CHAPTER SIX

"This plant is the first that vegetates on naked rocks, covering them with a kind of tapestry and draws its nourishment perhaps chiefly from the air; after it perishes, earth enough is left for other mosses to root themselves; and after some ages soil is produced sufficient for the growth of more succulent and larger vegetables. In this manner perhaps the whole earth has been gradually covered with vegetation, after it was raised out of the primeval ocean by subterraneous fires."


6 Successional Models and Other Primary Sites

This chapter compares the mechanisms and processes of vegetation succession in the bing habitat as observed and measured in this study with examples from literature of successional models and the development of vegetation on other primary sites.

In earlier chapters the causal mechanisms and processes of vegetation dynamics on oil-shale bings have been discussed in relation to various spatial scales: the combined data from all bing sites, the individual bing sites, positions over all sites, positions-on-site and individual quadrats. In Chapter Three classification and ordination established that there were recognisable patterns in the vegetation and in Chapter Four the plant communities within and between the shale bings were associated with physical and chemical environmental gradients. Nutrient availability and lack of competition were established as determining factors in many species associations as was the availability of suitable sites.

Having established some of the mechanisms and processes producing the patterns in vegetation on the shale bings, a more detailed investigation was made using individual species. A series of trials established the complexity of variations in their physiological traits (Chapter Five) and identified the importance of seed production and dispersal as major contributors to the outcome of succession.
The aims of this chapter are to produce a model of the succession patterns on the bings that can be compared with models of succession from the literature and to test whether the plant species strategies and dispersal processes recognised in the primary succession of vegetation on oil-shale bings are similar to those found on other primary succession sites, both natural and man-made by addressing the questions:

Do bings provide acceptable models of primary succession?
Does succession on shale bings follow previously identified ‘rules’?
Do the patterns of succession follow the same trends as those recorded on other primary sites, both natural and man-made?
Does the vegetation on oil-shale bings develop in an analogous way to other island communities, particularly those found on volcanoes and oceanic islands?

6.1 Primary Succession on Bings

A conceptual model of vegetation succession on the oil-shale bings of West Lothian was constructed using the vegetation data collected in this study and the results of the trials to formulate a sequence of early and later seral stages of primary succession on shale bings, both temporal and spatial. The model describes colonisation by plants on shale bings from the date of cessation of dumping. The bings are potentially an inhospitable habitat where establishment of vegetation is affected by steep slopes, altitude and a substrate that differs both chemically and physically from the surrounding area.

6.1.1 A model of bing succession

The model is constructed with a combined hierarchical and modular structure based on the ModMED modelling environment (Legg et al., 1998). The structure of the model allows succession to be described at several levels, reflecting the different scales of processes and mechanisms determining vegetation dynamics, from region to individual plant (Figures 6.1 and 6.2). Several of the individual species modules can be represented within each of the community modules: these symbolise the numbers and diversity of seeds invading from the surrounding landscape. Equally several of the community level modules can be represented within each of the landscape modules: these symbolise the effects of within site variation in physical
and chemical environment on the germination and establishment of the invading species (Legg et al., 1995). Finally at the landscape scale the influence of the size of individual sites, particularly altitude and aspect, on the distribution of invading species produces a vegetation map of the bings within the surrounding countryside.

**Figure 6.1 The hierarchical and modular structure of the bing succession**

The development of different hierarchical levels each with modular components allows variation within modules at landscape level to be described by several alternative bing community level models. In addition several different individual species models can be represented within the same bing community. Adapted from Legg et al. (1998)
Regional scale: the county
The vegetation map of West Lothian. The physical environmental factors of bing size, basal area, height and aspect determine rates of invasion from seed sources in the surrounding countryside. Their effect varies between bings reflecting distance from existing vegetation and the efficiency of dispersal mechanisms and seed production of individual species in other habitats to reach the bare substrate.

Landscape scale: between bing sites
The bing sites are modelled in three divisions according to physical structure:
- Base - where the site meets the existing, lower vegetation and general topography is usually at a slope less than 30° – seeds invade readily from the surrounding landscape in large numbers.
- Middle - the area of the site where general topography is usually at a slope greater than 30° or there is more than 5 metres separation from the existing, lower vegetation – the overall number of invading seeds will decrease with increased distance from local seed source and the proportion of wind and animal dispersed species will increase.
- Top/plateau - the highest area of the site where general topography is usually at a slope less than 30° (often horizontal) or within 10 metres of the summit or within 5 metres below the plateau vegetation – seed numbers and species variation will be lower than base and middle areas and will be almost wholly wind and bird dispersed with a higher number of species invading from great distances.
In all three divisions aspect will determine the direction of prevailing winds and location of nearest seed sources and physical size the bing will govern the dispersal distances.

Community scale: within and between bing sites
Physical environmental factors of management, angle of slope and percentage bare ground and chemical environmental factors of pH and available nutrients combine to determine the success of ecesis and survival within the large scale divisions. These factors influence which of the invading seeds germinate, establish as seedlings and develop into mature plants with the capacity to reproduce. The most successful species will be those whose seeds are deposited in suitable microsites and are best suited to the new environment resulting in:
- Base – composition of surviving plants is similar to the vegetation surrounding the bings with an increase in abundance of species better suited to the new environment and a decrease in abundance or loss of unsuited species.
- Middle – surviving species composition is less representative of the vegetation immediately surrounding the bings due to greater distance from seed sources and higher mortality rates caused by lack of safe sites on steep slopes - this leads to low species diversity and numbers, sparse vegetation and remote individuals of large seeded species (usually small trees and shrubs) whose seeds have become trapped in the substrate. Top/plateau – surviving species will reflect the higher proportions of invading wind and bird dispersed seeds and will often represent well suited species that have been dispersed over great distances – the resulting vegetation is more abundant than in the middle slopes but species composition bears little resemblance to the surrounding landscape, often including locally rare species.
At the base and top/plateau of the bings the survival and establishment of invading species is influenced mainly by the chemical environment and in the middle slopes by the physical environment, particularly disturbance.

Individual scale: within and between plant species
Morphology, seed production and dispersal mechanisms of individual reproducing species determine their colonisation success. The size and composition of individual vegetation patches and continued successful invasion of individual species is influenced at this level: once established individual successful species contribute more to the seed input and amplify the variations in vegetation composition caused by the larger scale processes described above.

Figure 6.2: Descriptive summary of the bing succession model

The vegetation succession of the bings is summarised in terms of region, landscape, bing community and individual plants. The smaller scalar levels describe mechanisms and processes within, and contributing to, the large-scale processes. Adapted from Legg et al. (1998).
6.1.2 Describing the bing succession

The model simplifies the complex series of mechanisms and processes that are interacting at each spatial and temporal level of the bing succession. A more detailed description of the succession was compiled: predominantly from the data collected in the baseline survey and giving more weighting to evidence collected from the unmanaged sites as these were considered to be more representative of natural invasion.

