1989). However, the availability of open sites with disturbed, litter free soils is highest in heathlands that have been recently burnt. Where severe fires have occurred conditions are believed to be particularly favourable for *Betula* regeneration; the above ground vegetation is destroyed, bare mineral soil is exposed and nutrient availability temporarily rises as a result of ash deposits (Bullock & Webb 1995; Allchin 1997). Bullock & Webb (1995) found that although there had been a general increase in the cover of *Betula* on the Dorset Heaths between 1978 and 1987 this was greater in areas that had been severely burnt in the uncontrolled fires of 1976. *Betula* often appeared to replace *Ulex* on burnt sites. However, not all burning equates with *Betula* invasion. Allchin (1997) for instance, found virtually no evidence of *Betula* invasion in experimental heathland plots subjected to controlled fires. The apparent discordance of these results is most probably attributable to the temperatures of the fires. At lower temperatures *Calluna* regeneration occurs via resprouting of rootstocks but the shallow transient seedbank of *Betula* will be largely destroyed, as the seed is not fire tolerant (Atkinson 1992). At higher temperatures dwarf shrub rootstocks, and sometimes their seedbanks, are destroyed allowing for the establishment of non-heathland species, e.g. *Betula*, which disperse into the 'sterile' soils and grow in the absence of pre-established competitors. Although *Calluna* may regenerate from the seedbank *Betula* spp. grow faster from seed and may therefore exclude *Calluna*. In a study of post-burn succession on the Brittany heathlands (Clement & Touffet 1990) *Betula* was found to establish most successfully where there had been high fuel loads and therefore high temperatures and nutrient rich ash deposits. Gloaguen (1990; 1993) also observed the post burn colonisation of *Betula* on the Brittany heaths but noted that establishment appeared to be restricted to the first few years following burning, presumably when competition was less severe. In heaths that are regularly burnt by controlled fires *Calluna* rootstocks are maintained, therefore, competitive stresses persist making *Betula* establishment unlikely but the relationship between the dwarf shrubs, *Betula* and fires could be further complicated by the degree of invasion that had occurred before the site was burnt. Birch may coppice following burning after it has reached a few years of age (Rackham 1986). Because of this coppicing the burning of pre-invaded heathland may stimulate invasion, as *Betula* growth from an existing rootstock is likely to be more rapid than that of the dwarf shrubs in the post-burn environment.

In summary, the overall balance to *Betula* colonists between the inhibitory and facilitative aspects of heathland fires depends on the severity of the fire, its degree of damage to the existing vegetation and seedbank, the proximity of the site to *Betula* seed sources and the spatio-temporal scale of interest.

HEATHER BEETLE OUTBREAKS

Marrs (1986) studied the invasion of *Betula* on heather beetle (*Lochmaea suturalis*) attacked areas of *Calluna* in East Anglia with a combination of aerial photos and ground survey methods. This provided evidence to suggest that invasion was more frequent during periods following beetle outbreak because severely attacked areas had taller individuals at greater densities than intact patches, presumably resulting from beetle effected reductions in interspecific competition and raised soil nutrient levels (Brunstig & Heil 1985).

Like so many processes in heathland ecosystems beetle outbreaks interact with the nutritional status of the system with outbreaks occurring more frequently in regions with high nitrogen deposition inputs (Diemont & Heil 1984; Brunsting & Heil 1985). The processes of eutrophication and beetle outbreak may therefore behave synergistically with respect to *Betula* establishment, with colonists invading competition free sites that are doubly eutrophicated from both aerial inputs and releases from vegetation pools.

MOWING, TURF CUTTING & AMENITY USE OF HEATHLANDS

A number of other disturbances including mowing (Sedláková & Chytrý 1999), turf cutting (Traynor 1995) and a variety of amenity practices (Harrison 1976) also affect the dynamics of lowland heaths. Mowing is likely to have a similar, if more homogeneous, effect to grazing with its exact effect on *Betula* colonisation depending greatly on the height and frequency of mowing, the degree of mechanical disturbance, and the amount and redistribution of harvested shoot removal. Turf cutting on the other hand is perhaps more similar to intense burning in that soils and vegetation are removed altogether, the difference being that smaller areas are affected, nutrients are directly transported off the heath and that soil is usually reduced to a greater depth.

Modern amenity uses of heathlands are wide ranging and are generally more intensive on the heaths close to London (Webb 1986). Dog walking plays a particularly significant role on many urban heaths as trampling causes direct damage, reducing the cover of dwarf shrubs and causing soil compaction (Gallet & Roze 2001), while acetic acid extractable soil P is raised by dog fouling. These effects may affect community composition with *D.flexuosa* being more common in the compacted, eutrophic zones close to footpaths (Shaw *et al.* 1995). Eutrophication caused by intersecting roads (e.g. Angold 1997) and dog fouling may effect *Betula* establishment in many similar ways to those described for endogenous and N deposition enrichment (see above). Many amenity uses that cause physical disturbance to the soil e.g. military training and biking are also thought to promote *Betula* invasion, particularly when they are inconsistent and allow temporal and spatial establishment opportunities.

Aims, Objectives and Rationale

The invasion of *Betula* spp. is a genuine threat to the conservation and persistence of Britain's lowland heaths. Despite a wealth of information on the ecology of *Betula* there are still many questions regarding its regeneration that remain unanswered. Although the process of invasion and establishment of *Betula* in the uplands has been extensively studied (e.g. Gong & Gimingham 1984; Kinnaird 1974; Miles & Young 1980) many of the results may not translate to lowland heaths because they differ in their species composition, soil nutrient status (including P availability) and climate (Chapman & Clarke 1980). Furthermore, a unified synthesis of the exact mechanisms by which some heathland communities inhibit the invasion of *Betula* and thus maintain stability has yet to be developed. Although a number of factors responsible for invasion success have been identified their relative importance and the way in which they interact to form an invasion threshold is unknown. Therefore, the overall aim of this research was:

To identify the key factors that determine transitions between heath and Betula scrub ecosystem states and to quantify their interactions and relative importance in the overall pattern of invasion on lowland heaths.

Although the study focuses on the critical point of change in the system, *Betula* invasion, it is the failure of this process to occur results in the maintenance of the heath ecosystem state. The aim of the study is therefore not only to discover the determinants of invasion success but also their inverse, the ecosystem properties that contribute to the resistance and persistence (*sensu* Pimm 1991) of heathland ecosystems.

The starting point for this research was an investigation of the hypothesis of Chapman *et al.* (1989b) who postulated that the threshold for *Betula* invasion on heathlands was regulated by phosphorus availability and that invasion was likely where soils had PSC >700μg P g^{-1}. However, "The multi-causal world of ecology makes it likely that a single hypothesis, even if valid, will be rejected" (Holling 1992) making the incorporation of numerous factors and the interactions between them a necessary element of a research programme aiming to describe the determinants of invasion.

As the review above demonstrates the number of potential determinants is vast making it impossible to study all possible factors in a single PhD project. Therefore a subset of determinants which are of high potential importance were selected for study. The central hypotheses of the project were as follows:

1. Transition from lowland heath to the *Betula* scrub ecosystem state is limited by numerous factors that may be subdivided into safe-site and seed limitation.

2. A key axis in the determination of a *Betula* safe-site is phosphorus availability. Where soil PSC is low, phosphorus availability limits *Betula* establishment. In sites with a high PSC (>700μg P g^{-1}), phosphorus availability is not limiting.

3. Spatial variation in the determinant factors accounts for much of the observed variation in *Betula* establishment. The effects of this variation operate on a number of spatial scales.

The testing of these hypotheses was implemented in a number of strongly linked studies, which form the remainder of this thesis. Although emphasis in the early stages of the research was on hypothesis testing the overall aim of the research project was to produce a general model describing the threshold of transition and inversely, heathland persistence. This combination of modelling and experimental approaches was achieved with multisite, multifactorial field experiments in which numerous covariates were measured. The factorial treatments were later converted into a continuous form and used alongside the covariate data in general linear regression models. Spatial relationships in the identified determinants were explored through the use of field survey data and geostatistics. It was intended, that if the project was successful and the conditions that preclude *Betula* invasion were understood, that management techniques might be adapted to increase the stability of heathlands and inhibit future *Betula* establishment. This would aid managers by reducing the need for costly maintenance and restoration projects.

Chapter 2: Effects of soil phosphorus sorption characteristics on the soil and vegetation dynamics of European Lowland Heath.

Abstract

1. Previous research on UK lowland heath has found that the likelihood of phase transition between heath and scrub ecosystems correlates with soil phosphorus sorption capacity (PSC). PSC has also been postulated as a key variable in the determination of leaching losses and productivity within lowland heath ecosystems.
2. An implicit assumption of this research was that PSC affects phosphate retention and therefore availability of P to heathland plants and scrub colonists. Here, I explore this assumption through a combination of descriptive and experimental studies.
3. A statistical model fitted to soil data from three experimental sites reveals that although soil organic matter (SOM) accounted for most of the variation in available P, PSC was also able to account for a significant, unique portion of the variance in P availability.
4. Additional models suggest that P saturation (P_{sat}) and the proportion of available P in water desorbable form (%WDP), both indicators of leaching losses, are highly dependent on PSC.
5. These findings are supported by the results of experimental studies. Greater amounts of added P were retained, and held in plant available form, on soils of high PSC. Soils from a low PSC site appeared to become saturated at low levels of P addition.
6. These studies validate the assumption that PSC affects bio-available P and demonstrate that this relationship operates through a variety of mechanisms functioning at different spatio-temporal scales. E.g. PSC may influence the rate at which SOM accumulates.
7. These findings allow the initial hypothesis, that PSC determines heath-scrub phase-transition, to be tested within an experimental framework, which examines the relationship between available phosphorus and scrub invasion success.

Introduction

Changes in the biological availability of nutrients have been shown to provoke phase transitions between alternate 'stable' states (May 1977; Scheffer *et al.* 2001) in a variety of ecosystems e.g. rivers, grasslands, coral-reefs, lakes and heathlands (Scheffer *et al.* 2001; Huppert *et al.* 2002 Aerts 1989; Pearce & van der Wal 2002). The majority of these studies have focussed upon anthropogenic nutrient inputs but variation in nutrient supply rates can also occur as a result of regional differences and autogenic processes. These natural differences may also influence the likelihood of phase transition and therefore impact significantly upon ecosystem function and community structure.

European lowland heaths, although not always intrinsically nutrient poor, have a low P and N bio-availability as a result of the large proportions of these nutrients in organic compartments and slow rates of mineralisation from these pools (Gimingham *et al.* 1979; Berendse *et al.* 1989). Accumulated evidence would suggest that heathland persistence is a consequence of this oligotrophy in that phase transition to alternate stable states such as grassland and scrub appears to be largely determined by changes in nutrient availability and cycling, whether driven by anthropogenic disturbance, autogenic accumulation of nutrients, positive feedbacks in supply driven by invading species or as a combination of these factors (Marrs 1993; Aerts 1989; Aerts & Chapin 2000). Evidence of this community and ecosystem level sensitivity to rates of nutrient supply comes from a number of experimental studies on the heaths of the UK and Netherlands. These researches have demonstrated that changes in productivity, and the abundance of numerous species including grasses (Aerts & Berendse 1988), lichens, bryophytes (Helsper *et al.* 1983) and herbivorous beetles (Brunsting & Heil 1985) occur when nutrients are added.

Although the majority of work on heathland nutrient dynamics has focussed upon nitrogen (e.g. Power *et al.* 1998; van Vuuren *et al.* 1992) the potential importance of P availability in determining the dynamics of European lowland heath was indicated by two papers by Chapman *et al.* (1989a,b) that related several major heathland processes including productivity and successional change to the phosphorus sorption capacity (PSC) of the soil. Heathlands, it is speculated, differ from fertilised agricultural soils in that soils with a high PSC are believed to have higher levels of plant available phosphorus than those with a low PSC. This is thought to arise from the low rates of P input and the constant leaching losses that occur in heathland soils. The modelling studies of Chapman *et al.* (1989a) suggested that PSC could, by determining the retention of phosphate and therefore both leaching losses and plant-availability, drive growth and soil organic matter accumulation rates in heathland ecosystems. These variables are in turn, likely to affect the speed of vegetation cycling (Watt 1947; Gimingham 1988; Chapman & Clarke 1980), the frequency at which fire outbreaks are likely to occur and the rate of nitrogen mineralisation (Berendse 1990). Direct evidence for the higher P availability of high PSC heathland soils is, however, currently lacking.

A survey of 68 heathland sites in southern Britain found that the PSC of their soils varied greatly (16-4000μg P g^{-1}) across the UK (Chapman *et al.* 1989b). Despite the wide range of

PSC values most sites could be categorised into 3 main types that coincided with certain major regions of UK heathland, the Dorset, New Forest and Dartmoor types (Described in Chapter 1.). These results, when coupled with the assumptions of the modelling studies, indicate that P retention and availability may differ greatly between heaths. If it is taken that the establishment of invading tree seedlings is sensitive to P availability and that this is determined by PSC then, by extension, it may be reasonable to suppose that the transition between heathland and scrub is more likely on some heaths, and in some regions, than it is on others. This deduction is supported by the observations of Chapman *et al.* (1989b) who identified a correlative relationship between the likelihood of scrub invasion and the PSC of the soil in the region leading them to hypothesise that invasion by trees was likely where soils had PSC >700μg P g^{-1} and where traditional management had ceased.

REANALYSIS

This relationship between PSC and successional change was given further consideration in a reanalysis of the original Chapman *et al.* 1989b data (provided in the appendix of Chapman *et al.* 1989b). These data provide details of the grazing regime, successional history, PSC, isotopically exchangeable P (IEP), acetic acid extractable P (AEP), soil organic matter content (SOM) and pH of the sites. As invasion by trees did not occur on any of the sites that had been persistently grazed by ponies, sheep or cattle the probability of invasion on a grazed site was zero, irrespective of the other variables, and these sites were therefore excluded from the analysis. The remaining, ungrazed, sites were classified as being invaded by trees (1) or not (0). The General Linear Model procedure of S+ 2000 was used specifying binomial errors and a logit link. Parameter values were estimated by maximum likelihood. A minimum-adequate model (Crawley 1993; 2002) was achieved through stepwise deletion of non-significant variables using T statistics (see methods below for further details of the statistical modelling procedure). The resulting model contained two significant variables PSC, which had a positive relationship with the probability of invasion and IEP, which displayed a negative relationship with the likelihood of invasion (Table 2.1). This result was unexpected; soils with a high PSC but low IEP were the most likely to be invaded. A more detailed examination, however, found that IEP was unable to account for any deviance in the absence of the PSC variable and that the heaths of Devon and Cornwall had a high PSC and IEP but were rarely invaded by trees. These phenomena suggest that this apparent discrepancy in the relationship between phosphorus availability and heathland persistence may in fact reflect regional differences in other possible determinants of scrub colonisation e.g. disturbance regimes, climate and dispersal.

Table 2.1. Minimum adequate model (MAM, binomial error, logit link) describing the relationship between heathland soil PSC (phosphorus sorption capacity), IEP (isotopically exchangeable phosphorus) and the probability of tree invasion. Explained deviance = 44.3%, residual d.f. = 47. Deleted terms: ACP, pH, SOM.

	Parameter Values	Standard Error	Explained Deviance	*p* (T-Test)
Intercept	-3.103	0.883		
IEP ($\mu g\ P\ g^{-1}$)	-0.077	0.0379	12.8%	<0.05
PSC ($\mu g\ P\ g^{-1}$)	0.006	0.00173	44.3%	<0.001

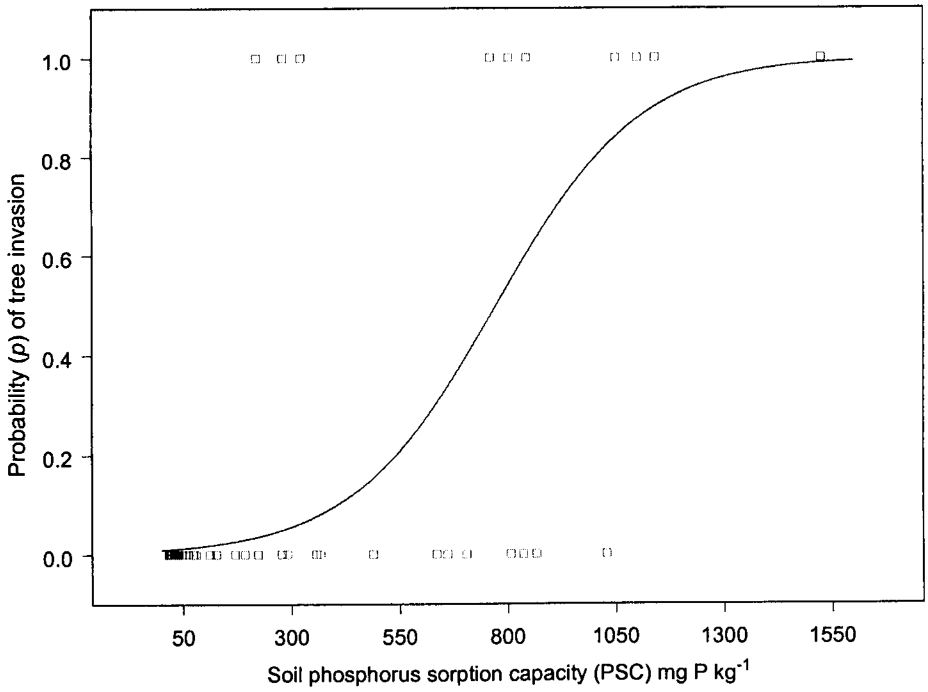


Fig 2.1. Fitted logit curve describing the relationship between PSC and the probability of invasion when IEP is held constant at 20mg P kg^{-1}. Square points represent the original data.

An examination of the fitted model, when IEP is held constant at 20, reveals that the critical region determining invasion success is between PSC of around 550 and 1050 in which the probability of invasion rises from 0.2 to 0.8 (Fig 2.1). The probability of invasion at the PSC of 700μg P g^{-1}, the arbitrary threshold of Chapman *et al.* (1989b), is 0.39.

Although this analysis places the relationship between PSC and invasion in a more quantitatively probabilistic framework the conclusion remains broadly similar; the higher the PSC of a site the more likely it is to be invaded by trees. The probable artefact that is the inclusion of IEP in the fitted model and the unexplained deviance suggest, however, that other factors, e.g. disturbance regime, may influence the likelihood of tree invasion and/or interact with PSC.

Although both papers described above (Chapman *et al.* 1989a;b) suggest that PSC plays a crucial role in determining heathland dynamics the conclusions of one are grounded on correlative relationships (Chapman *et al.* 1989b), whilst the other is based on a simulation model with a large number of assumed parameters and relationships (Chapman *et al.* 1989a). Complications also arise from the fact that the observations of Chapman *et al.* (1989b) are not statistically independent (e.g. all grazed sites and low PSC sites are in one or two geographic regions). The correlation between PSC and invasion may therefore reflect other regional trends or be a statistical artefact of two spatially autocorrelated variables (Lennon 2000). There is also an implicit assumption in the Chapman *et al.* (1989b) research that PSC influences productivity and phase-transition by affecting the P available to both heathland and invading scrub species. These drawbacks prevent the formation of firm conclusions and leave a number of major questions about the true role of PSC in heath dynamics unanswered. In this chapter I describe work that forms the initial framework of a study in which the Chapman *et al.* (1989b) hypothesis; that PSC determines plant available P, the probability of tree invasion, and therefore the state of the ecosystem, is tested experimentally. This comprised 3 component studies in which I:

1. Describe the soil P characteristics of different sites and soil depths
2. Model the relationships between soil properties and phosphorus characteristics.
3. Experimentally examine the relationship between PSC and plant-available P.

1. A DESCRIPTION OF SOIL PHOSPHORUS CHARACTERISTICS

The research that comprises the remainder of this chapter is itself a component of several closely integrated studies into the factors that determine the colonisation of *Betula* species on lowland heath and therefore, the persistence of the heathland ecosystem state. The majority of these studies were conducted on three experimental sites that were believed to differ with respect to their soil phosphorus characteristics (see Chapters 3 & 4). In the first section of this chapter I describe the soil properties of the three sites with respect to the findings of

Chapman *et al.* (1989b) and expand upon this framework by describing the changes in phosphorus characteristics with soil depth.

2. RELATIONSHIPS BETWEEN SOIL PHOSPHORUS PROPERTIES

The variables discussed in section 1. are given further consideration in the second section of the chapter, which describes statistical models of the relationships between key soil phosphorus characteristics. These are, specifically, the determinants of: plant-available phosphorus, soil phosphorus saturation and the proportion of plant-available phosphorus in water desorbable form.

3. EFFECTS OF P SUPPLY AND SORPTION CHARACTERISTICS ON AVAILABLE P

The third section of this chapter relates to experimental work in which P addition and disturbance treatments were applied to the aforementioned experimental sites. A sub-experiment nested within the plots of the experimental blocks was conducted to uncover the quantitative differences in plant available P that were generated by these treatments and therefore allow, amongst other benefits, for a more precise critique of the plant response results (see Chapters 3 & 4). This experiment, although primarily conducted as a means of assessing the impact of the P additions on the plant-available P within the larger experiment, allowed for an examination of the effect of PSC and disturbance on phosphorus retention and availability.

The overall hypotheses of these studies are that:

1. A greater proportion of added or mineralised P will be retained on high PSC sites. This P will be retained in a plant-available form.

2. As P retention is lower on low PSC soils leaching losses will be greater. Therefore, in the long-term, higher PSC soils will have greater P availability.

3. PSC increases with soil depth as result of leached Fe and Al compounds. Therefore, disturbance brings soils of a higher PSC to the surface (Chapman *et al.* 1989b), increasing the P available to seedling plants.

Methods

PART 1. SOIL PHOSPHORUS CHARACTERISTICS OF THE EXPERIMENTAL SITES

SOIL SAMPLING AND PREPARATION

Soils were collected from three heathland sites in Southern England that doubled as experimental sites used to study the determinants of *Betula* invasion on lowland heath (see Chapters 3 & 4). The sites were chosen for their similarities with respect to vegetation type, (the M16 of the National Vegetation Classification (Rodwell 1992)), topography (flat), soil type (humus-iron podsol) and proximity to mature *Betula*. A major distinction between the sites was believed to be their soil phosphorus sorption characteristics. The first site at Arne, Dorset (see Chapter 3.) was thought to possess sorption characteristics of the Dorset Type (PSC = <100μg P g^{-1}) (*sensu* Chapman *et al.* 1989b). The other two sites were believed to be of the New Forest type (with PSC c.1500μg P g^{-1}). The first of these sites at Denny wood, New Forest has a history of free ranging grazing while the other, on Horsell Common, Surrey has seen little management in the last 50 years. The Management histories of the three sites are described in greater detail in Chapters 3 & 4.

Samples were taken on a regular sampling grid that provided maximum coverage of the study sites and ensured the production of interpolated grids to be used in the derivation of soil covariate values (see Chapters 3 & 4.) The study sites occupied areas of 41 x 8m at the Surrey and New Forest sites and 78 x 11m at the Dorset site. The number of sampling points was 30 at the New Forest and Surrey sites and 72 at the larger Dorset site.

Soil core samples were taken to a depth of 150mm with a 20mm diameter cylindrical soil borer and divided into two depths: 0-50mm and 50-150mm. The top 50mm sample typically included the L (litter), F (decomposing organic) and H (completely humified organic matter) layers of the podsol. The 50-150mm portion contained the A (humic dark sand) and Ea (grey sand) layers. The Bh (iron pan) layer was infrequently observed in the samples. After sampling, soils were returned to the lab and stored at <4°C as soon as possible. They were then weighed, air dried, weighed again, passed through a 2mm sieve and weighed again. Estimates of pH were made for all samples by mixing soil and distilled water at a 1:2 ratio, shaking the mixture intermittently for 20 minutes, standing for ten minutes and then reading from the meter. Total moisture and SOM contents were estimated by placing 5g of air-dried soil in a crucible and re-weighing after 12 hours of oven drying at 100°C. The remainder was then placed in a muffle furnace at 450°C for 12 hours and re-weighed.

CHEMICAL ANALYSIS:

PHOSPHORUS ADSORPTION ISOTHERM

A subset of 5 samples were selected randomly from both depth categories for each of the three sites and used in soil P sorption isotherm analysis. 2g of air-dry soil were transferred into 50ml polypropylene tubes and 40ml of standard phosphate solution was added (0, 5, 10, 20, 30, 40, 60, 70, 100 and 150mg P l^{-1} in 0.02M KCl). Three drops of chloroform (to inhibit microbial activity) were also added. Bottles were then well shaken and placed in an orbital incubator at 10°C for 24 hours at 100 rev/min after which the suspensions were left to settle for 1 hour at 10°C. After settling, the supernatant was removed, filtered through 0.45µm cellulose nitrate membrane filter paper and analysed colorimetrically. The amount of P sorbed to the soil was calculated as the amount initially in solution minus the amount remaining. No attempts were made to control for pH and so the pH in the tube will have approximated field conditions. This method conformed to the original Chapman *et al.* (1989b) method as closely as possible so that results were directly comparable. The only major differences between the two methods is the separation of the 0-150mm depth used by Chapman into 2 depths, and a possible discrepancy in sorption temperature, which was not specified by Chapman *et al.* (1989b).

ACIDIFIED AMMONIUM OXALATE EXTRACTABLE P (P_{OX})

An acidified ammonium oxalate extractant was used to measure the total of sorbed P and water-soluble P fractions. Acidified ammonium oxalate extractable P (P_{ox}) has been found to be a good predictor of the available P in weathered soils (Guo & Yost 1999). 100% of P_{ox} is thought to be desorbable in sandy soils (Lookman *et al.* 1995) and has been used as a measure of sorbed P in acidic grassland soils (e.g. Pote *et al.* 1996). In laboratory conditions, practically all P_{ox} is thought to be desorbable within 100-400 days (Lookman *et al.* 1995).

The combined mix of ammonium oxalate and oxalic acid dissolves non-crystalline oxides of Fe and Al. These non-crystalline forms may be important in plant nutrition as they are less stable than crystalline phases in the presence of organic acids e.g. plant root exudates (Wang *et al.* 1991). Readsorption is lower in oxalate extract than other extractants because Fe and

Al are complexed and Ca is precipitated. P_{ox} is therefore more comparable to the combined fractions of the Hedley P test than it is to the P desorbed by resins and Fe oxide strips.

Measurements of P_{ox} were obtained by mixing 2g of soil with 40ml of acidified ammonium oxalate (0.2M ammonium oxalate mixed with 0.2M oxalic acid until a solution pH of 3 was reached) and placed in a orbital incubator at 15°C for 2 hours at 100 rev/min after which the suspensions were left to settle for 1 hour at 10°C. After settling, the supernatant was removed and filtered through a 0.45μm cellulose nitrate membrane filter paper. 3ml of filtered sample was evaporated to dryness and ashed at 500 °C for 1hr. Ashed samples were re-dissolved in 1M HCl and analysed colorimetrically. In all cases, phosphate was measured colourimetrically as 'soluble reactive phosphorus' using the method of Murphy & Riley (1962). Colouration of the filtrate by the sample was found to have little effect on the absorbance measurements. At least two blanks were used per 20 samples analysed. P_{ox} was estimated for all soil samples of the 0-50mm depth and for the same 15 samples that were used in the sorption isotherm analysis for the 50-150mm depth.

MODEL FITTING TO SORPTION DATA

Description of soil phosphorus sorption characteristics is achieved by the fitting of statistical models to quantity/intensity (Q/I) plots which describe the amount of phosphorus adsorbed to the soil (*x*) at known soil solution P concentrations (*c*). The amount of P currently absorbed to the soil (P_{ox}) is added to the estimate of sorption at that concentration.

The most popular equation used to describe P sorption, is the Langmuir two-surface equation, a mechanistic two-component model based on the assumption of low and high energy sorption sites (Equation 1).

$$(1)\, x = \frac{a_1 x m_1 c}{(1 + a_1 c)} + \frac{a_2 x m_2 c}{(1 + a_1 c)}$$

Each component of the Langmuir equation contains two key parameters: *a*, which describes the steepness of the slope and therefore the phosphate affinity of the soil, and *xm* which, when summed for the two surfaces, represents PSC (Barrow 1978). There is however, great difficulty in measuring the true PSC, especially on low sorption soils. This is for two reasons; first the proportion of phosphorus remaining in solution rises with solution concentration, with an associated rise in error. The other major problem is that at high tube P concentrations (*c.*100mg P l^{-1}) (Prof. Alan House, CEH Dorset, personal communication), P is not adsorbed but precipitated as insoluble mineral phosphates (Holford *et al.* 1974). In some cases a modified version of the Langmuir two-surface equation, in which the second surface is represented by a constant, is used. This has found to be a good fit for soils in which the high-energy surface is saturated (Holford *et al.* 1974).

Three variants of the Langmuir equation (the one surface, two surface and one plus constant models) were fitted to the Q/I plot data. At high solution concentrations (e.g. 150mg P l^{-1}) many sorption estimates on low sorption soils appeared unreliable and so were omitted from the analysis. Curves from low sorption soils were therefore constructed from fewer data.
Curve fitting was achieved by using the S+ 2000 non-linear least squares procedure. Residual sum of squares was used as the measure of curve fit with the model possessing the minimum residual deviance being selected as the best model. This procedure found that the Q/I plot data of the soils were best described by the Langmuir 1 surface + constant model.

P SATURATION

Phosphorus saturation has been found to be a good estimator of P runoff from agricultural systems (Pote *et al.* 1996) and it is therefore likely to be a good indicator of leaching losses. The degree of soil phosphorus saturation (%P_{sat}) was calculated using a modified form of the molar ratio method used by Lookman *et al.* (1995) and Pote *et al.* (1996) in which:

$$(2)\ \text{Molar ratio} = \frac{P_{ox}}{Fe_{ox} + Al_{ox}}$$

However, as actual PSC estimates were available they were used to substitute the bottom half of the equation in which the Fe_{ox} and Al_{ox} estimates are used to estimate soil PSC.

WATER DESORBABLE P

The fraction of P_{ox} that is water desorbable (%WDP) represents that which is in solution or is weakly adsorbed. This is the fraction that is most readily available to plants but also the most likely to be leached (Lookman *et al.* 1995). This fraction was calculated as:

$$(3)\ \%\ \text{WDP} = \frac{\text{WDP}}{P_{ox}}$$

When WDP is that measured in the 0 mg P l^{-1} concentration of the sorption isotherm.

PART 2. STATISTICAL MODELLING OF SOIL PHOSPHORUS PROPERTIES

Statistical models were formulated that described three key soil phosphorus properties; plant-available phosphorus (as estimated by P_{ox}), P_{sat} and %WDP. In each case, it was the soil data collected from the five randomly selected samples taken from each site and depth that were utilised. The procedure of model fitting followed the guidelines of Crawley (1993 and 2002) in that all measured variables, P_{ox}, SOM, pH, PSC, Langmuir a, site and depth categories, were tested and systematically deleted until a 'minimum adequate' model was reached.

The major difference in this statistical approach to that of traditional ANOVA and regression methods is that traditional techniques use standardised, *a priori* statistical models and test the data against them. The general linear modelling (GLM) approach, on the other hand, allows the user to specify the structure of the model permitting the modification and maximisation of the model to fit the data. This 'best' model, known as the minimum adequate model (MAM), has the smallest minimal residual deviance (analogous to r^2) possible with the constraint of all parameters being statistically significant. The MAM is arrived at through the fitting of a maximal model (by maximum likelihood) containing all possible parameters and the stepwise deletion of parameters that do not account for significant proportion of the deviance. Error distributions and link functions are also flexible. Significance in general linear modelling is estimated using deletion tests in which a variable is removed and the corresponding change in deviance is assessed with T, F or χ^2 tests, depending on the link function, error distribution and residual dispersion. Exact probability values cannot be prescribed when using these methods unless normal (Gaussian) errors and an identity link are used. By using the GLM approach, hypotheses may be tested while simultaneously finding the best possible model fit to the data, a process that may, in its own right, reveal properties of the relationship of interest.

Once the MAM was fitted, the relative contribution of each explanatory variable was obtained through its deletion from the model and measured as the change in explained deviance over the total deviance. I have expressed this value as deviance change on deletion (%DCD). DCD values for main effects include the effect of removing any interaction terms that contained the main effect.

PART 3. EXPERIMENTAL PHOSPHORUS ADDITION

At each of the three experimental sites three (Surrey and New Forest), or four (Dorset), plots of 50 x 50 cm were placed in a chequered arrangement (see Fig 2.2.) and randomly allocated to 4 2m x 1m plots within each block of the larger experiments (see Chapters 3 & 4). At the Dorset site there were 8 treatment combinations of phosphorus and disturbance and 4 experimental blocks. This gave a total replication of 8 for each treatment combination. The study was repeated, with a lower level of replication (6 per treatment combination), in a 3 x 2 factorial design within 3 experimental blocks at the Surrey and New Forest sites.

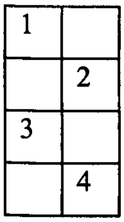


Fig 2.2. Arrangement of sub-plots within the larger experimental plots.

TREATMENTS:

DISTURBANCE

Disturbance was manually applied with a 3-pronged mattock to generate a non-specific form of disturbance to soils and vegetation that simulated many aspects of heathland disturbances e.g. plant death and soil mixing. Disturbed plots were struck and turned with the mattock for 150 seconds m^{-2}. This was the time taken to generate realistic levels of disturbance i.e. when much of the vegetation had been destroyed and the top 100mm of soil was disrupted. Disturbance treatments were applied to the three sites between the 17th and 24th June 1999.

P ADDITION

Phosphorus was applied at a constant concentration and amount with the number of additions differentiating the treatment levels. The concentration of each pulse was believed to be equivalent to that released in the burning of a 30yr old heath. Chapman (1967) estimated the total aboveground P of a Dorset heathland to be c.18.5kg ha^{-1} and therefore a 2 x 1m plot would contain approximately 3.7g of P. Assuming that 5% of P is lost in smoke (Chapman *et al.* 1989a; Allen 1964) 3.52g would remain in the ash; it is this amount that was deposited in each addition. The form of this P was 45% triple super-phosphate dissolved in 500ml of water. It was thought that if the soil of each larger plot is perceived as a volume of water 150mm x 2000mm x 1000mm then the P concentration following an addition will be 11.7µg per ml. This concentration is, according to the results of Chapman *et al.* (1989b), sufficient to differentiate between the different P adsorption types especially considering that the real soil solution volume is likely to be much lower. The post-burn soil-solution P concentration that was deemed to be typical of upland heath by Allen (1964) was 22mg P l^{-1}.

The four Treatment levels used at the Dorset site were: 1= no added P, 2= 1 P addition, 3= 2 P additions and 4= 3 P additions. The levels used at the Surrey and New Forest sites were 1, 2 and 4. The first addition of P was applied between the 30th June 1999 and the 5th July 1999, the 2nd between the 5th and 10th of January 2000, and the 3rd between the 5th and 7th June 2000. Applications were made using a watering can with a fine rose. Care was taken to ensure that the distribution of the solution was as even as possible.

SAMPLING & ANALYSIS

Soil cores were taken with a 150mm diameter cylindrical borer from the central area of the 50cm^2 plot. Sampling took place between the 7th and 15th of November 2000. This period coincided with the flooding of November 2000 and so soils were heavily waterlogged at the time of sampling. After sampling, samples were divided into depths, stored and prepared according to the methods described above. A 2g sub-sample of the 0-50mm soil from every sample was analysed for P_{ox} according to the method described above. The data were then analysed using the ANOVA procedure of S+ 2000 specifying Tukeys HSD as the post-hoc test for the comparison of means. Variance in the data from all three sites was standardised through log *e* transformation. Block effects at all three sites were not significant and so were removed from the ANOVA models.

Results

SOIL PHOSPHORUS CHARACTERISTICS OF THE SITES

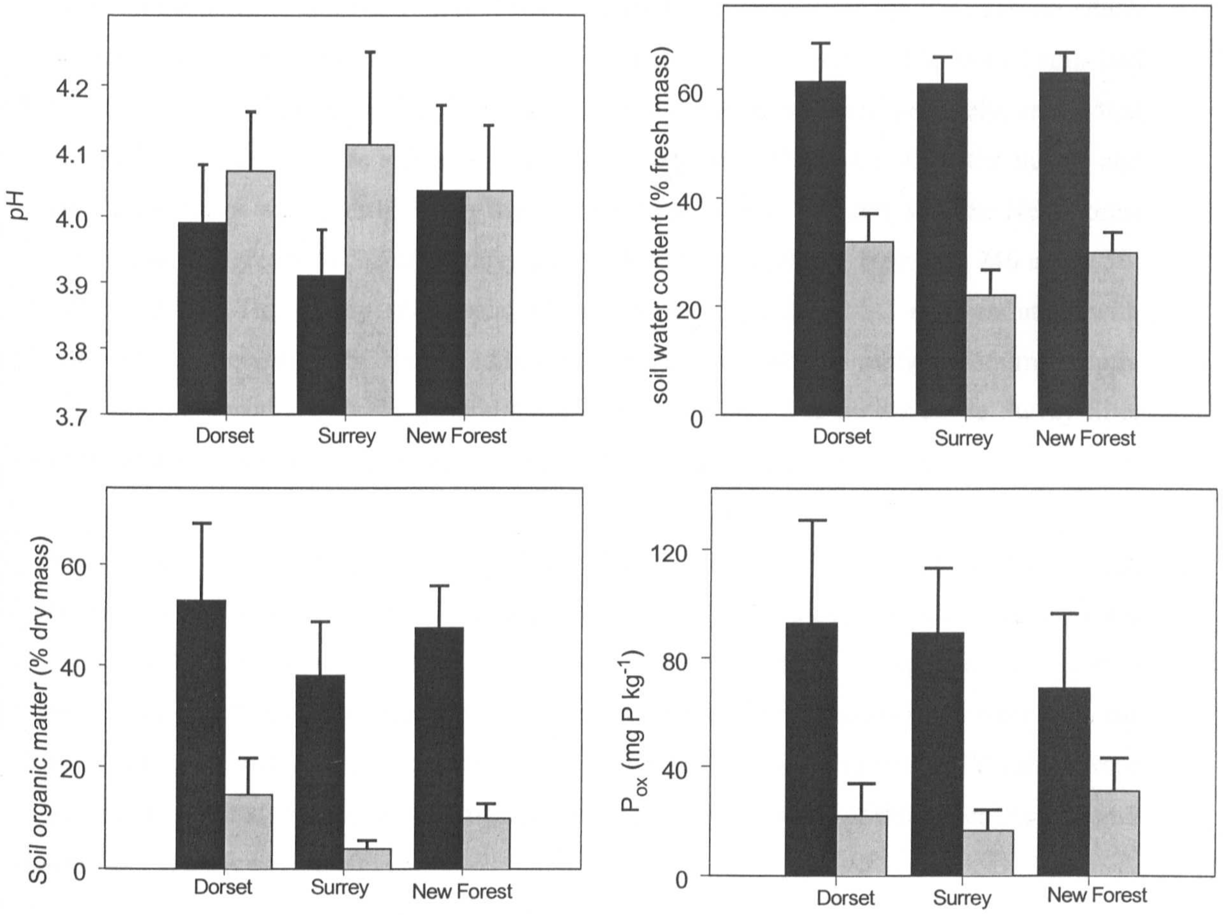


Fig 2.3. Soil properties of the three experimental sites. Dark shaded bars indicate soils taken from the 0-50mm depth. Lighter shading indicates soils of the 50-150mm depth. Error bars represent ±1 standard deviation.

The soil of the three experimental sites displayed remarkably similar properties with respect to most of the measured variables including, pH (c. pH 4), water content (c.60% for the 0-50mm zone and c.25 for the 50-150mm depth) and to a lesser extent SOM (0-50mm = c.45%, 50-150mm = c.10%) and phosphorus availability (0-50mm= P_{ox} c.70μg g^{-1}, 50-150mm = P_{ox} c.20μg g^{-1} (Fig 2.3). An exception to this trend was, as hypothesised, soil PSC, which differed greatly between both sites and soil depths (Fig 2.4, Table 2.2.)

Although Langmuir *a* or separate surface sorption values were not given in the original Chapman *et al.* (1989b) appendix it can be seen by comparing the form of the fitted curves (Fig 2.4) with the examples given in Chapman *et al.* (1989b) that initial sorption/affinity was lower in the soils of this study. What remain consistent however, are the PSC values, which coincide with the regional values described by Chapman *et al* (1989b). The Dorset soils had PSC (μg P g^{-1}) of 231 and 323 at the 0-50mm and 50-150mm depths respectively, values that are slightly higher than the regional 'type' but not atypical. The soil PSC of the Surrey and New Forest sites was slightly below the regional 'type' values of 1500 with the New Forest site having the greatest PSC of all three sites; 1463 at the 0-50mm depth and 746 at the 50-150mm depth. The Surrey site displayed the greatest degree of PSC differentiation with depth of the three sites. PSC was 1112 at the 0-50mm depth and 251 in the 50-150mm depth. This finding concurs with the general trend of greater depth differences at the Surrey Site; SOM and pH were also more dependent on depth than at the other two sites.

Values for %WDP and P_{sat} correlated fairly closely (Pearson's r=0.70) and like PSC varied greatly both between and within sites and depths. The mean values for both variables were highest at the Dorset site, lowest at the New Forest and tended to be higher in the 0-50mm soil depth (Table 2.2). Standard deviations and coefficients of variation (CV) were high for all variables indicating small-scale spatial heterogeneity in soil P properties. CV values were generally higher at the Dorset site, most probably as a consequence of the larger site size and therefore sample coverage.

Table 2.2 Mean values and coefficient of variation of the soil phosphorus properties of the experimental sites: Phosphorus sorption capacity (PSC μg P g^{-1}), Langmuir *a* parameter, P saturation (P_{sat}) and water-desorbable P (WDP). Numbers in parentheses represent ±1 standard deviation.

Site & Depth	PSC	PSC CV	Langmuir *a*	Langmuir *a* CV	%P_{sat}	%P_{sat} CV	%WDP	%WDP CV
Dorset 0-50mm	231 (165)	71.4	0.048 (0.032)	66.7	32.8 (23.4)	71.3	72.8 (22.9)	16.67
Dorset 50-150mm	323 (253)	78.3	0.038 (0.034)	115.8	10.3 (7.6)	73.8	59.9 (32.8)	54.8
Surrey 0-50mm	1112 (460)	41.4	0.011 (0.005)	45.5	8.75 (4.0)	45.7	24.1 (15.0)	62.2
Surrey 50-150mm	251 (106)	42.2	0.038 (0.019)	50.0	7.54 (2.15)	28.5	11.6 (9.46)	81.6
New Forest 0-50mm	1463 (531)	36.3	0.013 (0.004)	30.1	4.63 (1.49)	32.2	12.3 (6.93)	56.3
New Forest 50-150mm	746 (326)	43.7	0.031 (0.03)	96.8	4.71 (2.03)	43.1	6.63 (9.54)	143.9

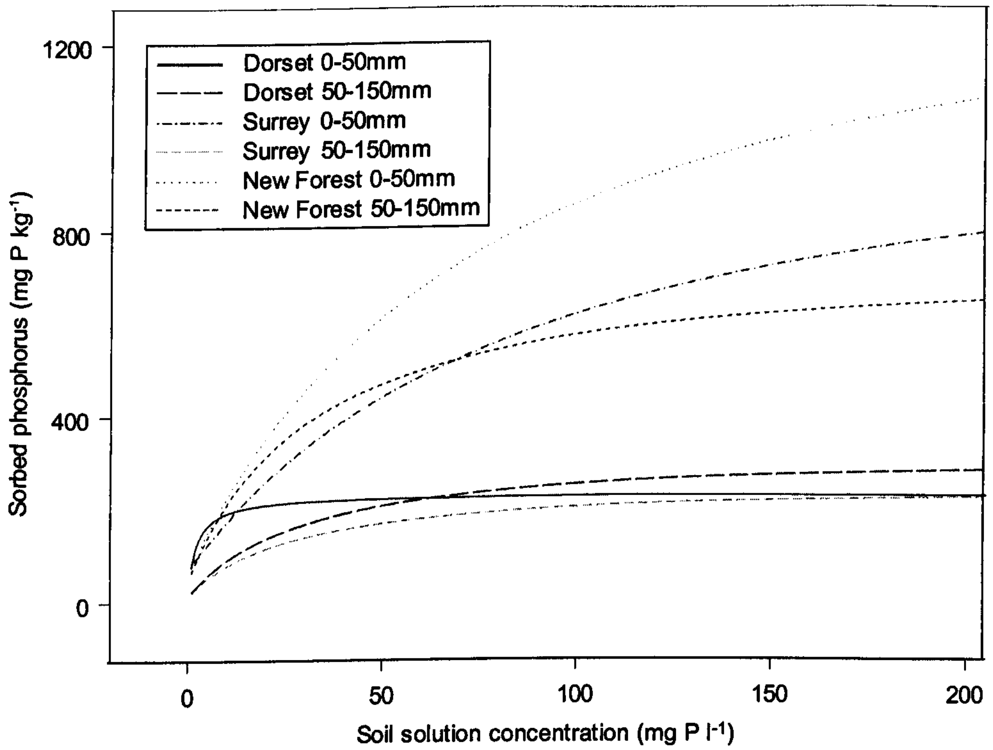


Fig 2.4. Phosphorus sorption characteristics of the three experimental sites. Lines are derived from the mean parameter values of fitted (by non-linear least squares) Langmuir 1 surface + constant equations.

RELATIONSHIPS BETWEEN SOIL P PROPERTIES

AVAILABLE P (P_{OX}) MODEL

Statistical models were formulated that were capable of describing a large proportion of the deviance (84-95%) for all three variables of interest. The first of these, which described long-term available-P as estimated by P_{ox}, was of the standard multiple linear regression form with Gaussian error, three descriptive variables, SOM, pH, PSC, and an interaction term (Table 2.3.). These accounted for 84.1% of the deviance in the response variable (P_{ox}). Deletion tests found there to be little overlap between the descriptors with the majority of the explained deviance unique to each variable. The most important of the three descriptors was SOM (p=<0.001, DCD=43.4%), which displayed a positive relationship with P_{ox} (Fig 2.5a). In contrast to expectation, it was soil PSC rather than the affinity term Langmuir a that was able to explain variation in P_{ox} (p=<0.05, DCD=8.63%). PSC displayed a positive logarithmic relationship with available P (Fig 2.5b) that presumably represents a direct effect of phosphorus sorption on phosphate retention. It can be seen from the fitted relationship, in which the other variables were held constant at their mean, that small differences in PSC (between 50 and 500μg P g^{-1}) have a considerable impact on available P. The third significant descriptor in the model, pH, displayed a positive relationship with P_{ox} in that more neutral soils were found to have greater P availability (p=<0.01, DCD=8.4%). This may relate to more favourable conditions for microbial activity and therefore P mineralisation. This trend is complicated by the negative interaction of pH with SOM. P_{ox} was lower in high SOM soils with a more neutral pH. The balance between these conflicting relationships is best understood by an examination of the fitted model (Fig 2.5a) which reveals that the combined effect of these three terms leads to a largely negative relationship between pH and P_{ox} over the typical range of heathland conditions. Only in low SOM soils is the relationship positive.

Table 2.3. Minimum adequate model (Gaussian error, identity link) describing the relationship between available P (P_{ox}) and a number of soil properties including soil organic matter, pH and phosphorus sorption capacity (PSC). Explained deviance = 84.1%, residual d.f. =23, deleted terms = Langmuir *a*, water content, site and depth categories.