Originally the whole surface of the bing substrate was totally barren and contained no organic matter; the same is true for many other industrial waste sites. On the bings the unweathered shale has been deep mined and heated to 500°C making it completely sterile: there are therefore no organisms, spores or seeds in the substrate. The blue substrate of unweathered shale (blaes) can now only be seen after a landslip or when other major disturbance reveals the anaerobic layers of subsoil, and is the colour of newly dumped material. The shale weathers rapidly and the characteristic red of weathered shale (red blaes) is the colour usually associated with the shale bings. The change in colour is caused by oxidation of elements in the substrate when they are exposed to oxygen and moisture in the air.

Initial invasion is stochastic: individual plants developing from available seeds wherever they fall and most representing species from the surrounding agricultural and urban landscape. Near neighbours from local sources make a greater contribution to the seed rain than more distant seed sources and have an increased probability of colonisation. The numbers of seeds produced by individual plants, the abundance of the species and dispersal mechanisms all affect the amount and composition of the seed rain. With increased distance (both length and height) from the source, the total numbers of seeds decrease while the proportion of wind and bird, or other animal, dispersed seeds increase. This combination of events and processes is theoretical as no data were collected from seed trapping in this study. Locally abundant species, like *Vicia cracca* and *Achillea millefolium*, that are limited in distribution to the lower slopes of the bings, even after more than 50 years of succession demonstrate that most seeds produced are deposited very close to the
parent plant however, and only a small proportion of seed from the surrounding landscape will be carried beyond the lower slopes of the bings to the middle slopes and summits of the bings.

Vegetation builds up around the pioneering individuals that first invade the site, and as plants become established and reproduce the seed rain gains a second component from seed produced within the site. In-site seed production is expected to remain the secondary seed source for many years because the vegetation remains sparse (Urbanska et al., 1998) nonetheless it determines the rapid incursion of individual species like *Reseda luteola*, *Senecio viscosus* and other transitory species that are rare in the surrounding landscape but suited to the bing environment. The result of these processes is evident from the patchiness of invasion, particularly the mosaic of vegetation interspersed with large areas of bare substrate after more than 50 years of colonisation on the unmanaged bing sites, and are the main cause of the variation in species composition between the base, middle and upper sections of the sites.

At the base of the bing the seed rain is expected to reflect species composition and abundance, plus seasonal fluctuations in seed production, of existing near neighbours in the local vegetation as described in the previous paragraph. The composition of surviving plants is similar to the local vegetation with an increase in some species that are better suited to the new environment and a decrease or total loss of species that are unsuited. Common agricultural escapes, like oil-seed rape, that are commonly recorded on road verges and other disturbed ground throughout the county have not been recorded even on bings that are surrounded by this crop. Species diversity and abundance is high in comparison with the rest of the bing site. When the spatial distribution of established seedlings is clustered to the extent suggested by the theories for invasion, germination and establishment presented in Chapter One (section 1.4), then competition should rapidly become an important factor in the survival of the species represented in areas of the bings where vegetation is well developed. There is no evidence of this successional stage developing from the data collected on the bings, although there are areas at the base of all of the sites where ground cover is complete and interactions between individual plants and species must be influencing the distribution of vegetation.
On the middle slopes of the bing the composition of seed rain will change with distance (length and height) from the local seed source, both in abundance and in composition. The overall number of seeds will decrease and the proportion of wind, and bird or animal, dispersed seeds will increase. The proportion of large seeds will decrease and only be represented by bird or animal dispersed species (Again this is hypothetical for the reasons described previously). The numbers of surviving individuals (per metre squared for example) on the middle slopes decrease with distance from the base and there is an increase in the proportion of species dispersed by wind and birds or animals, reflecting the change in composition of the seed rain. Where the sides are steep and the substrate is unstable there is a low survival rate in many species because of lack of safe sites as described by Jumponnen et al. (1999). Species diversity is lower than at the base of the site and vegetation is very sparse. Lack of competition and limited seed sources leads to strange combinations of plant species. On the middle slopes of unmanaged sites, patches of *Fragaria vesca* and *Leucanthemum vulgare* (wild strawberries and ox eye daisies) cover 100 m$^2$ patches of substrates and form a common combination on many sites although there is a distinct lack of other species (Figure 6.3). *Sedum acre* (biting stonecrop) also covers large areas but only on one bing site, Greendykes (Figure 6.3). This species is occasionally recorded in West Lothian, on dry-stone dykes and rocky outcrops (Smith et al., 2002), although this colony may be a garden escape. As already noted *Reseda luteola* (weld) is common to all bing sites, frequently in association with *Senecio viscosus* (sticky groundsel) although both of these are very rare in the surrounding landscape (Smith et al., 2002) (Figure 6.3). These and other similar bing vegetation 'types' have very sparsely distributed, or no, grass species associated with them. Continuing with the vegetation model on the middle slopes, there are also frequent but isolated, individual representatives of large seeded species, usually trees or shrubs, suggesting that a seed has become trapped and has germinated in a suitable microsite instead of rolling down the slope or being eaten. This appears to be the main situation when 'safe sites' are more important to the vegetation composition than seed dispersal and production. The vegetation patterns and species groupings are very dynamic, often due to physical disturbance, and are unlikely to become stable for many decades, even centuries.
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Figure 6.3  Examples of middle slope, bing vegetation types

The slopes of large, high bing sites like Greendykes, Five Sisters, Niddrie and Faucheldean, are unlikely to stabilise and the species composition of the middle sections of these bings will remain different from the vegetation at both the top and base. The middle slopes of smaller, lower bings like Mid Breich and Oakbank are likely to lose any distinctive, middle range of species as these areas become transition zones between top and base vegetation.

At the summit of the bings, on the top and plateau areas, numbers and abundance of species in the seed rain will initially be much lower than either the base or middle areas and almost wholly composed of wind and bird dispersed seeds. There will be a higher proportion of seeds from species outwith the vegetation surrounding the site represented because of this. Some species with particularly light seeds or spores will

<table>
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<th>Senecio viscosus and Reseda luteola</th>
<th>Sedum acre</th>
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<td>These represent some of the unusual vegetation combinations that are common to the middle slopes of the bing sites. Although they are comprised of locally rare and occasionally alien species, they are novel, natural communities.</td>
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Fragaria vesca and Leucanthemum vulgare
be carried from sites many kilometres distant. Food seeds and berries will be carried similar distances. The baseline survey data showed that 78% of the species recorded in the top and plateau recording quadrats employ wind or animal dispersal mechanisms compared with 66% of species recorded on the bings as a whole. There are still many local species but there are also a higher proportion of species dispersed from great distances. These are often locally uncommon or even rare species like *Epipactus helleborine, Orchis mascula* and *Platanthera chlorantha*, some of the orchid species that have been recorded on Faucheldean (Muscott, 1989). The proportion and, in some species, number of surviving individuals is high compared with those on the middle slopes, as survival is no longer limited by slope and the substrate is more stable. Competition is currently (2004) not a major limiting factor in the succession on the summits, but is expected to gradually play a part in stabilising the developing communities over time. The overall composition of vegetation on the tops and plateaux bears little resemblance to that at the base and middle reaches of the larger bings, or to the surrounding vegetation due to the predominance of wind and animal dispersed species.

The tops and plateaux of sites are where important refuge sites have developed for rare and endangered species of the region, both plant and animal. The plant communities include many locally rare species that are better suited to the different physical and chemical properties of the substrate on the bings and also invaders from other regions with similar substrates, like coastal dunes. Examples of these are *Anthyllis vulneraria*, first recorded in West Lothian in 1999 when it was found on Mid Breich bing. The nearest recorded seed sources are sand dunes at least 20 km away (Figure 6.4a). This species is rare throughout Scotland (Smith *et al.*, 2002; Preston *et al.*, 2002). *Lycopodium clavatum* is not so rare (Figure 6.4b) but had not been recorded in Central Scotland since before 1930 until it was discovered growing on several bing sites in the early 1970's (Smith *et al.*, 2002).
6.1.3 Seeds

The production and dispersal of seed are the main processes driving this model of primary succession on the bings. Seed rain from vegetation surrounding the site determines the species range and abundance of the initial colonisation. This, when combined with secondary seed production from established plants and long range seed dispersal from similar ecosystems, adds to the diversity of species within and between the 19 bings. Seeds from all of the sources contribute to the seed bank and can be retained for many years. The trials and measurements described in Chapter Five demonstrated the extent that mechanisms of seed ecology vary both within and between species and also that some of the variation is influenced by physical and chemical variables. Seed dynamics, however, are only one aspect of the succession and to truly reflect the process the model must include the effects of morphology and nutrient availability on the competitiveness and continued success of individual species.

6.1.4 Physiological variation within species

Once established, individual species can have greater seed input to patches within the site than species from nearby communities (Reseda luteola and Senecio viscosus). Perennial species, like Leucanthemum vulgare, spread vegetatively from an initial colonisation to gradually occupy more space, giving them a selective advantage over...
incoming species. Conversely, as the vegetation contributes to soil amelioration, some species that have remained dormant in the seed bank and previously unsuccessful species that are present in seed rain, will take advantage of the changes in available resources. Gradually, dominant species will become noticeable but due to the stochastic nature of the invasion processes these will not be the same species on all sites.

Vegetation types that are dependent on the suitability of the site for the initial invading species develop. Competition, both inter- and intra specific, slowly becomes an increasingly important factor in the development of plant communities. As demonstrated in Chapter Three, these species assemblages rarely resemble any existing or standard community-type: National Vegetation Classification for example (Rodwell, 1991a; 1991b; 1992; 1995; 2000).

The inherent plasticity of nine species was demonstrated in Chapter Five (*Trifolium campestre*, *Medicago lupulina*, *Leucanthemum vulgare*, *Tripleurospermum inodorum*, *Holcus lanatus*, *Plantago lanceolata*, *Centaurea nigra*). The causes of the variability in the physical properties of the species that were measured (plant height, flower-head and seed production, fecundity) were not always clarified but the amount of the variance that was explained by variation in the physical and chemical environment was described (Chapter Five). Morphological differences and reproductive success within these species plays a large role in their distribution and the resulting vegetation patterns. When habitat factors are less favourable the patterns caused by morphology in individual species changes. On shale bings for example, extreme physical demands can be made on shallow-rooting species and seedlings by the rapid drying out of the soil/substrate, even when there is considerable rooting depth.

### 6.1.5 Reactions and interactions

The physical effects of wind, rain and changes in temperature influence soil structure and, to a lesser extent, the nutrient content in the substrate. These abiotic reactions and the interactions between them are important to the bing succession as weathering has a more rapid and direct effect on the substrate structure than vegetation in the
early stages. Large laminar fragments in the top few centimetres of the bings are rapidly split into layers by a combination of freezing and thawing in winter and drying and wetting in the summer. Once separated the thin layers quickly crumble to become a more suitable growth medium for invading species. Any high concentrations of salts retained from the oil extraction processes are rapidly leached from the bing surface by rain (Chapter Three).

The colonising vegetation modifies the microclimate by shading and transpiration, and the influence of some species is intensified by allelopathy, the ability to produce toxins that inhibit the growth of other species, and sometimes their own seedlings, in the immediate vicinity. Allelopathic interactions are known to occur in several of the species that have been recorded on the bings. *Plantago lanceolata*, one of the nine species studied in Chapter Five, was demonstrated to interact, both positively and negatively, with many other species by Sagar and Harper (1961). Myster and Pickett (1992) presented evidence of strong allelopathic interference by grass species on a range of other vascular plants, for example a negative effect of *Dactylis glomerata* on *Rumex acetosella*. They also demonstrated the negative allelopathic effect of *Poa pratensis* on *Plantago lanceolata* and of *Trifolium pratense* on *P. pratensis*, and the positive effect of *Plantago lanceolata* on *Achillea millefolium* in a series of pairwise experiments. The effect of allelopathy was not measured in relation to the bing succession in this study but will have increased influence on species composition as vegetation cover intensifies and there is more competition for space.

The bing succession is highly complex. The initial invasions and aggregations of species have developed into a mosaic of patterns of vegetation over a range of spatial scales. The combined hierarchical and modular structure of the bing succession has described a model of bing succession (Figure 6.1 and 6.2) that can be evaluated with published successional models. The described mechanisms and processes of the vegetation dynamics of the succession on the bings can be compared with descriptions of other successional communities from literature.
6.2 Succession Models in Literature

Regular, short-term changes in vegetation were recognised and utilised by human, hunter-gatherer ancestors, and determine behaviour patterns in animals. Farmers have exploited seasonal variation in vegetation in the production of crops and management of animals for thousands of years. Around 300 BC Theophrastus produced the first written record of the spatial and temporal variations in the vegetation of river floodplains (Wali, 1999). The first scientific writing on succession is attributed to William King (1685) in a paper presented to the Philosophical Transactions of the Royal Society, London. This is a description of the long-term orderly patterns of vegetation change in an Irish bog. Modern authors have decried this work as representing "common knowledge" (Golley, 1977) but this is an unjust criticism considering the level of much of the scientific research that was being published at the time.

Models of primary succession are not a new concept in natural sciences. Erasmus Darwin (the grandfather of Charles) introduced an outline model in the notes accompanying a set of rhyming couplets on Lichen in his book 'The Botanic Garden' (Introductory quote to this chapter. Darwin, 1879) which, despite its brevity, describes the stages of succession from denuded substrate to climax vegetation.