	Parameter Values	Standard Error	Explained Deviance	*p* (F-Test)
Intercept	-3222.13	275.08		
pH	72.81	67.99	8.4%	<0.01
SOM content (% dry mass)	20.81	7.895	43.4%	<0.0001
log*e* (PSC (μg P g^{-1}))	7.80	2.54	8.63%	<0.05
pH* SOM	-4.95	1.95	4.4%	<0.05

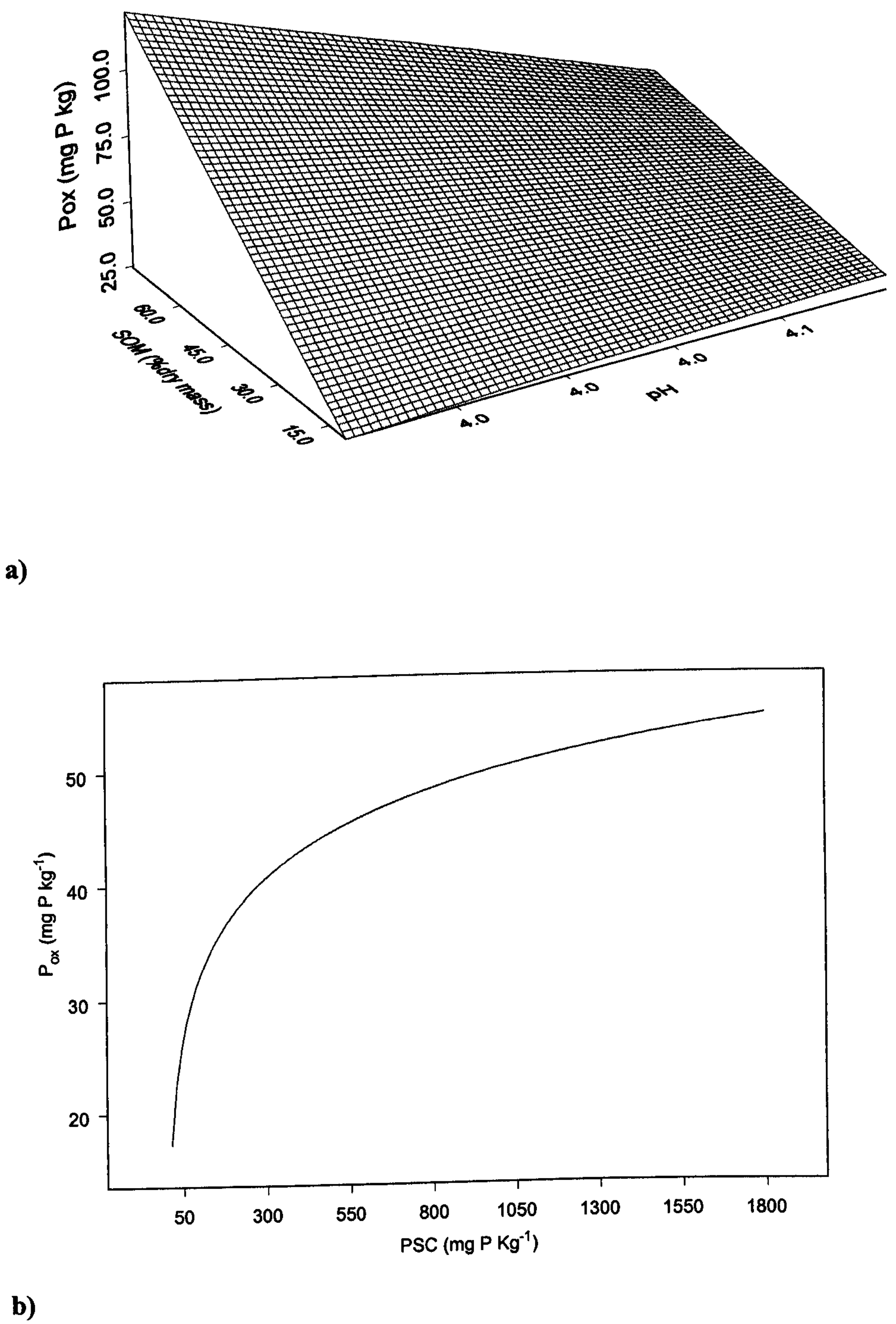


Fig 2.5. Fitted responses of P_{ox} to soil chemical properties. a) Response of P_{ox} to pH and SOM when PSC is held constant at the mean value of 666µg g^{-1}. b) Response of P_{ox} to PSC when pH and SOM are held constant at their mean values of 4.03 and 28.9 respectively.

P SATURATION MODEL

The P saturation of heathland soil was well described (Explained deviance = 95.2%) by a regression model with Poisson errors and a log link function containing two interacting variables, PSC and SOM, which accounted for distinct portions of the explained deviance (Table 2.4). The variable accounting for the greatest proportion of the explained deviance was log *e* transformed PSC (p=<0.001, DCD=73.2%). This effect is clearly a simple consequence of the greater capacity of high PSC soils, the greater the PSC the greater the quantity of P that is required to saturate the soil. The second variable in the model, SOM, accounted for a far smaller proportion of the deviance (p=<0.001, DCD=29.3%) and displayed a positive relationship with saturation i.e. samples containing high SOM contents were closer to saturation. A simple explanation for this trend is that SOM is the source of most soil phosphate and so mineralised phosphorus is found in association with organic matter. It would seem likely that much of this P initially remains sorbed or in solution close to the location of its mineralisation.

A small interaction between the two variables (p=<0.01, DCD=2.0%) suggests that the degree of saturation rises steeply when SOM is high and PSC is low but the conclusion that P saturation and by extension, leaching losses, is greatest in high SOM soils with a low sorption capacity remains unchanged (Fig 2.6).

Table 2.4. Minimum adequate model (log link, Poisson error) describing the relationship between soil phosphorus saturation (%P_{sat}) and two soil properties, soil organic matter (SOM) and phosphorus sorption capacity (PSC). Explained deviance = 95.2%, residual d.f. = 24. Deleted terms = pH, Langmuir *a*, water content, site and depth categories

	Parameter Values	Standard Error	Explained Deviance	p (χ^2-Test)
Intercept	4.17	0.870		
SOM content (% dry mass)	0.072	0.018	29.3%	<0.0001
log*e* (PSC (μg P g^{-1}))	-0.42	0.152	73.2%	<0.0001
PSC* SOM	-0.008	0.003	2.0%	<0.01

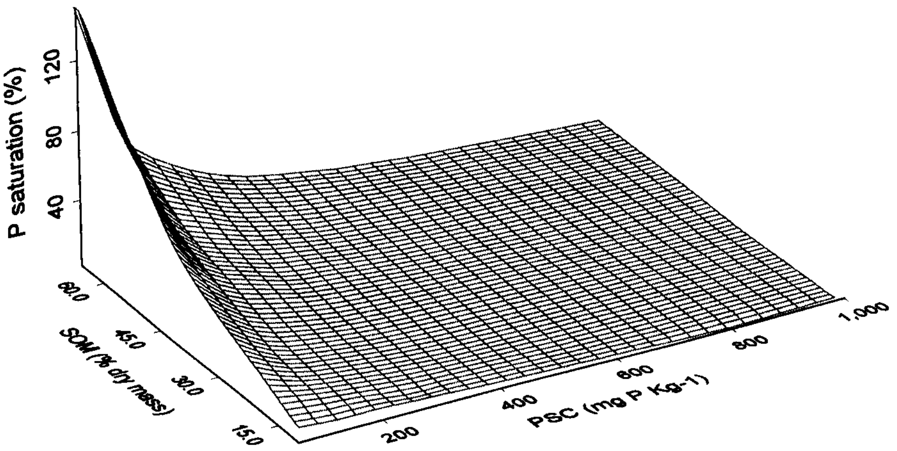


Fig. 2.6 Fitted response of P saturation (%P_{sat}) to soil organic matter content (SOM) and phosphorus sorption capacity (PSC).

WATER DESORBABLE P (%WDP) MODEL

Although the model fitted to explain the %WDP was able to account for a large proportion of the deviance (92.5%) its interpretation is more complex than those of the saturation and P_{ox} models (Table 2.5). %WDP was best described by an ANCOVA model with two continuous predictors, log (PSC) (p=<0.001, DCD=19.2%) and SOM (p=<0.05, DCD=2.0%), one categorical predictor, site (p=<0.01, DCD=36.7%), and an interaction term (p=<0.001, DCD=15.1%) which indicated that the relationship between %WDP and PSC was site-specific. The Dorset and New Forest sites displayed a negative relationship between PSC and %WDP, i.e. lower PSC soils at these sites had a greater proportion of P_{ox} in readily desorbable or solution pools. These observations are consistent with the theory of soil P sorption; as soils become saturated, a process, which occurs more rapidly on low PSC soils, the energy of sorption declines and so a larger proportion will be found in water-soluble forms. The fitted relationship between SOM and %WDP is also consistent with theory as mineralised P is initially likely to be associated with SOM and in a soluble form.

Converse to the findings at Dorset and the New Forest is the relationship observed at the Surrey site, which displayed an opposing trend i.e. %WDP was lowest in high PSC soils. The most likely explanation for this trend is that greater vegetation densities at the Surrey site resulted in greater plant P uptake and so the high PSC soil of the 0-50mm zone was relatively more depleted of readily available P than at the other sites.

Table 2.5. Minimum adequate model (identity link, Gaussian error) describing the site-specific relationship between the proportion of available P (P_{ox}) in water-soluble form (%WDP) and two descriptors, phosphorus sorption capacity (PSC) and soil organic matter (SOM). Explained deviance = 92.54%, residual d.f. = 21, deleted terms = Langmuir a, pH, soil water content, depth category.

	Parameter Values	Standard Error	Explained Deviance	p (χ^2-Test)
Intercept	39.06	3.93		
Site	New Forest =-15.27 Surrey = -40.15	2.80 4.41	36.7%	<0.0001
SOM content (% dry mass)	0.188	0.078	2.0%	<0.05
PSC (μg P g^{-1})	-0.045	0.0067	19.2%	<0.001
PSC* Site	New Forest = 0.019 Surrey = 0.064	0.0038 0.0098	15.1%	<0.0001

EXPERIMENTAL P-ADDITION

ANOVA found a significant difference between the soil P_{ox} content of the four phosphorus addition levels of the Dorset site (F= $4.95_{3,56}$, p=<0.01). There was no significant effect of disturbance either as a main effect or as an interaction with the phosphorus treatments. Comparison of means found the difference to occur between the control (P_{ox} = 103μg g^{-1}) and high treatment level plots (two additions P_{ox}=191μg g^{-1}or three additions P_{ox}= 189μg g^{-1}). These results indicate that low levels of phosphorus addition had either little effect on P_{ox} or that the added P had been immobilised or leached from the upper layer of the soil. The failure to detect any significant differences between the different levels of P amended plots suggests that the soils had rapidly reached saturation (Fig 2.7a).

At the Surrey site, P addition was found to have a significant effect on P_{ox} (F =$13.4_{2,29}$, p=<0.001) but again there was no significant effect of disturbance as either a main or interactive effect. Differences between the P treatment levels were only found to occur between high level plots (P_{ox} = 563μg g`1) and the other treatment levels (control P_{ox} =195μg g^{-1}, one addition P_{ox} =239μg g^{-1}). There were therefore no significant differences in P_{ox} between control plots and those subjected to a single P addition. At the Surrey site, the first phosphorus addition seems to either to have leached out or, as is more likely, been taken up by the surrounding vegetation. The higher-level additions resulted in the highest mean P availabilities of any of the sites; P_{ox} was 591µg g^{-1} in the disturbed plots (Fig 2.7b).

The New-Forest site displayed the most dramatic differences in P_{ox} between the treatment levels with both the phosphorus ($F=30.4_{2,30}$, $p=<0.001$) and disturbance treatments ($F=5.8_{1,30}$, $p=<0.05$) having significant main effects on P_{ox}. The interaction between the two variables was not significant. The effect size of the disturbance treatment ($eta^2=0.06$) was small in comparison with that of the P additions ($eta^2 = 0.61$). Post-hoc comparison of means found that all levels of phosphorus, control (P_{ox} = 113µg g^{-1}), one addition (P_{ox} = 234µg g^{-1}) and three additions (P_{ox} = 472µg g^{-1}), were significantly different to the others. The high PSC of the soil at this site appeared to exaggerate the effect of the P additions resulting in very different levels in the soil (Fig 2.8c).

An overall view of the study reveals that the relative effect of phosphorus addition on P_{ox} was greater on the high PSC sites and a larger amount of the added P remained in an available form in the topsoil where PSC was high. The hypothesis that leaching losses are greater at low PSC sites is supported by approximate values of P saturation estimated by dividing the P_{ox} of the undisturbed, 3 addition experimental soils by the mean PSC of the sites at the 0-50mm depth. The Dorset site (PSC=231µg g^{-1}) reached a saturation of 75.3% in the three additions treatment level compared to 53.2% in the Surrey site (PSC=1112µg g^{-1}) and 30.3% at the New Forest site (PSC=1463µg g^{-1}).

Although a significant interactive effect between the treatments was not observed at any of the sites there was a salient and consistent pattern that indicated that there was a small interactive effect between phosphorus addition and disturbance. Disturbance appeared to reduce P_{ox} at low levels of P addition but increase P availability at high levels of P application (Fig 2.7a-c). This is most easily explained by the temporal pattern of addition. Lower vegetation densities in disturbed plots are likely to result in less plant P uptake. This P is therefore, in the short term, available. On longer timescales, however, more of this P may be lost from the cycle of plant uptake, litterfall and mineralization and subsequently leached out of the system.

The phosphorus availabilities of control plots reveal a worrying trend that suggests that they may have been contaminated by horizontal transfer of P from other plots as phosphorus availabilities were considerably higher than they had been in the surrounding areas in the previous year (see Figs 2.3 and 2.7). This pattern may alternatively, be a consequence of the conditions of the time of sampling; P mineralisation may have been higher in the period preceding sampling than it had been in the previous year.

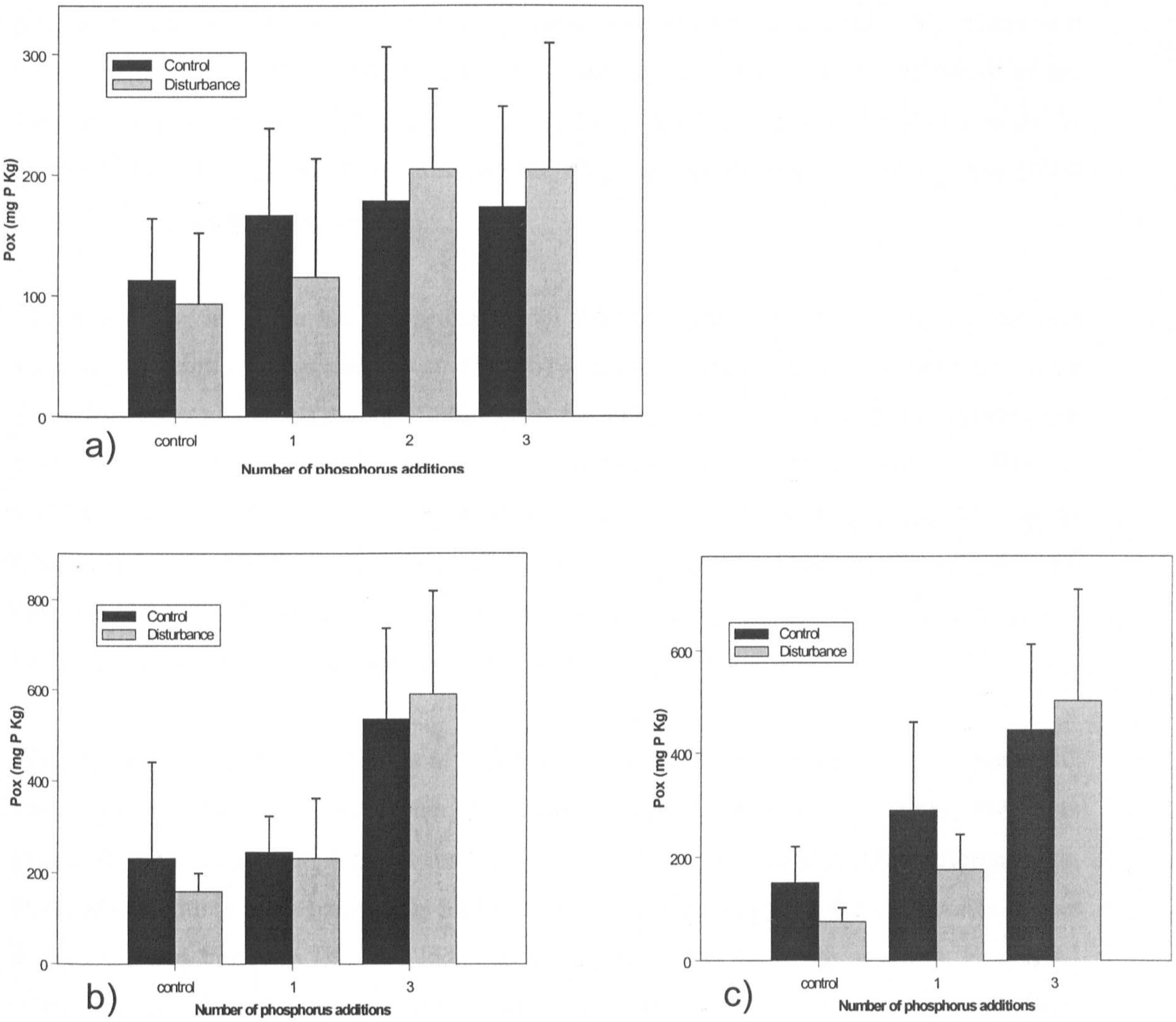


Fig 2.7 a-c. The effects of phosphorus addition and disturbance on the availability of inorganic phosphate (P_{ox}) at the three experimental sites. Dorset (a), Surrey (b) and New Forest (c). Error bars represent 1 standard deviation.

Discussion

Evidence drawn and amalgamated from the results of each of the component studies support hypotheses 1 and 2 by demonstrating that soils of high PSC retain greater amounts of phosphate resulting in both lower leaching losses and greater plant availability where soil PSC is high. The third hypothesis, that soil disturbances increase plant-available P at the surface is rejected in part. PSC was found to be lower at the 50-150mm depth than at the 0-50mm zone at two of the three sites and the only significant effect of disturbance (New Forest) was found to be negative.

The first study, in which the soil properties of the three study sites are described, concurs with the findings of Chapman *et al.* (1989b) and other heathland researchers (e.g. Allen 1964; Pywell *et al* 1994; Traynor 1995) in that the soils of the study sites display declines in P availability and SOM content with depth and a have a fairly consistent soil pH. The soil PSC of the sites, if not their sorption affinity, was also consistent with the findings of Chapman *et al.* (1989b) in that the soil phosphorus sorption characteristics of each site conformed to their regional types, despite being taken from distinct depths and from wet heath sites as opposed to *Calluna* dominated and presumably drier soils.

What the results add to the findings of Chapman *et al.* (1989a,b) is a description of how PSC varies greatly over both soil depths and short horizontal separation distances. PSC was greater in the 0-50mm soil depth at the New Forest site and showed particular differentiation at the Surrey site but was marginally higher in the 50-150mm depth of the Dorset site. These differences and trends in PSC are likely to be dependent on the depth at which Fe and Al oxides are precipitated in the soil profile and it was observed that the characteristic 'iron pan' of humus–iron podsols was sampled in few of the soils of this study thus explaining the failure to observe greater PSC at greater soil depths. Fe and Al oxides are, however, also likely to be sorbed onto organic colloids in the topsoil (White 1980), a phenomenon that explains the higher PSC at this depth in the Surrey and New Forest site soils. The consequences and implications of this dual peak in soil PSC across the soil profile is that only extreme soil disturbances e.g. rotavation, are likely to increase the PSC of the soil surface and that turf stripping of the organic zone (typically 0-50mm in this study) may be an effective means of reducing surface PSC, providing the iron pan is still several centimetres below the surface.

These results support and help explain the findings of upland heath studies. In laboratory conditions, experimental burning of soil cores found that there was almost no nutrients lost when the organic layer was >5cm thick (Allen *et al.* 1969), a result that supported earlier findings where most nutrients released as ash were held by the litter and upper peat layers (top 20mm of the profile) (Allen 1964).

As mentioned previously, the results of this study demonstrate that considerable spatial heterogeneity in PSC may occur across both vertical and horizontal spatial dimensions. This implies that although the majority of variation in heathland soil PSC occurs at the regional scale, there is also within-region (Chapman *et al.* 1989b) and within-patch heterogeneity that may have considerable impact on local processes. Further study is required to acquire a full understanding of the extent and influence of this heterogeneity.

MODELLING THE INTER-RELATIONSHIPS BETWEEN SOIL P PROPERTIES

The fitted statistical models support the ideas of Chapman *et al.* (1989a) whose models assumed that soils with high PSC would lose less P through leaching and, in the long term, have higher levels of plant-available P. Although the data used in the models were taken from only three sites and from two depths with fairly distinct soil properties the failure of the site and depth categories to account for significant proportions of variance in the presence of the soil factor variables as either main effects or interaction terms (with the exception of the %WDP model), their lower explanatory power than these variables when used in isolation, and the excellent fit of the models to the data presented indicates that the descriptive model variables used here represent the determinants, or close correlates, of the response variables. Theoretically consistent mechanistic explanations for the majority of the relationships provide further support of this view.

P_{OX} MODEL

The fitted model and subsequent deletion tests suggest that there are numerous determinant factors and mechanisms that affect the bio-available P of heathland soils. The variable with the greatest explanatory power was SOM, which displayed a positive relationship with P_{ox}. This will almost certainly represent the mineralisation of P from plant litter and microbial pools in the organic matter. Its contribution in explaining P_{ox} is also likely to overlap with PSC as the Fe and Al oxides that influence PSC are often sorbed onto organic colloids. Unexplained deviance in the model may be associated with different species origins of the SOM in the soils as the two dominant species at the site, *Erica tetralix* and *Molinia caerulea*, were spatially aggregated and are thought to differ in their litter P mineralisation rates (Berendse *et al.* 1989).

The fitted relationship between pH and P_{ox} was more complex but was on the whole negative i.e. neutral soils had a lower availability. Available P is generally thought to be reduced by low pH because of the formation of iron and aluminium phosphates (Killham 1995). The acidified ammonium oxalate method however, dissolves these, and so recognises that the P remains bound within that region of the soil and may actually become available over long time periods (Frossard *et al.* 1995). Phosphorus sorption capacity was also found to affect P_{ox}. Though its effect was found to be small and probably a result of greater retention, the effect of PSC on phosphorus availability over longer timescales is likely to be far greater. The simulation modelling of Chapman *et al.* (1989a) and the empirical studies of Chapman & Clarke (1980) suggest that the cumulative effect of greater P availability in high PSC soil enables faster plant growth (biomass accumulation) and therefore, more rapid SOM accumulation rates. Direct observations of different aged heath stands have found that P content accumulates alongside SOM in post-fire heath development (Chapman *et al.* 1975). Although the ratio between soil organic and inorganic P remains relatively constant with age (Chapman 1970) the organic zone of the soil becomes deeper as the stand develops resulting in an increase in the total budget of available inorganic P as the stand approaches the degenerate state. This synopsis is given further support by the higher P_{ox} found in high SOM soils in this study and the greater P availability in degenerate as compared to mature stands found by Alchin (1997).

In conclusion, soil PSC is responsible for a small, direct, effect on P availability at this scale of study but will, by affecting SOM accumulation, play an important role in affecting P availability over decadal and landscape scales as high PSC regions (e.g. Surrey and the New Forest) will reach high P availabilities more rapidly after disturbance or abandonment than regions of lower PSC (e.g. Dorset). The models of Chapman *et al.* (1989a) also predicted that SOM accumulation would reach a plateau where PSC was low and that the rate of decline in SOM accumulation was not so rapid where PSC was high. If P availability is an important factor in scrub colonisation then it is late successional heaths that will be the most invasible. If all other influences are considered equal (e.g. time of management cessation) there will be a greater proportion of heath area in this more invasable state in high PSC regions. It would therefore follow that burning management needs to be applied more frequently in high PSC regions if available P is to be held at a low level.

P-SATURATION ANDWATER SOLUBLE-P MODELS

The proportion of water in readily desorbable pools (%WDP) and the degree of P saturation, both indicators of leaching losses, displayed a similarly moderate correlation to that found by Lookman *et al.* (1995). PSC was found to be an important determinant of both of these variables in the statistical models indicating that P_{sat} and %WDP will be greater in low PSC soils. This latter result suggests that phosphorus availability may be greater over short timescales (i.e. plants do not need to invest a great deal of effort to obtain the P available in the system) but also suggests that P mineralised from SOM, or released in pulses following disturbances, is more likely to be retained on high PSC soils. Findings at the more densely vegetated Surrey site, at which the proportion of water desorbable P was low are consistent with the modelling studies of Chapman *et al.* (1989a) which predicted a negative correlation between leaching losses and vegetation development. This balance between P release, sorption, plant uptake and leaching is likely to play an important role in the accumulation and loss of P from the system as a whole. The results of this study tentatively suggest that high SOM, low PSC heathlands such as the Dorset site will have considerable leaching losses and possibly a declining overall P budget while those of higher PSC sites like those of the New Forest and Surrey will continue to accumulate P.

EXPERIMENTAL PHOSPHORUS ADDITION

Further evidence of the greater P retention and availability of high PSC sites is provided by the results of the experimental study. This study of the P_{ox} content of the topsoil allowed the added P to be divided into two soil pools. The first, measured, fraction was adsorbed and soluble P in the upper soil and the second was a combination of leached, complexed, microbially immobilised and plant-absorbed P. Although this second fraction represents a number of fates of the added P, results from observational studies would suggest that much of the sorbed P would be in the organic layer where PSC is greater. P sorbed lower in the profile may effectively be lost as the roots of heathland plant species are concentrated in the organic zone. Despite this large number of 'black box' soil P pools the conclusion remains valid; retention and availability of added P was greater at the high PSC sites, while at the low PSC, Dorset site it reached saturating levels after a small number of additions.

Disturbance did not have the large effect on phosphorus availability that was hypothesised. Results of the descriptive studies reveal that this was due to the intensity of disturbance being insufficient to bring leached Fe and Al oxides to the surface. With the exception of plots that had received recent fertiliser applications P availability was lower in disturbed plots. This may reflect two opposing processes occurring over different temporal scales; disturbed plots will initially have higher available P amounts as a result of lower plant uptake but this will eventually be leached out of the topsoil. It may also be influenced or interact with the phenomenon of lower PSC soils being brought to the surface.

The results of the experimental studies are particularly relevant to the phenomena of fire and beetle outbreaks in heathland ecosystems in that large quantities of P are released over short periods of time. The implications are that greater amounts of P are likely to be retained after these events where soil PSC is high. These differences may have significant impact upon vegetation recovery in terms of both speed and community structure.

CONFOUNDING VARIABLES AND OTHER CAVEATS

Although this study has focussed upon the role of PSC a number of other factors will also affect retention, leaching losses and plant availability at both the study sites in question and on heathlands in general. Although the soil water content of the three study sites were similar, their drainage rates may not be and this is a factor that varies greatly between heathland and mire vegetation types. PSC itself could be affected by drainage as it depends greatly on Fe and Al oxides, and these are susceptible to leaching. Sorption-desorption processes are also affected in that the diffusion of P increases when soil water content increases so P is often released from waterlogged soils (Frossard *et al.* 1995). In such cases, leaching losses may depend greatly upon water flow and plant uptake rates of this 'standing soluble' pool. In opposing conditions, dry sandy soils are likely to display lower soil solution P concentrations but will drain quickly absorbing little of the soil solution P. This dependence on drainage was found in upland heath where it was found that nutrient leaching in a post burn heath depended on the structure, compactness and porosity of the soil (Allen 1964).

THE MEASUREMENT OF BIOAVAILABLE P IN HEATHLAND ECOSYSTEMS

The wider research project that this Chapter contributes towards concerns itself with the apparent relationship between soil phosphorus availability and phase-transition between heath and scrub ecosystem states. Comprehensive study and confirmation of this relationship, however, involves difficult challenges associated with the measurement and spatio-temporal scaling of bioavailable P.

The majority of heathland P studies have looked at extractable P as a measure of plant available phosphorus (e.g. Mitchell *et al.* 1997; Pywell *et al.* 1994) but simple measures of bio-available P have proven difficult (Frossard *et al.* 1995). This difficulty is caused by species-specific inequality in the availability of differing soil P pools, variation in the relative sizes of these pools and temporal dependence in what is considered an available fraction; all isotopically exchangeable P present on the solid phase can eventually come into solution (Frossard *et al* 1995). In their most simple interpretation the different extractable P measurements represent P availability on different timescales. It is for these reasons that the most appropriate measure of plant-available P is dependent on the species and spatio-temporal scale of the process in question.

In this research P_{ox} was chosen to represent P availability as experienced by heathland shrubs and seedling tree species (e.g. *Betula* and *Pinus* spp) as it measures all the solution and sorbed phosphate that may eventually become available. In the predominantly organic upper layers of podsols P mineralisation rates may also be a good indicator of seedling P availability as it is believed that P nutrition becomes increasingly dependent on decomposition rates as the proportion of P in SOM increases (Frossard *et al.* 1995). Both methods neglect the role of mycorrhizas which are not believed to enable greater access to sorbed or 'fixed' P (Lajtha & Harrison 1995) but may contribute significantly to the nutrition of both ecto- and ericoid mycorrhizal species through the acquisition of organic P sources (Perez-Moreno & Read 2000; 2001a,b; Allen 1991).

The synthesis presented here demonstrates that it is PSC, or another more inclusive measure e.g. total P, as opposed to extractable measurements of available P that may be the best predictor of P dependent processes at the landscape and decadal scales e.g. regional differences in productivity and invasion as it appears to play a role in influencing the overall P budget of the system.

CONCLUSIONS

The findings of the component studies presented here, when combined with the existing literature, provide support to the hypotheses that PSC, by affecting plant-available P, controls phase-transition in heathland ecosystems. This new synthesis complicates the originally simple model by suggesting that PSC influences available P through a variety of mechanisms which operate at different temporal scales. These include the greater direct sorption of mineralised phosphate and lower leaching losses on high PSC soils resulting in differences in the accumulation rate of the soil organic matter P pool.

Although this study demonstrates a link between PSC and P availability further study is required to see if the success of tree invasion responds to variance in P availability at the scale of the individual seedling recruit. Whether P limitation is a *major* determinant of tree colonisation and therefore persistence of heathland ecosystems also needs to be determined i.e. is its proportional contribution to invasion success large relative to that of other determinant factors?

Chapter 3: Identifying the determinants of a heath-scrub phase transition.

Abstract

1. The invasion of *Betula* spp. represents the moment of transition between lowland heath and scrub ecosystems. It was hypothesised that the invasion of *Betula* was controlled by a multivariate threshold, comprised of numerous determinant factors that may be subdivided into those contributing to seed and safe-site limitation. It was also hypothesised that P-availability represented a key axis in the determination of the *Betula* safe-site.
2. These hypotheses were tested in a multi-factorial field experiment in which 3 variables: seed rain, P-availability and disturbance, were manipulated to cover a wide, but typical, range of heath conditions. Numerous covariates, including the vegetation densities of competing species, were also measured.
3. Initial analysis was conducted using analysis of deviance with *Betula* seedling densities as the proxy response for invasion success. A more detailed description of the data was achieved by converting two of the factorial variables: seed rain and P availability to a continuous form, including a wide range of covariates and producing 'minimum adequate' statistical models (MAM's) that provided the best possible fit with the constraint of all parameters being significant. An additional model, describing the determinants of mammalian herbivore attack, was also formulated.
4. Analysis of deviance found that all three treatments had significant effects on *Betula* seedling densities, with seed availability proving to be the single greatest limitation. P availability had a small but non-significant effect in the germination stages but had highly significant effects on seedling numbers 4 and 12 months after germination. Disturbance had an initially large positive effect that dwindled over the 12 month duration covered by the data.
5. The MAM's provided consistently accurate descriptions of the data (explained deviance typically >70%) and quantitatively delimited the environmental conditions at the site in which transition was likely to occur. The models suggested a temporal accumulation of deterministic processes as evinced by greater parameterisation in models describing densities of more mature seedlings. MAM's allowed for the subdivision of disturbance effects revealing that in the long term its effects were mixed; positive effects emerged from the reduction of vegetation densities, these were balanced by the negative effects,

most probably representing exposure. The most important identified determinants of the *Betula* invasion threshold at this site were seed rain, plant neighbour effects and P-availability. Many co-variates may have lacked sufficient variance within the site to be recognised as determinants by the statistical models.

6. The model fitted to the herbivore data demonstrated that seedlings had a greater chance of attack when they were larger, in greater densities and where ericaceous species were scarce. The result of this selection is that the safe-site conditions or 'regeneration niche' of *Betula* appears to be extremely narrow when mammalian herbivores are present.
7. A major limitation of the models is their lack of generality, as they are specific to a single site. They are capable, however, of illuminating the mechanisms by which many larger scale processes e.g. burning and grazing regulate the persistence of lowland heath. The results also support the hypothesis that soil phosphorus sorption capacity (PSC) determines heath-scrub transition as many of the identified determinants e.g. P-availability and vegetation densities, are controlled either directly, or indirectly, by PSC.
8. Further study of a wider range of sites, conditions and scales is required if these determinants of invasion, and their relative significances are to be confirmed and if a general, multidimensional model describing the ecotonal conditions of the heath-scrub phase-transition is to be formulated.

Introduction

Transitions between alternate ecosystem states are of fundamental importance in both community and ecosystems ecology (Scheffer *et al.* 2001; May 1977). These transitions are often abrupt (ecotones) and are dependent upon the colonisation and rapid population growth of a single species or functional group within the community. This organism often modifies the environment to initiate successional change to the alternate ecosystem state (Chapin *et al.* 1997; Edmunds & Carpenter 2001; Hobbs 1996; Srivistava & Jeffries 1996; Petraitis & Latham 1999). The threshold of entry for this species or functional group often depends upon multiple variables, an example being the regulation of bacterial and algal populations, the drivers of the phase transition in lake ecosystems. Algal and bacterial population dynamics are dependent on the interaction between nutrient levels, carbon availability, the intensity of fish predation and grazing invertebrate densities (Jones *et al.* 2002; Scheffer *et al.* 2001). Invasion of any species is also likely to be affected by dispersal, establishment and reproductive success. In plant ecology these factors are, at smaller scales, usually reduced into factors controlling the presence of propagules (seed limitation) and the factors controlling establishment success (safe-site limitation). The majority of studies have found that a combination of seed and safe-site limitation is required if recruitment dynamics are to be explained (e.g. Eriksson & Ehrlén; 1992; Turnbull *et al.* 2000). Acquiring an understanding of factors controlling the invasion of the species that trigger phase transition is key to ecosystem management as it allows for the development of management strategies in which the species causing the transition may be encouraged or precluded. Ecosystems may therefore be held in the desired, 'suspended dynamic', state.

The last century has seen a large decline in the area of European lowland heath ecosystems (Moore 1962; Farrell 1993; Webb 1998). Although the majority of this change is attributed to direct conversion to alternate land uses (Webb 1990), e.g. forestry, urbanisation and agriculture, the major causes of heath decline have shifted in recent years to 'natural' transitions towards grassland and woodland ecosystem states (Heil & Diemont 1983; Rose *et al.* 1999). Transition to grassland has been the major change in continental lowland heath but transmutation in the UK has been predominantly towards woodland and scrub systems (Webb 1990; Rose *et al.* 1999). A number of species are responsible for this process but none is more prevalent or causes such widespread change as *Betula* (Mitchell *et al.* 1997).

At the patch scale and below, colonisation of heathlands by *Betula* (both *B.pubsecens* (Ehrh.) and *B.pendula* (Roth)) represents the moment of transition from a dwarf shrub to a scrub ecosystem state in which there are widespread and significant changes to both community composition and ecosystem properties (Chapter 1.). Once transition to *Betula* scrub has occurred the system proves highly resistant to restoration efforts (Mitchell *et al.* 1999), a possible indication of hysteresis, the requirement to shift conditions further back towards the original state than the point of transition (Scheffer *et al.* 2001).

The customary view of heath persistence is that it is dependent upon traditional management e.g. grazing and burning (Gimingham 1971; Webb 1998). More recent reviews have expanded this outlook by suggesting that lowland heath may persist, without human intervention, within a mosaic of ecosystem states in the presence of large free-ranging herbivores (e.g. Bokdam & Gleichman 2000; Olff *et al.* 1999; Vera 2000). Although management appears to be largely responsible for between-heath differences in encroachment in the UK there is considerable regional and patch scale variation in the extent and likelihood of scrub invasion in unmanaged heath, a pattern that correlates with the phosphorus sorption capacity (PSC) of the soil (Chapman *et al* 1989b; Chapter 2). Positive relationships between PSC and plant-available P have resulted in the formulation of the hypothesis that *Betula* invasion, and therefore heathland persistence, is sensitive to small differences in P availability (Chapter 2). Such a mechanism would be consistent with the patterns of nutrient dependent phase transition in continental heathlands in which shifts towards grassland are stimulated by anthropogenic nitrogen deposition (Aerts 1989; Aerts & Berendse 1988).

In reality, however, *Betula* invasion is unlikely to depend on P availability alone with the threshold of invasion being in all probability, controlled by numerous variables in a site and scale dependent manner. Although the process of *Betula* recruitment has received considerable attention (Atkinson 1992; Harding 1981; Perala & Alm 1990), with numerous factors being proposed as 'important' to seedling germination growth and survival (Chapter 1.), the relative contribution of these factors have not previously been assessed in an integrative fashion making an accurate description of the recruitment threshold problematic. The variables controlling this threshold may, however, be subdivided into those contributing to seed (e.g. dispersal, reproductive failure) and safe-site (e.g. competition, nutrition) limitation, the latter overlapping considerably with the concept of invasability – environment dependent variation in colonisation and establishment success.

It is therefore hypothesised that:

1. The likelihood of transition between lowland heath and *Betula* scrub states is determined by the degree of *Betula*: a) seed limitation and b) safe-site limitation.

2. A key axis in the determination of the *Betula* safe-site is P availability.

These hypotheses were tested in a single field experiment at the edge of a colonising population in which the effects of a multitude of proposed invasion determinants were simultaneously assessed for their impact on *Betula* seedling colonisation. This was achieved with a multi-factorial experimental design with 3 treatments: phosphorus, seeding, disturbance and numerous quantified co-variates (e.g. soil organic matter content, vegetation density). The significance and nature of the relationship between *Betula* colonisation and each of the proposed determinants was assessed with general linear modelling techniques. This approach enabled a simultaneous assessment of the variables that determine the phase transitional area (Loehle *et al.* 1996) or 'invasion threshold', their relative importance and the nature of their relationship with seedling success. Repeated survey of the experimental site allowed temporal shifts in the determinants of seedling recruitment to be assessed and also for an analysis of the factors determining herbivory, a major potential determinant. The overall aim of this process was to produce a general, multivariate model of invasion for the experimental site that described invasion success as a function of several determinant factors. As ecosystem persistence, in this case, is the inverse of invasion success a model describing the determinants of invasion is also a description of the determinants of heathland ecosystem persistence.

Methods

STUDY SITE

The experimental site was located on Crichton's heath of the Arne peninsula, Dorset (National Grid Ref: SY 976 894), an area managed as a nature reserve by the Royal Society for the Protection of Birds since 1966. Before this time it is thought that the site was low intensity farmland and cleared of trees for timber use. The heathland of Arne has not experienced widespread *Betula* invasion, even when left unmanaged. In a review of the management history of the site Pickess *et al.* (1992) state that "unlike many Southern English lowland heaths neither *Betula pendula* or *B.pubescens* present major management problems" and that "the cause of this stability is not at present understood". The geology of the region is clay overlain with sandy Tertiary deposits, the Bagshot Beds (Pickess *et al.* 1992), resulting in sandy podsols with the impedance of drainage in some areas.

The plant community of the site is best classified as a dry M16 (*Erica tetralix-Sphagnum compactum*) NVC community (Rodwell 1992) in that it is a flat patch of vegetation dominated by *Erica tetralix* (L.), *Molinia caerulea* ((L.) Moench) and *Calluna vulgaris* ((L.) Hull). The dwarf shrub species appear to have undergone the full heather cycle described by Watt (1947) and Gimingham (1988), as degenerate, pioneer and building phase vegetation are found in unison resulting in a wide variety of vegetation densities and some light gaps ≥ $25cm^2$. The experimental blocks run parallel to a linear strip of *Betula* at distances of 13-24m. Aerial photos inform us that these trees were largely absent in 1924 when the area now covered by *Betula* was an agricultural field (Oliver 1925). Locating the experiment at the edge of a colonising population ensured some background seed rain, it is also the area that intuition would tell us is the most likely to undergo transition.

The site of the experimental plots is not thought to have been actively managed before 1990 and has seen no active management in the 8 years previous to the experiment's inception. The site is not grazed by domestic animals but the Arne peninsula supports a large population (c.300) of Sika Deer (*Cervus nippon*) and evidence of their presence: browsing damage, tracks and droppings, can be seen on and around the site. Mean soil PSC values of the site were found to be $231\mu g$ P $g^{-1}$and $323\mu g$ P g^{-1}at the 0-50mm and 50-150mm depths respectively, values that are slightly higher than the regional 'type' (see Chapter 2) but not atypical.

In June 1999, before the onset of experimentation, the site was cleared of all visible *Betula* seedlings by hand pulling. Later in the year it became clear that some small seedlings had been missed and so these were also removed. In the summer of 1999, shortly after the experiment's inception, the site experienced a heather beetle (*Lochmaea suturalis*) outbreak which seriously damaged all and killed >50% of the *Calluna* bushes on the site. Although beetles and their larvae were sighted again in 2000 visible damage did not continue to be observed.

EXPERIMENTAL DESIGN

The experiment encompassed an orthogonal factorial 3 x 4 x 2 randomised block design (Dutilleul 1993) with all 2m x 1m plots in each of the 4 blocks approximately equidistant to the nearest source of seed rain. As there were 2 replicates per block there was a total of 192 plots with 8 replicates per treatment combination. There was a 50cm guard row between plots and a one metre guard row between blocks to minimise the effect of nutrient leaching between plots and allow access. The experiment covers an area of 78m x 11m.

TREATMENTS:

1. PHOSPHORUS ADDITION

The phosphorus addition treatment, which had 4 treatment levels: control, 1, 2 and 3 additions is described in full detail in Chapter 2.

2. SEEDING

Seed of *Betula pubescens* was collected from sources close to 3 heathland sites in late September and early October 1999. The sites were: Horsell Common, Surrey TQ014598 (38 trees), Beaulieu River, New Forest SU380060 (54 trees) and Crichton's Heath, Dorset SY974896 (65 trees). After collection, leaves and twigs were removed and the seed was thoroughly mixed. Five 100 seed sub samples were taken from each batch and tested for viability using the tetrazolium method described in Bullock (1996) but with a 24-hour period in the dark. Five 1g samples were also taken from each of the seed mixes and the number of seeds in these were counted. By using the results of the viability tests and seed counts a seed mix was prepared that contained equal proportions of viable seeds from the Dorset, New Forest and Surrey sites. A seed mix of multi-site origin was used to ensure that the emphasis of the seeding treatment was on the effect of seed numbers *per se* as opposed to the genotypic suitability of the invader. In the interim period between collection and application the seed was stored in sealed plastic bags in the dark in an outdoor shed at CEH Furzebrook Research Station, Dorset. The seeds were therefore subjected to a range of temperatures that approximated those of the external environment. Seed was applied at three densities: 1= no added seed, 2= 50 seeds m^{-2} and 3= 250 seeds m^{-2}. These application rates were chosen to coincide with the seedbank densities of $50\text{-}500m^{-2}$ that are typical of both *Betula* species (Granström 1988; Thompson *et al.* 1997). Seed rain was added to the experimental plots between the 3rd and the 5th of November 1999. This coincided with the cessation of the natural seed rain period. Seed was scattered as evenly as possible and close to the ground to avoid the contamination of other plots and the surrounding area, which was later sampled for background seedbank density (see Chapter 4).

3. DISTURBANCE

The disturbance treatment, which was of a non-specific form, was applied factorially at two levels, control and disturbance. It is described in detail in Chapter 2.

CO-VARIATES:

EDAPHIC FACTORS

In addition to the 3 manipulated factors several co-variates were measured. Soil cores were taken on a regular sampling grid of 72 sites, which maximised the coverage of the experimental site. Soil of the 0-50mm depth, that which the seedlings were assumed to be in contact with, was analysed for soil organic matter content (SOM), pH, moisture content and plant-available P (P_{ox}). A full description of the sampling and analysis procedures are provided in Chapter 2. SOM, moisture content and pH were also recorded for the 50-150mm depth.

SEED RAIN DENSITY

Background levels of *Betula* seed rain were monitored using seed traps positioned at regular intervals between the experimental plots. The traps used were blue sticky cards (Agralan Ltd.) coated in waterproof non-drying glue, positioned horizontally 50cm above the ground.

Trapping was initiated on the 6/7/99 and continued until 5/11/99. Trapping recommenced in the period between 27/6/00 and the 3/10/00; both periods were set to coincide with the observed natural seed-shedding period of that year. Trapped seed was tested for viability by visual assessment under x 40 magnification, because glue from the traps prevented tetrazolium tests from working effectively. Seed with a full oily content and spongy white tissue was classified as viable. The reliability of this method was confirmed by conducting both the visual and tetrazolium tests on the same 40 seeds. Results matched perfectly (100% agreement). This enabled natural and experimentally added seed rain values to be compared with confidence. As the seed rain of viable seeds was low an estimated seed rain value was calculated by multiplying the total seed rain of each trap by the mean percentage viability of each sampling period. There were no apparent spatial trends in seed viability.

VEGETATION STRUCTURE & COMPOSITION

Vegetation was recorded using a point quadrat method shortly after the disturbance treatment had been applied. Vegetation recording of the experimental plots was conducted in a random order between mid July and early September 1999. Each experimental plot was recorded separately with a 4 x 9 arrangement of 60mm diameter fibre canes with 20cm spacing. Therefore, 36 points representing the central 160cm x 60cm of each plot were measured. Presence/absence data was collected for all plant species at each 1cm interval of each cane, dead material (necromass) was also recorded, but not to species level. The basal substrate penetrated by each cane was recorded as being either a moss or lichen species, predominantly organic (litter or humus) or predominantly mineral material. All mosses and lichens were recorded to species level with the exception of *Sphagnum* spp. and *Cladonia* spp.

EFFECT OF P ADDITION AND DISTURBANCE ON PLANT AVAILABLE P

The effect of the P additions and disturbance treatments on plant-available P, as measured by ammonium oxalate extractable P (P_{ox}), was studied in a 4 x 2 factorial sub experiment located within the plots of the main experiment. The results of this experiment are presented in Chapter 2.

SEEDLING MONITORING

The abundance and status of *Betula* seedlings were recorded in June, late July/early August and September 2000, and again in May 2001. To record seedling abundance plots were divided into 50 20 x 20cm sub-plots and the numbers of *Betula* seedlings, including cotyledon stage plants, in each sub-plot were counted. The species of *Betula* the seedlings belonged to was not recorded as *Betula* spp. seedlings may only be differentiated to species level after several months of age (Atkinson 1992). Stem diameter at the soil surface (to the nearest 0.5mm) was also recorded. Conducting the final survey in May 2001 allowed the 2001 seedling cohort to be easily identified and subsequently removed from the analysis.