6.2.1 Descriptive models

Present day models of primary succession began in the early twentieth century with the pioneering work of Clements. Although the earliest stages of colonisation were recognised before this time, they were of no practical use to humans and so were not considered worthy of research. The first models of succession were mainly descriptive. As outlined in Chapter 1, Clements (1916) described a conventional view of the successional process in six sub-processes (seral stages).

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1 For example, an article 'proving from experiments' that larger wheels move more easily over obstacles (A member of the Philosophical Society, 1685), and another describing the difference between freshwater and seawater ice (Lister, 1685), appeared in the same volume of The Philosophical Transactions of the Royal Society of London as the article by King.
1. Denudation – the creation of a new environment.
2. Migration (immigration in a primary succession) – the arrival of spores and seeds.
3. Ecesis – the germination of seeds and establishment of the seedlings.
4. Competition - the contention between and within species for resources: for example nutrients and space.
5. Reaction – the modification of the environment by the vegetation from processes like transpiration, shading and mortality of individuals.
6. Stabilisation – the eventual development of a climax vegetation.

I use Clements’ (1916) model as the main example because it is the most frequently referred to, either in whole or in part, by other authors when describing succession. "At the simplest level, the mechanisms outlined by Clements in 1916 remain valid today" (Wali, M, 1999). The model is wholly deterministic and each of the sub-processes leads forward to the next, finally culminating in a self-maintaining and stable, climax type of vegetation. When the bing model of succession is compared with Clements’ model the first three sub-processes are comparable and each leads progressively on to the next, however, they are also happening concurrently, in different parts of the bing sites and seemingly all of the time.

New successional seres originate when an initiating process produces a bare area that is capable of ecesis and has physical factors that are essentially different from the surrounding area (Clements, 1916 - Chapter III). This describes the bing substrate immediately after dumping but also after any major disturbance event such as erosion. The sterile, bare area is first colonised by the process of migration/immigration, the movement of propagules from the parent area into the new habitat. The position of the bare area and the communities of the surrounding landscape are both briefly considered by Clements. In the bing model distance from seed source, particularly altitudinal, is shown to influence both the rate of invasion from the surrounding landscape but also, more significantly, the dispersal agencies of species that successfully colonise the tops and plateaux. These are predominantly animal or wind dispersed species in comparison with the species for the bings as a whole (Section 6.1.2). Clements gives an example of the ease with which forested areas
can be temporarily invaded by alpine species from nearby high ground and stresses the difficulty of species invading up a slope, suggesting that only man, animals and the wind can overcome this effect that supports the observations made in the description of bing succession.

Once the initial invaders have become established, the colonies develop by the process of association. The interaction of these two processes, establishment and association, originates each successional stage by introducing new species and establishing them as characteristic or locally dominant components of the vegetation. The study of bing vegetation did not reveal dominant species but there was evidence of species characteristic of particular conditions within the bing sites, as discussed in Chapter Four. The results of the field measurements in this study showed that the mechanisms of seed production and dispersal are very strong influences on the processes of invasion and species association, a finding that is supported by Clements (1916 - Chapter IV).

"Ecesis is the adjustment of the plant to a new home" (Clements, 1916). In the field measurements and greenhouse trials on the germination success and establishment of species associated with the shale bing succession the processes of ecesis, variability in plant height, flower-head and seed production and fecundity, were demonstrated to have different influences on the success of individual species (Chapter Five). The high loss of seedlings was also discussed in the previous chapter, both the loss to predators and to desiccation. Clements describes the processes of ecesis in great detail and corroborates the findings of this study: stressing the importance of habitat on germination success, how seed dormancy can overcome temporarily unfavourable conditions and the massive loss of seeds to predation.

Sub-processes four and five are less distinctly separate in the bing model than described by Clements. Interactions between species and their reactions to the environment on the bings are a series of complex processes that are happening concurrently with stages two and three of the succession model. Indeed in the bing model, as with many primary successions, there is a frequent denudation of large areas due to the physical instability of their steep slopes. Clements suggests that well
adapted species that form mats or rosettes and have long tap-roots will ultimately stabilise the substrate on these habitats and allow a continuation of succession through to climax (Clements, 1916 - Chapter V). Such species are frequently recorded on the bings and are often abundant and the description fits the unusual association of *Leucanthemum vulgare* and *Fragaria vesca* described in Section 6.1.2. Although Clements later appears to contradict his earlier statement by declaring that the significance of the stabilisation mechanism is only revealed when the cover is destroyed.

In a primary succession each pioneer exerts some reaction in or on the substrate, through removal of nutrients and water or by shading for example. Clements argues from this that the reactions caused by pioneer species alter the microenvironment until habitat becomes unfavourable to themselves, or becomes more favourable to later invading species. It is difficult to accept that this would make evolutionary sense for species in any habitat, including the bings, as it must ultimately lead to their extinction. The inherent plasticity of many early successional species is a trait that has possibly evolved to prevent their demise under such circumstances.

The final stage in Clements' succession model is stabilisation, the eventual development of climax vegetation. The environmental changes that are caused by reaction and interaction between species in earlier sub-processes become "more favourable to the occupants than the invaders and the existing community becomes permanent constituting a climax." (Clements, 1916). The data collected in this thesis suggests that the bing succession is either still developing towards climax vegetation or that the final stage of Clements' model can not be achieved in all successions. However stability is a relative term that is scale dependant, both spatially and temporally.

Bings are far short of achieving Clements’ idea of climax, but there is considerable difference of opinion in the literature on the final outcome(s) of the vegetation development in succession and also on the sub-processes within the successional processes (Gleason, 1927; Bradshaw *et al.*, 1975; Austin, 1977; Gray *et al.*, 1987; Glenn-Lewin, *et al.*, 1992; Eriksson and Eriksson, 1998; and many others). Connell
and Slayter (1977) proposed three alternative succession models based on the ability of species to modify the environment.

The facilitation model describes a succession where only certain species are able to establish on a new site and these early invaders then modify the environment making it better suited to other species. The succession continues on a forward progression towards stabilisation. This describes the succession found in the middle of the bings where species that are particularly suited to the habitat have established. The vegetation on these slopes may “progress” if the substrate becomes more physically stable as a result of this initial colonisation and this could lead to increased invasion from more competitive species that are established on the already stable lower slopes.

The tolerance model describes a succession where any species that survives can establish. The sequence of species is determined solely by their life-history characteristics and implication is that newly invading individuals of one species, if they survive and establish, will always be more tolerant of the modified environment than those species already present. Ultimately only one species will remain which cannot be invaded unless individuals die or are killed, resulting in a stable, climax vegetation. The first part of this model describes the findings of Chapter Three in this study. There was a clear link between species with the same life history characteristics within the bing habitats. However there was no evidence to suggest that more tolerant (competitive) species or groups were excluding others.