An additional investigation into the effect of the measured variables on the likelihood of attack by mammalian herbivores was conducted by recording a binary response for each seedling noting whether the plant displayed damage inflicted by mammalian herbivores. This was classified as damage to the plant stem, small losses of leaf tissue were assumed to be the result of invertebrate herbivores.

ANALYSIS

An overall assessment of treatment effects in the experiment was achieved by analysing the experiment as a standard factorial design. A more detailed description of the determinants of *Betula* colonisation was achieved by fitting general linear regression models to seedling data, where the descriptive variables were continuous measurements of the heathland environment derived from the experimental site.

MEASURING THE LIKELIHOOD OF PHASE TRANSITION

A full study of the determinants of *Betula* colonisation and establishment, the factors controlling phase-transition and heathland persistence, would require a period of 10-20 years. Although long-term study of the experimental site is intended, the response variable in the research presented here is a proxy of the true threshold of invasion - seedling densities. A number of variables were considered as the measure of *Betula* invasion success including seedling biomass and total basal area. The relationship between seedling biomass and basal area was explored in a study in which the aboveground parts of 160 small birches were harvested from 3 sites on the Dorset heaths in April 1999. Sampling was non-random, instead a wide variety of growth forms (e.g. spindly and prostrate, grazed and ungrazed) were selected to account for natural variability. Both *B.pendula* and *B.pubescens* were present in approximately even numbers. Linear regression found seedling dry weight to be accurately described by seedling basal area (r^2 = 0.85, F = 884.1, p = <0.0001). Total basal area, as predicted from stem diameter was also found to correlate with seedling numbers in the surveys (September 2000, Pearson's r = 0.93, May 2001, Pearson's r = 0.94) suggesting that seedling densities were not only a measure of seedling abundance but also biomass. It is therefore assumed here that seedling numbers are indicative of later invasive success, i.e. conditions resulting in high seedling densities indicate a high probability of phase-transition.

ANALYSIS OF DEVIANCE

Evaluation of experimental treatment effects was conducted by using seedling count data of the four surveys as the response variable in a fixed form Analysis of Deviance general linear model with the four factors, block, seed, phosphorus and disturbance in an orthogonal design. A log-link and Poisson errors were specified, block was treated as a fixed factor and therefore block-treatment interactions were not calculated. This had the additional advantage of reducing the number of model parameters. Analysis was conducted in S+6 for Windows (Insightful).

STATISTICAL MODELLING:

KRIGING

Within this thesis there is considerable use of the geostatistical method of kriging. Kriging is an advanced interpolation procedure that provides estimates for unrecorded locations (Rossi *et al.* 1992; Robertson 1987). This is achieved by measuring the degree of spatial autocorrelation at several distances and subsequently using these measures as the weights in interpolation. The effectiveness of kriging as an interpolation technique was confirmed by the mathematical experiments of Zimmerman *et al.* (1999) who found ordinary and universal kriging to be superior to inverse distance weighting methods for all levels of surface type, sampling pattern, noise and correlation.

The pre-requisite of kriging interpolation is the calculation of co-variance (γ), the average product of the differences between two variables and their respective means, at varying degrees of separation, or lag, distance (h) and the subsequent fitting of a mathematical model that describes these data; the variogram. The variogram is a mathematical description of the degree of spatial autocorrelation of a variable that describes the average degree of correlation in the value of a variate at sampling points as a function of their spatial separation (Rossi *et al* 1992).

Certain variogram models (see McBratney & Webster 1986) allow for the estimation of parameters describing the distance over which autocorrelation occurs and the proportion of variance that is spatially autocorrelated. The 'nugget' variance ($\gamma(0)$) is that at the intercept. It is the combination of sampling error and autocorrelated variance on a scale below that of the minimum measured lag distance. A flat line or 'pure nugget' variogram therefore represents a total lack of spatial structure; i.e. covariance is equal over the entire measured range. Two other key parameters, the range (*a*), which represents the lag distance at which autocorrelation ceases and the sill (*C*), the covariance value at the range, allow for an estimate of the degree of spatial dependency; $1 - (\gamma(0) / C)$ = the proportion of total variance that is autocorrelated. The parameters of the variogram therefore provide an index of both the magnitude and scale of spatial heterogeneity in the variable (Gross, Pregitzer & Burton 1995); e.g. a variogram describing a line curving towards a peak represents patchiness, with the point at which the curve flattens representing the average patch size. Once a suitable variogram model has been fitted to the covariance data it may be utilised in kriging interpolation. In ordinary kriging the weighting of interpolation is based upon the variogram model, which provides information on the degree of influence that each sampled point will have on each unsampled point (Burrough 1995). The end result of this process, where point estimates are calculated, is the production of a grid of interpolated values covering the sampled area. The mean value of a variable for any given area may be estimated from this grid.

Ordinary kriging (conducted using the spatial extension of S+6 for Windows) was used in this study to provide covariate estimates for background levels of seed rain and several edaphic factors including P_{ox} and SOM. As anisotropy (directional dependence of spatial covariance structure), was not detected in any of the variables omnidirectional semi-variograms were calculated for all distance lags up to 40m with the constraint of each lag estimate being based upon a minimum of 30 distance pairs. The best model for each empirical variogram was selected by choosing the fitted model with the lowest residual sum of squares (fitted by weighted non-linear least squares) from the standard asymptotic variogram models; spherical, exponential and Gaussian (McBratney & Webster 1986). A grid of point estimates containing a covariate value for the central position of each square metre of the experimental plots was then calculated by using ordinary kriging with the selected model. The covariate value for each plot was obtained by taking the mean of the two central points.

For two variables, P_{ox} and SOM 50-150mm, the distances in the empirical variograms were restricted to 12m and 20m respectively as preliminary analysis indicated that there was genuine spatial structure within this range that was clouded by the reoccurrence of similar patches at larger scales. The fit of the models was assessed by comparing the fitted models against a linear model with the overall sample variance at the intercept and a slope of zero. The pH data displayed little variation and no spatial structure and so were omitted from the analysis.

The variogram model selected by this process was, for all variables, the spherical model. The fit and form of the models differed considerably between the variables (Table 3.1) with seed rain, moisture content (50-150mm) and SOM (50-150mm) showing the greatest degree of spatial dependency and P_{ox}, moisture content (0-50mm) and SOM (0-50mm) displaying patterns that can be considered 'pure nugget' variance as linear models with a slope of zero had a superior fit to the fitted spherical model. The models fitted to these latter data, and used in the kriging process, were initially steep slopes with a short range.

Table 3.1. Variogram models fitted to the covariate data and used in subsequent kriging interpolation.

	Seed (Background)	P_{ox} (Background)	Moisture 0-50mm	Moisture 50-150mm	SOM 0-50mm	SOM 50-150mm
Best fit model	Spherical	Spherical	Spherical	Spherical	Spherical	Spherical
Range (a)	36.50	1.19	6.74	38.49	6.42	0
Sill (C)	231.45	1331	80.1	22.9	238	19.1
Nugget ($\gamma(0)$)	48.70	52.5	0	18.9	7.85	5.36
Spatially structured covariance $1-(\gamma(0)/C)$	0.79	0.96	1	17.5	97	71.9
Explained deviance (%)(fitted/null)	88.2	-0.06	-4.65	84.2	-5.33	84.2

STATISTICAL MODELLING

Statistical models were fitted to the seedling density data with the GLM procedure of S+6 for Windows, and using the deletion-test procedure described in Chapter 2 (see also Crawley 1993; 2002). Two of the factorial variables, P addition and seed addition were converted into a continuous form to reduce parameterisation and increase the generality of the fitted models. This was, in the case of the seed addition, simple; estimates of background seedrain were added to the values of those that were added experimentally. A single measure of P availability was calculated by taking the mean P_{ox} availability of the various P and disturbance treatment combinations (see Chapter 2) and adding the difference from mean background P_{ox} levels, as estimated from the kriged grid, for each individual plot. Using P_{ox} estimates that were specific to both the number of additions and the disturbance treatment will have had the effect of removing any P effects from the disturbance variable and will have reduced the likelihood of observing an interaction between disturbance and P_{ox} variables. The third of the factorial treatments, disturbance, was subdivided into a number of separate variables including proportional substrate cover and plant and litter abundances. In most studies of safe-site and seed limitation safe-site conditions are assumed to be those that have received some sort of disturbance, often rotavation. Disturbance benefits plant establishment by reducing competition for light, water, nutrients and space. It also creates microenvironments that are more suitable for seedlings than those of intact vegetation. It may however, contain negative influences e.g. exposure to abiotic stresses, greater apparency to herbivores and the destruction of mycorrhizal mycelium. These effects were to some degree separated by including, in the models, both continuous measures of the substrate cover and species abundances and the binary disturbance variable. Because substrate and vegetation data were collected shortly after the disturbance treatment was applied, any effect of disturbance that was observed when the vegetation variables were included could be attributed to disturbance effects independent of vegetation and substrate. Excessive correlation between plant density and disturbance was avoided as de-vegetated beetle attacked, disturbance resistant and naturally low density plots resulted in a wide variation of vegetation densities in both control and disturbed plots.

The requirement for species-specific vegetation terms was assessed using likelihood ratio deletion tests to compare the fit of models containing either individual species variables or sum totals of all live ‘hits’ (biomass density). The resulting parameter values of these variables in the fitted model provided an indication of the relative competitive strength of each species. These parameters cannot be considered as representing competition alone because the observed effect of neighbouring plant biomass on *Betula* seedling densities will represent an assumed net balance between both facilitation and inhibition (Connell & Slayter 1977; Holzapfel & Mahall 1999; Callaway & Walker 1997) which also incorporates indirect effects such as associated soil environments.

The form of the relationship between *Betula* seedling numbers and each descriptor was explored by fitting polynomial regression models and the subsequent testing of any deviance changes with likelihood ratio tests. Relationships were assumed to be linear where the adding of quadratic and cubic terms did not significantly improve the fit of the model.

HERBIVORY MODEL

A model describing the proportion of seedlings that had suffered attack from mammalian herbivores in September 2000 was formulated by using the statistical modelling approach described in Chapter 2. The specified model was fitted by weighted regression using a logit link function, binomial error distribution, the proportion of seedlings attacked as the response and the individual sample sizes (total number of seedlings in the plot) as weights.

Results

Analysis of deviance found that all three of the proposed major determinants: disturbance, phosphorus availability and seed limitation had highly significant effects on the success of *Betula* colonisation (Table 3.2), as defined in terms of seedling population density. The density of seedlings was greatest in disturbed, high P, high seed rain plots in all of the surveys. Although there was some degree of density-dependent compensation (see below) this was insufficient to have an exactly compensatory effect, i.e. plots with initially high seedling densities remained at a greater density throughout the experiment (Figs 3.1a,b,c). Despite the overall trend of initial invasion success equating with long-term success there were considerable changes in the effect strength of each of the treatments over time that are reflected in the changes in the F ratios and *p* values over time.

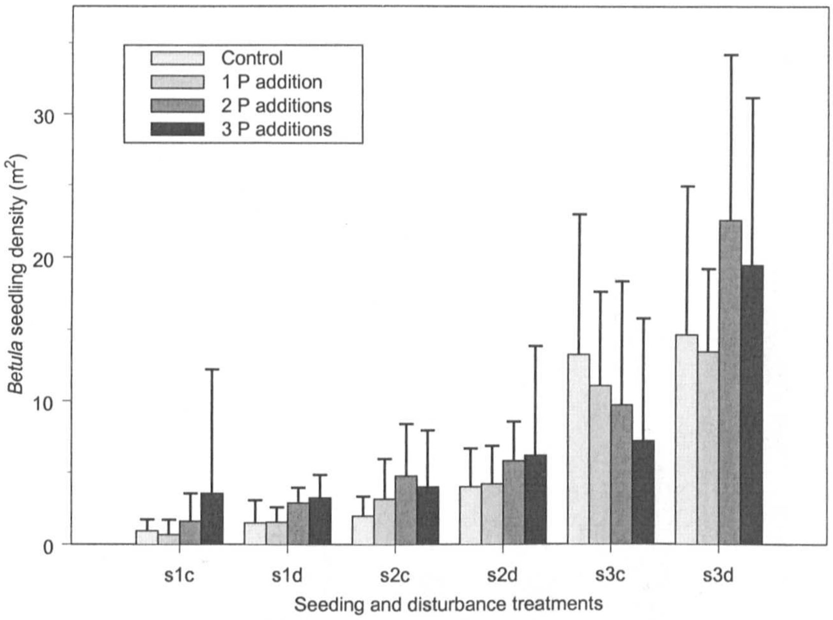
The significance of disturbance peaked in August 2000 ($F = 31.03_{1,165}$, $p = <0.0001$, explained deviance (ED) = 7.53%) when the seedlings were approximately 3 months old. At this point in time the seedling densities were likely to be revealing responses to both superior germination conditions in disturbed plots and a lower intensity of competition. As the experiment progressed the benevolence of disturbed conditions declined (September 2000, $F = 27.3_{1,165}$ $p = <0.0001$, ED= 6.48%, May 2001, $F = 10.99_{1,165}$, $p = <0.01$ ED = 31.5%) as seedlings suffered the effects of greater exposure to herbivores (see below), abiotic stresses and possibly the regrowth of plant competitors.

The effects of P addition at the germination stage (June 2000 survey) were positive but of no statistical significance ($F = 2.17_{3,165}$, p = n.s. ED =1.58%). Several months later (August 2000) the seedlings showed a far greater response ($F = 11.64_{3,165}$, $p = <0.001$, ED = 8.48%), though not of the same magnitude as the seeding effects. The magnitude of the P addition effect declined later in the experiment (September 2000 $F = 9.00_{3,165}$ $p = <0.0001$ ED = 6.41%) but P remained an important determinant of seedling density for the entire year over which the surveys were conducted (May 2001 $F = 8.89_{3,165}$, $p = <0.0001$, ED = 7.65%). These trends are likely to reflect the balance between positive P availability effects on plant health and growth and the greater likelihood of mammalian herbivore attack experienced by larger seedlings (see below). Throughout the experiment, seedling responses to the additions appeared to correlate closely with measured availabilities with seedling responses to P, reaching a plateau at high addition levels in the same way as availabilities (see Chapter 2).

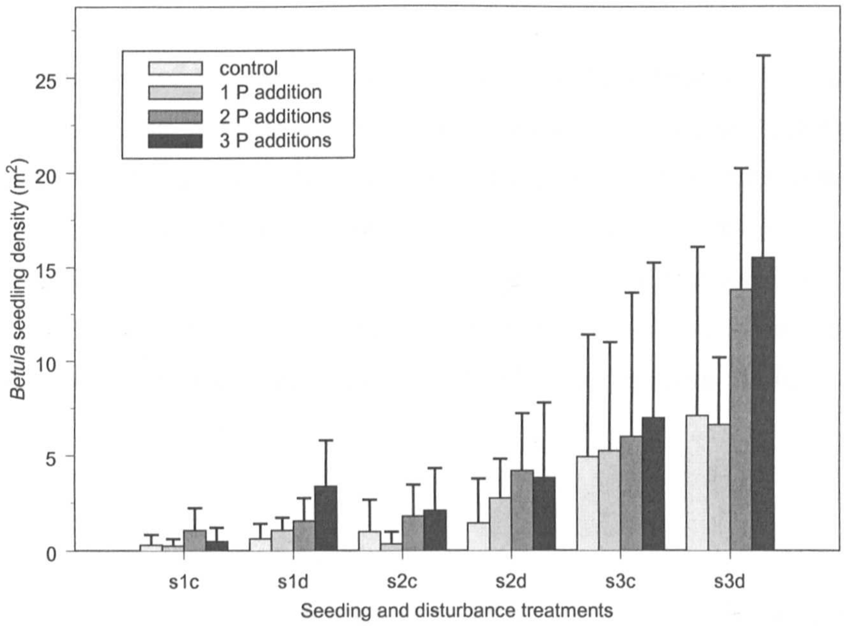
Seed addition provoked the greatest effect of the factorial treatments suggesting that the site experienced considerable seed limitation despite short distances from parent trees. The effect of seeding was particularly pronounced at the germination stages (June 2000 $F = 98.2_{2,165}$ $p = <0.0001$, ED=47.5%), as many factors influencing seedling survival, e.g. P nutrition, were probably not operating in a significant way at this stage. The general trend for the effect size of the seeding treatment was one of decline (May 2001, $F= 55.92_{2,165}$ $p = <0.0001$ ED =32.05%) as the influence of initially high seedling numbers was reduced by factors determining seedling survival and density-dependent processes (see modelling section). Despite these trends seed addition remained the single most important of the studied determinants throughout the course of the study period.

Table 3.2. Analysis of deviance of the seedling count data with a fixed form GLM (Poisson error/log link). Interaction terms were non significant and have not been presented here. ** = p <0.01, *** = p<0.001, ****=p<0.0001. Null *d.f.* = 191, Residual *d.f.* =165.

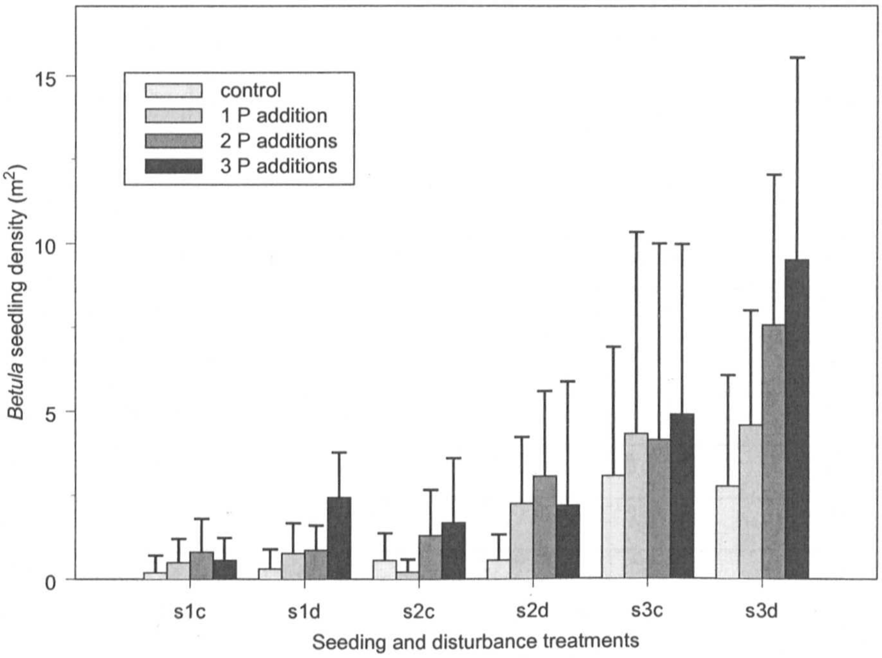
FACTOR		JUNE 2000		AUGUST 2000		SEPTEMBER 2000		MAY 2001	
	d.f.	F	*p*	F	*p*	F	*p*	F	*p*
Block	3	7.09	***	8.86	****	9.10	****	6.69	***
Disturbance	1	16.97	****	31.03	****	27.3	****	10.99	**
Phosphorus	3	2.17	n.s.	11.64	****	9.00	****	8.89	****
Seed	2	98.20	****	70.82	****	82.84	****	55.92	****



a)



b)



c)

Fig 3.1a-c. The effect of seed addition, disturbance and phosphorus treatments on *Betula* seedling densities for a) 1 month, b) 4 month and c) 1-year-old seedlings. s1=control, s2 = 50 seeds m^{-2}, s3 = 250 seeds m^{-2}, c= control, d=disturbance. Error bars represent 1 standard deviation.

DESCRIPTION OF THE CO-VARIATES

An examination of the variables used in the modelling process revealed several general patterns including a tendency for kriged variables to display little variation and for manipulated variables to display the greatest (Table 3,3). The former trend is an integral property of the kriging process, which by its very nature removes much of the background variation in the original data. Although as wide a range of heathland conditions as possible was generated by the experimental method variation in some variables was low, e.g. CV for moisture content 0-50mm was 0.07, and is unlikely to represent the full variety of naturally occurring heathland conditions.

Table 3.3. Descriptive statistics: mean, standard deviation (STD DEV) and coefficient of variation (CV), for the continuous variables used in the statistical models.

	MEAN	STD DEV	CV
Mean vegetation height (cm)	11.1	2.6	0.24
Molinia caerulea density (hits m^{-2})	15.1	20.3	1.35
Erica tetralix density (hits m^{-2})	20.2	15.5	0.77
Calluna vulgaris density (hits m^{-2})	10.5	14.7	1.40
Necromass density (hits m^{-2})	78.8	33.5	0.43
Biomass density (hits m^{-2})	46.3	27.4	0.59
Total moss and lichen density (hits m^{-2})	4.7	7.9	1.66
Total available P (P_{ox}) (μg P g^{-1})	156.0	41.3	0.27
Water 0-50mm (%total soil mass)	68.2	5.1	0.07
Water 50-150mm (% total soil mass)	33.7	3.1	0.09
SOM 0-50mm (% dry mass)	52.7	10.8	0.20
SOM 50-150mm (% dry mass)	13.3	3.0	0.22
Mineral substrate (% cover)	8.1	12.1	1.49
Organic substrate (%cover)	86.3	12.4	0.14
Seed rain (total m^{-2})	125.1	109.4	0.88

STATISTICAL MODELS

JUNE 2000 – 1 MONTH OLD SEEDLINGS

The formulation of statistical models provided a series of descriptions of the survey data that were more general, closer fitting, less parameterised and more detailed than those provided by the analysis of deviance results alone.

The model fitted to the June 2000 survey data (Table 3.4), which had Poisson error and a log link function, was able to explain 70.8% of the deviance in seedling densities shortly after germination had occurred. Its included variables and parameter values reflected the effects of seed addition and the interaction of this effect with the determinants of germination and early stage survival.

Table 3.4. Minimum Adequate Model MAM (log link, Poisson error) model describing *Betula* seedling densities (m^{-2}) approximately 1 month after germination (June 2000). Explained deviance = 70.8%, residual *d.f.* = 185. Deleted Terms: Disturbance, biomass density, all substrate measurements, all moss and lichen abundances, necromass density, mean vegetation height, water content (50-150mm), SOM (0-50mm), SOM (50-150mm), *Calluna vulgaris* density.

	Parameter Values	Standard Error	Explained Deviance	p (F-Test)
Intercept	-0.989	0.45		
Soil water content (%) (0-50mm)	0.0248	0.0063	0.98%	<0.05
Phosphorus availability (μg P g^{-1})	0.0029	0.00065	1.31%	<0.05
Molinia caerulea density (hits m^{-2})	-0.032	0.0044	14.33%	<0.0001
Erica tetralix density (hits m^{-2})	-0.003	0.0026	6.25%	<0.0001
Total seed rain (m^{-2})	0.0079	0.0004	46.1%	<0.0001
E.tetralix * Seed rain	-0.00007	0.00002	0.84%	<0.05

The variable of greatest influence in this model is seed rain density (DCD = 46.1%, p = <0.0001). Suggesting that seed limitation was of far greater importance than safe-site limitation in the determination of early stage seedling densities. The abundance of *Molinia* *caerulea* (DCD = 14.3%, p = <0.0001) and *Erica tetralix* (DCD = 6.3%, p = <0.0001) were found to have significant, negative relationships suggesting that inhibition of germination and/or very early seedling establishment was occurring where these species were present. The effect was more pronounced for *M.caerulea*, presumably as a result of the thick litter associated with live stems. *C.vulgaris* densities did not affect germination or early stage survival; possible causes being lower light absorbance and/or the previous years heather beetle outbreak. Disturbance failed to elicit any significant effects other than through the reduction of *E.tetralix* and *M.caerulea*.

Edaphic factors played a minimal role in seedling germination with most measured factors e.g. SOM and substrate type being unable to account for significant proportions of the deviance. Soil water content in the 0-50mm depth (DCD = 1.31%, p = <0.05) and P_{ox} availability (DCD = 1.31%, p = <0.05), did however, demonstrate positive relationships with seedling numbers that were able to account for small, unique portions of the deviance. These parameters are likely to represent the beginnings of seedling dependency on the external soil environment. The water effect is likely to result from seedling droughting at a stage when roots are not fully developed and also from the effect of soil water content on seed germination. The significant P_{ox} effect is apparently contrary to the results of the factorial analysis but merely reflects the lower parameterisation of the P variate in this model *d.f.* = 1 as opposed to 3.

The final effect detected by the modelling process was a small interaction between seed and safe-site limitation, as represented by total seed rain and *E.tetralix* density (DCD = 0.84%, p = <0.05). This reflects the proportionally lower co-incidence of seed and safe-site when both are limiting and vice versa.

SEPTEMBER 2000: 4-MONTH OLD SEEDLINGS

The MAM fitted to the September 2000 survey data, which was a log link, Poisson error model explaining 73.9% of the deviance, retained factors affecting germination but also included additional variables, which reflect environmental factors affecting seedling survival (Table 3.5). This temporal variation of the determinants of seedling densities is revealed not only in the parameters included in the model but also by the changes in their parameter values and the proportion of explained deviance that is unique to them. The main shift in determinant factors is a general increase in the number and importance of factors associated with safe-site limitation in relation to seed limitation. Despite this trend, total seed rain remained the factor with the single greatest independent contribution to the explained deviance (DCD = 40%, p = <0.0001).

Table 3.5. MAM model (log link, Poisson error) describing *Betula* seedling densities (m^{-2}) approximately 4 months after germination (September 2000). Explained deviance = 73.9%, Residual *d.f.* = 181. Deleted Terms: biomass density, All substrate measurements, all moss and lichen abundances, necromass density, water content (50-150mm), water content (0-50mm), SOM (50-150mm).

	Parameter Values	Standard Error	Explained Deviance	p (F-Test)
Intercept	-1.829	0.332		
Calluna vulgaris density (hits m^{-2})	-0.0175	0.0031	2.93%	<0.0001
Molinia caerulea density (hits m^{-2})	-0.0212	0.0056	13.52%	<0.0001
Erica tetralix density (hits m^{-2})	-0.0524	0.0046	11.78%	<0.0001
Phosphorus availability (P_{ox} μg P g^{-1})	0.0073	0.0009	5.81%	<0.0001
Disturbance (binomial variable)	0.0121	0.112	2.38%	<0.001
Total seed rain (m^{-2})	0.0073	0.0005	40.0%	<0.0001
Mean vegetation height (cm)	0.1234	0.021	2.74%	<0.0001
SOM (% dry mass) (0-50mm)	0.0108	0.0039	0.63%	<0.05
Disturbance * Seed rain	0.0028	0.0008	0.92%	<0.05
M.caerulea * Seed rain	-0.0001	0.00002	0.69%	<0.05

The net effect of facilitative and inhibitory processes associated with the surrounding vegetation remained strongly negative with all three dominant plant species; *C.vulgaris* (DCD = 2.93%, p = <0.0001), *M.caerulea* (DCD = 13.52%, p = <0.0001) and *E.tetralix* (DCD = 11.78%, p = <0.0001) having highly significant effects on *Betula* seedling density. An additional factor, mean vegetation height, was also included in the model (DCD = 2.74%, p = <0.0001). This effect, which could account for a significant proportion of deviance in the presence of measures of vegetation density, may represent differences in the invasability of different vegetation structures (physiognomy). As the relationship is positive it reveals that shorter vegetation was less invasable than taller vegetation of the same density. This may result from the greater homogeneity of the shorter vegetation e.g. building phase dwarf shrub vegetation. Taller vegetation of the same density is likely to be more heterogeneous in form and so have a greater likelihood of containing light gaps.

Disturbance accounted for a small portion of the variance in addition to its effects on plant competition and P availability (DCD = 2.38%, p = <0.001). P availability was a more important factor than it had been in June, with high P plots containing higher densities of seedlings (DCD = 5.81%, p = <0.0001). Seedling densities were also found to respond positively to the SOM content of the topsoil (DCD = 0.63%, p = <0.05), probably through a combination of its effects on moisture retention and nutrient availability. The September 2000 model contained two interaction terms, both of which reflected interactions between safe-site and seed limitation. The first interaction, between disturbance and seed rain, revealed the proportionately greater effect of adding seed in a disturbed plot (DCD = 0.92%, p = <0.05), while the other, between *M.caerulea* and seedrain (DCD = 0.69%, p = <0.05) also exhibited the greater proportional effect of adding seed where safe-sites are non-limiting – a similar effect to that which had been observed for *E.tetralix* in June.

SPRING 2001 – 1-YEAR OLD SEEDLINGS

The MAM fitted to the May 2001 survey data had a log link, Poisson error and 14 significant parameters. It accounted for 69.3% of the total deviance (Table 3.6). The identity and nature of the determinant factors and their effects was broadly similar to those observed in September 2000 but herbivory and other forms of mortality appear to have had a greater compensatory effect on higher density plots which reduced the perceived impact (shallower slope, and lower intercept within the models) of many of the positive variables.

Despite considerable seedling mortality, seed rain remained the single most important variable in the model (DCD = 31.74%, p = <0.0001). Its interactions with disturbance (DCD = 0.86, p = <0.05) and *M.caerulea* (DCD = 0.76%, p = <0.05) were also retained (Fig 3.3). The interaction between disturbance and seed rain had however, switched to being negative (i.e. the effect of adding seed had become proportionately lower in disturbed plots), a pattern that may be explained by the seedling density and size dependent actions of herbivores (see below).

Disturbance as a main effect also shifted towards having an overall negative effect on seedling numbers when separated from the effects of competition reduction (DCD = 4.53%, p = <0.0001). This finding, which is consistent with the decreasing significance of the disturbance treatment in the original factorial analysis, may reflect greater exposure in disturbed conditions which although having positive effects on growth may also result in greater contact with herbivores and abiotic stresses e.g. frost heaving.

Table 3.6. MAM model (log link, Poisson error) describing *Betula* seedling densities (m^{-2}) approximately 1 year after germination (May 2001). Explained deviance = 69.27%, residual d.f. = 177. Deleted Terms: biomass density, All substrate measurements, all moss and lichen abundances, necromass density, water content (50-150mm), water content (0-50mm).

	Parameter Values	Standard Error	Explained Deviance	p (F-Test)
Intercept	-0.7136	0.575		
Calluna vulgaris density (hits m^{-2})	-0.0185	0.004	5.33%	<0.0001
Molinia caerulea density (hits m^{-2})	-0.0161	0.006	11.29%	<0.0001
Erica tetralix density (hits m^{-2})	-0.1826	0.036	12.64%	<0.0001
Phosphorus availability (P_{ox} μg P g^{-1})	0.0045	0.0018	6.82%	<0.0001
Disturbance (binomial variable)	-0.1981	0.132	4.53%	<0.0001
Total seed rain (m^{-2})	0.0080	0.0006	31.74%	<0.0001
Mean vegetation height (cm)	0.0705	0.035	3.62%	<0.0001
SOM (% dry mass) (0-50mm)	0.0191	0.0054	1.53%	<0.01
SOM (% dry mass) (50-150mm)	-0.476	0.0191	0.76%	<0.05
E.tetralix * P availability	0.0004	0.0001	0.86%	<0.05
C.vulgaris * *M.caerulea*	-0.0021	0.0008	0.98%	<0.05
Disturbance * Seed rain	-0.0013	0.0005	0.86%	<0.05
E.tetralix * Vegetation height	0.0052	0.0016	1.09%	<0.05
M.caerulea * Seed rain	0.0007	0.00003	0.76%	<0.05

Vegetation densities of competing species retained strong effects upon seedling densities and were found to interact (DCD = 0.98%, p = <0.05) in the case of *M.caerulea* (main effect DCD = 11.29%, p = <0.0001) and *C.vulgaris* (main effect DCD = 5.33%, p = <0.0001), revealing that seedling densities were particularly high where the abundance of both species was low. *E.tetralix* appeared by this stage to have the greatest negative effect on *Betula* densities of all the identified factors (DCD = 12.64%, p = <0.0001); where *E.tetralix* was dense virtually no seedlings occurred. The effect was particularly pronounced where mean vegetation height (DCD = 3.62%, p = <0.0001) was short with the two factors interacting (DCD = 1.09%, p = <0.05) to produce extremely low seedling densities where *E.tetralix* was dense and in the building phase (see Fig 3.2).

The increase in the relative importance of *E.tetralix* may reflect seasonality in the biomass allocation of *M.caerulea*. Seedlings surviving the autumn, winter and early spring in dense *M.caerulea* are likely to have escaped competition for several months in which they benefited from the shelter of the plant litter whilst avoiding the incessant competition suffered by seedlings growing within *E.tetralix*. These differences are highlighted in the different parameter values of the two species (*E.tetralix* = -0.1826, *M.caerulea* = -0.0161).

Another trend identified by this model is the increasing importance, over time, of edaphic factors in determining seedling densities. The soil environment is represented by not only its likely inclusion in plant abundance effects but also directly with an increase in the importance of SOM in the 0-50mm depth (DCD = 1.53%, p = <0.01), a small, negative, somewhat inexplicable and previously non-significant negative effect of SOM at the 50-150mm depth ((DCD = 0.76, p = <0.05) and a rise in the proportion of variance explained by P_{ox} (DCD = 6.82%, p = <0.0001). An interaction between *E.tetralix* and P_{ox} (DCD = 0.86%, p = <0.05) seems to reflect the failure of *Betula* seedling densities to respond to phosphorus addition where *E.tetralix* was dense (Fig 3.4).

In summary, the model suggests that it is intermediate conditions, i.e. those with some shelter and good nutrition but not too much competition, where transition to scrub is the most likely to occur.

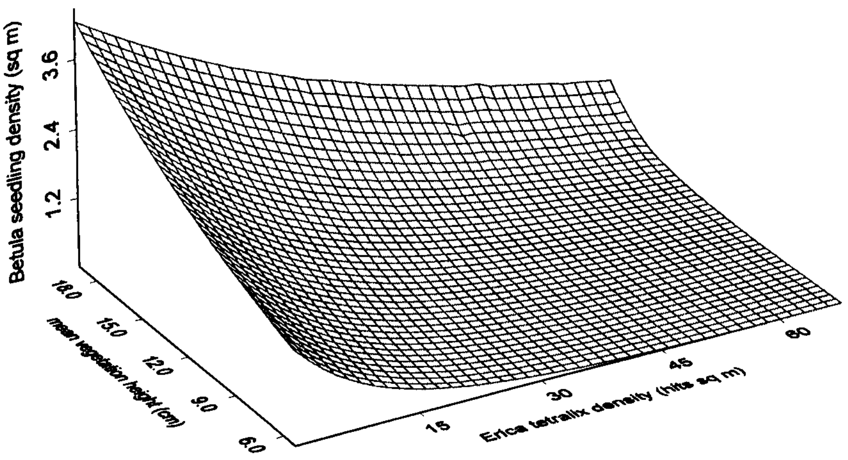


Fig 3.2. Fitted response surface of *Betula* seedling density (1-year-old seedlings) as affected by mean vegetation height and *Erica tetralix* density. All other variables in the fitted model (Table 3.6) were held constant at their mean.

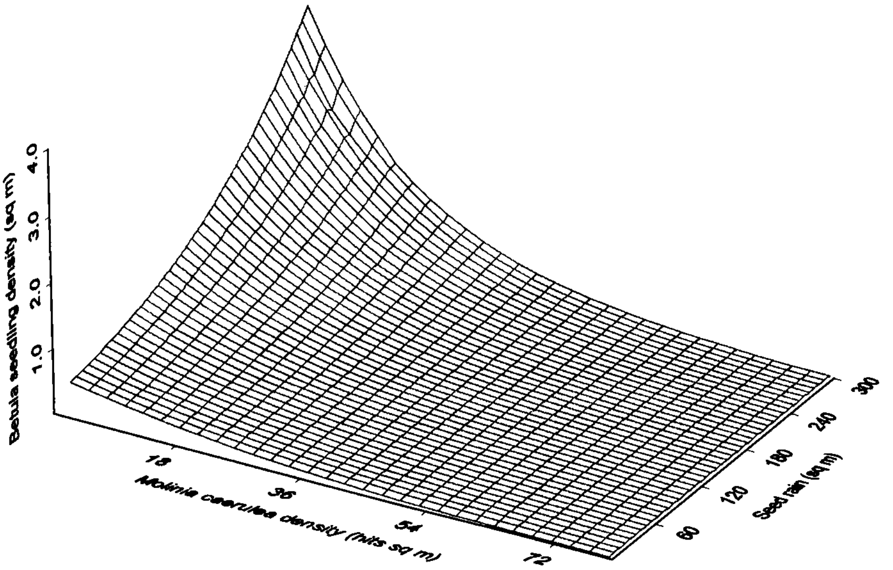


Fig 3.3. The fitted effects of *Molinia caerulea* and seedrain density on the density of 1-year-old *Betula* seedlings. All other variables from the fitted model (Table 3.6) were held constant at their mean.

The large number of significant parameters in this model highlights a temporal trend towards complexity in the fitted models. This may represent the accumulation of factors having an effect on the response variable, *Betula* seedling density, because the survival of seedlings is influenced by different determinants at different stages in their life cycle. However, despite increased parameterisation the capacity of the model to explain variance is not improved, suggesting that unmeasured or effectively stochastic factors (e.g. herbivory – see below) also play a role in determining seedling densities as they approach the sapling stage of the life cycle.

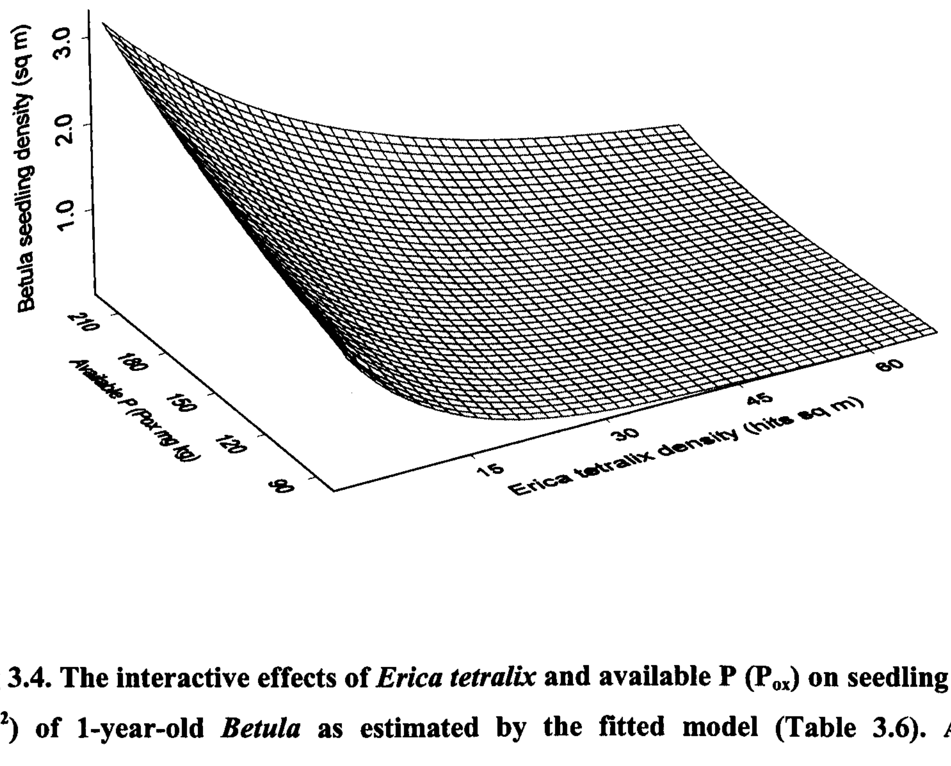


Fig 3.4. The interactive effects of *Erica tetralix* and available P (P_{ox}) on seedling densities (m^{-2}) of 1-year-old *Betula* as estimated by the fitted model (Table 3.6). All other variables were held constant at their mean.

HERBIVORY

A major, but unquantified, factor in the determination of seedling numbers appeared to be predation by mammalian herbivores. By May 2001 40% of seedling survivors displayed mammalian herbivore damage and many seedlings are likely to have been destroyed altogether. This predation is likely to be responsible for much of the temporal 'levelling out' or density dependent compensation that is observed in both the factorial and modelling analysis.

Table 3.7. Minimum adequate model (binomial error/logit link) describing the determinants of mammalian herbivore attack, as represented by the proportion of *Betula* seedlings displaying herbivore damage (September 2000). Explained deviance =64.8%, Residual d.f. = 146. Deleted Terms: *Molinia caerulea* density, phosphorus availability (P_{ox}), necromass density, and disturbance.

	Parameter Values	Standard Error	Explained Deviance	p (χ^2-Test)
Intercept	-3.184	0.41		
Mean seedling basal area (mm^{-2})	1.634	0.16	33.3%	<0.0001
Mean vegetation height (cm)	0.069	0.034	1.11%	<0.05
Seedling density (m^{-2})	0.0185	0.007	1.81%	<0.05
Erica tetralix density (hits m^{-2})	-0.0262	0.0087	2.64%	<0.01
Calluna vulgaris density (m^{-2})	-0.0122	0.0053	1.54%	<0.05

Although not measured directly, the processes determining herbivore attack were described by a statistical model having binomial error, a logit link and explaining 64.8% of the deviance in the proportion of seedlings attacked (Table 3.7). The fitted model suggests that the proportion of seedlings attacked was greatest where seedlings were large, aggregated and open to attack. All significant variables, with the exception of *C.vulgaris* and *E.tetralix* density, correlate with open conditions and so deviance overlap in the models descriptors is considerable. However, the model shows that there are small effects which are independent of seedling size as reflected by the key determinant, seedling basal area (DCD = 33.3%, p =<0.0001). Additional effects included positive density-dependent predation (DCD = 1.81%, p =<0.05) (Fig 3.6.) and a shelter or avoidance effect of the surrounding species that appears to be independent of their effect on growth suppression and was strongest for *Erica tetralix*

(DCD = 2.64%, *p* =<0.01) dominated vegetation (Fig 3.5). This effect was weaker in *Calluna vulgaris* dominated vegetation (DCD = 1.54%, *p* =<0.05) and not significant where *Molinia caerulea* was dominant i.e. it had no effect on herbivory other than the suppression of seedling germination and growth. A greater proportion of seedlings were attacked where the vegetation was taller (DCD = 1.11%, *p* =<0.05) possibly due to greater openness of the vegetation (apparency) or attraction of herbivores to these areas of the vegetation. Disturbance, like *M.caerulea* had no significant effect other than its effects upon seedling growth, survival and the destruction of surrounding vegetation, as did the phosphorus conditions of the seedlings. The non-significance of the phosphorus variable suggests that herbivore selection was more sensitive to food availability and quantity than quality. The model does not distinguish clearly between the separate effects of size and apparency in determining herbivory but it would appear that both factors influenced herbivore selection.

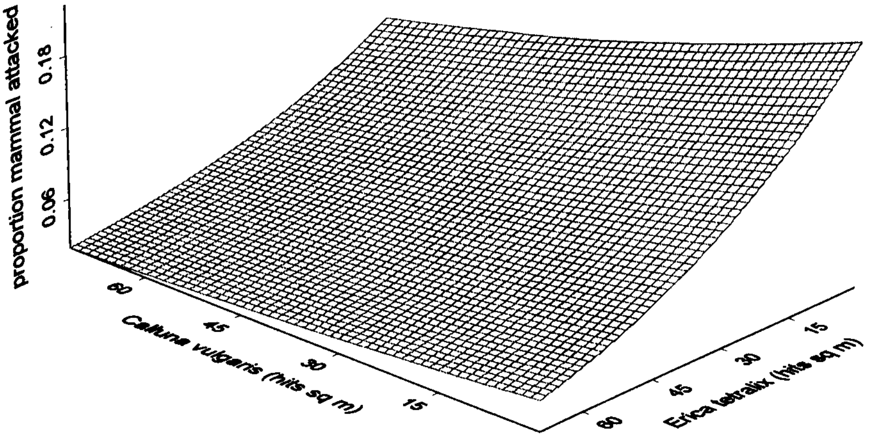


Fig 3.5. The fitted response surface for the effects of *Erica tetralix* and *Calluna vulgaris* density on the proportion of *Betula* seedlings displaying damage caused by mammalian herbivores. All other variables from the fitted model (Table 3.7) were held constant at their mean.

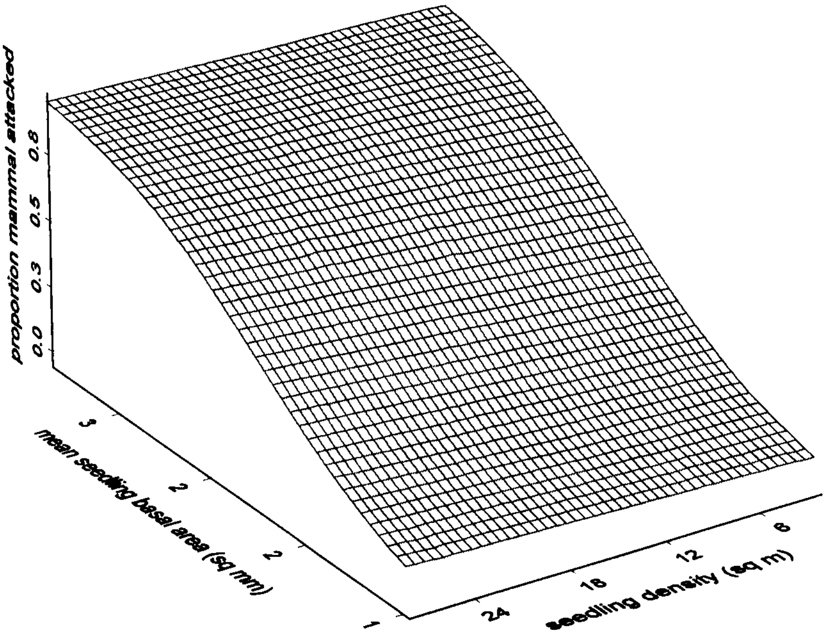


Fig 3.6. Fitted response surface for the proportion of *Betula* seedlings displaying evidence of mammalian herbivore attack as described by seedling basal area and density. All other variables in the fitted model (Table 3.7) were held constant at their mean.

Discussion

The results show that both seed and safe-site limitation affect the likelihood of *Betula* invasion at the study site and that phosphorus availability can play a major role in the determination of the *Betula* safe-site. These results validate the original suggestion that the phase-transitional area between heath and scrub systems is determined by numerous variables and highlight the requirement to provide multivariate descriptions of the 'conditions' (Scheffer *et al.* 2001) at which ecological state shifts occur. The study finds agreement with the majority of plant population studies in finding invasion to be limited by both safe-site and seed limitation (e.g. Mazia *et al.* 2001). The fitted models can be thought of as representing descriptions of the phase-transitional area or threshold conditions of the heath-scrub ecotone (Loehle *et al.* 1996) which is conceptually similar to the basin of attraction around the F_2 conditions of state shift identified by Scheffer *et al.* (2001) and Carpenter (2001). Numerical combinations of predictor variables resulting in seedling densities of zero represent stable, uninvasable heath conditions. Conditions resulting in predicted seedling densities >0 represent the conditions within which transition may occur.

Despite the formulation of these closely fitting statistical models it cannot be concluded that the threshold of invasion (and therefore transition) has been accurately defined as the response of the model is dependent upon the assumption that seedling densities are indicative of the likelihood of transition to scrub. The presence of seedlings does not always equate with adult survivors. In a review of seed addition studies Turnbull *et al.* (2000) found that seedlings were present at 64% of seed introduction study sites (those outside existing populations) but that adults were only present at 23%. Further, long-term study of seedling and sapling demographics will therefore be required if seedling abundance is to be validated as representative of the likelihood of transition. The temporal trend in the fitted models suggests that models describing numbers of sapling or reproductively viable trees are likely to be of greater complexity and of lower predictive power than those presented here.

The other major drawback in the use of the statistical models as descriptors of the threshold is their lack of generality, i.e. they are likely to be specific to the Arne study site. Although attempts were made to represent as wide a range of typical heathland conditions as possible the variance and effect of each determinant is likely to differ between heathland sites and regions. In other words, the numerical combinations of the predictor variables and the unmeasured site conditions do not cover all of the multidimensional space of 'typical' heathland conditions. What can be derived from these models however, is a description of *some* conditions in which phase transition definitely does and does not occur i.e. heathlands would appear to remain stable where there is low seed rain, dense ericaceous vegetation and nutrient poor conditions.

Experimental manipulation of the heathland environment revealed that tree colonisation failure at the study site was dependent upon a number of determinant factors that operated at different stages in seedling development. Statistical modelling demonstrated tradeoffs between environmental conditions that favoured survival at different stages of seedling development (e.g. disturbed conditions were highly favourable for seedling germination and early stage survival but had more negative consequences for later survival) and highlighted the increasing specificity of conditions for establishment as the seedlings passed through a series of 'windows of survival'. Long-term monitoring may therefore be required if accurate models are to be formulated.

SEED LIMITATION

Of all the factors identified seed availability was the single most limiting, even a full year after germination. This result is surprising, considering that the plots were a mere 13-24 metres away from a large number of parent trees.

Seed limitation may emerge as a result of the density and dispersion of adults, reproductive output, dispersal distances (Clark *et al.* 1998), germination failure and seed predation. The main cause of seed limitation at this site however, was almost certainly wind direction; the prevailing southwesterly wind of the region would blow seeds in the opposite direction to the experimental plots. Short distance dispersal limitation in *Betula* has been previously observed on eroded Icelandic lava fields by Arradóttir *et al.* (1997) who found that the saturation of safe sites occurred only at distances <4m from parent trees and that the colonisation of seedlings was strongly directional. Such results, when coupled with those presented here, question the dogma of hugely effective dispersal in *Betula* spp. which, although more widely dispersing than many tree species have obvious limits to seed production and dispersal.

This observed degree of seed limitation at the edge of an extant population suggests that seed limitation is likely to be great on many lowland heath patches, which are often at far greater distances from seed sources than the plots of this experiment.

SAFE-SITE LIMITATION

A number of factors were identified that could be classified as axes of the *Betula* safe-site or regeneration niche (*sensu* Grubb 1977). These included the density and height of the surrounding vegetation, its species composition, soil organic matter content, phosphorus availability and disturbance. These factors, when combined, were able to explain a large proportion of the variance in *Betula* seedling densities, especially those of more mature seedlings.

DISTURBANCE

Disturbance played a large role in determining invasion success both positively, by reducing competition and negatively by exposing the plants to herbivores and physical stresses. The overall effect of disturbance was, as revealed in the factorial analysis, positive. This effect of disturbance, supports the widely held view and physiological evidence (e.g. Gilbert *et al.*

2001) that *Betula* spp. have growth characteristics that suit them to gap colonisation as opposed to the colonisation of intact canopies. However, the results of the statistical modelling approach reveal that, in the long term, positive effects of disturbance were entirely the product of competition reduction and that other disturbance effects were negative.

The majority of previous studies looking at safe-site and seed limitation have assumed that suitable microsites are simply areas where disturbance has occurred (e.g. Eriksson & Ehrlén 1992). In this study, disturbance is likely to have initially provided the high light, high temperature conditions that favour birch germination (Black & Wareing 1954). Later in seedling development disturbance became a negative influence when isolated from the effects of competition reduction. Although I suspect that this effect was associated with the greater size and apparency of seedlings in disturbed plots attracting herbivores it may also have emerged from the regrowth of unmeasured vegetation in the disturbed plots. If this were the major source of the effect, however, a disturbance-vegetation density interaction would be expected. These results demonstrate the point that viewing safe-sites as merely any disturbed conditions is an oversimplification and that the regeneration niche (Grubb 1977) of any plant species is likely to be complex, multidimensional and context dependent. The effects of disturbance, for instance are likely to have been different in the absence of herbivores.

PLANT EFFECTS

The largest of the safe-site effects were those mediated by the three principal competitor species at the site: *Erica tetralix*, *Molinia caerulea* and *Calluna vulgaris*. The net effect of all three species, which incorporate indirect and potentially facilitative effects such as soil modification and shelter, fluctuated over time but was always negative. However, the late appearance of disturbance as a negative factor and the competition independent effects of *E.tetralix* and *C.vulgaris* in the herbivory models suggest that plant cover does provide some shelter. This apparent temporal shift in the balance between positive and negative plant interactions has similarly been found in experimental studies of annuals and desert shrubs (Holzapfell & Mahall 1999).

Although the parameter values and response curve to each species depend upon the biomass represented by each 'hit', the models suggest that *Betula* responds most negatively to the presence of *E.tetralix*. This response may represent not only direct competition effects but also lower rates of nutrient supply. Van Vuuren *et al.* (1992) found that total P was lower in the soil of *E.tetralix* communities than that of *M.caerulea*. N mineralization rates were 4.4g N m^{-2} y^{-1} in *Erica tetralix* soil compared to 7.8g N m^{-2} y^{-1} *Molinia* soil, and in dry soil *Calluna* communities, 6.2g N m^{-2} y^{-1}. P mineralization may also be greater in *M.caerulea* soils than in those dominated by *E.tetralix* (Berendse *et al.* 1989).

Although the net effect of *M.caerulea* appeared to be lesser than that of *E.tetralix* its abundance was able to explain considerable portions of the variance in *Betula* seedling densities, particularly those of recently germinated seedlings. These effects are likely to contain the influences of light and root competition and also inhibitory effects of the litter associated with the plant, it was noted that germination was extremely poor where *M.caerulea* litter was present (personal observation). These results concur with a number of plant ecological studies in which litter was found to inhibit seed germination (e.g. Mazia *et al.* 2001; Wilby & Brown 2001). Failure to detect this effect in the measure of necromass density is probably a result of the lack of species specificity in the measure, i.e. only *M.caerulea* litter inhibited germination. These results appear to conflict with those of Bodkam & Gleichamn (2000) who found that *Betula* seedlings appeared but did not survive in Mollinetum, their study was however, conducted over a longer period of time.

A potentially confounding factor is the currently undetected interaction between P additions and *Molinia.* Aerts & Berendse (1988) found that P added at 1.9 g m^{-2} y^{-1} (higher than this study but not greatly so) to a wet heath site for 3 years, caused significant increases in *Molinia* cover but no change in overall biomass. *Molinia* did appear to reach larger biomass densities in P added plots in this experiment (personal observation) but did not appear to do this to the exclusion of *Betula.*

The third of the dominant plant species, *Calluna vulgaris*, appeared to have a lesser effect on *Betula* seedling densities. The low 'per hit' parameter value of this species may be a result of the damage caused by the heather beetle outbreak at the start of the experiment with plant death and the allocation of resources to recovery in survivors making the plants, on the whole, less competitive. Another factor associated with the vegetation of the site is the greater invasability of taller vegetation. It is well known that heath vegetation is at its most 'vigorous' in the short, compact building phase and it is this vigour, which may include effects such as greater root competition, coupled with greater heterogeneity, and therefore light gap availability, in taller vegetation that this effect is likely to reflect.

These results, when synthesised, suggest that the invasability of heathland communities by *Betula* is dependent on not only the biomass of vegetation and its growth phase (as found by Gong & Gimingham 1984), but also its species composition. Such species specificity and the greater invisibility of *Molinia* dominated communities was also observed by Miles (1972) who found that experimentally sown *Betula* of both species performed best on *Agrosto-Molinetum* and *Sphagnetum* communities and that neither species grew well in *Callunetum*.

SOM

A small but significant positive effect of SOM was detected that, due to the structure of the models, may be considered independent of its effects on P-availability (see Chapter 2). There are likely to be two main factors contained within this relationship. The first appears as a separate but correlated variable in the early stages; a positive association with soil water content in which seedlings are more likely to germinate and less likely to die of droughting at a stage in which roots are poorly developed and temperatures are high. The second component of the SOM effect was associated with later stage seedling survival and is likely to represent N mineralization. N mineralization increases with the post burn successional age of heathland vegetation (Berendse 1990) and may be a key determinant of seedling success in some situations. This experiment, however, was conducted on late stage vegetation in which N is likely to be less limiting, hence the small effect size of SOM.

Although nitrogen availability was not directly measured in this study Berendse (1990) found that 84% of the variance in N mineralization rates in Dutch heathland soils was accounted for by soil organic matter content and the abundance of *Molinia*. As both of these factors have been measured it is likely that any nitrogen effects will be included within these terms.

PHOSPHORUS

A key result of this experiment is the finding that *Betula* seedling densities are, in natural field conditions, responsive to differences in available P, represented here by P_{ox}, a variable that can be explained in part by PSC (Chapter 2). It should be noted however that the scale of response to P_{ox} enrichment appeared to be dependent on the density of *E.tetralix*. This adds mechanistic validation and overall support to the original hypothesis of Chapman *et al.* (1989b, see also Chapter 2); that the likelihood of phase-transition in heathland ecosystems is dependent upon soil PSC. What my own research also shows, however, is that the degree of dependency on P availability is small when compared with other factors, i.e. competition and seed limitation, at least at this site and over the range of P availabilities that were generated there. Nutrient limitation of *Betula* seedlings is likely to result from low inorganic P availability in heathland ecosystems and the ecophysiology of the species. Birch seeds are small and, unlike many tree species, lack nutrient stores resulting in a dependency on exogenous nutrient sources soon after germination (Perez-Moreno & Read 2001a; Newton & Pigott 1991a).

The scale of the response to P availabilities may be underestimated by the P_{ox} measurement as there is likely to be considerably more measurement error in this variable than there is in the other identified determinants. The rise in the importance of P as a variable indicates that P may be important to long term growth and survival, a hypothesis that will be confirmed by long-term monitoring. Alternatively, older *Betula* saplings may exploit large P pools beyond the physical reach of the dwarf shrubs and so P availability may only be of importance in the early growth stages.

A point of consideration when interpreting the relationship between P availability and *Betula* invasion of heathland is the pathways by which the species of the original community and the invader acquire their nutrients. Although both dwarf shrub and *Betula* species utilise inorganic and organic P sources their proportional use of these pools and their physiological responses to different supply rates are believed to be considerably different. Ericoid species primarily utilise organic nutrient sources, accessed via their mycorrhizal partners (Read 1983), and may not show the degree of morphological plasticity that is typical of *Betula* spp. (e.g. Harrison and Helliwell 1979). In the plots of this experiment, and possibly on high PSC, high SOM heaths (Chapter 2) inorganic P levels may exceed those over which ericoid species may respond i.e. they reach their maximum growth rate at a P concentration below that of *Betula*.

The results of this experiment appear consistent with a general trend in succession in which fertilisation of systems (in heathlands a natural temporal process – see Chapter 2) increases the growth of all species but proportionately increases the growth of fast growing species, thus accelerating successional change (Huston & Smith 1987). This hypothesis is further supported by the finding of Helsper *et al.* (1983) who found that P additions had little effect on *Calluna* communities at 57kg ha applications (approximately equal to the total deposited in this studies high level treatments) other than a stimulatory effect upon the lichen flora. Gimingham (1972) also states that "*Calluna* does not respond to phosphate by itself". These results appear to contradict the models presented in Chapter 2 and those of Chapman *et al.* (1989a) but in reality *Calluna* is most likely to respond to differences at the low end of the heathland nutrient range and over long timescales. A similar relationship is believed to occur in nitrogen enriched continental heathland in which *M.caerulea* is believed to be a superior competitor and show a greater degree of responsiveness to elevated concentrations of inorganic nitrogen (Aerts & Chapin 2000) resulting in species replacement and phase transition.

This apparently simple model, describing the mechanism by which high inorganic P availability may enable *Betula* to replace dwarf shrub species, is likely to be confounded by the presence and activity of ectomycorrhizal fungi on *Betula* roots. It was noted (personal observation) that ectomycorrhizas were present on all *Betula* seedlings occurring outside the experimental area. It is also a generally accepted fact that *Betula* are effectively obligately mycorrhizal in the majority of habitats (Atkinson 1992); they have been seen to form an ectomycorrhizal association within 3 weeks of germination (Newton & Piggott 1991a). Recent research has found that *Betula* seedlings may, via mycorrhiza, acquire significant portions of their phosphorus from organic sources e.g. Pollen may account for 7.9% of P and nematodes 7.4% (Perez-Moreno & Read 2000; 2001a;b), a result which indicates that ectomycorrhizal *Betula* seedlings may bypass limitations in inorganic phosphorus. However, Newton & Piggot (1991b) found that there was an inverse relationship between soil fertility and ectomycorrhizal colonisation with infection being significantly reduced by P application in both pot and field experiments. They also found that seedling growth was poorly correlated with ectomycorrhizal colonisation with the exception of one site (Newton & Piggot 1991c). Similarly, Harrison & Helliwell (1979) found that ectomycorrhizal root colonisation could not account for variation in the uptake of P by *B.verrucosa*.

A mechanistically consistent synthesis of these results, including those presented here would be that *Betula* seedlings are more dependent upon organic P sources supplied via their mycorrhizal partners where nutrient availabilities are low and that they disassociate or reduce the degree of dependency on the symbiosis in high P conditions, freeing carbon resources that may then be utilised in overcoming alternative stresses (e.g. greater shoot elongation), thus boosting survival.

A second potentially confounding effect of mycorrhizas in this study is the transfer of P between plots via a mycelial network. If this phenomenon was in operation within the experimental site then it is likely that it would have an averaging effect on the seedling survival and therefore P-limitation would be underestimated.

In this study it is possible that some seedlings were able to access ectomycorrhizal networks directly from the intact mycelium of nearby adult trees. However, the availability of ecotmycorrhizal partners may be limiting in the interior of large uninvaded heaths, a possibility that would depend upon the dispersal of early-stage ectomyocrrhizal spores (see

Chapter 1) and the abundance of facultatively ectomycorrhizal saprophytes that were previously existing in a non-mycorrhizal form within the predominantly ericoid mycorrhizal heathland habitat. This limitation may interact with seed limitation in the centre of large, uninvaded heath patches which are not only likely to be seed limited but also mycorrhiza limited, resulting in a particularly low probability of transition especially in low P, high competition conditions.

HERBIVORY

Attack by mammalian herbivores only occurred in the later stages of seedling growth but it appeared to have a major effect on the recruitment dynamics of the seedlings. As all the experimental plots were open to herbivores the relative impact of herbivory on plant recruitment cannot be quantified.

Although herbivore preferences can be obscured by spatial autocorrelation in herbivore activity, i.e. particular areas of the experiment or the whole experiment itself can be targeted by herbivores (e.g. Manson 2000; Marrs & Le Duc 2000) the fitted model suggested that herbivores had distinct preferences and that they are likely to have been responsible for much of the compensation in seedling densities - conditions which produced large seedlings at high densities e.g. high seed rain, low competition, high phosphorus, were those selected by herbivores. The other, contrasting, effects of *E.tetralix* and *C.vulgaris* are likely to be related to the browsing behaviour of the deer at the site. *M.caerulea*, which had no significant effect on *Betula* herbivory was browsed regularly by the deer (personal observation) and is unlikely to have provided physical shelter. *E.tetralix* on the other hand, displayed a negative relationship with herbivory. *E.tetralix* is thought to be less palatable than *Calluna* (Bannister 1966) and it would seem likely that herbivores avoided grazing areas where *E.tetralix* was more common. It may also have provided physical protection.

These phenomena suggest that, when herbivores are present, there is a narrow regeneration niche or 'window of opportunity' in which *Betula* seedlings may survive. This appears at the Arne site, to be qualitatively best represented by plots attacked by heather beetles, particularly those in which P additions had occurred (personal observation). In these conditions seedlings seem to have avoided the biotic pressures of both herbivory and competition and reached considerable size without attack as a result of protection from dead standing woody material. In these environments there are also likely to be greater nutrient availabilities as heather beetle attack is known to result in considerable release of nutrients (Heil & Diemont 1983; Diemont & Heil 1984; Brunsting & Heil 1985). An examination of the site in September 2001 suggested that in all other conditions seedlings had been bitten down to the level of the field layer or ground, a result that concurs with Kinnaird (1974) who found that seedling densities were unrelated to grazing but that if seedlings were not protected then they were dwarfed and distorted.

These findings lead to the conclusion that the determinants of the *Betula* phase transition in the absence of herbivores may be simply defined and possibly well described by the early stage seedling density model (September 2000) that is presented here. In such situations competition effects are likely to remain important until the plant overtops the dwarf shrub vegetation. Where herbivores are present at high densities, temporary exclusion of a sufficient duration for seedlings to overtop the browse line may be necessary if transition is to occur. Where grazers are present, seedlings that survive the early stages of colonisation e.g. 1 year may be able to persist in the 'bonsai' state for considerable periods of time. Kinnaird (1974) found, for instance, that although mortality was in the order of 96-98% *Betula* saplings could live for 31 years within taller *Calluna* communities. Because larger seedlings (>1.5mm stem diameter) have a capacity to resprout (personal observation) invasion may, if grazing pressure were to subside, occur in conditions that bear little relation to those in which the initial stages of colonisation occurred.

LANDSCAPE SCALE IMPLICATIONS

Caution is required in the extrapolation of these results to larger spatial and temporal scales. The first drawback is that the identity of the determinants of phase transition and the relative contributions of various seed and safe-site sources of limitation is temporally dependent and further affected by the exact definition of the 'moment of transition'. From a population biology perspective transition has occurred when reproductive maturity of the invaders is reached and it is only at this point that the relative contributions of seed and safe-site limitation may be quantified. Measurement of the determinants of transition from a community or ecosystems ecology viewpoint would depend greatly upon the spatial scale of the measurement and the definition of the scrub state. The models given here describe the ecotone region of transition at small spatial and temporal scales and it is not possible to state whether the same variables play a deterministic role at the landscape level of organisation as the determinant factors that vary, and thus explain variation at one scale e.g. climate, soils, vegetation, may be uniform or effectively random at another.

Despite these drawbacks, the relationships described by the fitted models are capable of describing landscape scale trends as many of the major, large scale processes of heathlands, e.g. grazing regimes, burning, beetle outbreaks and soil and climate trends, have significant impacts on the variables identified here over large areas of heath. Soil PSC, for instance, has direct effects upon P availability but may also drive the speed of heathland vegetation production and soil development (Chapter 2; Chapman *et al* 1989a). Lowland heath in high PSC regions is likely to reach the low competition, high SOM, high P state more readily than low PSC regions and will therefore require more intensive or regular management if it is to be held in a non-invasable condition. Burning of degenerate stage heath in high PSC regions, is for example, not only likely to result in hot fires that destroy the dwarf shrub rootstock but also in a considerable increase in soil nutrient availability (Chapter 2).

The process of seed limitation at larger scales is likely to be largely dependent on the degree of both safe-site and seed limitation in the previous generation. Seed and safe-site limitation are therefore likely to interact significantly at the landscape scale resulting in a range of outcomes varying between an 'epidemic' of transition and absolute stasis. Iterative simulation modelling (e.g. Clark *et al.* 2001) would be required to see how these processes may, in fact, operate.

CONCLUSION

The models presented in this study provide a detailed and accurate description of the early stages of *Betula* invasion, the critical point in heath-scrub phase transition, and suggest the controlling mechanisms. They validate the original hypotheses of the study in showing the determinants of invasion to be, at least in potential, dependent upon seed and safe-site limitation, as represented by the effects of plant neighbours, vegetation structure, edaphic factors and 'pure' disturbance effects. These findings are consistent with both mainstream views of heathland persistence and the Chapman *et al.* (1989b) hypothesis (Chapter 2), which states that PSC is a key determinant of scrub invasion, as both PSC and traditional management affect the determinant variables.

The major drawback of the models is their specificity to a single site and a small spatio-temporal scale. Generalisation of the models or confirmation of their generality will require multi-site and multi-scale studies in which a wider range of the multidimensional space of heath conditions is covered. An accurate picture of natural variation in determinant factors at larger scales is also required before the identity, role and relative impact of the determinants of heath-scrub phase transition are confirmed.

Chapter 4: Formulation of a general statistical model describing the determinants of a heath–scrub phase transition

Abstract

1. Numerous studies have provided descriptions of the thresholds or phase transitional areas at which transition to alternate ecosystem states occurs but few have quantitatively delimited these conditions.
2. Previous research on heathland ecosystems provided a single-site statistical model, which described the determinants of *Betula* spp. seedling colonisation, the critical point in heath-scrub phase transition. The general applicability of this model to a wider range of environments was unknown.
3. Multi-site experimental manipulation and statistical modelling suggested that the identity of the factors controlling the degree of *Betula* colonisation (which included seed density, P availability and vegetation effects) was broadly similar between sites but that their relative contributions to within-site heterogeneity varied widely.
4. A single statistical model was fitted to data collected from three experimental sites. The model, which explained 59.8% of the deviance in seedling densities, describes *Betula* seedling densities as a function of biomass and necromass density, vegetation height, seedbank density, phosphorus availability, and to a lesser extent, soil water content. The form of the fitted relationships was complex with numerous interaction and polynomial terms.
5. If the model is applicable to a wider range of conditions then it may be concluded that it is heathlands in close proximity to seed sources, in the degenerate state, and possibly those subjected to severe burns, that are the most likely to shift to the *Betula* scrub state. At larger spatial scales these conditions are probably most common in low management intensity, high phosphorus sorption capacity (PSC) regions.
6. The major caveat attached to these conclusions is that the model is derived from data taken from a single heath community type. An understanding of the model's applicability to a wider range of conditions and a knowledge of natural variation in the identified determinants is required if the above conclusions are to be accepted as a general model with confidence.

Introduction

Thresholds at which multispecies assemblies shift from one 'stable' state to another are an accepted part of theoretical ecology (May 1977; Scheffer *et al.* 2001) and there are numerous field studies that support these ideas (Carpenter 2001; Van de Koeppel 2001; Jones *et al.* 2002). There have been, however, few experimental studies of, and little empirical information gathered, on the nature and parameter values, of these critical points at which state transition occurs (Petraitis & Latham 1999).

In many cases shifts between alternate states, or phase transitions as they are analogously known (Loelhe *et al.* 1996), are controlled by the population densities of 'foundation' species which engineer the new ecosystem state (Jones and Lawton 1997; Wilson & Agnew 1992; Peterson 1984) and which are themselves responding to a variety of biotic and abiotic influences (Petraitis & Latham 1999; Laycock 1991). In such cases the threshold of transition is likely to be multidimensional, as opposed to being driven by a single 'control factor' (e.g. Carpenter 2001), because recruitment depends upon not only the availability of propagules but also a wide range of environmental conditions (Bazzaz 1996; Mazia *et al.* 2001; Meekins & McCarthy 2001). A description of the threshold or phase transitional area, as it is perhaps more accurately defined (Loehle *et al.* 1996), can therefore be obtained by defining the determinants of colonisation and establishment for the species or functional group that defines and drives the condition of the ecosystem state.

Invasion of *Betula* spp. (*B.pendula* and *B.pubescens*) has the capacity to drive transitions between heath and scrub vegetation states (Mitchell *et al.* 1997; Miles & Young 1980; Hester *et al.* 1991 a,b,c) and is a major threat to the conservation of lowland heath (Marrs 1984; Marrs *et al.* 1986; Rose *et al.* 1999). *Betula* scrub-heath state shifts have not been measured or formally tested (e.g. Carpenter 2001; Connell & Sousa 1983) but there is considerable anecdotal and experimental evidence for bi-directional shifts, originating from numerous sources. This evidence ranges from recent studies of invasion and restoration (e.g. Mitchell *et al.* 1997 and 1999) to historical records of heathland formation and decline (see Chapter 1).

Experimentation has demonstrated that the likelihood of *Betula* driven heath-scrub shifts can be influenced by factors related to both seed and safe-site limitation (Eriksson & Ehrlén; 1992; Turnbull *et al.* 2000), with vegetation structure and density and P-availability being potentially important axes of the safe-site or regeneration niche (*sensu* Grubb 1977). Statistical models derived from the experimental data have defined the phase transitional area of the shift (Chapter 3). However, the single-site nature of the study in question generates doubt as to the generality of the findings as both local and landscape scale differences occur in many of the proposed determinants of invasion (Chapter1). The problem this creates is that many typical heath conditions may not be present within the site from which these conclusions were drawn. The observable degree of limitation caused by each of the determinants may also operate in a context dependent manner, thus precluding generalisation. An example of these shortcomings is the potential for regional variation in the importance and nature of the phosphorus component of the threshold as caused by phosphorus sorption capacity (PSC). PSC has been found to correlate with landscape-scale patterns of invasion (Chapman *et al.* 1989b). The higher PSC of some regions, which has been found to directly influence plant-available P (Chapter 2) may alter the degree of P limitation in these areas and thus reduce its observed effect in determining phase-transition within those regions i.e. P availability may exceed limiting concentrations across entire regions. Alternatively, the identity and importance of the factors controlling heath-scrub state-shifts may be universal to all sites.

The overall aim of the research presented in this chapter was to experimentally evaluate and derive models that describe what Petraitis and Latham (1999) term "the origins of an assemblage". The means of doing this were twofold; the first component of the research was to describe *Betula* recruitment limitations and the phase transitional area in a variety of heathland environments. Experimental study of recruitment limitation over entire regions is impractical and so in this study, 3 sites, located within geographically distinct heathland regions were selected and the same experiment was conducted at all 3 sites. Such a design precludes the formation of regionally applicable conclusions but does allow for an evaluation of potential between-site differences in the determinants of the phase-transitional area. The consistency of results from these geographically distinct areas, assessed with both experimental tests and statistical modelling, allowed for an evaluation of the conclusions presented in Chapter 3.

The second component of this research involved the combination of data from the experimental sites into a single set so that a general model describing the heath-scrub phase transition could be formulated. It was decided *a priori* that this would only be attempted if the second of the above hypotheses, that the determinants of invasion were universal, was, at least in part, supported by the experimental studies. Such a model would sacrifice any local, site-specific relationships and patterns in exchange for coarse, but general, descriptions of the identity and form of universally operating recruitment limitations.

The combination of these divergent studies has provided a description of both factors that limit recruitment at many sites and those that only play a role in specific circumstances. The general, combined site model should, in principle provide a quantitative description of the phase-transitional area over a wide range of heathland conditions. The results of these studies are presented and discussed with reference to both the ecological understanding of phase transitions between alternate vegetation states and the management of heathlands in which shifts to scrub are considered undesirable.

Methods

SITE CRITERIA AND DESCRIPTIONS:

The experiment was been replicated in 3 regions, each of which displays a different pattern of *Betula* invasion and PSC type. Soil phosphorus sorption characteristics were initially hypothesised to control the degree of P limitation at each site but its relationship with available P has since been found to be more complex (Chapter 2). The regions are:

1. Dorset, an area typified by a slow but increasing rate of birch invasion. The PSC of the soil is low in this region (c.70µg P g^{-1})
2. New Forest. This is the largest and most important lowland heath in Britain covering an area of c.15, 000 ha (Westerhoff 1992) and therefore representing around 6% of European lowland heath area. The soil PSC here tends to be high (c.1500µg P g^{-1}) but the rate of *Betula* invasion is probably lower than that of Dorset. This is thought to be a function of the free ranging grazing animals of this region that have continuously grazed the region since medieval times (Westerhoff 1992). However, although grazing densities are high in the New Forest relatively little of the animals' time is spent on the heath (Putman 1986). Section II of the New Forest act of 1949 also places an obligation on the Forestry Commission to keep the "grazings sufficiently clear of coarse herbage, scrub and self sown trees" (Tubbs 1974).
3. Surrey. *Betula* invasion is a severe problem in this region (Rackham 1986, Harrison 1976). The soil PSC in this region is intermediate to Dorset and the New Forest (c.700µg P g^{-1}).

The experimental sites within these regions were chosen to fit 3 criteria:

1. Vegetation of the National Vegetation Classification M16 *Erica tetralix-Sphagnum compactum* type (Rodwell 1992) with some gaps $\geq 25\text{cm}^2$ in the canopy. All sites contained an M16c community type i.e. dominated by dwarf shrubs as opposed to *Sphagnum* spp.
2. Approximately equidistant, and running parallel, to a linear patch of mature *Betula* and therefore receiving some background seed rain
3. Flat so that the transfer of P from P amended plots into control and lower level plots was minimised.

Within these limitations there was considerable variation, particularly in PSC (Chapter 2). All three sites lie upon the Bagshot (Barton & Bracklesham) beds; Tertiary (Eocene) sandy deposits.

SITE 1. CRICHTONS HEATH, ARNE PENINSULA, DORSET.

The Dorset site (National Grid ref. SY 976 894) is located upon the generally uninvaded Arne Peninsula. A full description of the site's vegetation and management history is given in Chapter 3. Although the PSC of the sites soil is low (231μg P $g^{-1}$and 323μg P g^{-1}at the 0-50mm and 50-150mm depths respectively) its higher SOM content results in similar background available-P levels to the other two sites (Chapter 2). Research conducted at the site found the most important factors in generating within-site variation in *Betula* recruitment limitation to be related to seed rain and vegetation density. Other factors contributing to the likelihood of transition were P-availability, SOM content, vegetation height and disturbance. There were numerous interactive relationships between the determinant factors (Chapter 3).

SITE 2. DENNY WOOD, NEW FOREST, HAMPSHIRE.

The New Forest Site (National Grid ref: SU 340062) is dominated by *Calluna vulgaris* ((L.) Hull) and *Erica tetralix* (L.) but the greater abundances of *E.tetralix*, *Sphagnum compactum* and the presence of *Tricophorum cespitosum* (L.) suggest that this site is slightly wetter than the others. The vegetation gap size here is intermediate to the other sites. As the site is within the New Forest boundary a greater grazing intensity than the other sites was expected. Fallow deer (*Dama dama*) have also been sighted close to the site but these are at far lower densities than those of Sika deer (*Cervus nippon*) at the Dorset site (Chapter 3). The site is regularly burnt and was last managed in the early 1990's. Soil PSC is the greatest of the three study sites (mean values: 1463μg P g^{-1} at the 0-50mm depth and 746μg P g^{-1} at the 50-150mm depth).

When the experiment was initiated the experimental plots were located in parallel with a linear strip of *Betula* (predominantly *B.pendula*). By April 2000, however, these were no longer present as the site manager had felled them. This had little effect on the experiment as felling occurred after the fall of seed that comprised the seedling cohort studied in the experiment. The experimental site was cleared of a small number of *B.pendula* saplings in the June 1999. This preceded the experiment's inception.

SITE 3. HORSELL COMMON, WOKING, SURREY

The Surrey site (National Grid ref: TQ 014 598) is also dominated by uneven-aged *C.vulgaris*, *Molinia caerulea* ((L.) Moench) and *E.tetralix*, with *T.cespitosum* present in some of the damper areas. Although vegetation gaps are present they are the smallest here of the three sites. This experimental site is located on a relict heathland surrounded by scrub and as some of the surrounding vegetation is *Betula* woodland higher seed rains were expected. The site and surrounding area display evidence of fairly recent (<10yrs) *Pinus sylvestris* and *Betula* invasion. Discussion with local people on the common has revealed that the majority of *Betula* invasion has occurred since the 1960's. There is virtually no evidence of grazing on the vegetation of the site although deer tracks and droppings can be seen nearby. The site itself had been colonised by *Betula* in some areas but these were removed in May 1999 to meet the site criteria. The site has been unmanaged for many years with the exception of some scrub clearance that was conducted in 1972. The PSC (mean values: 1112μg P g^{-1} at the 0-50mm depth and 251μg P g^{-1} in the 50-150mm depth) of this site was intermediate to the others. The site was cleared of *Betula* in May 1999, prior to the onset of experimentation.

EXPERIMENTAL DESIGN:

The only major difference in the experimental designs between the three sites was size, which was greater at the Dorset site (78 x 11m) than at the New Forest and Surrey Sites (41 x 8m). The Dorset site had a 3 x 4 x 2 factorial design with 2 replicates per block and 4 blocks equalling 192 2 x 1m plots. The smaller New Forest and Surrey sites had a 3 x 2 x 2 factorial design with 2 replicates per block and 3 blocks equalling 72 2 x 1m plots. The exact nature of the experimental treatments: disturbance, seeding and P addition, are described elsewhere (Chapters 2 & 3). The first treatment to be applied was disturbance, which was applied at two levels (control, disturbed) to all sites between the 17th and 24th June 1999. The second treatment, P addition, had 4 treatment levels at the Dorset site: control, 1, 2 and 3 additions, and 3 at the Surrey and New Forest sites: control, 1 and 3 additions. The first addition was applied between the 30th June and the 5th July 1999, the second between the 5th and 10th January 2000 and the third between the 5th and 7th June 2000. The third treatment, addition of seed, had 3 levels at the Dorset site: control, $50m^{-2}$ and $250m^{-2}$, and two at the New Forest and Surrey sites: control and $250m^{-2}$.

The experiments had a randomised block design with all 2m x 1m plots in each block approximately equidistant to the nearest source of seed rain. It was ensured that the blocks followed the same pattern of distances at each of the sites i.e. the front of the closest block was 13 metres from the strip of *Betula* with the others running parallel to this at distances of 16m, 19m and at the Dorset site, 21m. There was a 50cm guard row between plots and a 1m guard row between blocks to minimise the effect of nutrient transfer between plots and allow access.

EDAPHIC FACTORS

In addition to the experimental treatments, several covariates were measured. Soil cores were taken on a regular sampling grid that maximised the coverage of the experimental area. Sample sites, located between the plots and blocks, numbered 30 at the New Forest and Surrey sites and 72 at the larger Dorset site. Soil cores were taken between the 19th and 26th November 1999. Soil samples of the 0-50mm depth, that which the seedlings were assumed to be in contact with, were analysed for their pH, soil organic matter (SOM), water content and their long-term P-availability as measured by ammonium oxalate extractable P (P_{ox}). Full descriptions of sampling method, preparation and analysis procedures are given in Chapter 2.

SEED BANK ESTIMATION

The seed bank densities of *Betula* were investigated at all 3 sites. This was achieved by sampling from the same grid that was used for the soil cores. Samples were taken between the 20th and 28th of February 2000. At each sampling point, five 5cm diameter cylindrical cores were taken to a depth of 3cm, thus totalling an area of $98cm^2$. Samples were taken as close to the location of the soil nutrient samples as possible and were stored in sealed plastic bags at 4°C within 6 hours of sampling. They were removed from cold storage for approximately 24 hours on the 6th March 2000 when they were transported to the University of Liverpool.

The estimation of *Betula* seed density within the cores was conducted in a polythene tunnel at Ness Botanical Gardens, Cheshire between March and June 2000. Each sample was passed through a 5mm sieve and spread thinly onto a 2cm layer of compost in 21cm x 31cm seed trays. Sample soil was pressed gently against the compost to ensure contact. Trays were placed on a 20m x 3.5m sand bed irrigated by a 16mm porous pipe (LBS horticulture) and were arranged so that each tray was approximately equidistant to the water source. Samples were divided as evenly as possible into 4 blocks, each containing 3 controls. Within block sample order was random. *Betula* seedlings were removed from the trays upon identification. The species of *Betula* the seedlings belonged to was not recorded as *Betula* seedlings may only be differentiated to species level after several months of age (Atkinson 1992).

VEGETATION STRUCTURE AND COMPOSITION

Vegetation was recorded using point quadrat methods during the summer after the disturbance treatment was applied but before seedling monitoring began. The method is described in detail in Chapter 3. Recording took place between July and September for the Dorset site and in September 1999 at the Surrey and New Forest sites.

EFFECT OF P ADDITION AND DISTURBANCE ON PLANT AVAILABLE P

The effect of the P additions and disturbance treatments on plant available P, as measured by ammonium oxalate extractable P (P_{ox}), was studied in a 4 x 2 factorial experiment at the Dorset site and in a 3 x 2 design at the New Forest and Surrey sites. The results of this experiment are presented in Chapter 2.

SEEDLING MONITORING

The size and abundance of *Betula* seedlings was recorded when the seedlings were approximately 1 month (5th May-16th June 2000), 4 months (14th September-12th October) and 1 year old (4th-15th May 2001). A description of the seedling survey protocol is given in Chapter 3. Throughout this paper it is assumed that *Betula* seedling densities are indicative of the likelihood of heath-scrub phase transition. Both *Betula* species, *B.pendula* (Roth) and *B.pubescens* (Ehrh), were grouped together in analysis. The rationale underpinning these assumptions is presented in Chapter 3.

CALIBRATION OF SEED BANK AND SEED RAIN VALUES

Although background seed rain was measured at the Dorset site, practical limitations prevented the measurement of background *Betula* seed rain at the Surrey and New Forest sites. It was hoped that the generation of a single measure of propagule availability could be achieved by using a calibration model derived from the Dorset site where both seed bank and seed rain densities had been measured. However, poor resolution in seed bank data at this site (i.e. most samples contained one or no germinable seeds) precluded the formation of a meaningful, predictive model of the relationship between the two variables. Their means at the site however, were remarkably similar (Seed rain 25.75m^{-2} ±15.6, Seed bank 26.14m^{-2} ±38.8). This was not unexpected as seed bank sampling occurred at the end of the seed shedding period but before germination is likely to occur (Atkinson 1992) and seed bank persistence is uncommon in *Betula* (Thompson *et al.* 1997). It is therefore assumed here that the seed bank:seed rain ratio is 1:1 and that there is little or no seed persistence between years.

ANALYSIS

An experimental evaluation of the degree of seed and safe-site limitation (as represented by a lack of disturbance and low P-availability) at each of the sites was achieved by analysing the seedling density data using a fixed-form Analysis of Deviance general linear model with a log link and Poisson errors. Block was treated as a fixed factor and therefore block-treatment interactions were not calculated. This had the additional advantage of reducing the number of model parameters. Analysis was conducted in S+6 for Windows (Insightful).

Detailed descriptions of the factors that explained variation in the densities of 1-year-old *Betula* seedlings were achieved by converting the manipulated variables into a continuous form and then combining these with the covariate data to formulate best-fit minimum adequate statistical models (MAM). (see Chapter 2 and Crawley 2002 for an introduction to statistical modelling). Several preliminary data manipulations were required before this could be achieved.

KRIGING

Individual plot values for seedbank and edaphic data were acquired from kriged output grids. The process of kriging, in which spatial autocorrelation is first modelled and then used in optimum interpolation, was performed in S+ 6 for Windows and is described in Chapter 3. The kriging models used for the data from the Dorset site is also presented there. Variograms of asymptotic form: the Spherical, Exponential and Gaussian models, were fitted to the ommnidirectional variogram data calculated from the P_{ox}, SOM, soil water content and seedbank data of the New Forest and Surrey sites. Low numbers of equidistant data pairs at larger distances underpinned the decision to limit the calculation of variogram data to distances of ≤10m. Empirical variogram calculation found that there was little variation and no spatial structure in the pH data from both sites and so this has been omitted from the study.

Table 4.1. a & b. Variogram models fitted to the covariate data from a) the New Forest site and b) the Surrey site and used in subsequent kriging interpolation.

NEW FOREST	Seed bank (Backgroud)	P_{ox} (Background)	Moisture 0-50mm	SOM 0-50mm
Best fit model	Gaussian	Gaussian	Spherical	Spherical
Range (a)	3.39	4.04	3.96	6.954
Sill (*C*)	90105	1020.8	21.93	45.4
Nugget ($\gamma(0)$)	5006	0	0	1.43
Spatially structured covariance $1-(\gamma(0)/C)$	0.94	1	1	0.97
Explained deviance (%)(fitted/null)	32.54	75.84	2.82	31.18

a)

SURREY	Seed bank (Background)	P_{ox} (Background)	Moisture 0-50mm	SOM 0-50mm
Best fit model	Gaussian	Gaussian	Spherical	Gaussian
Range (a)	2.70	3.17	4.25	2.56
Sill (*C*)	2144	567	32.22	64.34
Nugget ($\gamma(0)$)	0	0	0	0
Spatially structured covariance $1-(\gamma(0)/C)$	1	1	1	1
Explained deviance (%)(fitted/null)	15.54	54.85	42.71	78.98

b)

Fitted variogram models, the key parameters of which are presented in tables 4.1a & b, were then used in ordinary kriging. Two point estimates were calculated for the central point of each square metre of each 2 x 1 m plot. The mean of these two estimates was then used in the modelling process.

CONVERSION OF FACTOR VARIABLES INTO CONTINUOUS FORM

Converting data from the seeding treatment plots into a continuous form was simple; a total seed density value was acquired by adding background seed rain to the added seed rain at the Dorset site and by adding seed bank density to added seed rain at the Surrey and New Forest sites. A single measure of P availability was calculated by taking the mean P_{ox} availability of the various P and disturbance treatment combinations (see Chapter 2) and adding the difference from mean background P_{ox} levels, as estimated from the kriged grid, for each individual plot. Using P_{ox} estimates that were specific to both the number of additions and the disturbance treatment will have had the effect of removing any P effects from the disturbance variable and will have reduced the likelihood of observing an interaction between disturbance and P_{ox} variables. Disturbance was retained as a factor variable, alongside many variables that it was related to including vegetation height, density and the availability of mineral substrates.

Models were fitted by maximum likelihood to seedling density data with the GLM procedure of S+ 6 for Windows and using the deletion test procedure described in Chapter 2 (see also Crawley 2002). Further description of the modelling process, including discussion of the fitting of polynomial and species-specific terms, is provided in Chapter 3.

Caution must be applied when comparing the results of both the factorial and modelling analysis of the various sites. The far greater replication of the Dorset site (null *d.f.* = 191) is likely to result in more significant *p* values and in the retention of more variables in the modelling procedure than at the New Forest and Surrey sites (null *d.f.* = 71). Models and conclusions derived from the Dorset site are therefore likely to be more detailed than those from the smaller sites.

FORMULATION OF A GENERAL MODEL

The data from all three sites was combined to form a single data set containing descriptions of: *Betula* seedling densities, seed densities, SOM content (0-50mm), water content (0-50mm), mineral substrate cover, mean vegetation height, P_{ox} availability (0-50mm) and the density of *E.tetralix*, *M.caerulea*, *C.vulgaris*, *T.cespitosum*, necromass and a sum total for biomass density. As data from different sites was collected in accordance with standardised sampling methodologies and at similar times it was considered equivalent. A preliminary inspection of these data using univariate and ordination methods was conducted so that the degree of overlap between the conditions at the sites, in both single and multidimensional space, could be assessed. This was done to ensure that the fitted relationships were constructed from data of multi-site origin over at least the majority of their range. An erroneous model is less likely to arise if this is the case e.g. if high vegetation density, high P plots are found at all sites.

Ordination was performed in S+6 for Windows using Principal Components Analysis (PCA). This was selected in preference to other ordination methods, because trends within the data were believed to be of a linear as opposed to Gaussian, form (ter Braak 1995). Data was scaled to provide unit variance to control for the different measurement scales of the variables.

A single model was fitted to the combined-site data using the GLM procedure described in Chapter 2 and in more detail by Crawley (2002). Interaction terms were restricted to first order as there were insufficient degrees of freedom to fit all higher order interactions and it was intended that the model should be of a fairly simple form. Linearity of the relationships was assessed by fitting polynomial terms, these were retained if found to significantly improve model fit in likelihood ratio tests. It was decided *a posteriori* that as the intention of the modelling process was to produce a general model that was applicable to a wide range of heath conditions, species-specific vegetation density terms were to be omitted from the models. Preliminary analysis found that this had little effect on the fit of the model, it was also advantageous from the perspective of model simplification; division of the vegetation density data into two basic categories, biomass and necromass density, reduced model parameterisation considerably.

Once the final, minimum adequate model was formulated a site interaction term was systematically added and removed for each term in the model, i.e. a separate, site-specific, regression slope was fitted for each term while the rest of the model structure remained unchanged. The significance of these site-specific terms was assessed using likelihood ratio tests. The aim of this process was to provide a rough assessment of the universality of the described relationships; if the fitted relationship was general to all three sites then model fit would not be significantly improved by the addition of site-specific terms.

Results

BETWEEN-SITE DIFFERENCES IN RECRUITMENT LIMITATION

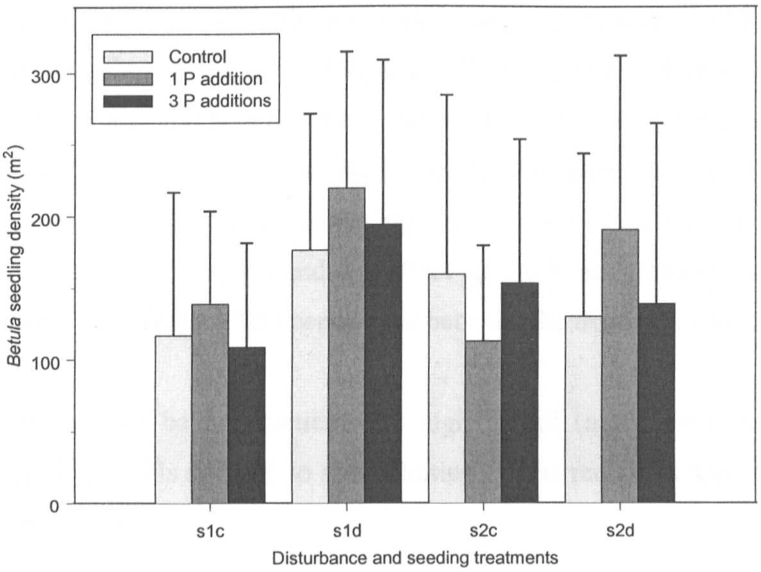
A) FACTORIAL ANALYSIS

Analysis of deviance demonstrated large differences in the degree of safe-site and seed limitation at the three experimental sites, with large temporal fluctuations in the importance of each of the manipulated factors. The effects of the experimental treatments at the Dorset site are discussed in detail in Chapter 3. Here it was found that seed limitation was the most important factor although both phosphorus and disturbance had highly significant effects.

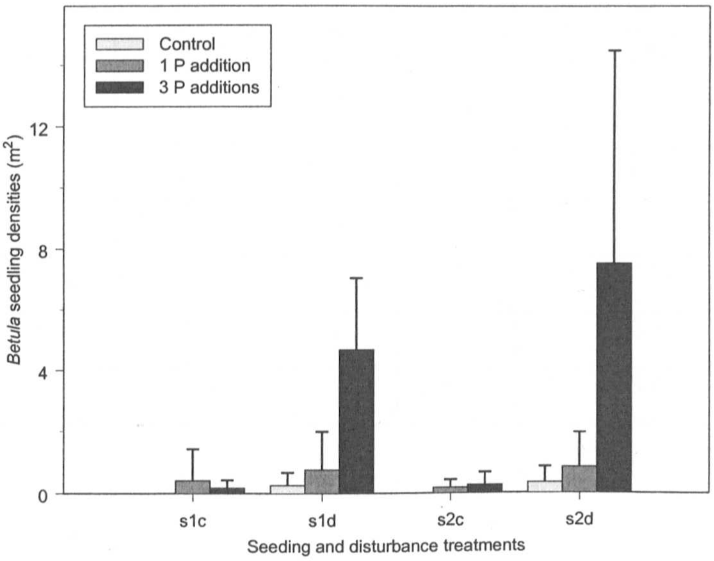
Of the experimental treatments, only disturbance had a significant effect on the densities of germinating seedlings at the New Forest site ($F= 5.5_{1,58}$, $p =<0.05$, Explained deviance (ED) = 4.82%), Fig 4.1 & Table 4.2. This effect was small however, compared to block effects ($F= 23.6_{2,58}$, $p =<0.0001$, ED = 41.4%), which are best explained by a possible moisture gradient; germination was earlier and markedly higher in damper conditions (personal observation). The initially high seedling densities, which were typically 100-200m^{-2}, were greatly reduced over the subsequent summer months with much mortality in all plots but particularly in undisturbed conditions. The effect of disturbance in September was highly significant ($F= 18.7_{1,58}$, $p =<0.0001$, ED = 19.75%). Mass mortality continued over the winter, resulting in seedling densities that were an order of magnitude lower (typically 0-4m^{-2}) than those of the germination stage (Fig 4.1).