The inhibition model describes a succession where the initial colonising species inhibit the invasion of subsequent species by securing all of the available space or resources. New individuals are only able to invade on the death of the original species and may be either the same species or a new species. This model will also eventually lead to stable, climax vegetation, as short-lived species are replaced more often than long-lived species. This model does not represent any described sequence of events within the bing succession. There is no evidence of initial colonising species holding a site and preventing invasion by other species except in very small areas.
These three models appear to be variations within Clements’ 1916 model in that each apply a particular set of rules to the interaction, reaction stage of succession. Each of these will be valid in particular circumstances and seem to occur in parallel in the overall bing succession. However they all suggest forward progression of succession to an ultimate stability of vegetation, a climax that is not evident even in the oldest bing, Mid Breich, which has been unmanaged since cessation of dumping in 1915.

Lawton (1987) adds a fourth model, the random colonisation model. Succession involves chance survival of different initial invading species and subsequent random colonisation by new species. Species then grow and mature at different rates. There is no facilitation and interspecific interaction is not important. This model also seems to describe some of the succession of the bing vegetation, particularly the initial random invasion and morphological variation found between and within species. The model does not, however, make provision for the consequent development of recognisable and recurring patterns within succession or the concept of assemblage of species, when established individuals of annual species, for example, have a greater input into local seed rain resulting in extension of the patch dominated, or individuals of perennial species will extend their group vegetatively.

### 6.2.2 Numerical models

Numerical techniques are used extensively in descriptive ecology to simplify multivariate data, to assist in hypothesis generation and to define the limits of extrapolation for results of experiments on a particular vegetation type (Austin, 1972). In this thesis, gradients, correlations and multivariate analyses were used with varying degrees of success to study the structural variations of vegetation and relate these to measured environmental factors. By these methods almost 50% of the variation in species distribution within and between bings was explained. When analysing abundance data using multivariate analysis, CCA as in this study, the percentages are expected to be at these levels (ter Braak and Šmilauer, 2002) and ordination that explains even lower percentages “may be quite informative”. The remaining variation could be attributed to a wide range of factors, some of which were discussed in earlier chapters and others which may not have been considered.
Early approaches to investigate non-randomness in vegetation patterns were based on the assumption that the main causal factor was vegetative propagation (Kershaw, 1963). Statistical evidence of non-randomness (as produced by Monte Carlo Analysis) was used in this thesis solely to demonstrate that particular small groups of species appeared together more frequently than expected by chance. As pointed out by Kershaw (1963) demonstration of the existence of non-randomness does not assist the understanding of the underlying mechanisms and processes causing non-random distribution. Numerical models can be used to provide empirical measurements within the structure of a subjective descriptive successional model. Difficulties arise with these analytical techniques because they are based on a mathematical model of linear correlation between sets of vegetation and environmental variables.

Multivariate correspondence analyses overcome the problems of violation of the assumption of linear response by adopting a unimodal response curve (ter Braak and Prentice, 1988). However despite their mathematical complexity the analyses can only be used to support existing or generate new hypotheses, they cannot use data to describe succession unless the data include a known time-line or chronosequence. In Chapter Four, Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) confirmed many of the vegetation patterns that had been detected using more simple mathematical tools and demonstrated the extent that environmental components were the correlated with the variation. The analyses also drew attention to species groupings that had not previously been evident. A mathematical assumption that can be problematic within correspondence analyses is that environmental factors are included as independent variables, and there is no consideration of detrimental, beneficial or otherwise proactive relationships between them.

6.2.3 Experimental models

The experimental approach to discovering the mechanisms and processes of succession is sometimes no more effective than the mathematical descriptive approach. The consequence of variation in each mechanism and process could be measured on every species in every community in every sub-process of the
succession. This is clearly impractical. However in experimental models the effects of many components of succession, competition for example, are often gauged on the measured reaction between only two species under artificial conditions. This is true of experimentation throughout the twentieth century from Gause's (1934) classical work on two species of laboratory Paramecium to more recent work on plant competition (Damgaard, 1998). Gibson et al. (1999) also suggest that simple pairwise species mixtures can be used to assess the effects of different treatments on competition and propose that "unless plant interactions can be demonstrated under green-house conditions they are unlikely to be of importance". Designs for multiple species glass house experiments tend to suffer from lack of randomisation or lack of independence (or both). Field conditions are so complex that manipulative experiments and field trials have to be designed to run over many seasons with a large number of replications and controls. When field measurements and measurements from greenhouse trials for the same trait are compared they often bear no resemblance to each other. As discussed in Chapter Five (5.7.3) for example, glasshouse experiments have been shown to result in higher germination rates than field trials for arable weeds (Roberts & Ricketts, 1970; Graham & Hutchings, 1988), and in this study when no Centaurea nigra seedlings emerged from the bing seedbanks germinating under greenhouse conditions yet large numbers of plants, including seedlings were recorded in the field.

6.3 Post-industrial Sites of Primary Succession

This section will compare the mechanisms and processes of succession described in the model of the bing vegetation with man-made waste and post industrial sites where primary succession has been described in literature (Salisbury, 1953; Marrs and Bradshaw, 1993; Zhang et al., 2001). Despite being described as bearing "a strong resemblance to cones of ash thrown out by modern volcanoes" and being "indeed volcanic in some respects" (Cadell, 1925) the bings are very much post industrial sites (Chapters One and Two) and, as determined in Chapter Four, the substrate of shale bings shares many physical properties with that of other types of large-scale industrial waste (china clay waste, colliery spoil, gravel pits, derelict land.
The range of post-industrial sites is as varied as the number of industries that created them.

In West Lothian there are 458 ha of designated derelict land, including 139 ha of oil-shale bings, and the total area of dereliction for Scotland is 7,741 ha (Scottish Executive, 2004). Most of the wasteland in Britain has resulted from the decline or disappearance of industries established during the Industrial Revolution and coal spoil forms some of the largest man-made waste sites in Europe.

6.3.1 Coal

There are two main methods of mining coal that each result in a different type of spoil: strip-mining and deep mining. Strip mining in the United Kingdom is small scale and current (2004) government legislation requires that restoration is closely monitored to the extent that arable crops can often be successfully grown immediately after the overburden has been replaced. This means that there is no opportunity to observe or record natural succession. In central Europe, however, large scale strip mining for lignite (brown coal) is carried out on a massive scale.

Prach et al. (1999) describe a succession on the mine spoil sites of North West Bohemia in the Czech Republic with steep, free-draining slopes in three stages beginning with a bare substrate and no vegetation at year one, followed by a stage with dominant perennial herbs from 2 years onward with a third stage of dominant grasses developing from fifteen years. The description of limited species assemblages and cover recorded on middle slopes in the succession model of vegetation on the bings, for example Sedum acre or Fragaria/Leucanthemum mix, corresponds to the early seral stage on steep slopes described by Prach et al. (1999).