Table 4.2. Analysis of deviance for seedling densities at the New Forest site with a fixed-form GLM (Poisson error/log link). Non-significant interaction terms have not been presented here. *=p <0.05 ** =p <0.01, *** =p<0.001, ****=p <0.0001

FACTOR		MAY 2000		SEPTEMBER 2000		MAY 2001	
	d.f.	F	*p*	F	*p*	F	*p*
Block	2	23.6	****	2.5	ns	13.7	****
Disturbance	1	5.5	*	18.7	****	89.4	****
Phosphorus	2	0.4	ns	2.0	ns	52.9	****
Seed	1	0.4	ns	0.5	ns	3.4	ns
Disturbance * Phosphorus	2	0.9	ns	0.2	ns	3.9	*



a)



b)

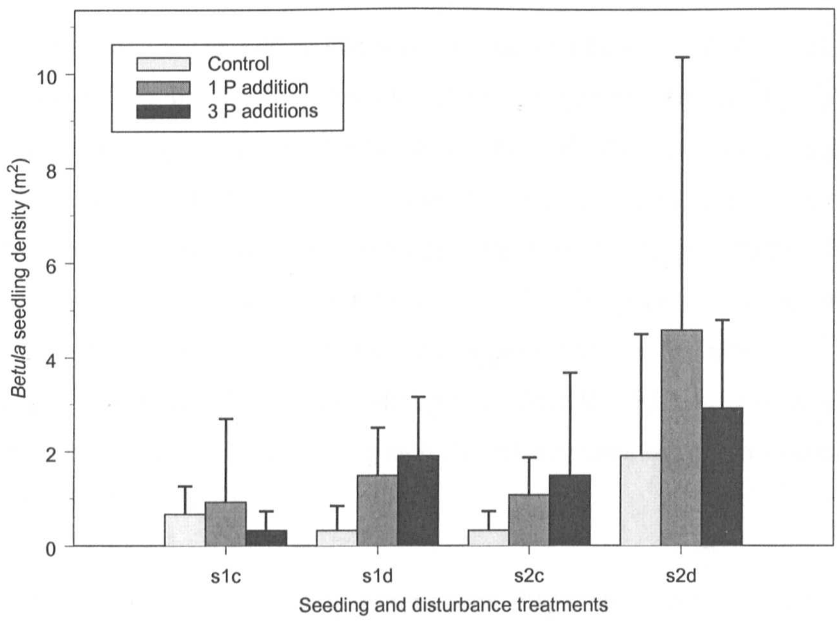
Fig 4.1.a &b. The effect of seeding, disturbance and phosphorus treatments on *Betula* seedling densities at the New Forest site for a) 1 month and b) 1-year old seedlings. s1 = control, s2 = 250 seeds m^{-2}, c = control, d = disturbance. Error bars represent ±1 standard deviation.

The over-winter mortality of all seedlings with stem diameters <1mm is reflected in densities of seedlings in May 2001, which revealed large disturbance ($F= 89.4_{1,58}$, $p =<0.0001$, ED = 30.1%) and phosphorus ($F= 52.9_{2,58}$, $p =<0.0001$, ED = 35.7%) effects and a small but significant interaction between these factors ($F= 3.9_{2,58}$, $p =<0.05$, ED = 2.62%); it was only in disturbed, high P conditions that seedlings were able to breach the >1mm size threshold during their first growth season. The high significance of the P factor can be attributed to both extreme safe-site limitation and the effect of the P additions at this site; there were large differences in available-P concentrations between the treatment levels (Chapter 2).

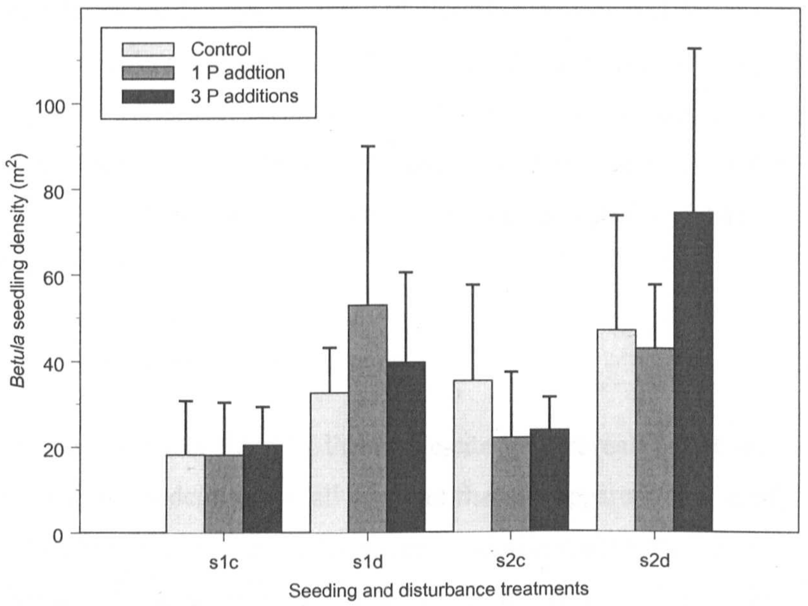
Background seed bank densities were high for all (mean seed bank densities = $337.9m^{-2}$ ±169.2) plots at this site and so seed addition effects remained non significant throughout the experiment.

Table 4.3. Analysis of deviance for seedling densities at the Surrey site with a fixed-form GLM (Poisson error/log link). Non-significant interaction terms have not been presented here. ** = p <0.01, *** = p<0.001, **** = p<0.0001

FACTOR		MAY 2000		SEPTEMBER 2000		MAY 2001	
	d.f.	F	*p*	F	*p*	F	*p*
Block	2	1.6	ns	1.6	ns	2.8	ns
Disturbance	1	30.3	****	20.1	****	13.6	***
Phosphorus	2	0.7	ns	3.5	*	3.8	*
Seed	1	5.2	*	12.5	***	8.6	**



a)



b)

Fig 4.2 a & b. The effect of seeding, disturbance and phosphorus treatments on *Betula* seedling densities at the Surrey site for a) 1 month and b) 1-year-old seedlings. s1 = control, s2 = 250 seeds m^{-2}, c = control, d = disturbance. Error bars represent ±1 standard deviation.

The largest effect at the Surrey site was disturbance (Table 4.3 & Fig 4.2), which had highly significant effects on seedling densities at the germination ($F= 30.3_{1,58}$, $p =<0.0001$, ED = 29.2%), 4-month ($F= 20.1_{1,58}$, $p =<0.0001$, ED = 18.6%) and 1-year stages ($F= 13.6_{1,58}$, $p =<0.001$, ED = 13.34%). Phosphorus played a small but significant role in the determination of later stage seedling densities (September 2000 $F= 3.5_{2,58}$, $p =<0.05$%, ED = 6.41%, May 2001 $F= 3.8_{2,58}$, $p =<0.05$, ED = 7.45%), with slightly greater densities in some P amended plots. The degree of seed limitation was intermediate to the other two sites with effects peaking in September, four months after germination ($F= 12.5_{1,58}$, $p =<0.001$, ED = 11.49%). The size of this effect is unsurprising as seedbank densities were also intermediate to the other two sites ($47.2m^{-2}$ ±32.65).

The demography of the seedling populations displayed dramatic between and within-site differences. Although the 3 sites displayed reasonably similar densities after 1 year (typically $<10m^{-2}$) their initial population sizes were greatest in sites that were non seed limited e.g. the New Forest (Fig 4.1a) with proportional mortality being greater where safe-sites were in short supply e.g. the New Forest and Surrey sites. Mortality was low at the Dorset site, 20% of germinating seedlings in control plots survived for 1-year while 52.5% survived 1-year in the disturbed, high seed, high P plots. At the New Forest and Surrey sites 1.13% and 4.8% survived 1-year in control plots while 7.20% and 4.57% survived in the disturbed, high seed, high P plots (respective, mean values). Another major difference between the sites was in herbivore attack rates. By May 2001 40% of seedling survivors at the Dorset site displayed evidence of attack from mammalian herbivores compared to 0.54% at the New Forest and 0.46% at the Surrey sites.

B) STATISTICAL MODELS

The statistical models fitted to the single-site data revealed that seed and safe-site factors explained seedling densities at all sites but that the apparent degree of the limitation and the exact identity of the safe-site determinants varied considerably between sites (Tables 4.4 and 4.5, Chapter 3). The model fitted to the Dorset site data is presented elsewhere (Chapter 3). It was found at this site that seedbank densities were able to explain the most variation in *Betula* seedling densities and that vegetation and nutritive effects were also important.

The model fitted to the New Forest site data (Table 4.4), which had a log link, Poisson error and an explained deviance of 83.2%, found seedling densities to be best described by a combination of 7 variables, the most important of which was P-availability (Deviance change on deletion (DCD) = 35.7% p = <0.0001). This, as discussed earlier (see above), is most likely to be a result of both strong background limitation and great within site variability (Coefficient of variation (CV) = 0.58 compared to 0.50 at Surrey and 0.27 at the Dorset site). The second largest contribution to explained deviance came from *M.caerulea* (DCD = 6.40%, p = <0.001), which was positively associated with *Betula* in control plots (an effect likely to originate from its associated environment) but proliferated in disturbed conditions to the exclusion of *Betula* (interaction term DCD =3.70%, p = <0.01).

The negative effects of *M.caerulea* in disturbed plots were balanced and in many cases exceeded by the positive effects of disturbance. Disturbance effects were better described by the availability of mineral substrates (DCD =2.72%, p = <0.01) than the binary factor descriptor, which would probably have been removed from the model if not for the aforementioned interaction. Mineral substrates were found in greater abundance in disturbed plots, their effect is likely to evince a *Betula* seedling requirement for soil microsites free of root competition and without the algal mat covering much of the site. It is less likely that they reflect the availability of light gaps, which appeared to be in fairly even supply across the site.

Table 4.4. MAM (log link/Poisson error) describing *Betula* seedling densities at the New Forest site approximately 1 year after germination (May 2001). Explained deviance = 83.2%, residual *d.f.*= 64). Deleted terms: *Erica tetralix* density, *Tricophorum cespitosum* density, soil water content (0-50mm), SOM (0-50mm), mean vegetation height, biomass density, necromass density, total vegetation density, all moss and lichen abundances

Variable	Parameter Values	Standard Error	Explained Deviance (% Null)	p (F-Test)
Calluna vulgaris density (hits m^{-2})	-0.10	0.037	3.71	<0.01
Molinia caerulea density (hits m^{-2})	0.039	0.037	6.40	<0.001
Disturbance	3.27	1.155	3.80	<0.001
P availability (P_{ox} μg P g^{-1})	0.007	0.00086	35.70	<0.0001
Mineral substrate (% cover)	0.059	0.021	2.72	<0.01
Seed bank density (m^{-2})	0.0016	0.0006	2.42	<0.01
M.caerulea density *Disturbance	-0.12	0.0369	3.70	<0.01

The final identified component of safe-site limitation was *Calluna vulgaris* density, which had a significant negative effect on seedling densities (DCD= 3.71%, p =<0.01). This effect, like that of *M.caerulea* is likely to represent the conditions associated with the species, which were dry and probably nutrient poor. It is interesting to note that *E.tetralix*, the dominant of this site, obviously had negative effects upon seedling survival (personal observation) but was not recognised by the modelling process, as its abundance was fairly uniform across the site. The final variable included in the New Forest MAM was seedbank density (DCD =2.42%, p = <0.01). Seedbank densities were extremely high for most plots (463m^{-2} ±204) but varied enough across the site to impact upon heterogeneity in seedling densities.

The model fitted to the Surrey site seedling data (Table 4.5) had a log link and Poisson error but a far poorer fit (Explained deviance = 38.4%), less parameterisation and a lower resolution than those of the New Forest and Dorset (Chapter 3). There was little overlap in the deviance explained by each term. The greatest contributions to explained deviance in the Surrey site model were those of the vegetation variables. At this site, species specific-biomass terms did not significantly improve the fit of the model and a similar lack of distinction was found for biomass and necromass. Instead, a single variable, total vegetation density (DCD =14.07%, p = <0.001) was retained. This effect was negative and is likely to reflect greater light interception in denser vegetation. The failure to detect separate bio- and necromass effects indicates that the effect is unlikely to represent belowground competition.

Table 4.5. MAM (log link/Poisson error) describing *Betula* seedling densities at the Surrey site approximately 1 year after germination (May 2001) Explained deviance = 38.4%, residual *d.f.*= 67). Deleted terms: all species-specific vegetation variables, soil water content (0-50mm), SOM (0-50mm), P-availability, all substrate variables, biomass density, necromass density.

Variable	Parameter Values	Standard Error	Explained Deviance (% Null)	p (F-Test)
Total vegetation density (hits m^{-2})	-0.0175	0.0035	14.07	<0.001
Disturbance	0.385	0.143	4.29	<0.05
Mean vegetation height (cm)	0.203	0.04	13.25	<0.001
Seed bank density (m^{-2})	0.0026	0.0008	6.25	<0.05

The second vegetation term, mean vegetation height, also explained a considerable portion of the variance (DCD=13.25%, p=<0.001) and displayed a positive relationship with seedling densities. As the effect is independent of vegetation density it is likely to represent the greater heterogeneity of taller vegetation and therefore the greater occurrence of light gaps in tall vegetation. The effect of disturbance at this site (DCD =4.29%, p = <0.05%) was likely to be of a similar nature to that represented by mineral substrate at the New Forest site in that it created small, competition free microsites within the typically dense vegetation. Flooding in many of the areas where mineral substrates were exposed accounts for the difference in descriptor variables between the sites. The size of the seedbank effect (DCD =6.25%, p = <0.05) was, like the seedbank density ($172m^{-2}$ ±130), intermediate to that observed at the other two sites (total seed bank densities were $125m^{-2}$ ±110 at the Dorset site).

The lack of inclusion of the phosphorus variable in the Surrey site model reveals a slight inconsistency with the factorial analysis in which P addition was significant at the 5% level (see above). This may reveal the shortcomings of estimating available-P from 'snapshot' measurements; at the time of sampling one addition and control plots had approximately equal availabilities (Chapter 2) but this is not what the factorial results would indicate (Fig 4.2a & b). Seedling densities were also found to decline in plots of exceptionally high P availability where the proliferation of algae occurred.

BETWEEN-SITE VARIATION IN THE NATURE AND COVERAGE OF HEATH CONDITIONS

Univariate examination of the data used in the fitting of the combined-site general model revealed that although there were large between-site differences in the values for most variables there was also considerable overlap (Fig 4.3 & 4.4) i.e. phosphorus availabilities were typically the lowest in the Dorset site plots but comparable levels of P-availability could also be found in some plots at the New Forest and Surrey sites. The exceptions to this trend were mineral substrate cover, which displayed a similar pattern at all sites and SOM content (0-50mm), which was substantially lower at the Surrey site. Variables appeared to cover a wide range of heathland conditions for most variables with the exception of soil water content, which displayed a range of 53.5 - 79.9% in the combined data set. The disadvantageous consequence of this lack of variation is that the model may be specific to wet heath conditions.

Table 4.6. Explained variance and loadings of the combined-site PCA ordination. Variables were scaled to provide unit variance. Loadings ≤±0.10 have been omitted.

	Component 1	**Component 2**	**Component 3**	**Component 4**
Erica tetralix	0.38	0.17	0.29	0.14
Molinia caerulea	0.12	0.48		-0.40
Calluna vulgaris	0.36	-0.20	-0.34	0.16
Tricophorum cespitosum	0.24	-0.19	0.33	-0.10
Biomass	0.52	0.20		
Necromass	-0.16	0.32		-0.63
Mean vegetation height	0.26	0.30	-0.48	
SOM content (0-50mm)	-0.32	0.40	0.10	0.40
Mineral substrate cover	-0.29	-0.29		-0.31
P-availability (P_{ox})	0.29	-0.16	0.22	-0.14
Soil water content	-0.13	0.38	0.18	0.32
Seedbank density			0.59	
Explained Variance (proportion)	**0.26**	**0.17**	**0.14**	**0.10**
Explained Variance (cumulative proportion)	**0.26**	**0.43**	**0.57**	**0.67**

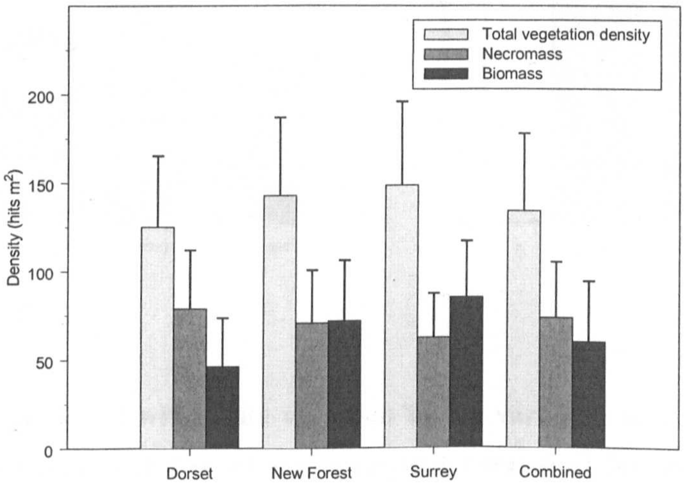


Fig 4.3. Between and within-site variation in the vegetation density data used in the combined-site general statistical model. Error bars represent ± 1 standard deviation.

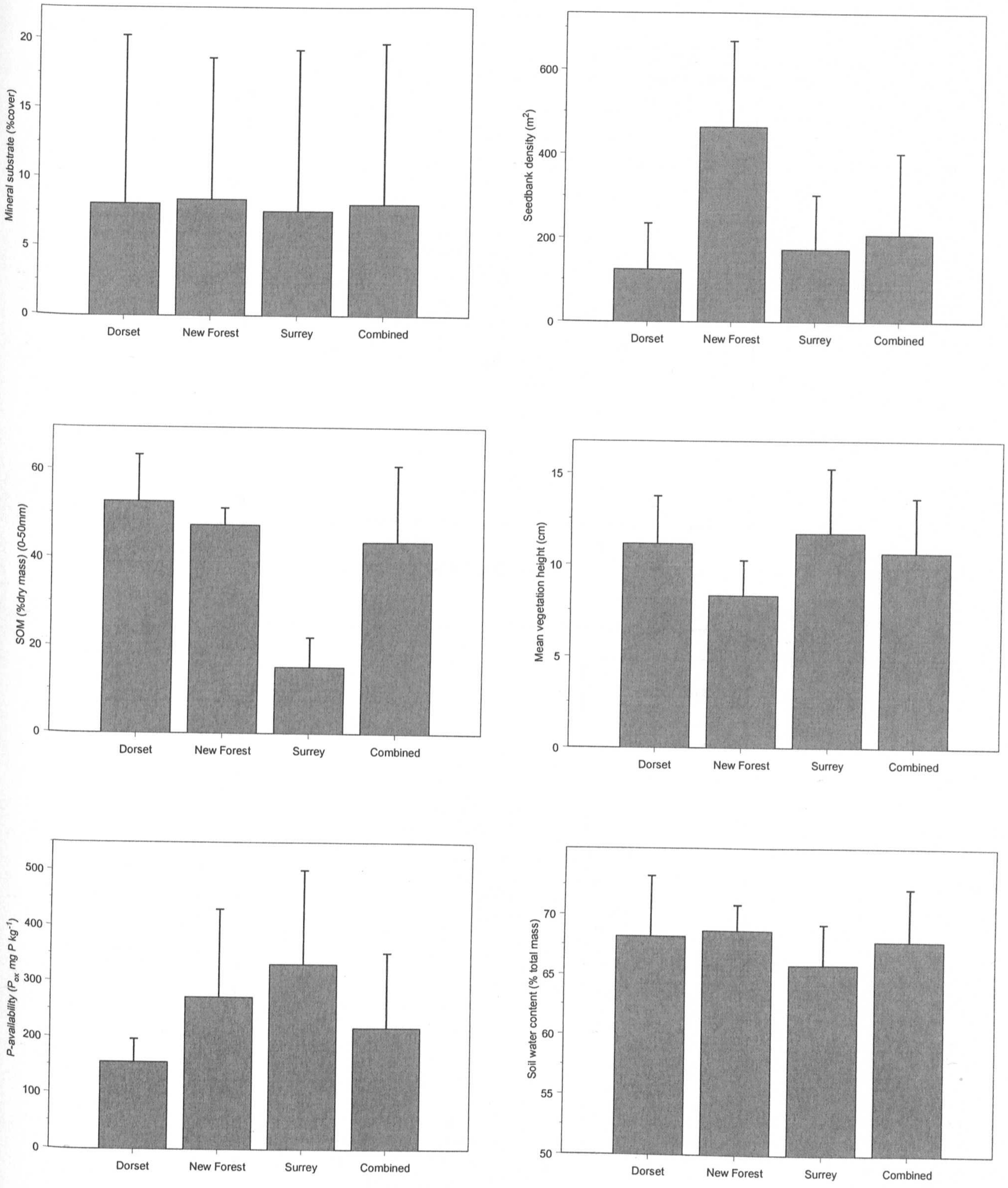


Fig 4.4. Between and within-site variation in the variables used in the combined-site general statistical model. Error bars represent ± 1 standard deviation.

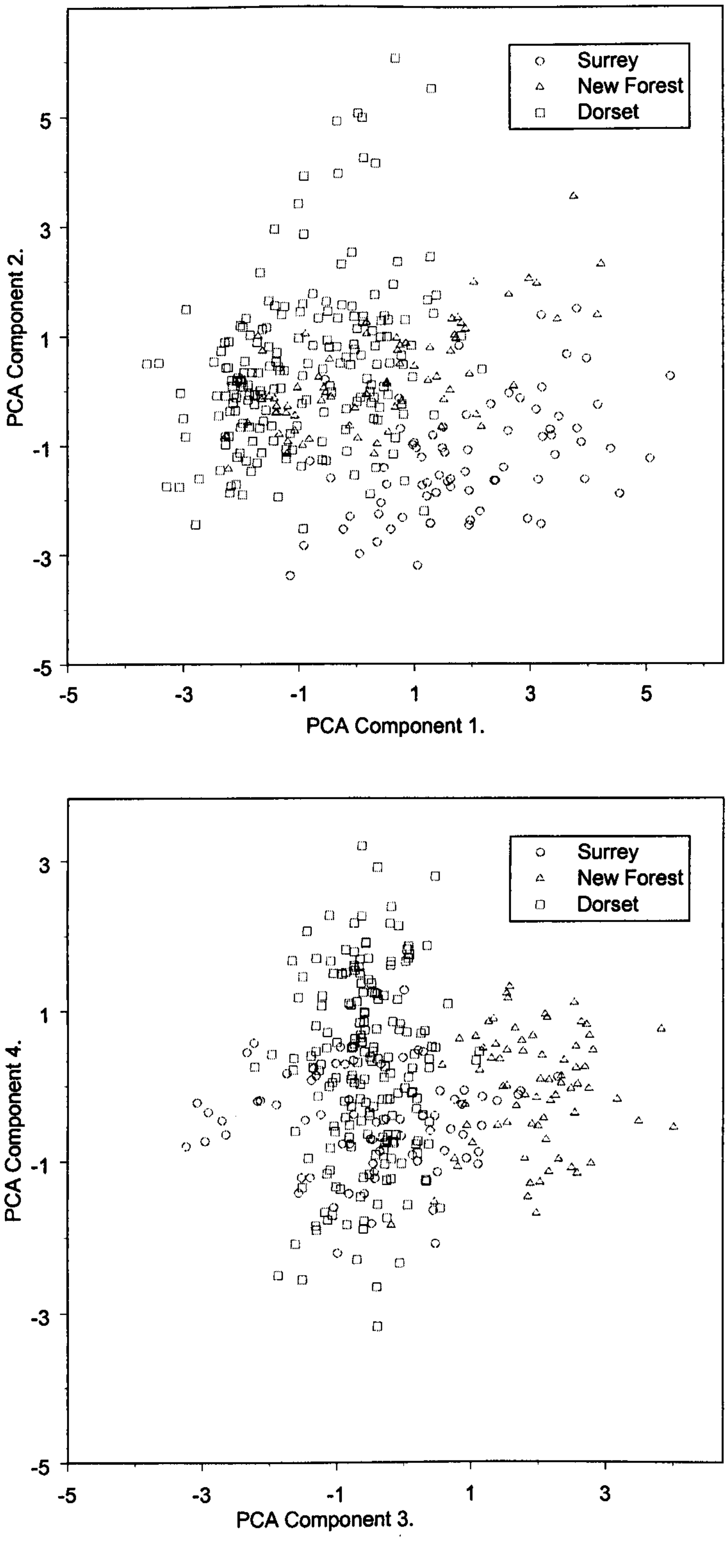


Fig 4.5. Principal components analysis of the data used in the combined-site general model. Components 1-4 account for 67% of the variance.

Multivariate analysis of the combined-site data (Table 4.6, Fig 4.5) found that the conditions within the experimental plots could be separated into distinct types (PCA components 1-4 accounted for 67% of the variance) but that these types were, in general, not specific to a particular site i.e. each site contained most conditions and therefore the model will be based on data from >1 site for the most of the typical numeric combinations. Relationships fitted to extremes of conditions are, however, likely to be based upon information from a single site.

COMBINED-SITE, GENERAL MODEL

The model fitted to the combined multi-site data, which had a log link and Poisson error, explained 59.8% of the deviance and contained six predictor variables (Table 4.7). Despite the low number of predictor variables there were 15 terms in the model as there were numerous polynomial and interaction terms, some of which were highly significant (Table 4.7). The greater complexity of the relationships observed in this general model, in comparison to the single-site models, are most likely to be a result of the larger sample size and wider range of conditions covered in the combined site data set. The variables used in the model are, to a greater or lesser extent, simple descriptions of the physical environment and the fitted relationships are not in principle, specific to a single community type. Another property of the general model was its failure to include many of the idiosyncrasies of the site-specific models (e.g. site-specific disturbance effects), only general, universal determinants were recognised.

It was found that the fit of some of the terms was significantly improved by fitting site-specific regression slopes (Table 4.7). This change in fit was, for 4 terms, significant at the 1% level. However, changes in explained deviance were always <2% of the null deviance. Context-dependence is therefore present, but only to a small degree; relationships were broadly similar at all sites. Although this bears out the generality of the model it must be acknowledged that the model was fitted to incorporate all sites and that this process will have been biased towards the fitting of general terms; i.e. a model fitting procedure that included site-specific terms from the offset would have resulted in a model of greatly different form.

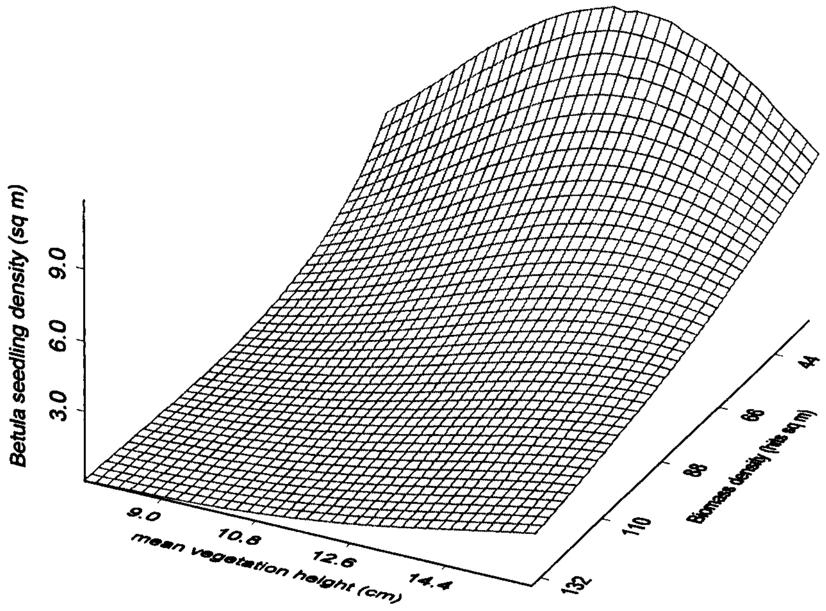
Variables	Parameter value	Standard Error	Explained deviance (% Null)	p (F-test)	Fit Improvement (% Null Dev.)	Site Specificity test (p)
Main effects:						
Soil water content (0-50mm)(% total mass)	3.23 *e*-002	9.67 *e*-003	0.84	<0.05	1.16	<0.05
Necromass density (hits m^{-2})	6.54 *e*-002	1.81 *e*-002	2.65	<0.01	1.45	<0.05
Biomass density (hits m^{-2})	-5.92 *e*-002	9.44 *e*-003	35.25	<0.0001	0.82	ns
Mean vegetation height (cm)	1.45	0.31 *e*-003	20.48	<0.0001	1.35	<0.05
Seedbank density (m^{-2})	-2.01 *e*-003	1.19 *e*-003	19.59	<0.0001	1.67	<0.01
Phosphorus availability (P_{ox} µg P g^{-1})	2.35 *e*-002	4.27 *e*-003	9.15	<0.0001	0.47	ns
Polynomial terms:						
P-availability^2	-5.81 *e*-005	1.51 *e*-005	3.22	<0.001	0.32	ns
P-availability^3	6.26 *e*-008	1.61 *e*-008	1.08	<0.05	0.30	ns
Mean Vegetation Height^2	-6.81 *e*-002	1.37 *e*-002	2.59	<0.001	1.35	<0.05
Interactions:						
Biomass * Seedbank	-8.28 *e*-005	1.11 *e*-005	5.20	<0.0001	1.48	<0.05
Biomass * Vegetation height	4.05 *e*-003	7.50 *e*-004	2.13	<0.001	0.94	ns
Seedbank * Vegetation height	9.83 *e*-004	1.34 *e*-004	4.70	<0.0001	1.79	<0.01
Vegetation height * P-availability^2	-8.64 *e*-007	2.22 *e*-007	1.25	<0.01	0.30	ns
Necromass * Vegetation height	-1.17 *e*-002	3.07 *e*-003	1.08	<0.05	1.62	<0.01
Necromass * Vegetation height^2	4.45 *e*-004	1.27 *e*-004	0.91	<0.05	1.55	<0.01

Table 4.7. General MAM for 1-year-old *Betula* seedlings in the M16 community (log link, Poisson error), explained deviance 59.8%, residual *d.f.* = 320. Deleted terms: SOM content (0-50mm) and mineral substrate cover. The data used in the modelling process was a combined set pooled from the three experimental sites. The final two columns display the results of generality tests in which site-specific regression slopes were fitted for each term of the model.

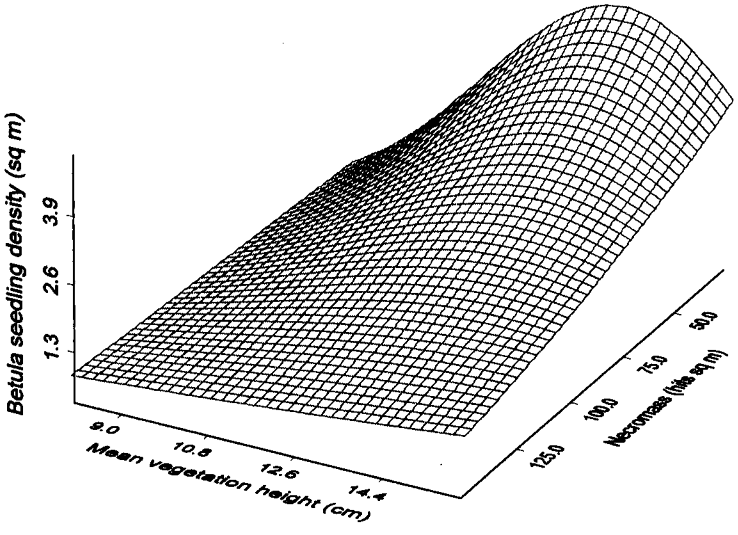
The relationships fitted by the modelling process can be divided into factors relating to safe-site and seed limitation, and additionally, the interaction between these factors. The variables accounting for the most deviance were the density of plant biomass (DCD = 35.25%, p=<0.0001), an independent effect of vegetation height (DCD = 20.48%, p=<0.0001), which can be thought of as representing the 'gapiness' of the vegetation, seedbank density (DCD = 19.59%, p=<0.0001) and phosphorus availability (DCD = 9.15%, p=<0.0001). Smaller effects were observed for the density of necromass (DCD = 2.65%, p=<0.01) and soil water content, the only non-interactive variable included in the model (DCD = 0.84%, p=<0.05). Two of the postulated predictor variables, SOM content (0-50mm) and mineral substrate cover did not explain a significant and unique portion of the deviance and so were removed during the modelling process.

An examination of the combined effects of main, polynomial and interactive terms reveals a number of consistent and revealing patterns. These patterns were explored through the plotting of spline fitted response surfaces to predictions from the fitted model (Figs 4.6, 4.7 & 4.8). The multidimensionality of the model required variables to be held constant while others were varied over their range within the combined data set. The first of these surfaces displays the relationship between seedling densities, vegetation density and height (Figs 4.6 a & b). At low densities of biomass and necromass vegetation height displayed a quadratic relationship with seedling densities, peaking in low-density vegetation of intermediate height (11-14cm). As vegetation density increased seedling densities declined, as did the curvature of their relationship with vegetation height, which had a small, positive, relationship with seedling densities where vegetation density is high. These relationships are more pronounced for living vegetation, a phenomenon that is likely to reflect competitive influences.

The overall trends displayed by these components of the model are likely to reflect the balance between inhibitory and facilitative components of vegetation effects, with the balance being at its most positive where light interception is low but where there is some shelter from herbivores and abiotic stresses such as drought. These conditions are most likely to occur in the early building and degenerate phases of the dwarf shrub cycle and in multi-species, beetle attacked vegetation. The contrasting, uninvasible conditions are dense, compact vegetation containing few light gaps e.g. the closed canopies of the later building and mature phases.



a)



b)

Fig 4.6 a & b. The interactive effects of: a) biomass density and vegetation height and b) necromass density and vegetation height on the density of 1-year old *Betula* seedlings as predicted by the general, combined-site statistical model (Table 4.7).

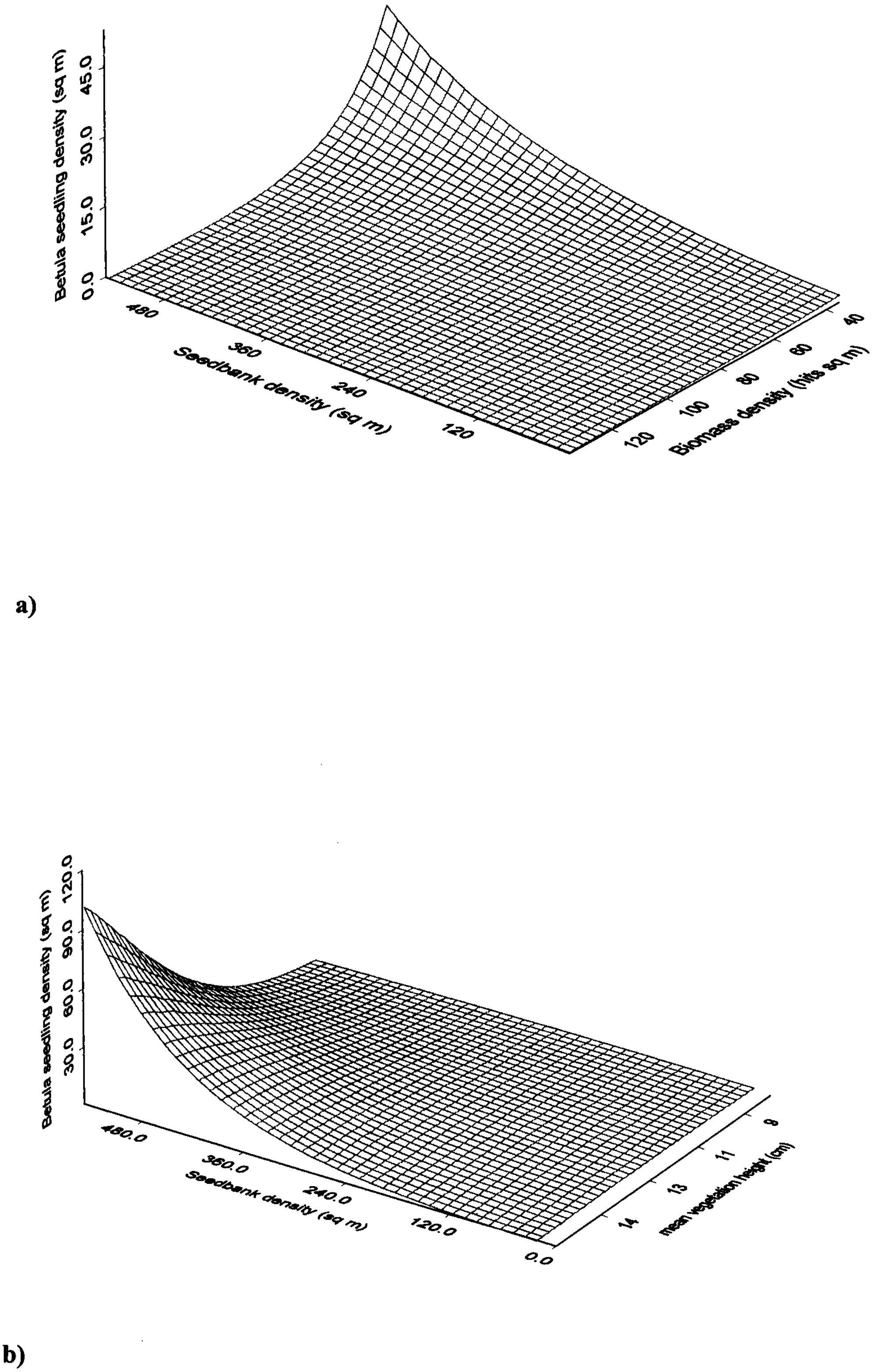


Fig 4.7a & b. Interactions between safe-site and seed limitation. a) Fitted response of 1-year-old *Betula* seedling densities as described by seed bank and biomass densities. b) Seedling response to seed bank density and vegetation height. All other variables in the fitted model (Table 4.7) were held constant at their mean.

The second major trend in the fitted relationships is the important interaction between seedbank density and the safe-site indicators biomass density (Interaction term DCD =5.20%, *p*= <0.0001) and vegetation height (Interaction term DCD=4.70%, *p*=<0.0001). The fitted response of *Betula* seedling densities to these factors reveal that high density *Betula* colonisation only occurred where both seed and safe-sites were non limiting (Fig 4.7a & b) and that phase transition, in conditions typical of the experimental plots, is likely to occur where seedbank densities are >200m^{-2}, if safe-sites are non-limiting. This exponential increase in seedling densities as they are freed from safe-site and seed limitation is evidence of the increasing likelihood of seed presence to coincide with safe sites as seed becomes more abundant. Safe-site limitation became total at densities of 88 biomass hits per m^{-2} and at vegetation heights of around 10cm, when the other variables in the fitted models were held constant at their mean. A phenomena swamped by the interactive effects of these variables is the potential for *Betula* to colonise at low densities where seed availability is low but safe-site conditions optimal.

The relationship between *Betula* seedling density and phosphorus availability was found to be complex and highly dependent upon vegetation structure (Fig 4.8); description of phosphorus relationships required both quadratic (DCD=3.22%, *p*=<0.001) and cubic terms (DCD =1.08%, *p*=<0.05) and an interaction term between P availability and vegetation height (DCD=2.59%, *p*=<0.001). Where vegetation was short (mean vegetation height <10cm) and therefore, for a fixed density, more compact, there was no response by *Betula* to increases in P-availability; only at extremely high P-concentrations (P_{ox} >400µg P g^{-1}) did *Betula* seedling density respond fully to increases in P availability. A completely contrasting response was fitted to the data from taller, more 'gappy', vegetation (mean vegetation height >10cm). In these conditions *Betula* seedling densities were dramatically responsive to differences in P-availability (P_{ox}) between 0 and 200µg P g^{-1}, the typical range of heathland conditions (Chapter 5). When the other variables in the model were held constant at their mean seedling densities peaked where P_{ox} was c.300 µg P g^{-1} and where vegetation was tall >12cm. Where vegetation was tall and P_{ox} was >400µg P g^{-1} seedling densities declined. This may be explained by the proliferation of algae in conditions that may be considered atypical of most heathlands.

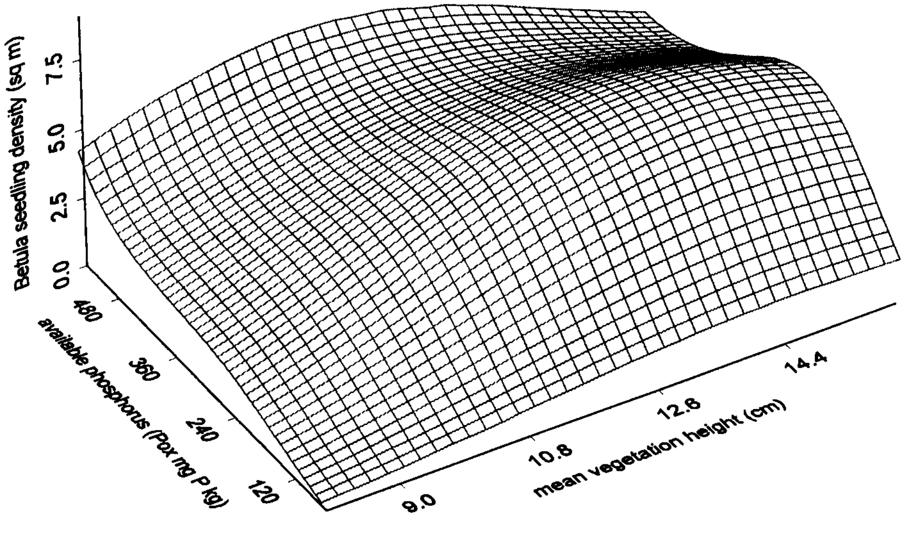


Fig. 4.8. The fitted response of 1-year-old *Betula* seedling density (m^{-2}) to phosphorus availability (P_{ox} μg g^{-1}) and vegetation height as estimated by the general model (Table 4.7). All other variables in the model were held constant at their men.

Discussion

The results demonstrate that the identity of the determinants of *Betula* colonisation are broadly similar between sites, that their relative importance varies widely and that a single statistical model is capable of explaining *Betula* seedling densities over a wide range of conditions. Results of the experimental and modelling analyses reveal, when combined, that *Betula* recruitment, and therefore the phase transitional area of the heath ecosystem, is controlled by both seed and safe-site limitation and that vegetation, disturbance and phosphorus effects can be key axes in the determination of the *Betula* safe-site; findings which extend and support to the conclusions of Chapter 3. The fitted relationships of the combined-site model reveal that the phase-transitional area of heathland ecosystems may be narrowly defined i.e. *Betula* colonisation of an extent likely to result in phase-transition is dependent upon the coincidence of a large number of favourable conditions; the non-optimality of a single important variable (e.g. vegetation density, seed bank density) may preclude invasion.

BETWEEN SITE DIFFERENCES IN THE DETERMINANTS OF INVASION

Large between-site differences in the degree of safe-site and seed limitation were found to occur, with seed limitation playing a larger role at the Dorset site than at the New Forest and Surrey sites and safe-site limitation being particularly strong at the New Forest site. The statistical models fitted to the experimental data indicate, somewhat unsurprisingly, that the variables accounting for variation in seedling densities at any given site were those which varied greatly, and over a critical range of values e.g. seedbank densities at the Dorset site and P-availability at the New Forest. The apparent inconsistency in the form of the site-specific models may be explained by 1) the apparent dissimilarity of predictor variables in the site-specific models, representing similar phenomena (e.g. disturbance/mineral substrate cover and various vegetation density terms, 2) failure of some variables to vary sufficiently at some sites i.e. they were universally limiting or non-limiting in all plots within the site and 3) site-specificity in the behaviour of the determinants e.g. non-competition disturbance influences.

At the Surrey site the failure of the experimental treatments to generate clear differences in seedling densities was exacerbated by flooding in many bare, disturbed sites and appeared to result in an entire-site negative interaction between seed and safe-site limitation and therefore low overall seedling densities. Submersion has previously been seen to promote *Betula* mortality in water meadows (Skoglund & Verjist 1989). Unlike those at the New Forest site, the few surviving seedlings were not associated with an easily definable set of conditions (upturned clumps of P rich, disturbed soil). Instead, seedling abundance was effectively stochastic; the best-fit model could account for little of the variation in seedling densities. This stochasticity is likely to be related to the low probability of seedling establishment when both seed and safe-sites are limiting; measurements of 'average' or 'overall' conditions like those used here probably lack the required fine-grained resolution that would be able to account for the infrequent coincidence of seed and microsite when both are strongly limiting. This concept is evinced by a comparison of the distribution of residuals at all sites and in all models, including the combined site model; overdispersion only occurred where predicted seedling densities were low.

Heterogeneity in seedling densities associated with broad differences in the overall invasability of entire plots (often caused by the experimental treatments) was more readily quantifiable. Between-site differences in seed limitation, which were large and surprising given that the sites were equidistant to seed sources may be easily explained by the site differences in seedbank density. Seedbank densities appeared to be controlled by two key factors, wind direction and source strength (*sensu* Clark *et al.* 1998). The New Forest site, for instance, was aligned with the prevailing wind direction and had a greater basal area of *Betula* in the strip adjacent to the experiment than at the other two sites. Clark *et al.* (1998) found that in closed forest stands "the most fundamental limitation on recruitment is the absence of parent trees", this limitation is likely to be of even greater importance where trees are colonising outside of their existing populations. If variation in seed availability was detected as a contributor to heterogeneity in seedling densities at all three experimental sites then it may be safe to assume that it plays a major role in determining the probability of phase transition in many heathland areas, which are typically more isolated from seed sources than the plots of these experiments.

The variety of safe-site limitations detected by the modelling process reveal that *Betula* seedlings respond to, and are limited by, a variety of environmental factors. Both the site-specific and combined-site models support the notion that disturbed conditions alone are not sufficient to describe a seedling safe-site, an assumption of many experimental studies (e.g. those reviewed by Eriksson & Ehrlén 1992). This study finds disturbance to have a net positive effect on seedling recruitment but one that appears to operate through a variety of mechanisms. The largest of these would appear to be its effect on vegetation structure and density. The identity and magnitude of vegetation effects differed greatly between the sites with negative effects of plant density being greatest at the Dorset and Surrey sites. This is more likely to reflect the greater heterogeneity of the biomass densities at these sites than limitation *per se*. The species-specific effects at the New Forest site are more likely to be linked to the associated environments of the identified species (discussed in Chapter 3), which were not the most abundant at the site. *Molinia caerulea*, for instance, is commonly associated with greater N (and possibly P) mineralization rates than dwarf shrub species (Berendse 1990; Berendse *et al.*1989). Another factor causing between-site differences in species-specific terms may be the different sampling times of the vegetation data. *M.caerulea* biomass, for example, is likely to be lower in the autumn when the New Forest and Surrey data was collected than in the summer when the Dorset site data was gathered (Aerts 1989).

Although there seemed to be greater germination of *Betula* in disturbed plots at all sites other effects mediated by disturbance varied between being positive at the Surrey and New Forest sites (a greater availability of small, competition free microsites e.g. upturned soil clumps), to being negative at the Dorset site. Disturbed plots contained larger gaps here, which were open to the herbivores of the site. This inconsistency in disturbance effects when isolated from vegetation effects may explain the failure of the disturbance indicator, mineral substrate cover, to be retained in the combined-site model; its effects were heavily context dependent.

Between-site differences in the P response of the *Betula* seedlings were a product of both the initial degree of limitation and the within-site variability of the P_{ox} variable. Low PSC resulted in fairly homogenous levels of P-availability across the Dorset site (Chapter 2) while at the New Forest site the high PSC generated great differences between control and high level P addition plots (Chapter 2). The lack of any major response at the Surrey site is explained by measurement error (see above) and/or P availabilities that were typically greater than the tall vegetation asymptote of the combined-site model (Fig. 4.8) in all plots (see Chapter 2 for values) i.e. P was possibly not limiting in any of the plots.

GENERAL MODEL

The general, combined site model provides a general and detailed description of the regeneration niche (*sensu* Grubb 1977), or safe-site of *Betula*, including density dependent factors, and in doing so describes, at least in part, the state-shift threshold or phase transitional area of the M16 heathland community. The model may be considered more generally applicable than the site-specific models as its fitted relationships are based upon a variety of sites, a larger number of replicates and a wider range of conditions. The nature of the six descriptor variables is also more generally applicable indicating that a large number of biotic effects may be reduced into simple descriptions of the physical environment without drastically reducing the explanatory power of the model. By describing the constraints on recruitment of a species known to activate a switch between ecosystem states it is one the first attempts to describe the threshold of transition (e.g. the F_2 point of Scheffer *et al.* 2001) in a general, quantitative and multidimensional fashion.

Despite these achievements the model is flawed in that it is probabilistic and reliant upon the assumption that the predicted response, seedling density, is indicative of the likelihood of transition rather than a clear distinction between the basins of attraction for the two alternate states. Again, as in Chapter 3, it must also be noted that accurate description of the phase transitional area requires long-term monitoring of the seedlings to adulthood, or at least until they have been deemed to have significantly altered the state of the system. The model does, however, delimit the conditions within which the threshold occurred at the experimental sites. The true threshold may not be greatly different to that described here for some situations e.g. the New Forest and Surrey sites, where herbivore induced mortality, a potentially major limitation in the later stages of seedling development, did not appear to be operating. Examination of the plots in September 2001 (personal observations) suggested that little mortality had occurred and that herbivory had not affected the seedlings at the New Forest, despite evidence of heavy browsing of *Betula* in nearby grassland patches and the breaching of the dwarf shrub field layer (seedlings were >30cm tall with stem diameters >5mm).

The factors recognised by the model are likely to be limiting and of importance at many sites. The greater replication and variety of conditions in the combined site data allowed for the detection of effects from factors which may not vary enough within a single site to explain heterogeneity there, despite the existence of limitation. This property suggests that the factors explaining heath-scrub transitions at any given scale will not only be those which limit at that scale but also those which are spatially heterogeneous, e.g. climate is unable to explain variation in the likelihood of transition within a small region. Likewise, the variables retained in the general, combined site model are likely to explain variation in the extent of invasion at the small, within-patch scale but only if the variety of conditions covered by the experimental plots are typical of many heathland sites. A lack of variation in some parameters, however, e.g. soil water content, may restrict the relevance of the model to a narrow range of conditions. These problems are discussed in further detail below. An enormous amount of further research, including a calibration of seedling densities to the likelihood of transition, would be required before a truly predictive model of the heath-scrub transition could be formulated.

Although the model was largely derived from experimentally manipulated plots of the M16 community the data do appear to cover a wide range of conditions and its fitted responses correspond closely to observations made by other researchers in a variety of heathland environments. Further study is required to see if the model can accurately describe seedling densities in a wider variety of conditions but these consistencies do provide some support to the general applicability of the model. Seed limitation, for instance, is likely to be well described. Mitchell *et al.* (1998) found in a study of several heathlands, that densities were <800m^{-2}, a range that is largely covered by the combined-site data. Overestimation by the model may occur however, where seedrain is low but other conditions are optimal; the model does not incorporate a function stating that 'predicted seedling densities cannot exceed seed bank densities'.

Vegetation conditions are also likely to be well represented by the model, which was constructed from data covering a wide range of vegetation densities and structures. An exception to this is recently burnt conditions, where vegetation densities and heights are potentially zero. Long-term behaviour of *Betula* seedlings in these conditions remains unknown. The fitted response does, however, describe the invasability of the various stages of the dwarf shrub cycle in a more quantitative fashion than has previously been attempted. The model suggests that low-density vegetation, of intermediate height, is the most invasable and that the facilitative-inhibitory balance of neighbour biomass is more negative than that of necromass. It should be noted in advance that the fitted model results are not directly comparable to the drier environments in which classic heath vegetation cycling (e.g. Watt 1947; Gimingham 1988) occurs as the phases are less distinct in the M16 community with vegetation density and gap size being more dependent on hydrology than the age of the vegetation (personal observation).

The almost total failure of *Betula* to penetrate thicker canopies is consistent with the findings of Gong & Gimingham (1984), de Hullu & Gimingham (1984) and Miles (1974) who stated that a gap of bare soil measuring at least $25cm^2$ was required for successful establishment in *Calluna* vegetation. Miles and Kinnaird (1979) revised these conclusions to state that gaps of $50\text{-}100cm^2$ were required, as smaller gaps saw early survival but competition driven mortality later on. The observed vegetation responses are also consistent with the findings of Marrs (1986) who found no *Betula* in the mature phase heath vegetation of Cavenham heath, in contrast with an area of pioneer and dead *Calluna,* which had a *Betula* cover of 38%.

Despite widespread canopy exclusion Gong & Gimingham (1984) found survival of seedling *Betula* in all ages of *Calluna* vegetation 14.5 months after experimental planting thus demonstrating that even dense canopies are occasionally invasable. This supports earlier proposals (see above) that low density, effectively stochastic invasion can occur in what are generally perceived as uninvasable conditions. This type of low-density invasion is unlikely to result in what would be perceived as a state shift at larger scales, though it may increase the likelihood of occurrence in the future.

The fitted response from the combined site model shows that *Betula* seedlings are responsive to variation in P-availability over ranges typical of heathland conditions. These results support the idea of Harrison and Helliwell (1979), who suggested that *Betula* spp. could tolerate low levels of P in the absence of competition (seedlings were present in some plots in low P conditions) but that high P conditions gave the seedlings a boost that increased their competiveness e.g. seedlings could survive at the safe-site limited New Forest site where P was extremely high.

The relationships of the fitted model also support ideas presented by Chapman *et al.* (1989b) and extended in Chapter 2. In the available P (P_{ox}) model presented in Chapter 2 (Table 2.3, Fig 2.5b) PSC increased P_{ox} from c.20µg Pg^{-1} to 55µg P g^{-1} over a PSC range of 50 to 1500 (e.g. from those typical of Dorset to those of Surrey and the New Forest). This difference, although small, coincides with the steep area of the fitted relationship (Fig 4.8) where vegetation is tall and may be sufficient to explain, at least in part, regional patterns of heath-scrub phase transition. Although there is thought to be some ecotypic variation in *Betula* response to low P concentration (Pelham & Mason 1981) with some types expressing P independent growth and others requiring high P concentrations to grow rapidly, more variation in seedling weight was accounted for by soil nutrient status than seed lots (genotype) in the studies of Helliwell & Harrison (1979). The fitted response is therefore likely to be reasonably general.

In synthesising the findings of the site-specific, combined-site and previously published studies it can be tentatively concluded that heath-scrub state shifts are most likely to occur in conditions where vegetation is sparse and of intermediate height, where propagule supply is plentiful, where P availability (P_{ox}) is >100μg g^{-1} and where herbivores are absent. This description of heathland conditions concurs closely with that of degenerate phase vegetation close to existing *Betula* scrub patches. Though the model does not include alternative heathland environments this conclusion appears to hold over them e.g. this description fits the successful colonisation of degenerate *Ulex europaeus* patches that is described by Grime *et al.* (1988). This conclusion also shows agreement with those of Marrs *et al.* (1986). He proposed that the success of *Betula* invasion in Breckland, East Anglia, UK was due to: "1. the presence of an abundant seed source, 2. seed dispersal, 3. a large number of 'safe-sites' for germination and establishment and 4. a low grazing pressure". These conclusions are also in accord with those of numerous ecological studies of invasion; e.g. Britton *et al.* (2000) who found that heathland invasion by *Deschampsia flexuosa* could be limited by gap availability and seed rain but that there was considerable between-site variation in the determinants of invasion and Burke & Grime (1996) who found that it was fertile, disturbed habitats that were the most invasable to exotics.

It is important to note that although invasion is greatest at the 'optima' described above invasion success is a product of multiple determinants, which interact in a complex fashion. There is, therefore, no single set of conditions in which transition is likely to occur but rather a suite of combinations that occupy a narrow area of multidimensional space. What is perhaps easier to define is the common and naturally occurring set of conditions in which transition does not occur; sites with seedbank densities of, or close to, zero and high density, short vegetation. Where invasion does occur, the contributions from various controlling factors (e.g. competition and phosphorus) are likely to vary. Transition events are therefore likely to be controlled by different factors at different sites and at different scales. A discussion of the factors that influence the identified determinants at larger scales, based on the assumption that the models findings are generally applicable, makes up the remainder of this chapter.

EXTRAPOLATION TO LARGER SCALES

Alternate ecosystem states are often viewed as plateaus between basins of attraction in phase space, which may be shifted by perturbations or endogenous processes (Scheffer *et al.* 2001; May 1977; Carpenter 2001; Doebeli in Calow 1998). In this study it is assumed that the predicted values (seedling densities) of the presented models are representative of the position of the system in phase space. Low predicted values represent stable heathland conditions while higher values indicate increased proximity to the unstable regions of phase space. Management regimes and inherent regional differences e.g. geology and climate may, by altering numerous components of the physical and biological environment, affect the mean values of the identified determinants over larger areas and timescales and therefore shift the average phase space position of the ecosystems in that region, making them more or less susceptible to invasion. At these scales it would seem that any factor which has allowed greater rates of invasion will result in greater a likelihood of seed presence in the next stage or generation of scrub colonisation. At larger scales seed availability is therefore representative of the success of previous invasions; the greater the invasion the more likely future invasions will be.

It has long been recognised that European heathlands undergo a characteristic cycle (Watt 1947; Gimingham 1988) over which most of the identified determinants vary. Although the dwarf shrubs of heathlands appear to exert a certain degree of conspecific facilitation, e.g. acidification and the slowing of nutrient supply rates (Aerts & Chapin 2000; Wilson & Agnew 1992), which along with the formation of a dense canopy promotes short-term heathland stability, heathland ecosystems also tend to exhibit a certain degree of 'self-organised criticality' in which they naturally progress towards the vulnerable, degenerate state. Long-term persistence is therefore seemingly dependent upon various regular disturbances, which the system may have evolved to attract (e.g. fire).

BURNING & BEETLE OUTBREAKS

Regular burning is likely to hold the environment within the heath stability domain as it promotes nutrient loss, maintains short dense vegetation and destroys *Betula* seed (see Chapter 1). Regular burning therefore resets the system within its basin of attraction, after its endogenous movement towards the vulnerable degenerate state. Infrequent burning events, however, are likely to initiate invasion as dwarf shrub rootstocks are destroyed and large quantities of nutrients are released (Bullock & Webb 1995; Clément & Touffet 1990; Allchin 1997), P for instance, can increase up to 60 times in the litter layer after burning (Allchin 1997). *Betula* spp. are also likely to be the superior competitors in the post-burn environment and so if seed rain is non-limiting then invasion is likely. These conclusions echo those of Gong & Gimingham (1984) who stated that: "Carefully controlled management of *Calluna* by regular burning can prevent the entry of birch even where seed is abundant but occasional fires followed by poor *Calluna* regeneration may promote it".

Outbreaks of heater beetles (*Lochmaea suturalis*) are likely to have similar effects to severe burning events in that vegetation is destroyed and large quantities of nutrients are released (Brunstig & Heil 1985) additional benefits to invading colonists may come from the physical protection from herbivores and abiotic stress that is provided by the dead stems.

GRAZING

Grazing is likely to affect shifts to *Betula* scrub not only through direct suppression and predation but also through its impacts upon nutrient cycling and vegetation physiognomy. Direct effects of heathland grazing appear to be specific to the species, context and temporal distribution of the herbivores (Bullock & Pakeman 1997; Chapter 1) and it is likely that their ecosystem level effects will be similarly varied.

The effects of herbivorous animals will depend upon the food preferences and behaviour of the animals. Deer and rabbits, as browsers, will have extremely strong direct effects upon scrub colonists when present in high densities (Chapter 3; Bokdam & Gleichman 2000) but may have little influence over the physical environment. Less selective herbivores, e.g. ponies, sheep and cattle, have been seen to feed on *Betula* (Westerhoff 1992; Auld *et al* 1992; Rose *et al.* 1999) but there is apparent disagreement over this (Bokdam & Gleichman 2000, this chapter) and so it would seem likely that they have a smaller direct effect on *Betula* colonists per unit biomass. Profound indirect effects of less selective herbivores may be expressed via the consumption of greater amounts of total biomass, which will play an important role in determining physical structure of the vegetation, rates of nutrient supply and the spatial pattern of the identified determinant factors such as P-availability and vegetation height. It is likely that the spatially aggregated behaviours of free ranging grazing animals (Putman 1986) will increase spatial heterogeneity in the likelihood of transition and strengthen the formation of a mosaic of vegetation states (Olff *et al.* 1999; Vera 2000; Bokdam & Gleichman 2000). Although the net effect of large grazing animals is likely to be a reduction of invasion and a generally stabilising effect on the heathland ecosystem there is likely to be great difficulty in extrapolating the effects of large free-ranging herbivores over extensive areas.

PSC

Although the direct effect of PSC on P availability may be sufficient to explain regional differences in *Betula* invasion (see above) it is its indirect influence through greater P retention that is most likely to explain the correlation between PSC and the likelihood of phase transition that are described by Chapman *et al.* (1989b) (see also Chapter 2). PSC not only affects P retention and availability but also controls the rates of vegetation cycling and organic matter accumulation (Chapman *et al.* 1989a; Chapter 2). Diemont (1994) stated that heathlands based upon soils that are inherently nutrient poor have a low productivity that slows the process of gap formation as a product of the longer lifespan of the ericoids. The build up of organic matter and hence available phosphorus will also be slower where PSC is low. There are several implications of these trends for landscape scale invasion dynamics. The first is that if all other components of the heathland environment are considered equal then there will be a greater proportion of vegetation in the invasable degenerate state after the abandonment of management (Chapter 2) and therefore management aiming hold the vegetation in the non-invasable state, e.g. burning and mowing, will need to be more frequent in high PSC regions. The second major implication of the PSC-vegetation cycling relationship is that slower cycling in low PSC regions increases the probability that a natural or accidental fire will occur during the 'safe' period of the cycle i.e. that in which the fire perturbation is likely to shift the conditions back towards the heath basin of attraction. Severe burn events are particularly likely to cause a shift towards the scrub state in high PSC areas as greater amounts of the released P are likely to be retained within the topsoil (Chapter 2).

As there has been no *direct* experimental test, I therefore provisionally conclude that PSC (which is itself determined by small variations in bedrock Fe and Al content) controls the likelihood of phase-transition between heath and *Betula* scrub ecosystem states at the landscape scale. Any effects of PSC are likely to interact with management regimes to determine the scale of scrub invasion within regions. This is best exemplified by the widespread invasion of the Surrey heaths that is described by Harrison (1976). The possibility of earlier abandonment than that of many heath areas (Webb & Haskins 1980; Rackham 1986) and a lack of fire management, due to the proximity of most heaths to residential areas, appear to have interacted with the high PSC of the region (Chapman *et al.* 1989b) to result in widespread invasion. This invasion, by increasing the propagule density of the region further increases the likelihood of transition to scrub in the remaining heath. Dorset, by contrast, is typified by low PSC (Chapman *et al.* 1989b), a later abandonment, more intensive management and therefore slower rates of invasion (Rose *et al.* 1999). Large deer populations may also have strengthened these stabilising interactions.

Petraitis & Latham (1999) present two models of vegetation state shifts, one in which the foundation species of the state enters, alters and out competes that of the original state in a constant process and a second in which disturbance allows for the rapid transition to the alternate state. The synopsis of new findings and published research presented here suggests that *Betula* is likely to achieve dominance through both mechanisms. The first through the invasion of degenerate heath vegetation and the exclusion of dwarf shrubs that is described by Hester *et al.* 1991a, b, c) and the second through disturbances such as high intensity fire and beetle outbreak. This appears to suggest that perturbation is not, as is often suggested (e.g. Scheffer *et al.* 2001), an essential pre-requisite of state shifts.

The major flaw that places doubt over these conclusions is that they are, in the main, extrapolated from small-scale studies of a single heath community type; experimentally manipulated plots of the M16 community of the National Vegetation Classification. Although the intermediacy of the M16 community between wet and dry heath communities is likely to increase its generality previous research has suggested that wet and dry heath sites differ in their community responses to inorganic nutrient availability (Heil & Diemont 1983; Aerts & Berendse 1988). The conclusions drawn from the experiments and derived models may also lack relevance to communities where alternative growth forms are present e.g. bracken patches or where previously unrecognised factors operate significantly.

Wide ranges of conditions were present in the experiments but it is important to know which of these conditions occur in unmanipulated heathland environments and whether they typically vary over the critical ranges identified by the fitted model. Study of variation in both seedling densities and the identified determinants over larger spatial scales and therefore community types will allow for both an initial test of the fitted statistical model and an evaluation of which variables are likely to contribute to observed heterogeneity in scrub invasion over a variety of spatial scales.

Chapter 5: Spatial heterogeneity in the determinants of a heath-scrub phase transition

Abstract

1. The invasion of *Betula* spp. represents the threshold at which transition between dwarf shrub and scrub ecosystem states occurs. The phase-transitional area of the threshold has previously been described with a statistical model derived from experimental data taken from wet heath communities. This model describes *Betula* seedling densities as a function of 6 'determinant' factors: biomass density, necromass density, mean vegetation height, P-availability, soil water content and seed bank density. The relevance of this model to a wider range of heathland environments and the natural extent, pattern and magnitude of variation in these variables remains unknown.
2. Both model testing and exploration of spatial heterogeneity were conducted using data collected from two, 130-point, regular sampling grids, each covering 5ha. The proposed determinants and *Betula* seedling densities were measured at each point.
3. Low model predictions and observed densities precluded formal model testing but predictions were qualitatively accurate. Total predicted and actual seedling densities at the two sites were 0.10m^{-2} (SE ± 0.02) and 0.11m^{-2} (SE ±0.05) at the Surrey site and 0.07m^{-2} (SE ±0.01) and 0.00m^{-2} (SE ±0.00) respectively.
4. Spatial heterogeneity in the determinant factors, which was assessed using variogram estimation and ordinary kriging interpolation, found that the nature of heterogeneity in the determinant factors varied between variables and sites. The two most salient trends were the tendency of edaphic factors and seedbank densities to display strong, positive autocorrelation over short distances (<50m) and the presence of autocorrelation that extended beyond the maximum range of the study sites (>150m) in the vegetation variables. This latter trend resulted in single across-site gradients, the former small distinct patches. Nugget variance i.e. that which occurred at distances lower than the minimum spatial lag (<17.6m) was high for many variables suggesting that much of the variation in the proposed determinants was not spatially structured at the patch scale.
5. The relative contributions of each of the determinant factors to within-site heterogeneity in predicted seedling densities was assessed by varying each of the measured variables over their full and interquartile ranges while the other variables were held constant and then subtracting maximum from minimum estimates. The estimated relative contribution

of the determinants to within-site heterogeneity varied greatly between sites, as did their mean values, suggesting that the nature of the processes underlying recruitment limitation was site specific at the patch scale.

6. It is suggested that easily identifiable spatial autocorrelation in the determinant factors (e.g. patches of mature trees and gradients in vegetation density) allows for the targeting of regions with a high probability of transition by heathland managers thus reducing required management intensities. Management techniques based upon the spatial de-coupling of *Betula* seed and safe-sites are proposed as a means of promoting heathland stability.

Introduction

Widespread invasion of woody plants into non-forested areas generates a phase transition between alternate ecosystem states that differ in ecosystem function and community composition (Scheffer *et al.* 2001; Petraitis & Latham 1999; Loehle *et al.* 1996; Laycock 1991). These tree species often act as the foundation of the woodland or scrub ecosystem state with their effects on the physical environment facilitating the invasion of associated species (Chapin *et al.* 1997; Wilson & Agnew 1992; Petraitis & Latham 1999; Jones *et al.* 1997; Hester *et al.* 1991a,b.c). Such invasions are often considered deleterious to the conservation of 'early successional' ecosystem types e.g. grasslands and heathlands, as restoration to the original, non-wooded, state is often difficult, expensive and sub-optimal (Carpenter 2001; Costello *et al.* 2000; Mitchell *et al.* 1999; Mitchell *et al.* 2000; Auld *et al.* 1992).

Transition to scrub and woodland systems is often, at least in the initial stages and at smaller spatial scales, patchy in nature (Bazzaz 1996; Milne *et al.* 1996), implying that there are spatially structured differences in either propagule availability or invasibility of the non-wooded system. These factors may be thought of as equivalent, at small spatial scales, to the safe-site and seed limitations of plant recruitment (Eriksson & Ehrlén 1992; Turnbull *et al.* 2000). Plant ecologists have long studied the determinants of recruitment in colonising tree populations (e.g. Li & Wilson 1998; Terwillinger & Pastor 1999; Burton & Bazzaz 1991). There have been, however, a limited number of studies (e.g. Gross *et al.* 1995) of the spatial pattern, extent and magnitude of variation in these factors and none which discusses the consequences that these may have in explaining heterogeneity in phase transition at patch and landscape scales. There has also been little discussion of the implications of spatial heterogeneity in recruitment limitation factors in habitat management strategies aiming to prevent woody plant invasion.

The invasion of *Betula* spp. (both *B.pubescens* (Ehrh.) and *B.pendula* (Roth)) represents the moment of transition between lowland heath and scrub ecosystem states, with significant transformations in both community structure and ecosystem function occurring within periods as short as 25 years (Satchell 1980a,b). The *Betula* scrub state is highly resistant to restoration efforts, effective restoration being both labour intensive and expensive (Mitchell *et al.* 1999; Auld *et al.* 1992). This invasion displays both within and between regional differences in its magnitude (Nolan 2000; Chapman *et al.* 1989b), a patchiness that can also be observed at the within-patch scale (0-5ha) (personal observation). A multi-site, multi-factorial field experiment situated parallel to existing *Betula* populations found that both seed and safe-site factors could limit *Betula* colonisation with vegetation height, vegetation density and phosphorus availability being identified as potentially important determinants of the *Betula* safe-site (Chapter 3; Chapter 4). A statistical model fitted to data from these experiments was able to account for 58.9% of the deviance in *Betula* seedling densities (which were assumed to be indicative of the likelihood of transition) and identified the above factors, necromass density, seedbank density, and soil water content as significant descriptor variables. There were also numerous interaction effects between these factors, particularly between vegetation factors and seedbank density. A major uncertainty associated with these conclusions is that the model was derived from experimentally manipulated plots of a single community type (the wet heath M16 community of the National Vegetation Classification (Rodwell 1992)) and so may be unrepresentative of a wider range of environments with respect to both the identity of the determinant factors and the form of the fitted relationships. If the models predictions do hold for a wider range of environments then it is important to know the extent, scale and pattern of variation in the identified determinants in typical heathland conditions and whether this variance occurs over the critical ranges that control densities; a large measured response of *Betula* over a wide range of experimentally manipulated conditions means little if this range does not occur in nature. Such an evaluation allows us to assess which factors are controlling heterogeneity in seedling densities at larger scales of study, and their relative contributions to this variation.

The research presented in this chapter comprised two closely linked studies. In the first data, equivalent to that used in the formulation of the model and sampled on a regular grid at two 5ha heathland sites, is used in an attempt to validate the model presented in Chapter 4. The second study uses the same data in an examination of the pattern, extent and magnitude of spatial variation in the previously identified determinant factors at within and between-patch scales. This was achieved using geostatistical tools (variogram estimation and kriging). The intention of these studies was to form a bridge in understanding between the small-scale experimental findings presented in Chapters 2-4 and the landscape scale patterns of transition to *Betula* scrub described by Chapman *et al.* (1989b), Harrison (1976) and Rose *et al.* (1999). The results of these studies are discussed with reference to the spatial pattern of ecological phase transitions and the management of heathland ecosystems. In this latter section the ecological understanding of lowland heath to *Betula* scrub shifts is synthesised and applied to provide suggestions of how management may be adapted to prevent *Betula* invasion whilst maintaining the populations of the characteristic species of heathland ecosystems.

Methods

STUDY SITES AND SAMPLING REGIME

Spatial heterogeneity in the factors identified as determinants of invasion in the combined-site statistical model (Chapter 4) was studied at heath patches within the Surrey and Dorset heath regions. Although the differences have not been directly quantified there is considerable anecdotal evidence, and it is readily observable that the invasion of *Betula* is infrequent and patchy on the Dorset heaths but relatively extensive and uniform in Surrey (Harrison 1976; Chapman *et al.* 1989b; Rose *et al.* 1999; Webb 1990; Rackham 1986; Nolan 2000). The sites are believed to be in many ways representative of their region and were also selected for their size and lack of fragmentation.

The basic sampling grid (Fig 5.1) consisted of 30 points spaced at 50m in a 5 x 6 arrangement of posts producing a 4 x 5 arrangement of 'cells'. In the centre of each 50m x 50m cell there was another sampling point, yet more sampling points were found between the central and corner points of each cell. This arrangement produced a regularly spaced grid of 130 sampling points with a fairly even spread of distance lags between 17.6m and 250m. The rationale for using this distance matrix is that smaller scale variation is effectively stochastic from the perspective of patch scale dynamics and ecosystem management while larger scale patterns are irrelevant to many heathland fragments, which are often very small. Webb & Haskins (1980), for example, found that 89% of the Dorset heath patches were <10ha). This pattern also gives a good coverage of the study area i.e. most areas are represented. Each study site covered an area of 250m x 200m (5ha). The variables examined were the same as those that were identified as descriptors of *Betula* seedling densities in a statistical model fitted to a large set of experimental data of a multi-site origin (see introduction and Chapter 4). The variables were recorded using the same standard procedures that are given in Chapters 2, 3 and 4 unless stated. Data were collected over a period of 1.5 years as logistical problems made a single intensive recording period impossible.

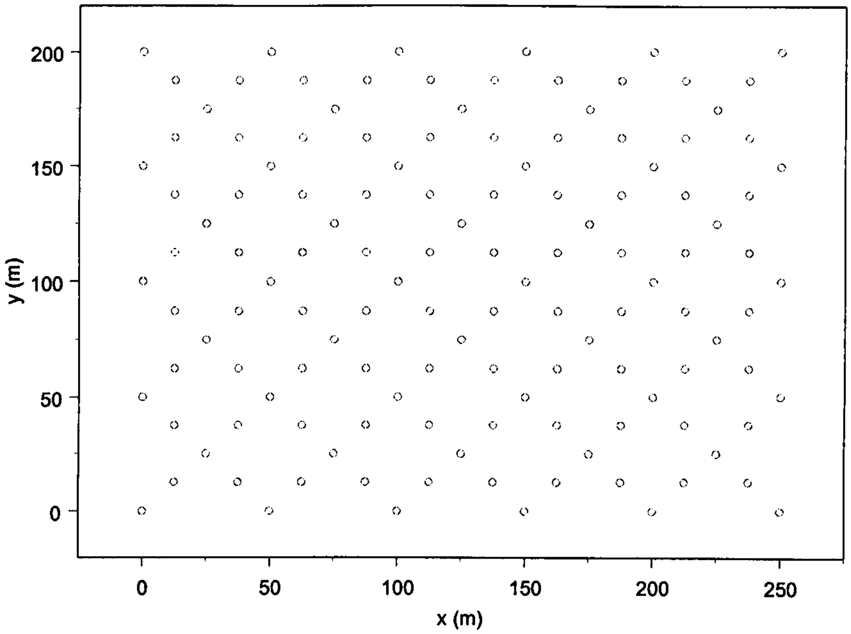


Fig 5.1. Spatial arrangement of sampling points at the Surrey and Dorset spatial sites.

SITE 1: ARNE HEATH, DORSET

This is an area of largely uninvaded heath located between Poole Harbour and the plantations of the Arne peninsula (central location national grid ref: SY 968890). The site is dominated by *Calluna vulgaris* (L. (Hull)) but a large patch of *Pteridium aquilinium* ((L.) Khun) occupies its centre. Although most of the vegetation of the site is in the mature and degenerate phases of the dwarf shrub cycle (Watt 1947; Gimingham 1988) it contains shorter vegetation of recolonised mown firebreaks. Wetter areas containing *Erica tetralix* (L.) and *Molinia caerulea* ((L.) Moench) are found in places. The site is bordered by *Betula* scrub on one corner and contains a few scattered *Betula* trees around its perimeter but there is little evidence of seedling stage plants and there has been no scrub clearance in the last 10 years. The site is closed to the public and is not grazed by domestic animals. Although Sika Deer (*Cervus nippon*) can often be seen nearby in large numbers there is little evidence of grazing on the site. The area appears to be undergoing invasion by bracken despite occasional spraying with the herbicide Asulox (last applied in the summer of 2001). Management within this area is of a low intensity and there has been no fire for over 30 years with the exception of a small patch in the corner of the study area, which was cut in November 1997 and burnt in March 1998. In contrast to the Horsell Common site the sampling grid here was permanently fixed. The ecological history of the Arne peninsula is discussed in further detail in Chapter 3 and in Pickess *et al.* (1992).

SITE 2: SURREY, HORSELL COMMON

Horsell Common is typical of many Surrey heaths in that traditional management ceased at an early date. Records show that its only commercial uses in 1904 were gravel raising and shooting and so traditional management on the common was abandoned before the Arne site, which was low intensity farmland until 1966. The area was used for military training in WWII, amenity being its only other use in the antecedent and following periods (Mrs P.M Lambert, Horsell Common Preservation Society, personal communication). Both local knowledge and the age structure of the local tree populations indicate that the area has seen extensive invasion by *Pinus sylvestris* and *Betula* spp. in the last 50-100 years.

The study area contains a typical heathland ecosystem with dry, wet and humid heath types (national grid ref: TQ 013612). The dominant species are *C.vulgaris*, *E.tetralix* and *M.caerulea*. The heath is typical of those in the region in that it is unmanaged by burning or domestic grazing, it also displays widespread invasion by scrub species despite non-intensive scrub clearance and heather cropping since 1972. Fire management has been avoided because of the proximity to housing but a fire did occur at one end of the site in 1970. Some areas of the site cover regions of recent scrub removal (*Pinus sylvestris* and *Betula* spp.) while others are overlain with young trees or display the evidence of resprouting cut *Betula*. Many of the managed areas have an incomplete plant cover and are covered more by mosses than vascular plants. The public uses the area intensively, predominantly for dog walking but also horse riding and cycling. This use has carved a number of footpaths into the site, and there is evidence of the eutrophication caused by litter and dog faeces that is described by Shaw *et al.* (1995) along the sides of these. The site was expected to have a high seedbank density of *Betula* spp. as mature trees are found abundantly along its perimeter.

VEGETATION COMPOSITION AND STRUCTURE

Vegetation was recorded using the same point quadrat procedure that was used for the experimental plot surveys that are described in Chapter 3. However, the density of points was lower: 2 x 9 points per plot. The data collected therefore covered the same area as the experimental plots (2 x 1m) but with half the number of samples within it. All seedling stage *Betula* (both *B.pendula* (Roth) and *B.pubescens* (Ehrh)) within the quadrats were surveyed according to the method given in Chapter 3. The positioning of the quadrats was standardised by placing the quadrat directly to the north of the sampling point. Vegetation surveys were conducted between the 29th June and the 15th July 2000 at the Dorset site and the 14th June and the 2nd July 2001 at the Surrey site.

EDAPHIC CONDITIONS

Soil sampling at the Dorset site was conducted between the 21st and 25th of November 1999, at the Surrey site it was conducted between 26th of November and the 3rd of December 1999. Samples were analysed for pH, soil organic matter content (SOM) (% dry mass) and soil water content (% total mass) for both the 0-50mm and 50-150mm depths and for P availability (P_{ox} μg P g^{-1}) at the 0-50mm depth (methods can be found in Chapter 2). Seedbank samples were taken at the Surrey site between the 28th February and the 2nd of March 2000 and between the 22nd and 25th of February 2000 at the Dorset site. Seedbank estimation was conducted using the same methods and in the same conditions as the experimental site samples (see Chapter 4), i.e. samples from the spatial and experimental sites were mixed together in a random order.

ANALYSIS

MODEL VALIDATION

An estimation of the experimental data, and therefore the combined site models', representation of typical heath conditions was achieved through univariate and multivariate (Principal components analysis (PCA)) comparisons of the 'determinant factor' data. The relevance of the combined-site model of the experimental sites (presented in Chapter 4) to a wider range of heathland conditions was tested by placing the 'determinant factor' data of the spatial sites within the fitted model to acquire predicted values that could be compared with actual seedling density values. As the location of both sites is within 2 kilometres of their respective experimental sites, there is the possibility of bias towards agreement with the combined-site model. The model was derived from seedlings of a single age (approximately one-year-old) so cannot be expected to predict numbers of more mature seedlings but merely the number of recruits (m^{-2}) from the previous year that have survived. It was for this reason that all *Betula* seedlings in the cotyledon stage or with stem diameters ≥ 3.5mm were excluded from the measurements of actual seedling densities at the two sites. Observations from the experiments (see Chapters 3 & 4) showed that even highly favourable growth conditions were unlikely to result in seedling sizes in excess of this size within a single year. At the Surrey site six plots were removed from the analysis. These represented scrub invaded conditions in which transition had already occurred i.e. with a dense wooded canopy overhead.

VARIOGRAM FITTING AND KRIGING INTERPOLATION

The pattern, extent and magnitude of within-patch heterogeneity were explored with standard geostatistical tools: variogram estimation and kriging interpolation (Mc Bratney & Webster 1986; Robertson 1987). An introduction to geostatistics and the methods used here can be found in Chapter 3 and in Burrough (1995). An initial inspection of the data from both sites found that anisotropy (directional dependence in spatial autocorrelation), if present, was weak and so it was thought that the assumption of isotropy (a constant trend of autocorrelation over the surface) had been met. The estimated variograms were therefore ommnidirectional, with the restriction of each lag estimate being based upon a minimum of 30 distance pairs.

Variogram models were fitted to empirical variogram data for all measured variables and the predicted seedling density values within the spatial extension module of S+6 for Windows (Insightful). The three standard variogram models in which both range and sill values can be estimated: spherical, exponential and Gaussian models, (see McBratney and Webster (1986)) were fitted using weighted non-linear least squares and the model with the minimum residual sum of squares (objective) was selected. The goodness of fit of each of the models was compared with a linear null model with a slope of zero and an intercept value equal to the estimate of overall population variance. Fitted variogram models were subsequently used in ordinary kriging, which was again, computed in S+6 for Windows. A kriged grid of 900 (30 x 30) estimates and their standard errors was computed for each variable.

The necessity of using variograms of asymptotic form in kriging interpolation meant that many models were fitted with range and sill values that were far greater than those of the study area and population variance respectively. The resulting estimates of spatially structured variance (calculated as $1-(\gamma(0)/C)$, see Chapter 3) that were taken from these fitted variogram models have little relevance as much of the supposed spatially structured variance was assumed from extrapolation of existing trends.

Overall between site-differences in the mean values of the determinant factors were assessed using t-tests and, where appropriate, analysis of deviance with a log link function and Poisson errors.

DETERMINANTS OF WITHIN PATCH HETEROGENEITY

The relative impact on within-patch heterogeneity of each of the determinant factors at the two spatial sites was coarsely estimated by varying each of the determinant variables over its full and interquartile range while the other variables in the model were held constant at their mean. The difference between the maximum and minimum predicted values was then calculated. Drawbacks of this approach are that it does not take into account the interactions between the variables and that the operation of the determinant factors is assumed to be equal to that of the experimental sites.

A number of data were removed from the Surrey site set when calculating empirical variograms and other summary statistics. This was due to both *a priori* reasoning (i.e. plots coinciding with mature *Betula* and footpaths were removed) and the loss of two soil samples during sampling and analysis. The maximum number of data removed was 18 but this depended on the variable in question.

Results

Univariate examination of the proposed determinants of *Betula* invasion revealed that many conditions of the spatial sites varied over larger, or different ranges than those of the experimental sites (Fig 5.2a-f). Two of the six variables were adequately described by the experimental plot data i.e. the mean, range and deviation of values was approximately equal at both the experimental and spatial sites. Seed bank densities and phosphorus availabilities were, in the main, far greater within the experimental plots than at the spatial sites (Seed bank (m^{-2}): Dorset = 1.81 ±4.85, Surrey = 74.4 ±230.7, Experimental = 207.6 ±193.7; P_{ox} (μg g^{-1}): Dorset = 48.4 ±24.7, Surrey = 45.2 ±11.7, Experimental = 218.7 ±133.8. Soil water content was also greater within the experimental plots, with most plots of the spatial sites being considerably drier (Soil water content (% total mass): Dorset = 55.7 ±12.3, Surrey = 45.0 ±10.9, Experimental = 67.8 ±4.4). Mean vegetation height, however, was greater at the spatial sites, particularly at the Dorset site where the presence of tall, mature-phase, *Calluna* communities and patches of Bracken (*Pteridium aquilinum*) raised mean values considerably (Mean vegetation height (cm): Dorset =17.03 ±5.50, Surrey =14.4 ±5.47, Experimental =10.64 ±2.99).

Multivariate analysis (PCA) of the combined, unit scaled, data from both the experimental and spatial sites (Table 5.1, Fig 5.3a & b) found similar trends to the univariate analysis in that the conditions of the sites displayed some overlap but also a large degree of differentiation on the first component (which accounted for 36% of the variance). The first component distinguished between the wet, high P, high seed experimental plots and the taller, low P, low seedbank, dry conditions of the spatial site plots. These latter conditions, as mentioned above, were not present within the experimental plots. Components 2-4, which cumulatively accounted for 50% of the variance, made no clear distinction between the plots of the experimental and spatial sites indicating that these represented gradients that were found within both the spatial site and experimental data. The problem that these between-site differences reveal is that the predicted values used in model validification are, to a certain extent, based upon extrapolations of the fitted model relationships or derived from areas of multidimensional numerical space that are poorly represented by the experimental data.

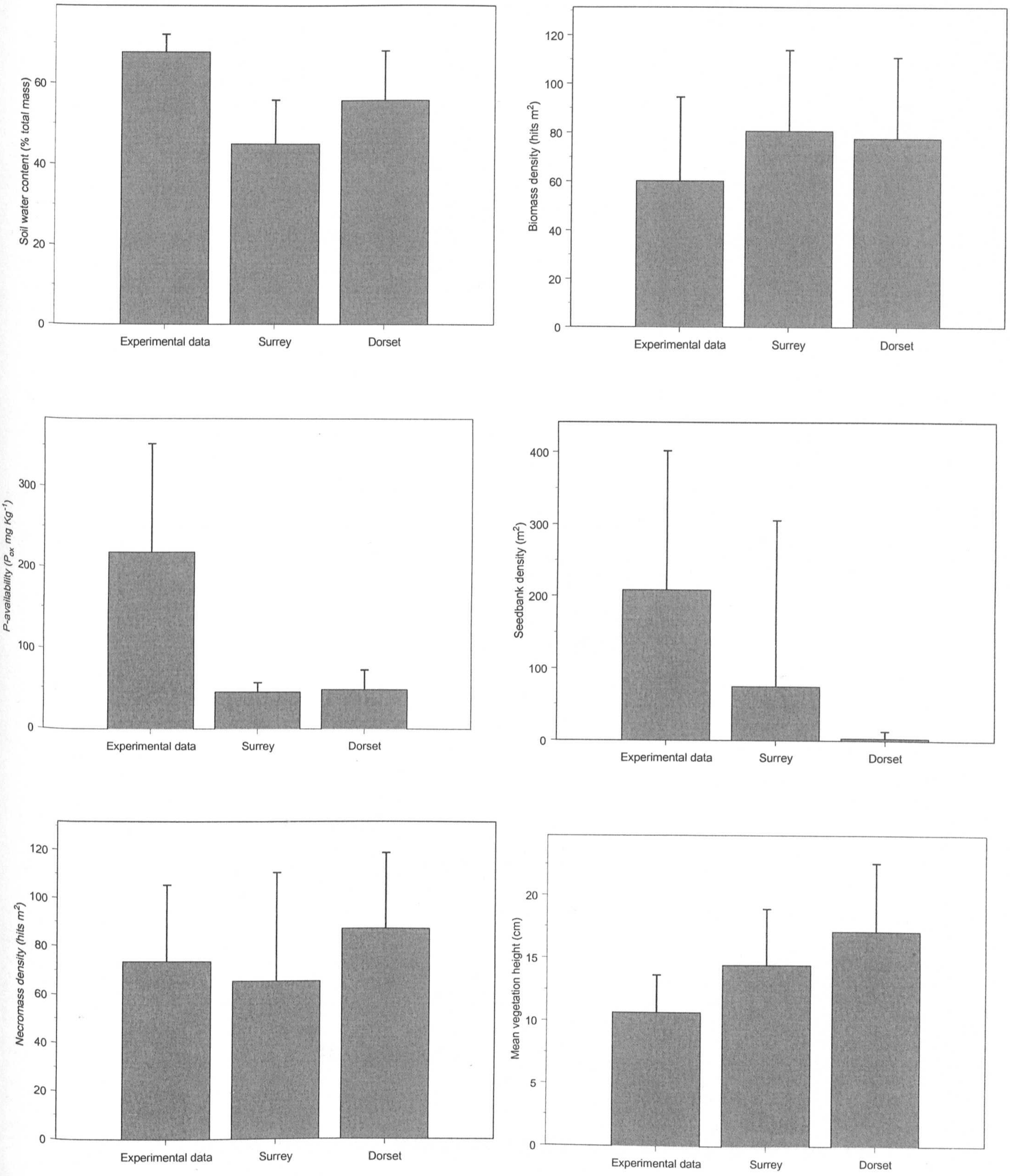
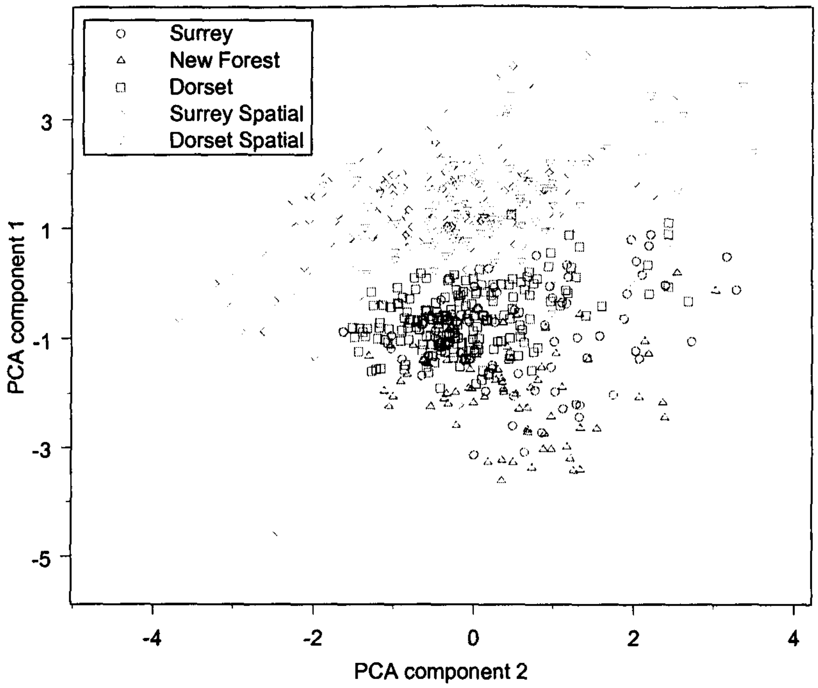


Fig 5.2 Univariate description of the proposed determinants at the spatial and experimental sites. Error bars represent ±1 standard deviation.



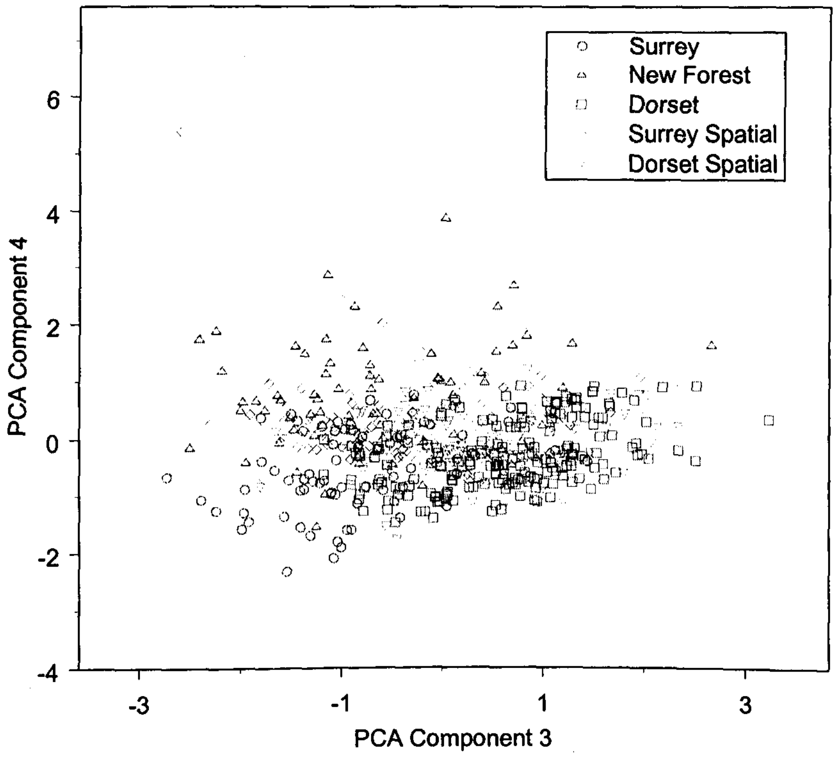


Fig 5.3. Principal components analysis of the data from the spatial sites and the 3 experimental sites: Surrey, New Forest and Dorset, from which the combined-site model was derived. All variables identified as significant in the combined-site model (Chapter 4) were included in the analysis

Table 5.1. Loadings and explained variance of PCA components 1-4 from the ordination of experimental and spatial site data. Loadings ≤±0.10 are not shown.