In sites with no steep slopes, but still free draining, they describe a seven-stage succession (Table 6.1). Succession on these sites is rapid by comparison with that recorded on the shale bings and after thirty years there is a near complete herb layer cover dominated by Arrhenatherum elatius, with Betula pendula and Sambucus nigra constituting a strong woody species presence (Prach et al., 1999). In contrast a stand of B. pendula has established naturally in one small flat area at the base of Mid
Breich bing over the last twenty years, although it is now almost 90 years since dumping ceased, and there are a few individuals of *S. nigra* established at Greendykes after 80 years. There is, however, strong evidence that the succession on the strip-mine spoil of North West Bohemia is following the sub-processes as those found on the shale bings, although the exact species compositions are not the same and the rate of succession is much more rapid in the Czech Republic.

Table 6.1 The seven stage succession of coal strip mine spoil

<table>
<thead>
<tr>
<th>description of seral stages</th>
<th>years from cessation of dumping</th>
<th>typical species</th>
<th>comments</th>
</tr>
</thead>
</table>
| initial stage or pioneer plants | 1-3                            | *Polygonum lapathifolium**,  
|                                |                                 | *Senecio viscosus*  
|                                |                                 | *Chenopodium spp.*  
|                                |                                 | *Atriplex sagittata*  |
| initial stage or pioneer plants | 4-6                            | *Carduus acanthoides**,  
| initial stage or pioneer plants | 7-8                            | *Sisymbrium loeselii*  
| stage with dominant perennial herbs | 9-16                           | *Tanacetum vulgaris*  
| stage with dominant grasses | 17 onwards                      | *Artemisia vulgaris*  
|                                |                                 | *Cirsium arvense*  
|                                |                                 | *Calamagrostis epigeios*  
|                                |                                 | *Arrhenatherum elatius*  
|                                |                                 | *Agropyron repens*  |
| stage with shrubs            | 17 onwards                      | *Sambucus nigra*  
|                                |                                 | *Rubus spp.*  
| stage with trees             | 17 onwards                      | *Betula pendula*  
|                                |                                 | *Acer pseudoplatanus*  
|                                |                                 | *Fraxinus excelsior*  |

Richardson (1975) indicates that in coal spoil from deep-mined coal extraction the physical properties of the substrate control plant growth and the rate of succession, particularly particle size and water holding capacity. Immediately after tipping the coal spoil is free draining, like oil shale spoil, but weathering rapidly reduces permeability so that the surface becomes waterlogged in wet weather and in dry conditions a crust forms that does not allow seedling penetration. The greatest
difference between the substrate of coal spoil heaps and the bings, however, is pH. The oil-shale spoil is neutral to basic on all bing sites, even after more than ninety years, however acidity develops extremely rapidly on most coal spoil heaps (Gemmel, 1977) although Hall (1957) recorded tips that were still neutral after 40 years. These differences in the chemical properties oil-shale and coal spoil do not affect the successional process but influence the species composition of the communities that develop. The literature describes two main vegetation outcomes of succession on coal spoil (Table 6.2), the first leads to woody communities (Hall, 1957; Titlyanova and Mironychevka-Tokareva, 1990) and the other arrests as grass- or heath-land (Hall, 1957; Weigleb and Felinks, 2001). The successions follow the same initial stages but demonstrate the variability of time scale that can occur between the sub-processes in different geographical regions, although this is less extreme in the woodland sites.

**Table 6.2 Examples of temporal variation in successional stages of coal spoil**

*The two main vegetation outcomes on coal spoil described in the text: one succession results in woodland and the other succession arrests as a grass/heathland. Adapted from Hall, 1957; Titlyanova and Mironychevka-Tokareva, 1990; Weigleb and Felinks, 2001.*

<table>
<thead>
<tr>
<th>reference</th>
<th>pioneer</th>
<th>forb/ grass</th>
<th>grass/ scrub</th>
<th>climax (sic)</th>
<th>vegetation type</th>
<th>region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hall, 1957</td>
<td>10-15</td>
<td>15-80</td>
<td>60+</td>
<td></td>
<td>grass/heath</td>
<td>NE. England</td>
</tr>
<tr>
<td>Titlyanova &amp; Mironychevka-Tokareva, 1990</td>
<td>4-15</td>
<td>15-40</td>
<td>30+</td>
<td></td>
<td>meadow steppe</td>
<td>Siberia</td>
</tr>
<tr>
<td>Hall, 1957</td>
<td>4-10</td>
<td>10-30</td>
<td>30-100</td>
<td>80+</td>
<td>oak woodland</td>
<td>SW. England</td>
</tr>
<tr>
<td>Weigleb &amp; Felinks, 2001</td>
<td>4-10</td>
<td>10-20</td>
<td>20→</td>
<td>100+</td>
<td>woodland</td>
<td>Lusatia, Germany</td>
</tr>
</tbody>
</table>

On the oil-shale bings there is evidence of different successional stages occurring simultaneously within sites and some sites retain pioneer vegetation after more than 90 years, suggesting that the temporal discrepancy in sub-processes is being driven by variation in the environment.
6.3.2 China clay (Kaolin)

The waste material from the production of china clay (kaolin) is mostly deposited as rolling hills of quartz crystals (sand) interspersed with mica lagoons and occasional dumps of overburden, although these are usually covered with sand (Bradshaw et al., 1975). Much of the research in Britain has been carried out on the sand deposits, by the Department of Botany in the University of Liverpool (Bradshaw et al., 1975; Marrs et al., 1980a; Roberts et al., 1980; Marrs and Bradshaw, 1980; Marrs et al., 1980b; Roberts et al., 1981; Marrs et al., 1981). This series of papers describes ecosystem development in relation to nutrient availability in the substrate. There is also some literature from the University of Georgia in the United States of America on the restoration of overburden (May, 1975; Haddock, 1997).

The quartz sand deposits studied by the Liverpool group are large mounds of open free-draining material in an area of high rainfall so that surface desiccation occurs only in summer making them physically similar to shale bings. The chemistry of the substrate is also similar to the bings, the main exception being the significantly lower levels of calcium, which are reflected in the lower measures of pH (Table 6.3).

Table 6.3 Comparison of the substrate chemistry in China clay waste and oil-shale spoil

The results of nutrient analysis of substrate at two china clay spoil heaps, Maggie Pie and Lee Moor (adapted from Bradshaw et al., 1977), and two shale bings, Mid Breich and Greendykes (from this study). The mean measure of K, Mg, Ca, P and N in parts per million and the pH are recorded for each site. All four sites are unmanaged. * Nitrogen values were not available for the two unmanaged bing sites but measurements at two managed bings were less than 2 parts per million.