	Component 1	**Component 2**	**Component 3**	**Component 4**
Biomass density (hits m^{-2})	0.313	0.500	-0.574	
Necromass density (hits (m^{-2})	0.116	0.544	0.652	0.358
Mean vegetation height (cm)	0.511	0.371		-0.112
P-availability (P_{ox} µg g^{-1})	-0.471	0.364	-0.320	-0.328
Soil water content (% total mass)	-0.455	0.411	0.264	-0.394
Seedbank density (m^{-2})	-0.445	0.116	-0.258	0.768
Explained Variance (proportion)	**0.36**	**0.19**	**0.19**	**0.12**
Explained variance (cumulative proportion)	**0.36**	**0.55**	**0.74**	**0.86**

MODEL VALIDATION

Low seedling densities at both spatial sites precluded formal testing of the accuracy of model predictions. Most predictions were for densities $<0.3m^{-2}$ but the minimum actual figure was $0.5m^{-2}$; a consequence of quadrat size. Mean and total densities were compared so that a coarse estimate of model accuracy could be calculated. Despite the requirement to extrapolate from the fitted responses (see above), the model fits were generally good approximations of actual seedling densities, with predictions being reasonably accurate and correct about which site would have the greater seedling densities.

The mean predicted seedling density of the Surrey site was $0.10m^{-2}$ (SE±0.02), the mean actual seedling density was $0.11m^{-2}$ (SE±0.05). It would be expected, from the predicted values, that seedlings, when present, would be found singly (actual density $0.5m^{-2}$) but this was not the case at the Surrey site, with seedlings displaying far more aggregation than would be expected. These findings concur with previous conclusions (Chapter 4) that seedling densities in generally uninvasible conditions are broadly predictable but effectively stochastic at smaller scales; there was considerable overdispersion around the lower predicted values of the original fitted model (Chapter 4).

At the Dorset site the mean predicted seedling density was 0.07m^{-2} (SE±0.01) and the mean actual density was 0.00m^{-2} (SE±0.00) i.e. there were no seedlings in any of the plots. Seedling densities were therefore slightly overestimated at this site. This may have occurred as a result of erroneous extrapolation (e.g. an underestimation of seed limitation or overestimates of invasion in drier soils) or the operation of an important limiting factor that may not have been included or recognised by the approach detailed in Chapters 2-4 (e.g. mycorrhiza, nitrogen, herbivory).

The failure, on the part of the data, to be able to demonstrate accurate positive predictions on this occasion means that further testing and refinement is required before the model is truly validated. What does appear to be true is that the model can predict where invasion does not occur; model predictions were broadly correct in predicting low densities at both sites. The model is therefore likely to be useful in formulating general, non-quantitative predictions that are of use to managers.

WITHIN PATCH HETEROGENEITY

Projections of within-site spatial variation in the determinant factors provided by the geostatistical analyses revealed that some of the determinants e.g. phosphorus availability, had a small scale patchiness of around 50m, while others, like biomass density displayed non patchy and extensive continuous trends (Fig 5.4 a-f, Tables 5.2 and 5.3). The size of patches (as estimated by the range parameter) and the degree of spatial dependency was found to vary for a single variable between sites and between variables within a single site. There were, however, some salient trends e.g. patchiness in most factors was more distinct at the Dorset site, a probable consequence of its more variable topography, to which much of the observed patchiness conforms (personal observation).

Table 5.2. Key parameters of the variogram models fitted to the data from the Surrey spatial site. Spher = Spherical model, Exp = Exponential model. Gauss = Gaussian model. The last two rows present the mean value of estimates derived from the use of models in kriging interpolation and the mean standard error of these estimates.

SURREY	Seedbank density (m^{-2})	Biomass density (hits m^{-2})	Necromass density (hits m^{-2})	Total vegetation density (hits m^{-2})	Mean vegetation height (cm)	P availability (P_{ox} µg g^{-1}) (0-50mm)	Soil water content (%total mass) (0-50mm)	Soil water content (%total mass) (50-150mm)	pH 50-150mm)	pH (0-50mm)	SOM (0-50mm)	SOM (50-150mm)
Best fit model	Exp	Exp	Gauss	Exp	Spher	Spher	Exp	Exp	Exp	Exp	Exp	Spher
Range (a)	137.48	268819	177.3	4310476	69.31	36.00	22.18	128.9	73.82	413745	1012740	27.69
Sill (C)	48425	4507375	2142.5	47107015	1.75	71.80	82.74	14.30	0	7.07	206635	8.50
Nugget (γ(0))	21661	861.8	1305.6	2497.1	27.19	60.00	34.18	19.31	0.0249	0.0235	79.99	0
Spatially structured covariance 1-(γ(0)/ C)	55.27	99.98	39.06	99.99	93.56	16.43	58.69	85.02	100	99.66	99.96	100
Explained deviance (%) (fitted/null)	76.09	63.63	95.99	88.73	28.2	63.4	82.25	72.1	0	0	78.12	38.25
Mean kriged estimate	73.72	80.56	65.47	146.12	14.39	45.37	45.00	18.79	4.16	4.10	24.79	5.95
Mean SE of estimates	170.67	30.65	37.08	55.56	5.37	10.38	8.80	4.76	0.16	0.16	9.41	2.18

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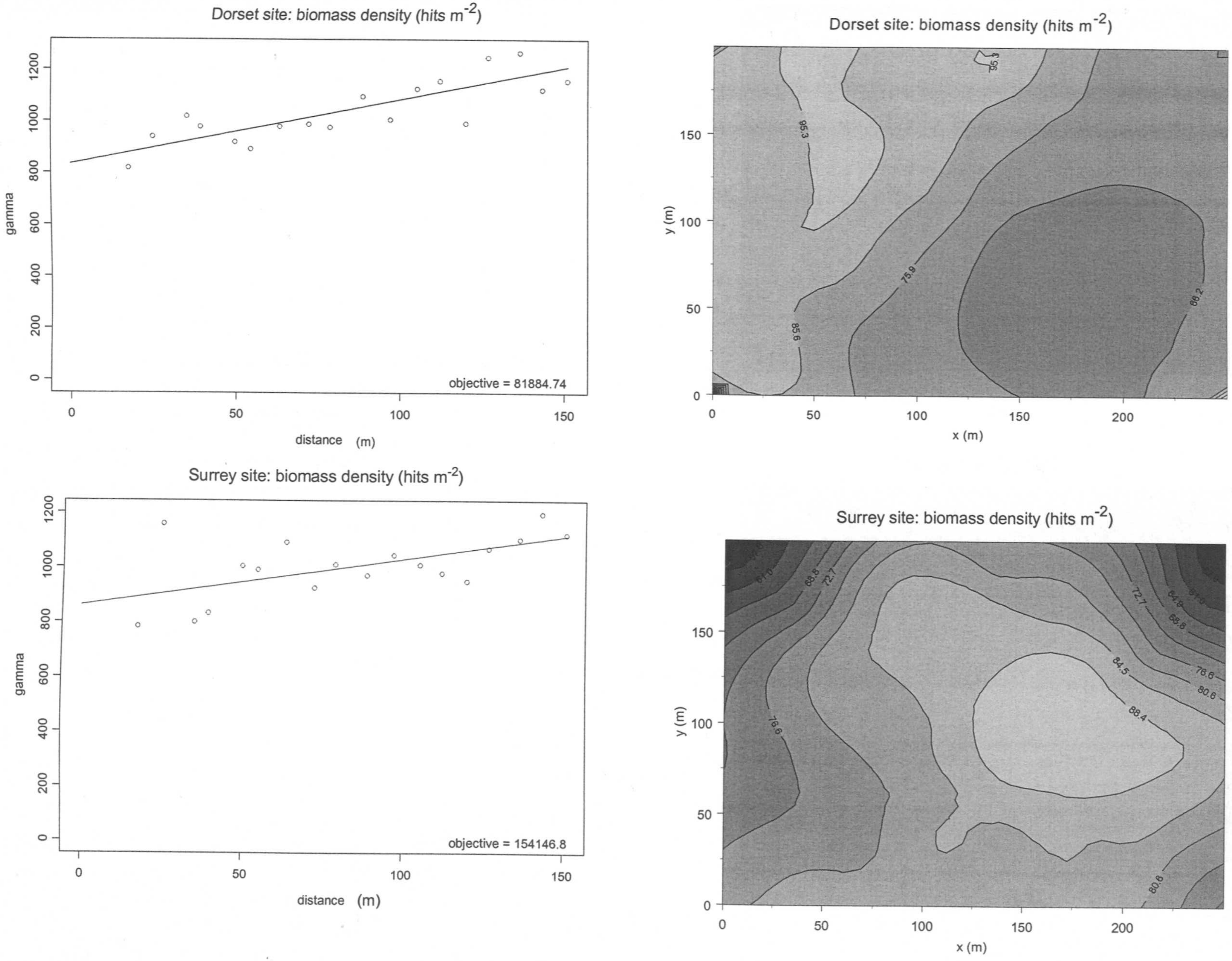
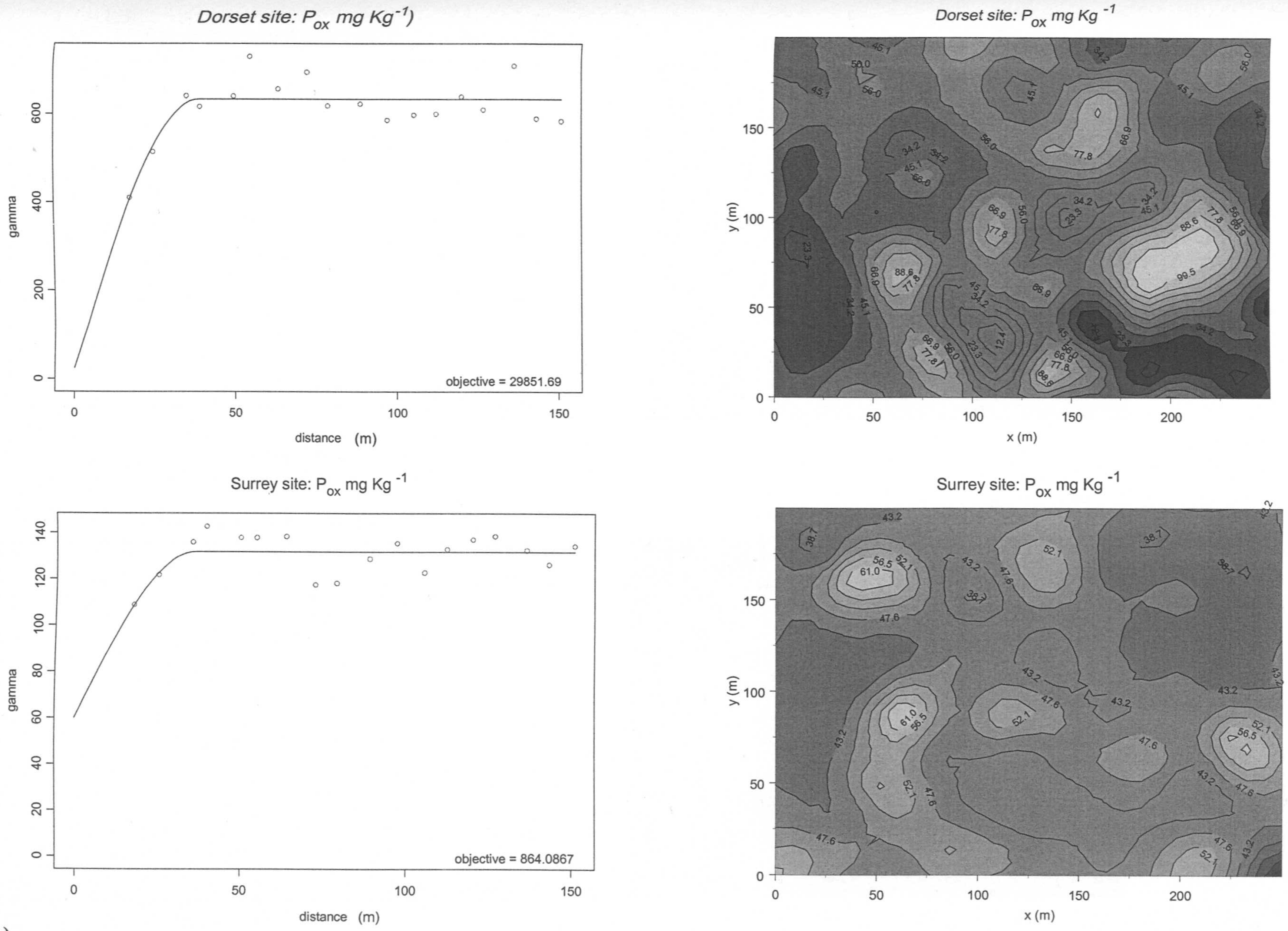
Table 5.3. Key parameters of the variogram models fitted to the data from the Dorset spatial site. Spher = Spherical model, Exp = Exponential model. The last two rows present the mean value of estimates derived from the use of models in kriging interpolation and the mean standard error of these estimates.

DORSET	Seedbank density (m^{-2})	Biomass density (hits m^{-2})	Necromass density (hits m^{-2})	Total vegetation density (hits m^{-2})	Mean vegetation height (cm)	P availability (P_{ox} μg g^{-1}) (0-50mm)	Soil water content (%total mass) (0-50mm)	Soil water content (% total mass) (50-150mm)	pH (0-50mm)	pH (50-150mm)	SOM (0-50mm)	SOM (50-150mm)
Best fit model	Exp	Spher	Exp	Exp	Exp	Spher	Exp	Spher	Exp	Exp	Spher	Spher
Range (a)	1465987	768729	29.36	983455	22.36	39.26	30.98	26.20	14.1	21.76	26.73	49.96
Sill (C)	4438.6	1271846	234.45	3696668	13.15	608.6	81.24	67.57	0.023	0.0289	279.9	0
Nugget ($\gamma(0)$)	0.4927	834.9	738.97	2449	17.87	24.57	66.64	0	0	0.0299	0	37.72
Spatially structured variance $1-(\gamma(0)/C)$	1	1	0.68	1	0.26	0.96	0.18	1	1	0.33	1	1
Explained deviance (%)(fitted/null)	94.00	75.41	75.41	76.53	61.4	65.55	88.50	18.76	100	25.00	33.3	34.6
Mean kriged estimate	0.58	77.57	87.03	163.93	17.04	48.62	55.72	27.35	4.09	4.02	46.4	14.94
Mean SE of estimates	0.76	30.44	29.98	51.93	5.13	16.34	10.28	6.28	0.11	0.22	12.65	6.17


Dorset site: biomass density (hits m^{-2})
gamma
0
200
400
600
800
1000
1200
objective = 81884.74
0
50
100
150
distance (m)
Dorset site: biomass density (hits m^{-2})
y (m)
x (m)
0
50
100
150
200
95.3
85.6
75.9
66.2
Surrey site: biomass density (hits m^{-2})
gamma
objective = 154146.8
distance (m)
Surrey site: biomass density (hits m^{-2})
y (m)
x (m)
61.0
64.9
68.8
72.7
76.6
80.6
84.5
88.4

a)


Dorset site: P_{ox} mg Kg^{-1})
gamma
0
200
400
600
0
50
100
150
distance (m)
objective = 29851.69
Dorset site: P_{ox} mg Kg $^{-1}$
y (m)
x (m)
0
50
100
150
200
23.3
34.2
45.1
56.0
66.9
77.8
88.6
99.5
12.4
Surrey site: P_{ox} mg Kg $^{-1}$
gamma
0
20
40
60
80
100
120
140
distance (m)
objective = 864.0867
Surrey site: P_{ox} mg Kg $^{-1}$
y (m)
x (m)
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47.6
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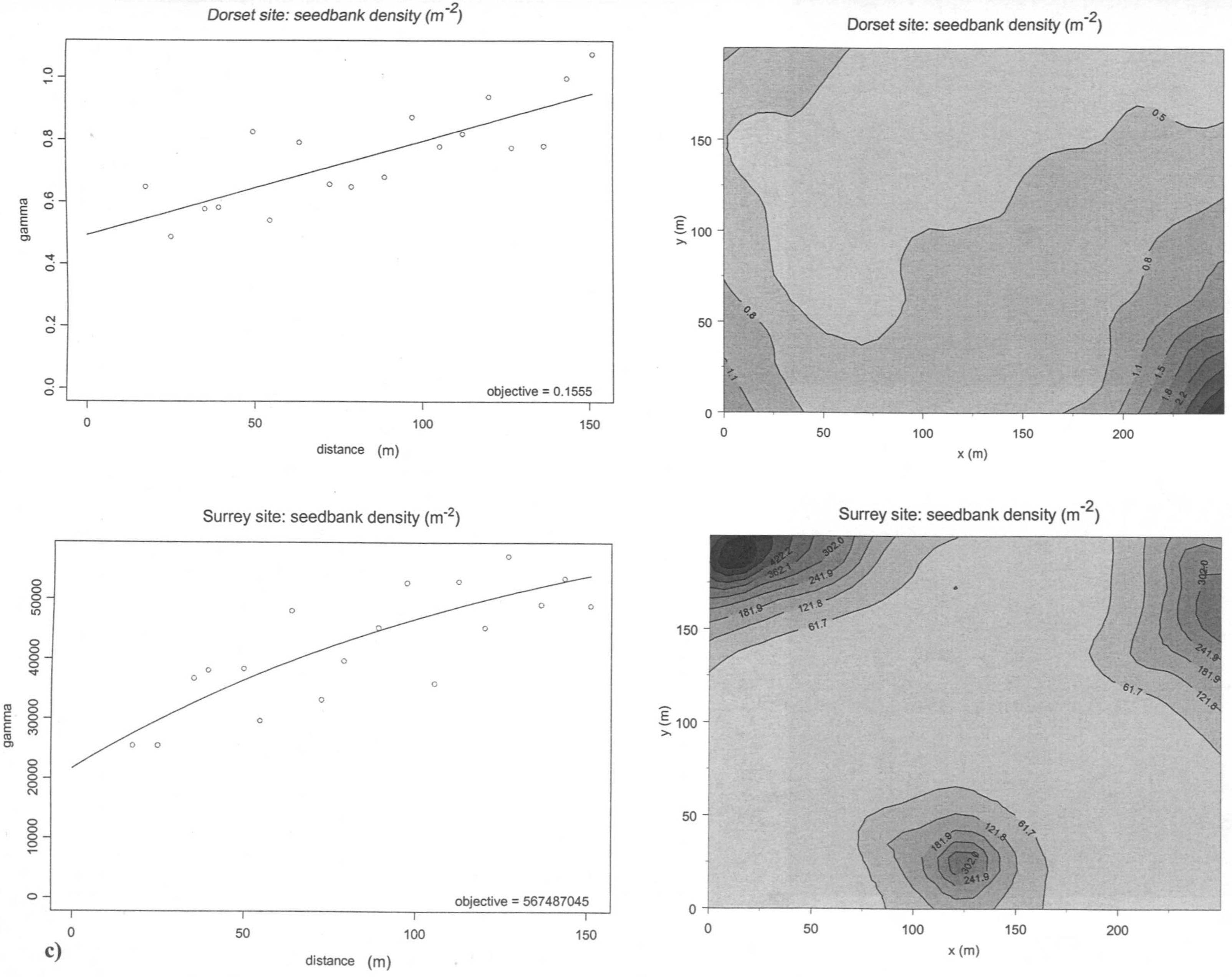
56.5
61.0

b)

Dorset site: seedbank density (m^-2)
gamma
1.0
0.8
0.6
0.4
0.2
0.0
objective = 0.1555
0
50
100
150
distance (m)
Dorset site: seedbank density (m^-2)
y (m)
150
100
50
0
0.5
0.8
1.1
1.5
1.8
2.2
x (m)
200
Surrey site: seedbank density (m^-2)
gamma
50000
40000
30000
20000
10000
0
objective = 567487045
distance (m)
Surrey site: seedbank density (m^-2)
y (m)
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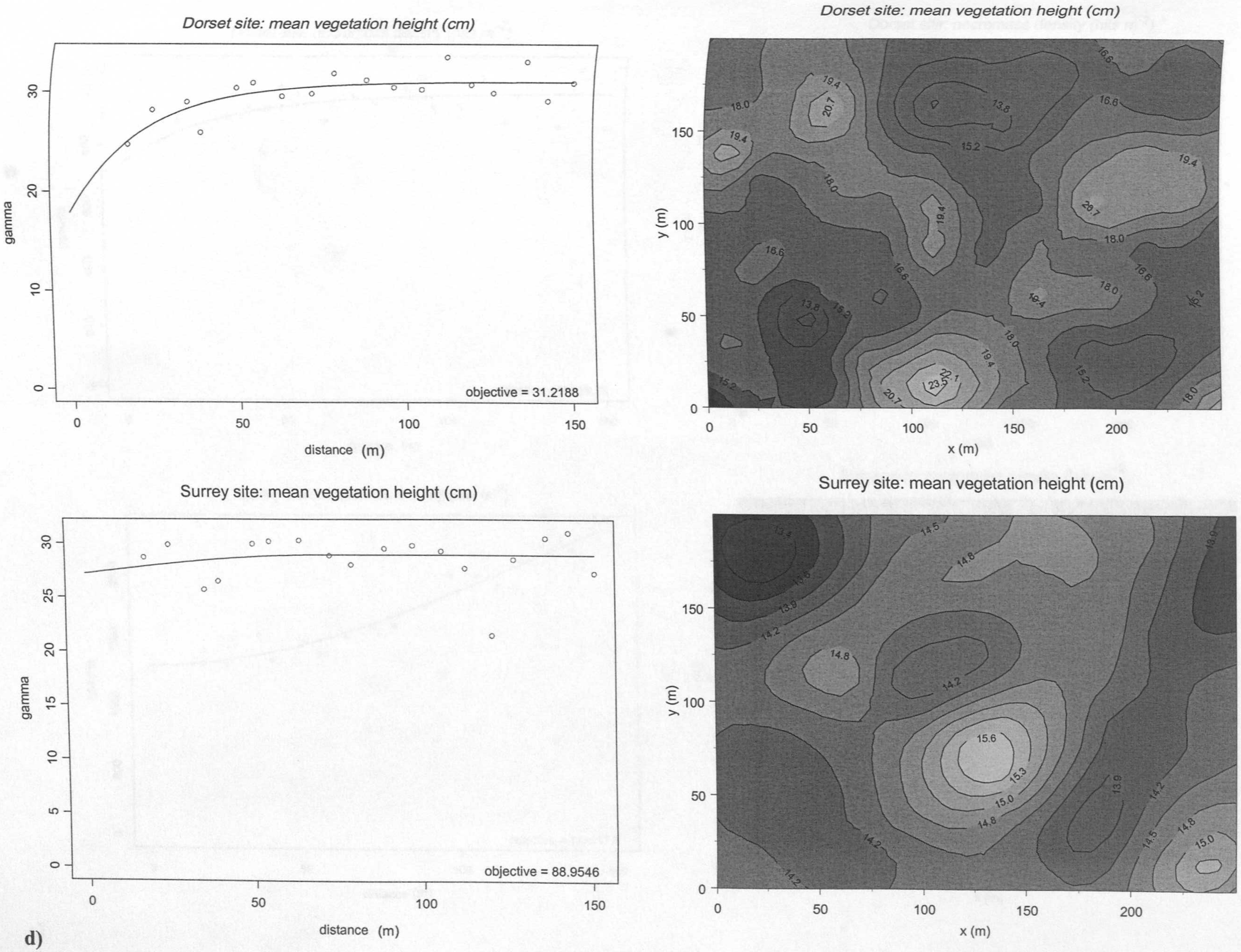
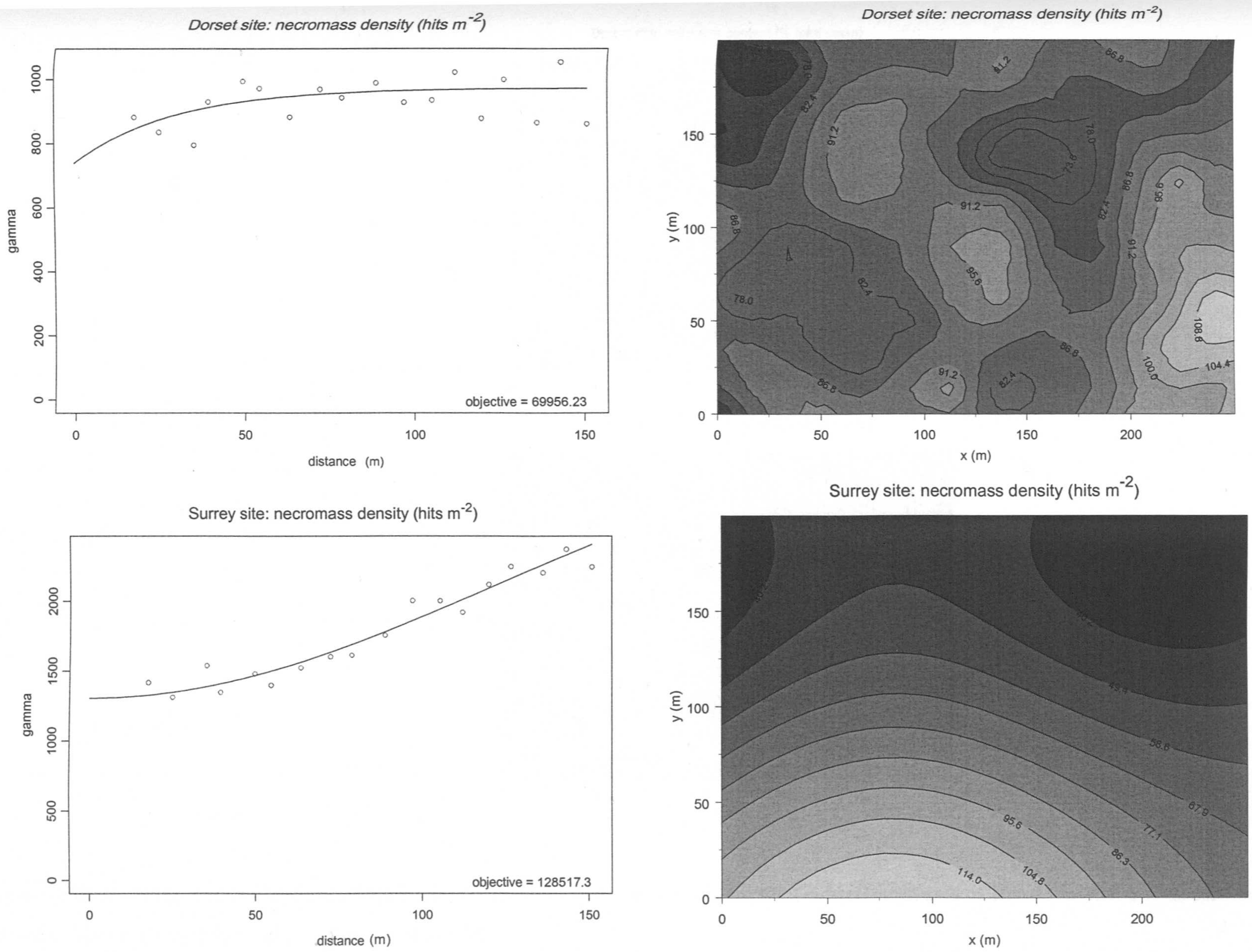
362.1
302.0
241.9
181.9
121.8
61.7
x (m)

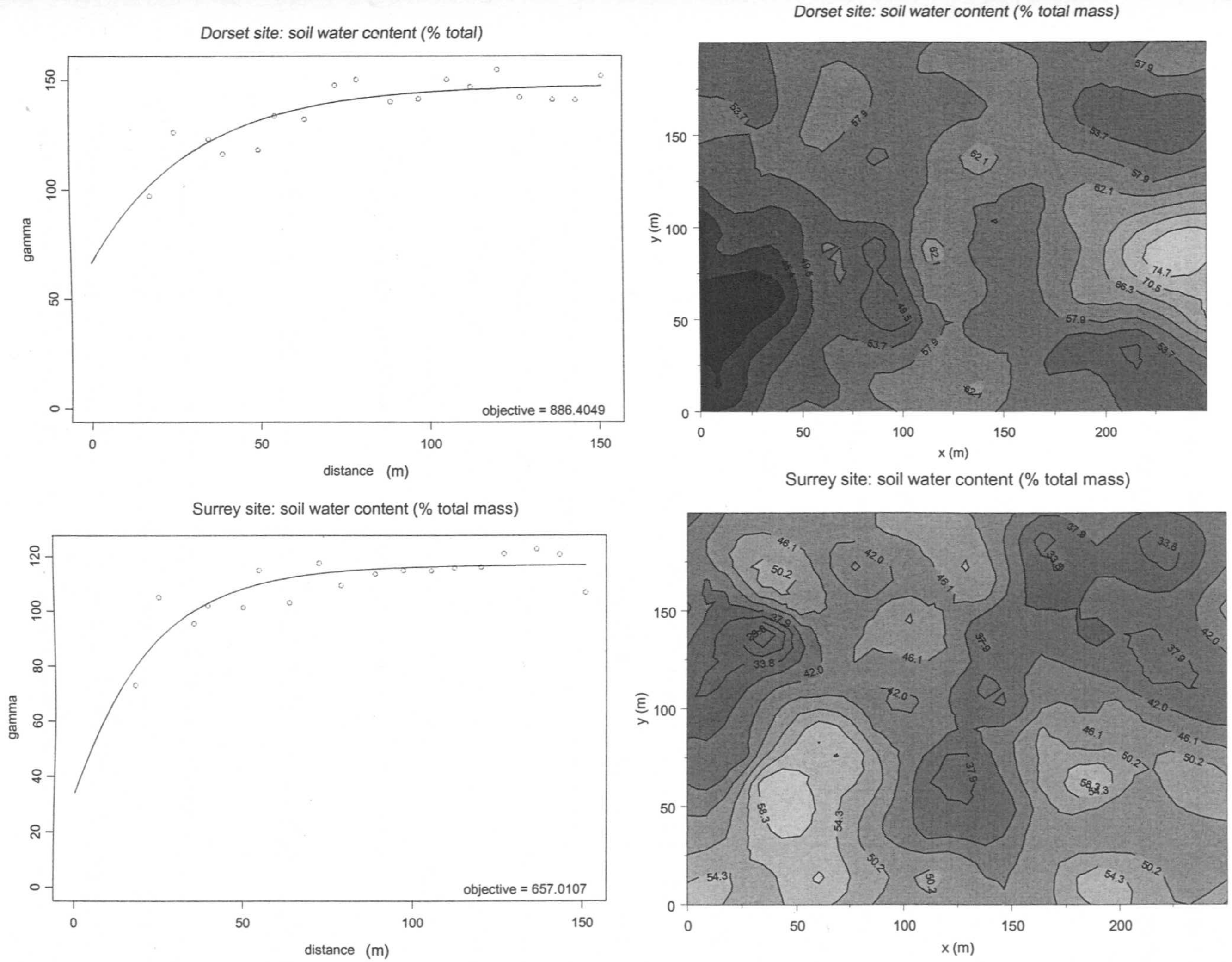
c)

d)


Dorset site: mean vegetation height (cm)
gamma
distance (m)
objective = 31.2188
Dorset site: mean vegetation height (cm)
y (m)
x (m)
13.8
15.2
16.6
18.0
19.4
20.7
22.1
23.5
Surrey site: mean vegetation height (cm)
gamma
distance (m)
objective = 88.9546
Surrey site: mean vegetation height (cm)
y (m)
x (m)
13.4
13.6
13.9
14.2
14.5
14.8
15.0
15.3
15.6


Dorset site: necromass density (hits m^{-2})
gamma
0
200
400
600
800
1000
objective = 69956.23
0
50
100
150
distance (m)
Dorset site: necromass density (hits m^{-2})
y (m)
0
50
100
150
x (m)
0
50
100
150
200
86.8
91.2
82.4
78.0
73.6
95.6
100.0
104.4
108.8
Surrey site: necromass density (hits m^{-2})
gamma
0
500
1000
1500
2000
objective = 128517.3
0
50
100
150
distance (m)
Surrey site: necromass density (hits m^{-2})
y (m)
0
50
100
150
x (m)
0
50
100
150
200
114.0
104.8
95.6
86.3
77.1
67.9
58.6
49.4

e)



f)

Fig 5.4 a-f. Fitted variogram models and kriged output grids for the variables identified as determinants of *Betula* invasion in heathland ecosystems. Gamma = variance, objective = residual SS.

Small-scale patchiness was greatest in the edaphic variables (soil water content and P availability), which displayed distinct patches with radii of c.25m. Vegetation variables (biomass density, necromass density and mean vegetation height) typically had large nugget values i.e. much of the variance occurred at scales below that of the minimum lag size (<17.6m). Spatial trends in the vegetation data (biomass density, necromass density and mean vegetation height) were typically extensive with range values that exceeded the maximum lag size i.e. patches were of a size greater than that of the study area. The large patch size of vegetation variables resulted in clearly identifiable gradients in vegetation properties but within these there was considerable small-scale variation (<17.7m), evinced by the low proportion of within-site variance that was spatially structured (see Fig 5.4). The error on seedbank density estimates was high for both sites but kriged grids displayed patterns that were consistent with the distribution of mature trees (personal observation) and revealed that seedbank densities declined sharply over distances of c.50m, approximately 2-3 times the height of adult trees.

BETWEEN PATCH HETEROGENEITY

Significant differences between the two spatial sites were found to occur in the values of necromass density ($T = 4.45$, *d.f.* = 240, $p = <0.0001$), seedbank density ($F = 27.27$, *d.f.* 240, $p = <0.001$), vegetation height ($T = 3.84$, *d.f.* = 251, $p = <0.001$), and soil water content (0-50mm) ($T = 7.37$, *d.f.* = 240, $p = <0.0001$). There were no significant between-site differences in biomass densities ($T = -0.73$, *d.f.* = 240, $p = >0.05$), and phosphorus availabilities ($T=1.30$, *d.f.* = 240, $p = >0.05$), the latter being likely to result from the neutralising effect of greater SOM content (0-50mm) at the Dorset site and higher PSC at the Surrey site. Mean values and standard deviations of the determinant factors are presented in Fig 5.2. The largest difference between the two sites was in seedbank densities, which were >41 times higher at the Surrey site; an observation which suggests that significant differences in the likelihood of invasion and the factors contributing to it exist at the between-patch scale i.e. some patches are more likely to undergo transition than others.

WITHIN PATCH HETEROGENEITY IN PREDICTED SEEDLING DENSITY

Geostatistical analysis of predicted seedling densities found that there was little spatial structure in the estimated probability of transition at the Surrey site but that small invasion hotspots did occur at the Dorset site (Fig 5.5, Table 5.4). Kriged grids derived from the predictions of seedling densities were again qualitatively accurate. Areas with higher predicted seedling densities concurred with the most heavily invaded areas of the sites (personal observation); a relationship that could be confirmed by an additional survey of *Betula* seedling densities using larger quadrat sizes. It is worth noting that there was little correlation between the determinant factors at the sites and so the co-incidence of conditions which favour *Betula* recruitment did not occur greatly more often than would be expected by chance (*r* values were typically <±0.30). Exceptions to this were phosphorus availability and soil water content, particularly at the Surrey site (Pearson's *r*: Surrey = 0.84, Dorset = 0.40), a likely association of both variables with SOM content. The only other strong correlation (>±0.50) was between vegetation height and biomass density (*r* = 0.51) at the Surrey site. This lack of association between the determinant factors is likely to have contributed to the low overall estimates and lack of strong spatial structure in predicted seedling densities at the sites.

Estimates of each determinant factors' contribution to within-site heterogeneity demonstrated that some variables, such as seed availability at the Dorset site and the gap indicator mean vegetation height at the Surrey site, could be clearly limiting but lacked sufficient variation within the sites to explain heterogeneity in seedling densities (Table 5.5). Other variables, particularly the edaphic factors that displayed a small scale patchiness (phosphorus & soil water content) appeared able to cause larger within-patch differences, even over the typical, non manipulated, ranges of availability that were found at the spatial sites. The differences between the interquartile and full range variations show that some variables could explain much of the variance at the patch scale e.g. vegetation height at the Dorset site but that extreme values may explain occasional high densities e.g. seedbank density at Surrey. These findings also indicate that it is safe-site factors that account for the majority of within-patch heterogeneity in the likelihood of invasion at the study sites. Occasional high seed densities may, however, explain some small hotspots of invasion.

Table 5.4 Fitted variogram models for predicted *Betula* seedling densities. Explained deviance was of too small a magnitude to be calculated using the S+ software for the Dorset site and so is not presented here.

	DORSET SITE	SURREY SITE
Best fit model	Spherical	Exponential
Range (a)	33.84	1758845
Sill (C)	0.0069	43.02
Nugget ($\gamma(0)$)	0	0
Spatially structured variance ($1-(\gamma(0)/C)$)	100%	86.7%
Explained deviance (%)(fitted/null)	N/A. (0)	11.5
Mean kriged estimate	0.072	0.116
Mean SE of estimates	0.059	0.098

Table 5.5. Estimated within-patch heterogeneity accounted for by each of the identified determinants. Values represent the difference between maximum and minimum predicted *Betula* seedling densities (m^{-2}) when the variables of the fitted, combined-site model were varied over their observed interquartile (IQ) and full ranges of the Dorset and Surrey spatial sites. Other variables in the model were held constant at their mean.

	Dorset: IQ Range	Dorset: Full Range	Surrey: IQ Range	Surrey: Full Range
Seedbank density (m^{-2})	0.0039	0.01	0.0114	175.27
Biomass (hits m^{-2})	0.0216	0.25	0.0227	0.10
Necromass (hits m^{-2})	0.0090	0.04	0.0604	0.15
Mean vegetation height (cm)	0.0798	0.10	0.0192	0.09
P-availability (P_{ox} µg P g^{-1})	0.031	0.12	0.0148	0.14
Soil water content (% total mass)	0.0253	0.17	0.059	0.26

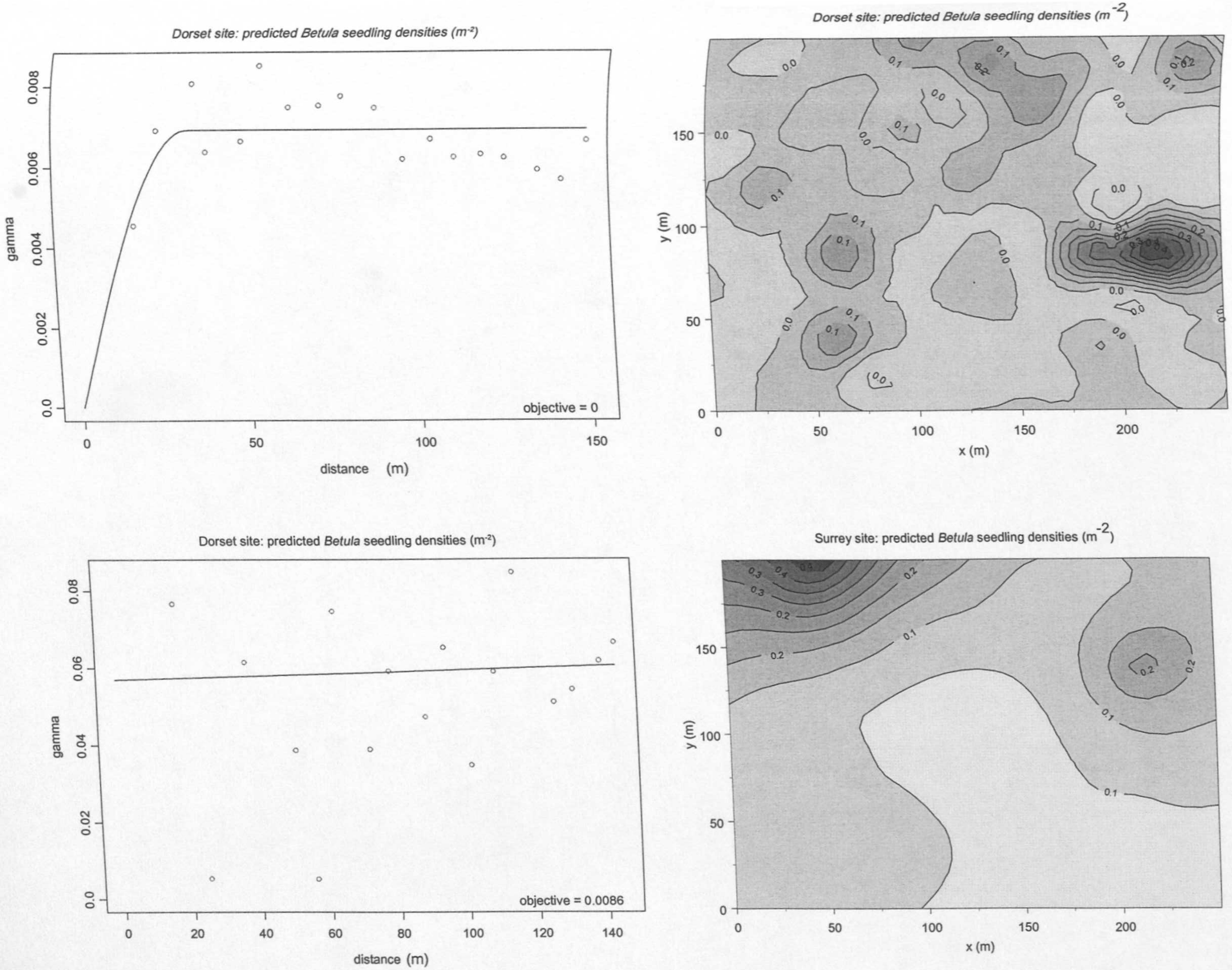


Fig 5.5 Fitted variogram models and kriged output grids for predicted *Betula* seedling densities (m^{-2}) at the Dorset and Surrey spatial sites.

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Discussion

VALIDATION AND EXTRAPOLATION OF THE GENERAL MODEL

The low seedling densities of the spatial sites precluded the confirmation of accurate model predictions of high-density seedling conditions. However, the broad, general accuracy of the model predictions would suggest that the identity and influence of predictor variables remained constant over a wide range of heathland conditions; i.e. the model is not entirely specific to the M16 community of the experimental plots. This was, in some respects, surprising as many predictions relied upon extrapolation of the fitted relationships or reliance upon relationships fitted to areas of multidimensional space that were poorly represented by the experimental data. The most likely explanation for the apparent accuracy of these extrapolations is that none of the variables requiring extrapolation had combinations of values that would result in high expected seedling densities. The taller vegetation heights of the spatial sites, for instance, result in lower predicted seedling densities than the intermediate height vegetation that commonly occurred within the experimental sites. As the experimental plots represent what may, in many respects, be 'ideal' conditions for establishment, extrapolations away from these optima will always result in low predicted densities. If the selected spatial sites are indeed representative of 'typical' heathland conditions then it is these sub-optimal conditions that are the most commonly occurring. This is what would be expected, if all conditions were likely to undergo transition then heathland ecosystems would not persist at all. The major question associated with extrapolation of inadequately represented variables such as P-availability and seedbank densities is not 'do seedling densities decline at low levels?' but 'what is gradient and form of this decline?' Although there may be exceptions to the suitability of these extrapolations (e.g. water content may be better represented by a quadratic relationship over wide ranges) the general accuracy of the model predictions suggests that major revision of the combined-site model presented in Chapter 4 is not required.

Although the model predictions were broadly accurate (e.g. no gross under or overestimation and the successful prediction of the 'most invaded' site) there were a number of minor inaccuracies suggesting that some important processes are either inaccurately modelled or not represented by the combined site model of the experimental sites. This inaccuracy was greatest at the Dorset site where predicted seedling densities exceeded actual observed densities. There are two likely causes of this inaccuracy. The first is an underestimation of seed limitation at low seedbank densities. As the model contains no quantitative restriction stating that 'seedling densities should always be a probabilistic function of seedbank densities' optimal safe-site plots with low seed input are likely to result in overestimation of seedling densities. Such a function may be of great benefit in a revised version of the model. A second cause of inaccurate prediction may originate from the *P.aquilinium* dominated environments that cover much of the Dorset site. *P.aquilinium* has a very different growth form and life history strategy to the species of the dwarf shrub and grass dominated communities that the model was based on. Extrapolations from the fitted models are therefore extreme; apparent biomass densities and vegetation heights may not have the same effects in these two communities. Additionally, the model does not include the effect of *P.aquilinium's* deep 'fluffy' litter, which may inhibit invasion and play a greater role in doing so than direct competition. Marrs (1987b) found that *Betula* seedling establishment was significantly lower under bracken than in late mature-early degenerate *Calluna* vegetation.

The conclusion of this sub-component of the study is that the model is qualitatively accurate and therefore of broad relevance to most dwarf shrub UK lowland heath communities. Further testing and modification is required before it can be concluded that the model is capable of exact predictions but this is not massively relevant to conservation managers who need only know what types of conditions should be promoted and avoided when aiming to extend heathland persistence. There is little evidence to dispute the broad conclusions presented in Chapter 4.

WHICH VARIABLES ARE IMPORTANT?

Low actual seedling densities were a largely inevitable finding of this study (see above). In many conditions where transition to scrub is likely it will have already occurred, only areas that have recently increased their likelihood of transition will usually be detected in 'heathland' surveys. For this reason many 'high likelihood' environments will rarely be observed in 'typical' heathland environments like those studied here. The typical values and ranges of the determinant factors do indicate, however, the identity of the factors that are the most likely to contribute to within-patch heterogeneity and halt invasion altogether at a site. Raising seed bank densities at both sites for example, is likely to greatly increase the likelihood of invasion (unpublished data). The data also reveal that the degree of safe-site and seed limitation can vary both within and between patches. This is most clearly exemplified by the seedbank density results. The almost total absence of *Betula* at the Dorset site would suggest that seed limitation is an extremely important component of the patches' stability. Its effect on within site heterogeneity in seedling density is, in contrast, tiny; seed was universally limiting to a similar degree across the whole site. At the Surrey site higher mean densities meant that seed was, overall, less limiting but an extreme patchiness in seedbank densities resulted in huge potential contributions to within-site variation.

No single factor could be identified as the key determinant of within-patch heterogeneity in seedling densities, the degree of importance assigned to each variable was site-specific with some variables accounting for much of the within-site heterogeneity at one site and little at the other (e.g. mean vegetation height). The most consistently high ranking factor was soil water content, though caution must be sanctioned when interpreting these results as much of the range in this variable at the spatial sites did not occur in the experiments and the measurements at all sites were based upon single 'snapshot' measurements. It is also worth noting that natural, non-manipulated variation in phosphorus availability could account for within site differences of a similar order to the other determinants, despite ranges of availability (c.0-100μg P g $^{-1}$) that were far lower than those of the experimental plots (39.3-649.1μg P g $^{-1}$). P_{ox} values >100μg P g $^{-1}$ may occur at high PSC high SOM sites but P_{ox} availabilities >200 μg P g^{-1} are only likely to occur in occasional circumstances e.g. near deposits of animal faeces or after extreme burning events in high PSC regions.

PATTERN, CAUSE AND CONSEQUENCE OF WITHIN REGION HETEROGENEITY

One of the major between-site differences was in seedbank density and it would seem reasonable to suggest that this was the key factor controlling the greater observed seedling densities of the Surrey site, which was surrounded by mature *Betula*. Such differences in seed input may be one of the greatest proximate causes of between-site variation in the extent of invasion. This variation in propagule availability is likely to originate from two main sources: the extent of previous invasion and the context of the heath i.e. the surrounding habitat. Nolan (2000), who studied heath-scrub vegetation shifts using the Dorset heathland database data (Webb 1990; Rose *et al.* 1999) found that the area of invasive species on the edge of a patch was the most accurate descriptor of vegetation change, but that internal fragmentation was also important.