<table>
<thead>
<tr>
<th>site</th>
<th>substrate</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
<th>P</th>
<th>N</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maggie Pie</td>
<td>china clay</td>
<td>10</td>
<td>16</td>
<td>85</td>
<td>2.0</td>
<td>9</td>
<td>4.5</td>
</tr>
<tr>
<td>Lee Moor</td>
<td>china clay</td>
<td>8</td>
<td>14</td>
<td>90</td>
<td>4.6</td>
<td>11</td>
<td>4.5</td>
</tr>
<tr>
<td>Mid Breich</td>
<td>oil-shale</td>
<td>11</td>
<td>17</td>
<td>300</td>
<td>1.9</td>
<td>*</td>
<td>6.6</td>
</tr>
<tr>
<td>Greendykes</td>
<td>oil-shale</td>
<td>21</td>
<td>51</td>
<td>398</td>
<td>5.1</td>
<td>*</td>
<td>6.5</td>
</tr>
</tbody>
</table>

The lower pH in the china clay waste also results in colonisation by a different group of vascular plant species. There is a slow invasion by calcifuge grasses and shrubs, a strong legume presence and Salix caprea and Rhododendron ponticum survive well in the later stages of succession. Bradshaw et al. (1977) suggest that the climax
vegetation will be acid oakwood. While this is similar to the findings on some coal spoil sites (Table 6.2) it is not comparable with the recorded vegetation on shale bings.

Roberts et al. (1981) outlined successional stages in natural colonisation of china clay waste in their description of vegetation changes on a group of sand tips ranging in age from 16-116 years. Most of the species recorded on the china clay waste are common native species and many of them also appear on the species list for the shale bings (Appendix 6). There are no annuals included in the vegetation descriptions, however, and eight species are recorded at more than 10% cover, all trees or shrubs. On the bing sites annuals were recorded in most areas and only two species, the grasses Holcus lanatus and Deschampsia flexuosa, were recorded at more than 10% cover. A low species diversity was recorded in the china clay waste study with the maximum number of species in any quadrat being 13, compared with 28 on the shale bings (the mean number of species over 340 bing quadrats was 13), and the china clay sites seem more homogeneous.

Recent studies, in the south eastern United States, to establish the soil conditions that encourage pine growth on kaolin spoil, compared stands of high productivity with those of low productivity (Haddock, 1997). Nutrient and physical properties of the spoil were measured but none of the measurements indicated significant or consistent differences in the soils where faster tree growth occurred. Similar inconsistent information was encountered in this study of the shale bings when trying to relate variation in the chemical and physical properties of the substrate to morphological variance in individual plant species (Chapter Five).

6.3.3 Quarries

Man-made primary sites resulting from non-ferrous ore extraction, sand and gravel workings, and stone and slate quarries are usually on a smaller scale than the massive waste from industry. In the past, most of the quarry and small-scale mining sites were abandoned to natural restoration, mainly because they were situated in rural areas. The scale of wasteland from quarrying has increased in recent years, however, with super-quarries being planned in very fragile ecosystems, including the Peak
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District National Park (Bradshaw and Chadwick, 1980) and restoration schemes are more prevalent. Unlike industrial man-made sites the successional time scales studied in some quarries can be measured in millennia, rather than decades, for example on the Stone Age flint mines in the chalk of Norfolk (Ranson and Doody, 1982).

Quarry substrates can be either acid or alkaline, with very low levels of plant nutrients. They also have combinations of extreme physical conditions; steep and flat surfaces, coarse and fine particles, stable and mobile spoil, and extremes of wetness and dryness; making them very similar in structure to shale bings. Most of the literature describes the vegetation of chalk, limestone and other carboniferous quarries (Davis, 1982; Bradshaw and Chadwick, 1980; Hepburn, 1955) but there is reference to the invasion of slate quarries, which have a hard acid substrate, by Bradshaw and Chadwick (1980). Many common species are recorded on quarry sites and on the quarry floors a varied but very evenly distributed flora develops (Davis, 1982). Descriptions of present vegetation and lists of common species are similar for alkaline quarry sites throughout the United Kingdom although there is considerable variation in the less common species both within and between sites (Hodgson, Davis, Ranson and Doody, Gray, Finegan and Harvey, all in Davis 1982; Hepburn 1955).

Regardless of the species composition of the vegetation, however, the mechanics and processes of succession follow those described in the descriptive models of bing succession summarised earlier in this chapter (Figures 6.1 and 6.2). The establishment of any species is a chance occurrence that depends on dispersability of propagules and tolerance of individuals to the biotic and abiotic conditions (Gray, 1982). The considerable diversity in the composition of vegetation within and between quarries is dependent on such factors as the time since abandonment and the heterogeneity of the physical and chemical environment (Finegan and Harvey, 1982). These are similar to the statements that have been made in this thesis regarding the variations in bing vegetation.
6.3.4 Other man-made sites

Other man-made habitats that are potential sites of primary succession include arable land, motorway verges, ski-slopes, derelict inner city sites, railway embankments and canal banks. The vegetation on many of these anthropogenic sites has been studied, usually with a view to restoration or reclamation to some degree of naturalness. With the exception of arable land, the physical properties of the sites are similar to those found on shale bings. The sites often have steep slopes with large particles, making them unstable, and are usually free-draining. Construction materials are often brought in from other parts of the country so the chemical composition and pH of the substrate are likely to be different from the surrounding landscape. Tsuyuzaki (2002) summarises the properties of the substrate on a skislope in Japan as "low in nutrients and the seedbank is absent" because of the erosion of all surface soil. This would make it a highly comparable site with bings and other industrial sites.

6.4 Natural Sites of Primary Succession

Many of the physical and chemical properties of man-made primary sites are also shared with natural primary sites (volcanoes, glaciers, scree, shingle and sand dunes). This section will continue the comparison of the model of bing vegetation described in this chapter (Section 6.2) with the processes of colonisation and succession described in literature from studies of islands (MacArthur and Wilson, 1967; Cronk, 1989; Schmidt and Schmincke, 2002), volcanoes (Ernst, 1908; del Moral, 1993; Lawrence and Ripple, 2000) and sand dunes (Cowles, 1899b; Lichter, 2000).

6.4.1 Islands

As described in Chapter 1 the oil-shale bings can be compared to islands. Their steep slopes and height, compared to the surrounding low-lying landscape, combined with the unique physical and chemical characteristics of the shale substrate, effectively isolates each bing from the surrounding area. The bings constitute islands of a different environment, in a sea of agricultural land. The individual area and height of these islands should be a determinant in regulating the occurrence and abundance of plant species (Wardle et al., 1997) and the colonisation by plants
should therefore follow the succession and vegetation patterns found on natural islands. The literature on island vegetation and successions is extensive and includes both general (Cronk, 1989; Schmidt and Schmincke, 2002) and very specific information (Holt, 1992; Smith and Steenkamp, 2001). A strategy of colonisation on islands is presented as a series of theoretical equations, structured around r and K, by MacArthur and Wilson (1967) and describes the processes whereby species richness per unit area should increase with island size. These are based on an assumption of both birth and death being density dependent. Holt (1992) elaborates on this model, pointing out that colonisation does not take place consistently over the whole island and that spatial structure and dynamics of populations within islands can both enhance the overall colonisation rate and reduce extinction rates. The model based on data from the bings would appear to support Holt’s suggestion of independently dynamic patches of vegetation within a site.