SPATIAL STRUCTURE & HETEROGENEITY IN INVASION

There was considerable between-patch and between variable differences in both mean values of and the scale, extent and magnitude of variation in the determinant factors. There was also little correlation between determinant factors. If this lack of consistent pattern is common to many heathland patches then it is likely that spatial heterogeneity in determinants results in idiosyncratic patterns of transition probability. These are most probably controlled by a complex combination of numerous factors including management histories, underlying geology and endogenous ecological processes (Chapter 4). Despite this overall variability, there were broad trends in spatial heterogeneity in that edaphic and seed variables tended to display smaller patch sizes than vegetation variables, which revealed broad spatial gradients rather than patches at the within-patch scale. The spatial patterns of the determinant factors may influence the way in which management is performed. Variables with spatially extensive trends e.g. the vegetation attributes are those that may be the easiest to manage as large 'invasable' regions can be identified and targeted. Although the small patch size of the edaphic factors means that, from a single-site management perspective, their variation is effectively random in space. The other variable with small patch size, seedbank density, is clearly identifiable and easy to manage for (see below). It was clear from the variograms and kriged grids of both sites that although displaying a large 'random' nugget variance seedbank densities had 'hotspots', which concurred with isolated trees and scrub patches.

These findings, when coupled with an acknowledgement of the large nugget variance of most variables indicates that patterns of invasion will exhibit a certain degree of noise at the patch scale as a consequence of small (<17.6m), high density, seedling patches that are not part of broader spatial trends. By extension larger-scale aggregations of seedlings are a likely consequence of spatially consistent patches of high transition probability e.g. compare the predicted seedling density (Fig 5.5) and the seed bank density patterns (Fig 5.4c) of the Surrey site. The significant between-patch differences in the values of some determinant factors, along with the differences in predicted and actual seedling densities support and further these conclusions to provide evidence of differences in the likelihood of phase transition at the between-patch scale. When these findings are synthesised with previous researches of within-patch and landscape scale differences in the determinants of heath-scrub phase-transition (Chapters 2-5; Chapman *et al.* 1989b) it becomes clear that heterogeneity in the likelihood of invasion exists and operates at all scales to produce the observed patterns of invasion. Many larger-scale studies discussing the origins of alternate ecosystem states cite disturbance regimes as the key control factor (e.g. Scheffer *et al.* 2001) while smaller studies usually propose the variables affecting recruitment of a 'foundation species' to be the control factor (e.g. Petraitis & Latham 1999). The research presented in this thesis suggests that these apparent differences in the determinants of transition may often reflect the fact that large-scale processes affect the mean value of the smaller scale determinant variable over large areas thus affecting the overall probability of invasion and therefore transition across larger areas. The common occurrence of *Betula* spp. in dense even aged stands, for instance, (Atkinson 1992) suggests that the conditions favouring establishment often occur in large patches within a narrow period of time. These patches probably correspond to low levels of seed and safe-site limitation over large areas e.g. severely burnt and degenerate stage patches with a high *Betula* seed rain. Areas with a few isolated trees, like the spatial sites studied here, represent areas with either low seed rains or small numbers of safe sites.

Simple deductive logic would suggest that the relative contributions of seed and safe-site limitation affect the pattern of encroachment and change at the landscape scale. If the largest component of heterogeneity at the patch scale (arbitrarily defined here as c.5ha) is seed limitation then phase transition is likely to follow a steady pattern of percolation across the landscape (spatial scales >5ha) (e.g. Milne *et al.* 1996). Alternatively, if safe-site limitation is the major contributor to within-patch heterogeneity, as is suggested by this research, then invasion may continue to form distinct patches thus slowing the rate, or precluding full transition at the landscape scale.

In summary, the central question of this thesis: 'what determines heath - *Betula* scrub state shifts?' (Chapter 1) requires a complex and scale-dependent answer. Further data collection coupled with a combination of statistical and simulation modelling of the process of invasion over larger temporal and spatial scales would aid greatly in the exploration of the ideas presented above.

CONTROL OF BETULA AT THE PATCH SCALE:

"Recruitment tends to be the Achilles heel of the invasive or unwanted plant" (Rees & Hill 2001) and *Betula* is almost certainly no exception to this rule. This means that careful management of recruitment opportunities has the potential to greatly reduce establishment and promote long-term heathland stability. The problem with *Betula* spp. that is not common to many exotic invaders is that outside of heathland ecosystems the species is not generally considered invasive and that the existence of some populations is desired e.g. for insect biodiversity. Management must therefore be applied at the patch scale. Exploration of the combined-site general model (Chapter 4) reveals that *Betula* recruitment limitation, and therefore the persistence of heath, can originate from a single variable e.g. a high vegetation density, even where other conditions are optimal. Therefore the phase transitional conditions exist within a narrow area of multidimensional space. What this means for heathland management is that effort can be concentrated on a single or a few of the determinant factors.

This will be easiest for factors that display a readily identifiable spatial structure e.g. vegetation density and seed density. Here I propose an integrated and non-intensive approach to *Betula* control that is sensitive to the needs of both open heath and scrub-heath ecotone dwelling species. The central tenet of the scheme is to manage for short, dense vegetation in high seed rain areas, therefore eliminating the majority of recruitment opportunities. The management strategy given here is specific to *Betula* spp. and therefore would need to be considered alongside, and integrated with other management aims before being realized. An assumption underpinning this plan is that the aim of the heathland manager is to halt transition to *Betula* scrub and maintain a mosaic of different aged heather stands, therefore supporting as many characteristic heathland species as possible.

Perhaps the simplest and most cost effective means of reducing the likelihood of transition to scrub is to remove isolated trees on open heath that will act as colonisation foci and then treat the stumps of these trees with herbicides to prevent resprouting (Marrs 1985). Isolated birch trees are often left during tree clearances and although these are thought to promote bird and invertebrate biodiversity (Pickess *et al.* 1992) it is non-heathland species that are most likely to benefit. As European lowland heath is an internationally endangered habitat heath patches should be managed for their characteristic species not overall within-patch diversity. I therefore suggest that this practice should be halted.

Removal of birch would benefit many of the endangered and characteristic species of heath. Van den Berg *et al.* (2001) for instance, state that Pine and scrub vegetation may provide habitat for *Sylvia undata* but its clearance often results in bare ground or heath which it is more positively associated with. Failure to clear this vegetation will lead to a long-term loss in the bare ground heath and the *Ulex europaeus* dominated habitats that it favours. The removal of *Betula* scrub should be executed in the winter to avoid nesting birds (Pickess *et al.* 1992) and as early as possible in the trees development. Waiting until trees have developed to maturity should be avoided as they will have probably transformed both soil and seedbank to favour regeneration of their own or associated species (see below and Chapter 1.).

A habitat type that may require conservation is the ecotone between the larger patches of scrub and heath. This habitat may provide warm and dry microhabitats that are required by some invertebrate species of the *Betula* scrub state (Dr L.K. Ward, CEH Dorset, Personal communication) and provide feeding and nesting habitat for the Nightjar (*Caprimulgus europaeus*) (Farrel 1993). In most cases this habitat will not need to be managed for at a national level it is currently increasing in area at an alarming rate. What may be desired, however, is that the position of the ecotone is stabilised. This could be achieved by creating uninvasible conditions in adjacent open heath ecosystems. Low intensity and regular mows or burns of heath areas near to *Betula* seed sources would maintain the dwarf-shrub vegetation in as competitive a phase as possible. Other, more invasible, phases of the dwarf shrub cycle e.g. degenerate and pioneer vegetation (Watt 1947; Gimingham 1988) should be maintained in an area remote from sources of *Betula* seed. By using this method of managing seed-proximate areas on a short cycle and those in the more isolated open heath areas on a long cycle, transitions to *Betula* scrub may be prevented, whilst also maintaining the mosaic of vegetation ages that is central to the maintenance of characteristic heathland species. Mowing and removing the shoots of the 'barricade' regions in autumn may also provide seed bearing shoots that may be used in the restoration of previously invaded areas (Pywell *et al.* 1996) and prevent the build up of phosphorus in soil organic matter that originates from plant litter (Chapman *et al.* 1989a; Chapter 2; Berendse *et al.* 1989).

This relatively simple plan is complicated by uncertainty as to what the required width of the 'barricade' zone should be. Kriged seed bank density maps suggest that twice the height of the adult tree (c.40-50m) may be adequate but an accurate model of *Betula* dispersal similar to those of Nathan *et al.* (2002) or Bullock & Clarke (2000) needs to be derived before this can be concluded with confidence. Results from the experimental sites suggest that prevailing wind direction may greatly influence the required width (Chapters 3 & 4). It may therefore, reduce the required management intensity if the length of heath-scrub ecotonal habitats that are aligned with the prevailing wind direction is minimised i.e. if the only *Betula* habitats that are maintained disperse the majority of their seed onto neighbouring non-heath habitats. The width of fortified regions may also need to be minimised on smaller heaths so that a variety of vegetation ages can be maintained and local extinction minimised. Such heaths will probably require more intensive management of other types if they are to remain stable.

The barricade method described above will, in principle, eradicate most *Betula* recruitment opportunities. However, the high levels of spatially unstructured variation in determinant factors suggests that low density invasion is still likely to occur in both the low seed, high safe-site 'centre' regions and the high seed, low safe-site barricade regions (Chapter 4). Heath should be monitored on a fairly regular basis (c.3 years) and sapling trees removed. This may be easily achieved with secateurs (personal observation) and is perhaps best done when the individuals are of intermediate age (i.e. when they have risen above the field layer but do not seem to be suppressed by herbivores). Resprouting of saplings may be minimised with the use of herbicide spot treatments. This method should halt the soil changes that follow invasion and aid in regulating the process of state shifts but will also prevent time-consuming and potentially unnecessary work of removing what could be unsuccessful invaders.

The importance of removing *Betula* colonists at an early stage should be emphasised, Both ecological surveys and management experience suggest that, in most restoration cases, litter stripping is necessary to return the ecosystem to the heathland state (Mitchell *et al.* 1999; Auld *et al.* 1992). The widespread changes brought about by *Betula* invasion have been described elsewhere (Chapter 1). A synthesis of the literature would suggest that these changes promote the maintenance of the *Betula* scrub vegetation state after the death of parent trees, the canopies of which tend to inhibit the establishment of conspecifics (Atkinson 1992). Evidence of this potentially 'community level' positive feedback mechanism (*sensu* Wilson & Agnew 1992) comes from several sources. A study of *Betula* managed sites, found that despite a reduced cover of *Betula* (1-39%), there were still elevated levels of extractable P and a seedbank of invasive species, including *Betula* itself, making re-invasion likely (Mitchell *et al.* 1999). Dimbleby (1952) found trees were concentrated around the old tree stumps of pine trees, usually within 6 yards. In these clusters mycorrhizal birch roots were concentrated around the humus pockets of the former tree roots, thus suggesting that there is a potential innoculum and sources of nutrition that may be unavailable to dwarf shrubs where there has been previous invasion. The third line of evidence comes from personal observations of cleared sites in which seedling densities have been seen to be extraordinarily high; probably as a combined result of high seed and phosphorus availability, low competition and the presence of suitable mycorrhizas. It has also been noted that ants (*Formica fusca* and *Lasius* spp.) living within the stumps of cleared *Betula* tend aphids on nearby *Betula* saplings. Although Madhi & Whittaker (1993) found, in similar circumstances, that ant tending provided no major benefits to the plant my own observations would suggest the contrary; ant 'protected' saplings were larger and healthier in appearance than their untended contemporaries. A final argument in support of the early removal of invading *Betula* is cost; removal of *Betula* (including litter stripping) costs £1507 (in 1992), a far greater expenditure than preventable methods e.g. mowing (£162) (Auld *et al.* 1992).

A huge number of other management tools are available to heathland managers and a discussion of their role their likely role in the control of heath-scrub phase transitions is either limited by space or presented elsewhere (e.g. Chapters 1 & 4). What should perhaps be reiterated is that burning and grazing, widely viewed as panacea for the regulation of heathland ecosystem 'stability', are complex processes that act in a context dependent manner and are associated with changes in factors that both stimulate and inhibit *Betula* colonisation.

Conclusion

The overall conclusions of this research are that:

1. The general combined-site statistical model appears to provide a coarse but fairly accurate definition of the phase transitional area between lowland heath and *Betula* scrub ecosystem states and therefore also describes conditions resulting in heathland persistence.
2. Both seed and safe-site limitations may determine the likelihood of heath-scrub transition at any given site. Results suggest that *Betula* safe-site is determined largely by vegetation attributes and phosphorus availability.
3. Both observational patch scale and experimental studies suggest that the identity of the determinants is broadly similar at different sites but their relative contributions to variance at that scale vary widely and in a site-specific manner.
4. The determinant factors are at larger scales governed by landscape-scale processes such as soil (PSC), climate and management regimes. Their effects on the determinant factors at smaller spatial scales are likely to explain regional differences in the degree of invasion.
5. Spatial autocorrelation of the determinant factors allows for the targeting of sites with a high probability of transition by heathland managers. Spatial decoupling of seed and safe-sites may promote heathland stability.

This model, when synthesised with the existing literature (Chapter 1) amalgamates thinking on safe-site and seed limitations on recruitment, transitions between alternate ecosystem states and the causes of ecosystem stability and contributes to the solution of a problem of conservation importance.

The results of this research indicate that many factors can influence *Betula* recruitment success, and that these may contribute to both within and between-patch variation in transition probabilities. The complex pattern of the determinants (conclusion 3) however, makes it difficult to estimate the overall importance of each factor at larger scales and so an overall aim of the research, quantifying the relative importance of determinants in the overall pattern of heath invasion, has not been met. The research simply does not cover a sufficiently wide range of sites, conditions, scales and variables; a fundamental criticism that may be aimed at the majority of ecological research. The relatively large number of screened variables and the qualitatively accurate fit of the combined-site model do suggest however, that many important factors have been identified. The mechanistic role of each of the identified determinants remains hypothetical. It is possible that in some cases they may represent close correlates of the true determinants.

An original hypotheses of this research was that phosphorus was not limiting where PSC was >700 $\mu g\ P\ g^{-1}$. The research presented here demonstrates that this is an oversimplification of the role of PSC, which like that of the other identified factors, is likely to have a complex, interactive, probabilistic and scale-dependent effect upon *Betula* recruitment. In reality it is unlikely that there is single transition point at which invasion occurs. Instead, the results suggest that there is a small, 'phase-transitional area' of multidimensional space in which transition is likely. Such a phenomenon may be common to many ecological state-shifts, which are often driven by the recruitment of a 'foundation' species (Chapter 1.) What is also likely to be common to many ecological state shifts, are scale dependency of identified determinants, and phase transitional areas described by resource availability and propagule pressure. The details of each state-shift are however, likely to differ greatly between systems and transitions.

The caveats of the studies' conclusions demonstrate that "unravelling the mechanisms governing the behaviour of spatially extensive ecosystems is notoriously difficult because it requires the interfacing of phenomena that occur on very different scales of space, time and ecological organisation" (Scheffer *et al.* 2001). The successes of the research however, indicate that these problems are not insurmountable. The existing conclusions can be drawn with a reasonable degree of confidence and small additive extensions to this research, e.g. the estimation of seed shadows, larger scale survey, statistical modelling at the patch scale and simulation modelling, could resolve many of the uncertainties and unanswered questions.

References

Abuzinadah, R.A & Read, D.J. (1989a) The role of proteins in the nitrogen nutrition of ectomycorrhizal plants IV. The utilisation of peptides by birch (*Betula pendula.* Roth) infected with different mycorrhizal fungi. *New Phytologist*, **112**, 55-60.

Abuzinadah, R.A & Read, D.J. (1989b) The role of proteins in the nitrogen nutrition of ectomycorrhizal plants V. Nitrogen transfer in birch (*Betula pendula.* Roth) grown in association with mycorrhizal and non-mycorrhizal fungi. *New Phytologist,* **112**, 61-68.

Aerts, R. (1989) Aboveground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. *Oikos*, **56**, 31-38.

Aerts, R. & Berendse, F. (1988) The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio,* **76**, 63-69.

Aerts. R. & Chapin III, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1-67.

Allchin, E.A. (1997) *Vegetation dynamics following management burning of lowland heathland.* PhD thesis, University of Liverpool.

Allen, M.F. (1991) *The Ecology of mycorrhizae.* Cambridge University Press, Cambridge.

Allen, S.E. (1964) Chemical aspects of heather burning. *Journal of Applied Ecology*, **1**. 347-367.

Allen, S.E., Evans, C.C. & Grimshaw, H.M. (1969) The distribution of mineral nutrients in soil after heather burning. *Oikos*, **20**, 16-25.

Angold, P.G. (1997) The impact of a road upon adjacent heathland vegetation: effects on plant species composition. *Journal of Applied Ecology*, **34**, 409-417.

Arradóttir, A.L., Robertson, A. & Moore, E. (1997) Circular statistical analysis of birch colonisation and the directional growth response of birch and black cottonwood in south Iceland. *Agricultural and Forest Meteorology*, **84**, 179-186.

Atkinson, M.D. (1992) Biological flora of the British Isles. *Betula pendula* Roth (*B.verrucosa* Ehrh.) and *B.pubescens* Ehrh. *Journal of Ecology*, **80**, 837-870.

Auld, M.D., Davies, S. & Pickess, B. (1992) Restoration of lowland heaths in Dorset. *RSPB Conservation review*, **6**, 68-73.

Bannister, P. (1966) Biological flora of the British Isles: *Erica tetralix*. *Journal of Ecology*, **54**, 795-813.

Barrow, N.J. (1978) The Description of phosphate adsorption curves. *Journal of Soil Science*, **29**, 447-462.

Bazzaz (1996) *Plants in changing environments*. Cambridge University Press, Cambridge.

Berendse, F. (1990) Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *Journal of Ecology*, **78**, 413-427.

Berendse, F. (1994) Competition between plant populations at low and high nutrient supplies. *Oikos*, **71**, 253-260.

Berendse, F., Bobbink, R. & Rouwenhorst, G. (1989) A comparative study of nutrient cycling on wet heathland ecosystems II. Litter decomposition and nutrient mineralization. *Oecologia*, **78**, 338-348.

Berendse, F., Schmitz, M. & de Visser, W. (1994) Experimental manipulation of succession in heathland ecosystems. *Oecologia,* **100**, 38-44.

Bjorkman, E. (1970) Forest Tree Mycorrhiza. The conditions for its formation and the significance for forest tree growth and afforestation. *Plant and Soil,* **32**, 589-610.

Black, M. & Wareing, P.F. (1954) Photoperiodic control of germination in seed of birch (*Betula pubescens*. Ehrh.) *Nature*, **174**, 705-707.

Bokdam, J. & Gleichman, J.M. (2000) Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology*. **37**, 415-431.

Britton, A.J., Carey, P.D., Pakeman, R.J. & Marrs, R.H. (2000) A comparison of regeneration dynamics following gap creation at two geographically contrasting heathland sites. *Journal of Applied Ecology*, **37**, 832-844.

Brunstig A.M.H. & Heil G.W. (1985) The role of nutrients in the interactions between a herbivorous beetle and some competing plant species in heathlands. *Oikos*, **44**, 23-26.

Bullock, J.M. (1996) Plants. *Ecological Census Techniques*. (ed. Sutherland W.J) pp 111-138. Cambridge University Press, Cambridge.

Bullock, J.M. & N.R. Webb. (1995) Responses to severe fires in heathland mosaics in Southern England. *Biological Conservation*, **73**, 207-214.

Bullock, J.M. & Pakeman, R.J. (1997) Grazing of lowland heath in England: management methods and their effects on heathland vegetation. *Biological Conservation*, **79**, 1-13.

Bullock, J.M. & Clarke, R.T. (2000) Long distance dispersal by wind: measuring and modelling the tail of the curve . *Oecologia*. **124**, 506-521.

Burke, M.J.W & Grime, J.P. (1996) An experimental study of plant community invasability. *Ecology*, **77**, 776-790.

Burrough, P.A. (1995) Spatial aspects of ecological data. *Data analysis in community and landscape ecology* (eds. Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R). Cambridge University Press, Cambridge.

Burton, P.J. & Bazzaz, F.A. (1991) Tree seedling emergence on interactive temperature and moisture gradients and in patches of old field vegetation. *American Journal of Botany*, **78** 131-149.

Calow, P. ed. (1998). *The Encyclopaedia of Ecology and Environmental Management*. Blackwell. London

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958-1965.

Carpenter, S.R. (2001) Alternate states of ecosystems: evidence and some implications. *Ecology: Achievement and Challenge.* (eds. Press, M.C., Huntly, N.J. & Levin, S) pp 357-383. Blackwell, Oxford, UK.

di Castri, F. Hansen, A.J. & Holland, M.M. (1988) *A new look at ecotones: Emerging International Projects on Landscape Boundaries. Biology International, Special Issue 17.* IUBS, Paris.

Chapin, F.S., Walker, B.H., Hobbs, R.J. Hooper, D.U. Lawton, J.H., Sala, O.E. Tilman, D. (1997) Biotic control over ecosystems. *Science*, **277**, 500-504.

Chapman, S.B. (1967) Nutrient budgets for a dry heath ecosystem in the south of England. *Journal of Ecology,* **55**, 677-689.

Chapman, S.B. (1970) The nutrient content of the soil and root system of a dry heath ecosystem. *Journal of Ecology*, **58**, 445-452.

Chapman, S.B., Hibble, J. & Rafarel, C.R. (1975) Litter accumulation under *Calluna vulgaris* on a lowland heathland in Britain. *Journal of Ecology*. **63**, 259-271.

Chapman, S.B. & Clarke, R.T. (1980) Some relationships between soil, climate, standing crop and organic matter accumulation within a range of *Calluna* heathlands in Britain. *Bulletin d' Ecologie*, **11**, 221-232.

Chapman, S.B., Rose, R.J. & Clarke, R.T. (1989a) A model of the phosphorus dynamics of *Calluna* heathland. *Journal of Ecology*, **77**, 35-48.

Chapman, S.B., Rose, R.J. & Basanta, M. (1989b) Phosphorus adsorption by soils from heathlands in Southern England in relation to successional change. *Journal of Applied Ecology*, **26**, 673-680.

Chapman, S.B., Clarke, R.T. & Webb, N.R. (1989c) The Survey and Assessment of Heathland in Dorset, England, for Conservation. *Biological Conservation*, **47**, 137-152.

CLAG (1997) Deposition fluxes of acidifying compounds in the United Kingdom, Institute of Terrestrial Ecology, UK.

Clark, J.S., Macklin, E., & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests *Ecological Monographs*, **68**, 213-235.

Clark, J.S., Lewis, M. & Horrath, L. (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, **157**, 537-554.

Clement, B. & Touffet, J. (1990) Plant strategies and secondary succession on Brittany heathlands after severe fire. *Journal of Vegetation Science*, **1**, 195-202.

Connell, J.H. & Slayter, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist*, **111**, 1119-1144.

Connell, J.H. & Sousa, W.P. (1983) On the evidence needed to judge ecological stability or persistence. *American Naturalist*. **121**, 789-824.

Costello, D.A. Lunt, I.D. & Williams, J.E. (2000) Effects of invasion by the indigenous shrub *Acacia sphoae* on plant composition of coastal grasslands in South Eastern Australia. *Biological Conservation*, **96**, 113-121.

Crawley, M.J. (1987) What makes a community invasable? *Colonisation, Succession and Stability* (eds. A.J. Gray, M.J. Crawley & P.J. Edwards) pp. 429-453. Blackwell, London.

Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell, London.

Crawley, M.J. (2002) *Statistical computing: An introduction to Data analysis using S+*, Wiley, Chichester, West Sussex, England.

Deacon, J.W., Donaldson, S.J. & Last F.T. (1983) Sequences and interactions of mycorrhizal fungi on birch. *Plant & Soil*, **71**, 257-262.

De Jong, T.J. & Klinkhamer, P.G.L. (1983) A simulation model for the effects of burning on the phosphorus and nitrogen cycle of a heathland ecosystem. *Ecological Modelling*, **19**, 263-284.

Diemont, W.H. (1994) Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science*, **5**, 409-414.

Diemont, W.H & Heil, G.W. (1984) Some long-term observations on cyclical and seral processes in Dutch heathlands. *Biological Conservation*, **30**, 283-290.

Dimbleby, G.W. (1952) Soil regeneration on the north-east Yorkshire moors. *Journal of Ecology*, **40**, 331-341.

Dutilleul, P. (1993) Spatial heterogeneity and the design of ecological field experiments. *Ecology,* **74**, 1646-1658.

Edmunds P.J. & Carpenter, R.C. (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5067-5071.

Eriksson, O. & Ehrlén, J. (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologia*, **91**, 360-364.

Farrell, L. (1993) *Lowland Heathland: the extent of habitat change.* English Nature Science no.12.

Frossard, E Brossard, M Hedley MJ & Mewtherell, A (1995) Reactions controlling the cycling of P soils. *Phosphorus in the Global Environment* (ed. H. Tiessen) pp. 107-137. Wiley. London.

Gallet, S. & Roze, F. (2001) Resistance of Atlantic Heathlands to trampling in Brittany (France): influence of vegetation type, season and weather conditions. *Biological Conservation.* **97**, 189-198.

Gilbert, I.R., Jarvis, P.G. & Smith, H. (2001) Proximity signal and shade avoidance differences between early and late successional trees. *Nature*, **411**, 792-795.

Gimingham, C.H. (1961) Biological flora of the British Isles: *Calluna vulgaris* (L.) Hull. *Journal of Ecology*, **52**, 285-97.

Gimingham, C.H. (1971) *Calluna* heathlands: use and conservation in the light of some ecological effects of management. *The scientific management of animal and plant communities for conservation* (eds. Duffer, E. & Watt, A.S.) pp. 91-103. Blackwell, London.

Gimingham, C.H. (1988) A reappraisal of cyclical processes in Calluna heath. *Vegetatio*, **77**, 61-64.

Gimingham, C.H., Chapman, S.B. & Webb, N.R. (1979) European Heathlands. *Ecosystems of the World 9A: heathlands and related shrublands*. (ed. Specht, R.L) pp.365-413. Elsevier, Amsterdam.

Gloaguen, J.C. (1990) Post-burn succession on Brittany heathlands. *Journal of Vegetation Science*. **1**, 147-152.

Gloaguen, J.C. (1993) Spatio-temporal patterns in post-burn succession on Brittany heathlands. *Journal of Vegetation Science*. **4**, 561-566.

Gong, W.K. & Gimingham, C.H. (1984) Birch regeneration in heath vegetation. *Proceedings of the Royal Society of Edinburgh*. **85B**, 73-81.

Gosz, J.R. (1992) Ecological functions in biome transition zones: Translating local responses to broad scale dynamics. *Landscape Boundaries: Consequences for Biotic Diversity and Landscape flows* (eds. A.J. Hansen & F. di Castri). Springer-Verlag. New York.

Granström, A. (1988) Seedbanks at six open and afforested heathland sites in Southern Sweden. *Journal of Applied Ecology*. **25**, 297-306.

Grime, J.P. (1979) *Plant strategies and Vegetation Processes*. Wiley, Chichester, U.K.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*, Unwin-Hyman, London.

Gross, K.L., Pregitzer, K.S. & Burton, A.J. (1995) Spatial variation in nitrogen availability in three successional plant communities. *Journal of Ecology,* **83**, 357-367.

Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52,** 107-145.

Guo, F. & Yost, R.S. (1999) Quantifying the available soil phosphorus pool with the acid ammonium oxalate method. *Soil Science Society of America. Journal*, **63**, 651-656.

Harding, J.S. (1981) Regeneration of Birch *(Betula pendula* Roth *and B.pubescens* Ehrh). *Appendix in The Regeneration of Oak and Beech Literature Review* (eds. Newbould, A.N. & Goldsmith, F.B.), pp. 83-112. Discussion papers in Conservation No. 33, University College, London.

Harrison, A.F. & Helliwell, D.R. (1979) A bioassay for comparing phosphorus availability in soils. *Journal of Applied Ecology*, **16**, 497-505.

Harrison, C.M. (1976) Heathland Management in Surrey, England. *Biological Conservation*, **10**, 21-220.

Heil G.W. & Diemont W.H. (1983) Raised nutrient levels change heathland to grassland. *Vegetatio*, **53**, 113-120.

Helsper, H.P.G., Glenn-Lewin, D. & Werger, M.J.A. (1983) Early regeneration of *Calluna* heathland under various fertilisation treatments. *Oecologia*, **58**, 208-214.

Hester, A.J. (1989) Successional vegetation change: the effect of shading on *Calluna vulgaris* (L.) Hull. *Transactions of the Botanical Society of Edinburgh*, **45**, 121-126.

Hester, A.J, Miles, J. & Gimingham, C.H. (1991a) Succession from Heather moorland to Birch Woodland. I. Experimental alteration of specific environmental conditions in the field. *Journal of Ecology*, **79**, 303-315.

Hester, A.J, Miles, J. & Gimingham, C.H. (1991b) Succession from Heather moorland to Birch Woodland. II. Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *Journal of Ecology*. **79**, 317-328.

Hester, A.J., Gimingham, C.H. & Miles, J. (1991c) Succession from Heather moorland to Birch Woodland. III. Seed availability, germination and early growth. *Journal of Ecology*, **79**, 329-344.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *Journal of wildlife management*, **60**, 695-713

Holford, I.C.R., Wedderburn, R.W.M., & Mattingly, G.E.G. (1974) A Langmuir two-surface equation as a model for phosphate adsorption by soils. *Journal of Soil Science*, **25**, 242-255.

Holling, C.S. (1992) Cross-scale morphology, geometry and the dynamics of ecosystems. *Ecological Monographs*, **62**, 447-502.

Holm, S.O. (1994a) Reproductive variability and pollen limitation in three *Betula* taxa in northern Sweden. *Ecography*, **17**, 73-81.

Holm, S.O. (1994b) Reproductive patterns of *Betula pendula* and *Betula pubescens* coll. Along a regional altitudinal gradient in Northern Sweden, *Ecography*, **17**, 60-72.

Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology*, **80**, 1747-1761.

de Hullu, E & Gimingham, C.H. (1984) Germination and establishment of seedlings in different phases of the *Calluna* life cycle in a Scottish heathland. *Vegetatio*, **58**, 115-121.

Huppert, A., Blasius, B. & Stone, L. (2002) A model of phytoplankton blooms. *American Naturalist*, **159**, 156-171.

Huston, M. & Smith, T. (1987) Plant succession: life history and competition. *American Naturalist*, **130**, 168-198.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946-1957.

Jones, J.I., Young, J.O., Eaton, J.W. & Moss, B. (2002) The influence of nutrient loading, dissolved organic carbon and higher trophic levels on the interaction between submerged plants and periphyton. *Journal of Ecology*, **90**, 12-24.

Killham, K. (1995) *Soil Ecology*. Cambridge University Press, Cambridge.

Kinnaird, J.W. (1974) Effect of site conditions on the regeneration of birch (*Betula pendula* Roth. and *B.pubescens* Ehrh.). *Journal of Ecology*, **62**, 467-472.

Kuiters, A.T. & Simm, P.A. (2002) Regeneration of mixed deciduous forest in a Dutch forest-heathland following a reduction of ungulate densities. *Biological Conservation*, **105**, 65-74.

Lajtha, K. & Harrison, A.F. (1995) Strategies of phosphorus acquisition and conservation by plant species and communities. *Phosphorus in the global environment* (ed. H.T Tiessen). Wiley, London

Laycock, W.A. (1991) Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management*, **44**, 427-433.

Lennon, J.J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, **23**, 101-113.

Li, X. & Wilson, S.D. (1998) Facilitation among woody plants establishing in an old field. *Ecology*, **79**, 2694-2705.

Loehle, C., Li, B.L. & Sundell, R.C. (1996) Forest spread and phase transitions at forest prairie ecotones in Kansas, USA. *Landscape Ecology*, **11**, 225-235.

Lookman, R., Freese, D., Merckx, R., Vlassak, K. & Van Riemsdijk, W.H. (1995) Long-term kinetics of phosphate release from the soil. *Environmental Science and Technology*, **29**, 1569-1575.

Mahdi, T. & Whittaker, J.B. (1993) Do birch trees (*Betula pendula*) grow better if foraged by wood ants? *Journal of Animal Ecology*, **62**, 101-116.

Manson, R.H. (2000) Spatial autocorrelation and the interpretation of patterns of tree seed and seedling predation by rodents in old fields. *Oikos*, **91**, 162-174.

Maron, J.L. & Gardner, S.N. (2000) Consumer pressure, seed versus safe-site limitation and plant population dynamics. *Oecologia*, **124**, 260-269.

Marrs, R.H. (1984) Birch control on lowland heaths: mechanical control and the application of selective herbicides by foliar spray. *Journal of Applied Ecology*, **21**, 703-716.

Marrs, R.H. (1985) The use of krenite to control birch on lowland heaths, *Biological Conservation*, **32**, 149-164.

Marrs, R.H. (1986) The role of catastrophic death of *Calluna* in heathland dynamics. *Vegetatio*, **66**, 109-115.

Marrs, R.H. (1987a.) Studies on the conservation of lowland *Calluna* heaths. I. Control of birch and bracken and its effect on heath vegetation. *Journal of Applied Ecology*, **24**, 163-175.

Marrs, R.H. (1987b.) Studies on the conservation of lowland *Calluna* heaths. II. Regeneration of *Calluna* and its relation to bracken infestation. *Journal of Applied Ecology*, **24**, 177-189.

Marrs, R.H. (1993) Soil fertility and nature conservation in Europe. Theoretical considerations and practical management solutions. *Advances in Ecological Research*, **24**, 241-300.

Marrs, R.H., Hicks, M.J. & Fuller, R.M. (1986) Losses of lowland heath through succession at four sites in Breckland, East Anglia, England. *Biological Conservation*, **36**, 19-38.

Marrs, R.H. & Le Duc, M.G. (2000) Factors controlling vegetation change in long term experiments designed to restore heathland in Breckland, UK. *Applied Vegetation Science*, **3**, 135-146.

May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, **269**, 471-477.

Mazia, C.N., Chaneton, E.J., Ghersha, C.M. & León, R.J.C. (2001) Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia*, **128**, 694-602.

Mc Bratney, A.B. & Webster, R. (1986) Choosing functions for semi-variograms of soil properties and fitting them to sampling estimates. *Journal of Soil Science*, **37**, 617-639.

Meekins, J.F. & McCarthy, B.C. (2001) Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecological Applications*, **11**, 1336-1348.

Miles, J. (1974) Experimental establishment of new species from seed in callunetum in North-East Scotland. *Journal of Ecology*, **62**, 675-687.

Miles, J. (1981) *The effects of birch on moorlands*. Institute of Terrestrial Ecology, Cambridge.

Miles, J. (1985) The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science*. **36**, 571-584.

Miles, J. & Kinnaird, J.W. (1979) The establishment and regeneration of birch, juniper and Scots pine in the Scottish Highlands. *Scottish Forestry*, **33**. 102-119.

Miles, J. & Young, W.F. (1980) The effects on heathland and moorland soils in Scotland and northern England following colonisation by birch (*Betula* spp.). *Bulletin d' Ecologie*, **11**, 233-242.

Milne, B.T., Johnson, A.R., Keitt, T.H., Hatfield, C.A., David, J. & Hraber, P.T. (1996) Detection of critical densities associated with Pinõn-Juniper woodland ecotones. *Ecology*, **77**, 805-821.

Mitchell, R.J., Marrs, R.H., Le Duc, M.G. & Auld, M.H.D. (1997) A study of succession on lowland heaths in Dorset, Southern England: changes in vegetation and soil chemical properties. *Journal of Applied Ecology*, **34**, 1426-1444.

Mitchell, R.J., Marrs, R.H. & Auld, M.H.D. (1998) A comparative study of the seedbanks and successional habitats in Dorset, Southern England. *Journal of Ecology*, **86**, 588-596.

Mitchell, R.J., Marrs, R.H., Le Duc, M.G. & Auld, M.H.D. (1999) A study of the restoration of heathland on successional sites: changes in vegetation and soil chemical properties. *Journal of Applied Ecology*, **36**, 770-783.

Mitchell, R.J., Auld, M.H.D., Hughes, J.M. & Marrs, R.H. (2000) Estimates of nutrient removal during heathland restoration on successional sites in Dorset, Southern England. *Biological Conservation*, **95**, 233-246.

Moore, N.W. (1962) The heaths of Dorset and their conservation. *Journal of Ecology*, **50**, 369-391.

Mozaffari, M. & Sims, J.I. (1994) Phosphorus availability and sorption in an Atlantic coastal plain watershed dominated by animal-based agriculture. *Soil Science*, **157**, 97-107.

Murphy, J. & Riley, J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31-36.

Nathan, R. Katul, G.G., Horn, H.S., Thomas, S.M. Oren, R., Avissar, R., Pacala, S.W., & Levin, S.A. (2002) Mechanisms of long distance dispersal of seeds by wind. *Nature,* **418,** 409-413.

Nolan, A.M. (2000) *Modelling change in the lowland heathlands of Dorset.* PhD Thesis. University of Southampton.

Newton, A.C. & Pigott, C.D. (1991) Mineral nutrition and mycorrhizal infection of seedling oak and birch I. Nutrient uptake and the development of mycorrhizal infection during seedling establishment. *New Phytologist,* **117**, 37-44

Newton, A.C. & Pigott, C.D. (1991) Mineral nutrition and mycorrhizal infection of seedling oak and birch I. II. The effect of fertilisers on growth, nutrient uptake and ectomycorrhizal infection. *New Phytologist,* **117**, 45-52.

Nziguheba, G., Palm, C.A., Buresh, R.J. & Smithson, P.C. (1998) Soil phosphorus fractions and adsorption as affected by organic and inorganic sources. *Plant & Soil,* **198**, 159-168.

Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., de Maeyer, K. & Smit, R. (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology,* **1**, 127-137.

Oliver, F.W. (1925) *Spartina* in Poole Harbour. *Journal of Ecology,* **13**, 74-91.

Pearce, I.S.K. & van der Wal, R. (2002) Effects of nitrogen deposition on growth and survival of montane *Racomitrium lanuginosum* heath. *Biological Conservation,* **104,** 83-89.

Pelham, J. & Mason, P.A. (1981) Nutritional variants of birch. *Forest and Woodland Ecology* (eds. Last, F.T. & Gardiner, A.S.) pp. 78-81. Institute of Terrestrial Ecology. Cambridge.

Perala, D.A. & Alm, A.A. (1990) Reproductive ecology of birch: a review. *Forest Ecology and Management,* **32,** 1-38.

Perez-Moreno, J. & Read, D.J. (2000) Mobilisation and transfer of nutrients from litter to tree seedlings via the vegetative mycelium of ectomycorrhizal plants. *New Phytologist,* **145**, 301-309.

Perez-Moreno, J. & Read, D.J. (2001a) Exploitation of pollen by mycorrhizal mycelial systems with special reference to nutrient recycling in boreal forests. *Proceedings of the Royal Society Series B*, **268**, 1329-1335.

Perez-Moreno, J. & Read, D.J. (2001b) Nutrient transfer from soil nematodes to plants: a direct pathway provided by the mycorrhizal mycelial network. *Plant, Cell & Environment*, **24**, 1219-2001.

Peterson, C.H. (1984) Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist*, **124**, 127-133.

Petraitis, P.S. & Latham, R.E. (1999) The importance of scale in testing the origins of alternative community states. *Ecology*, **80**, 429-442.

Pickess, B.P., Burgess, N.D. & Evans, C. (1992) The management of lowland heath from 1966-1989 at Arne nature reserve, Dorset, UK. *Proceedings of the Dorset Natural History and Archaeological Society*, **114**, 227-232.

Pickett, S.T.A., Collins, S.L. & Armeseto, J.J. (1987) A hierachical consideration of causes and mechanisms of succession. *Vegetatio*, **69**, 109-114

Pimm, S.L. (1991) *The Balance of Nature?* University of Chicago Press. London

Pote, D.H., Daniel, T.C., Sharpley, A.N., Moore, P.A., Edwards, D.R. & Nichols, D.J. (1996) Relating extractable soil phosphorus to phosphorus losses in runoff. *Soil. Science Society of America. Journal*, **60**, 855-859.

Power, S.A., Ashmore, M.R., & Cousins, D.A. (1998) Impacts and fate of experimentally enhanced nitrogen deposition on a British lowland heath. *Environmental Pollution*, **102**, 27-34.

Putman, R.J. (1986) *Grazing in temperate ecosystems, large herbivores and the ecology of the New Forest*. Croom Helm, London.

Pywell, R.F., Webb, N.R. & Putwain, P.D. (1994) Soil fertility and its implications for the restoration of heathland on farmland in southern Britain. *Biological Conservation*, **70**, 169-181.

Pywell, R.F., Webb, N.R. & Putwain, P.D. (1996) Harvested heather shoots as a resource for heathland restoration. *Biological conservation*, **75**, 247-254.

Rackham, O. (1986) *History of the countryside*. Dent, London.

Rand, T.A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient, *Journal of Ecology*, **88**, 608-621.

Rees M. & Hill, R.H. (2001) Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology*, **38**, 364-377.

Risse, P.G. (1995) The status of the science examining ecotones. *Bioscience*. **45**, 318-325.

Robertson, G.P. (1987) Geostatistics in ecology: interpolating with known variance. *Ecology*, **68**, 744-748.

Robinson, R.K. (1971) Importance of soil toxicity in relationship to the stability of plant communities *The scientific management of animal and plant communities for conservation*. (eds. E. Duffey & A.S. Watt) pp. 105-113. Blackwell, Oxford.

Rode, M.W. (1995) Aboveground nutrient cycling and forest development on poor sandy soil. *Plant and Soil*. **168-169**, 337-343.

Rodwell, J.S. (ed.) (1991) *British Plant Communities. Volume 1: Woodlands and Scrub*. Cambridge University Press, Cambridge.

Rodwell, J.S. (ed.) (1992) *British Plant Communities. Volume 2: Mires & Heaths*. Cambridge University Press, Cambridge.

Rose, R.J., Webb, N.R., Clarke, R.T. & Traynor, C.H. (1999) Changes on the heathlands in Dorset, England, between 1987 and 1996. *Biological Conservation*, **93**, 117-125.

Rossi, R.E., Mualla, D.J., Jarne, A.G. & Franz, E.H. (1992) Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological Monographs*, **62**, 277-314.

Satchell, J.E. (1980a) Soil and vegetation changes in experimental birch plots on a *Calluna* podzol. *Soil Biology and Biochemistry*, **12**, 303-310.

Satchell, J.E. (1980b) Earthworm populations of experimental birch plots on a *Calluna* podzol. *Soil Biology and Biochemistry*, **12**, 311-316.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*. **413**, 591-596.

Sedláková I. & Chytrý M. (1999) Regeneration patterns in a Central European dry heathland: effects of burning, sod-cutting and cutting. *Plant Ecology*, **143**, 77-87.

Shaw, P.J.A., Lankey, K. & Hollingham, S.A. (1995) Impacts of trampling and dog fouling on vegetation and soil conditions on Headley heath. *London Naturalist*, **75**, 77-82.

Shurin, J.B. (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology*, **81**, 3074-3086.

Skoglund, J. & Verwijst, T. (1989) Age structure of woody species populations in relation to seed rain, germination and establishment along the river Dalaven, Sweden. *Vegetatio*, **82**, 25-34.

Srivistava, D.S. & Jeffries, R.L. (1996) A positive feedback: herbivory, plant growth, salinity and the desertification of an Arctic salt marsh. *Journal of Ecology*, **84**, 31-42.

Stace C.A. (1997) *New Flora of the British Isles*. Cambridge University Press. Cambridge.

ter Braak, C.J.F. (1995) Ordination. *Data analysis in community and landscape ecology*. (eds. Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R.) pp. 91-173. Cambridge University Press, Cambridge.

Terwillinger, J. & Pastor, J. (1999) Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. *Oikos*, **85**, 83-94.

Thompson, K., Bakker, J. & Bekker, R. (1997) *The soil seedbanks of north west Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.

Traynor, C.H. (1995) *The Management of heathland by turf cutting: historical perspective and application to conservation*. PhD Thesis, University of Liverpool.

Tubbs, C.R. (1974) Heathland management in the New Forest, Hampshire, England. *Biological Conservation*, **6**, 308-306.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225-238.

Uzumov, D.I. (1993) *Introduction to the theory of critical phenomena: mean field fluctuations and renormalisations*. World Scientific, Singapore.

Vera, F.W.M. (2000) *Grazing Ecology and Forest History*. CABI Publishing, Oxford, UK.

Van den Berg, J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W. & Rose, R.J. (2001) Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biological Conservation*, **101**, 217-228.

Van de Koeppel, J., Herman, P.M.J., Thoolen, P. & Heip, C.H.R. (2001) Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology*, **82**, 3449-3461.

Van Vuuren, M.M.I., Aerts, R., Berendse, F. & De Wisser, W. (1992) Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry*, **16**, 151-166.

Veitch, N., Webb, N.R. & Wyatt, B.K. (1995) The application of geographic information systems and remotely sensed data to the conservation of heathland fragments. *Biological Conservation,* **72**, 91-97.

Vrålstad, T., Fossheim, T. & Schumacher, T. (2000) *Piceirhiza bicolorata* – the ectomycorrhizal expression of the *Hymenoscyphus ericae* aggregate? *New Phytologist*, **145**, 549-563.

Wang, H.D., Harris, W.G. Yuan, T.L. (1991) Noncrystalline phosphates in Florida phosphatic soils. *Soil Science Society of America. Journal*, **55**, 665-669.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1-22.

Webb, N.R. (1986) *Heathlands*, Collins, London.

Webb, N.R. (1990) Changes on the Heathlands of Dorset, England, between 1978 and 1987. *Biological Conservation*, **51**, 273-286.

Webb, N.R. (1998) The traditional management of European heathlands. *Journal of Applied Ecology*, **35**, 987-990.

Webb, N.R. & Haskins, L.E. (1980) An ecological survey of heathlands in the Poole Basin, Dorset, England, in 1980. *Biological Conservation,* **17**, 281-296.

Webb, N.R & Hopkins, P.J. (1984) Invertebrate diversity on fragmented *Calluna* heathland. *Journal of Applied Ecology*, **21**, 921-933.

Webb, N.R. & Vermaat, A.H. (1990) Changes in vegetational diversity on remnant heathland fragments. *Biological Conservation*, **53**, 253-264.

Westerhoff, D.V. (1992) *The New Forest Heathlands, Grasslands and Mires – a management review and strategy*. English Nature, Lyndhurst, UK.

White, R.E. (1980) Retention and release of phosphate by soil and soil constituents. *Critical reports on applied chemistry, Volume 2: Soils and Agriculture*. (ed.. Tinker, P.B.) pp. 71-114. Blackwell Scientific Publications, London.

Wilby, A. & Brown, V.K. (2001) Herbivory, litter & soil disturbance as determinants of vegetation dynamics during old field succession under set-aside. *Oecologia*, **127**, 259-265.

Willems, J.H. (1988) Soil seedbank and regeneration of a *Calluna vulgaris* community after forest clearing. *Acta Botanica Neerlandica,* **37**, 313-320.

Wilson, J.B. & Agnew, A.D.Q. (1992) Positive-feedback switches in plant communities. *Advances in Ecological Research*, **23**, 263-336.

Zimmerman, D., Parlik, C., Ruggles, A. & Armstrong, M.P. (1999) An experimental comparison of ordinary and universal kriging and inverse distance weighting. *Mathematical Geology*, **31**, 375-390.