However the island biogeography theory (MacArthur and Wilson, 1967) also assumes that the surrounding matrix (the sea) is totally incompatible with the island and so does not contain species or processes that can influence the island landscape. In a landscape context, the bings are islands in a sea of agricultural land, the matrix is not incompatible with the island and there is considerable recruitment of species from the surrounding area (Cook et al., 2002). This process was demonstrated by the invasion of immediately local species to the basal slopes of the bings, described in the model in Section 6.1.1, as was the relationship between the extent of this invasion and the size, or more importantly the height, of the site. The seed dispersal powers of most flowering plants are limited (Miles and Walton, 1993) and islands, including oil-shale bings and other islands of industrial waste, are often isolated from similar habitats. In the bing model, colonisation is dependent on the availability of suitable seed sources, in terms of habitat requirements, that occur in close proximity: a model that is supported by del Moral (1993) in his description of the succession on Mount St. Helens. Initially this leads to a species poor flora, as found on the steep middle slopes of the larger bings, that reflects the stochastic order of species arrival by dispersal and is supported by theory developed independently in the early 20th century by Gleason (1926), Lenoble (1926) and Ramensky (1926) as an alternative to
the deterministic succession model presented by Clements (1916). As the succession continues larger bings (or islands) and those near suitable propagule sources should have greater species richness than sites that are smaller and more distant (Holt et al., 1995).

### 6.4.2 Volcanoes

Volcanoes are effectively another type of island, indeed many oceanic islands are formed as the result of volcanic activity. The physical similarities between volcanoes and bings were pointed out by Cadell (1925) and have already been remarked on earlier in this chapter. The colonisation of volcanoes and volcanic islands has been the source of major long-term analyses of primary succession for more than a century (Ernst, 1908; van Borssum Waalkes, 1960; Bush et al., 1983; Whittaker et al., 1989; Partomihardjo et al., 1992 [Krakatau group]. Wood and del Moral, 1987 and 1988; Dale, 1989; del Moral, 1993; Lawrence and Ripple, 2000; del Moral and Jones, 2002 [Mount St. Helens]).

All life on the Krakatau island group was extinguished in August 1883 when the three islands, Pulau Rakáta, Pulau Sertung and Pulau Rakáta Keţiil\(^2\), were covered with up to 30 metres depth of ash and pumice when the supposedly extinct volcano, Krakatau, erupted (Ernst, 1908). Continuing volcanic activity over the next 50 years resulted in the emergence of the new island, Anak Krakatau, in 1930 (van Borssum Waalkes, 1960). The vegetation has been studied and recorded on both the original islands, since the 1883 eruption, and on Anak Krakatau, since its emergence. The vegetation of Mount St. Helens in Washington, USA was similarly devastated from a single eruption in 1980 (del Moral, 1983) but only towards the north, the vegetation on the southern flank of the volcano was not destroyed. The two sites had very

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\(^2\) Sertung is also referred to as Danan and Rakáta Keţiil as Panjang or Perboewatan in some texts and the Anglo/Dutch names of Krakatau (locally this is the name of only the volcano), Verlaten Eiland and Lang Eiland are also used. There are also various spellings of the Indonesian names for the three islands.
different vegetation prior to the volcanic activity that reflected their geographical location.

The Krakatau group is surrounded by the Selat Sunda, a strait between the Java Sea to the north and the Indian Ocean to the south, and is situated in a region of species rich tropical forest islands in Indonesia (Whittaker et al., 1989). Mount St Helens is a terrestrial volcano located in the Cascade Mountains on the west coast of the USA in a temperate region, with species poor sub-Alpine vegetation (USGS, 2003). The nearest seed sources were in close proximity to the new substrate due to the incomplete destruction of vegetation on the volcano but, despite this, invasion was slow and after six years colonising species were very sparsely distributed (Wood and del Moral, 1987). The invasion and succession of the Krakatua Group after the earlier volcanic activity was very rapid, despite the nearest seed sources being islands 19 - 27 Km away that were also damaged by the eruption, and mainland Java and Sumatra, 35-45 Km distant (Table 6.5).

Table 6.4 The vegetation recorded on the Krakatau Group

The number of species, and their dispersal mechanisms, recorded on the three islands of the Krakatau Group in 1886, 1896 and 1979-83; and on Pulau Sertung in 1897, 1906 and 1979-83 (adapted from Ernst 1908 and Whittaker et al., 1989).

<table>
<thead>
<tr>
<th>site</th>
<th>Years from eruption</th>
<th>no. of spp</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Krakatau group</td>
<td>3</td>
<td>28</td>
<td>11 cryptogams- only 2 belong to local islands 17 phanerogams - 11 sea dispersed, 6 wind dispersed (4 composites and 2 grasses) + 7 species represented only by seeds</td>
</tr>
<tr>
<td>Krakatua group</td>
<td>13</td>
<td>65</td>
<td>12 cryptogams 53 phanerogams - 32 sea dispersed, 17 wind dispersed, 4 animal dispersed + 26 species represented only by seeds</td>
</tr>
<tr>
<td>Krakatau group</td>
<td>96-100</td>
<td>76</td>
<td>17 cryptogams and 59 phanerogams - 42 sea dispersed, 13 wind dispersed, 21 animal dispersed cryptogams and phanerogams (numbers not given)</td>
</tr>
<tr>
<td>Pulau Sertung</td>
<td>14</td>
<td>15</td>
<td>recorded within 1 hour by 2 people 7 species not recorded on Pulau Rakáta</td>
</tr>
<tr>
<td>Pulau Sertung</td>
<td>23</td>
<td>42</td>
<td>6 cryptogams and 25 phanerogams The reduction in species numbers is probably due to volcanic activity in the 1950's (Whittaker et al., 1989)</td>
</tr>
<tr>
<td>Pulau Sertung</td>
<td>96-100</td>
<td>31</td>
<td></td>
</tr>
</tbody>
</table>
The early differences between the vegetation and species diversity on the islands have not levelled out in the ensuing decades, as might be expected if the succession was moving towards climax (Whittaker et al., 1989). There is evidence of a high species turnover on the Krakatau group between 1896 and 1983.

Many of the earlier studies of the Krakatau group (Ernst, 1908; Van Borssum Waalkes, 1960; Bush et al., 1983) concentrated on the analyses of species/area relationships rather than species/time relationships however these earlier data sets were used by Bush and Whittaker (1991) to investigate the primary colonisation of the islands. Their objective was to identify the patterns of recruitment and extinction in succession, for higher plants, birds and butterflies, from start (the eruption of 1883) to equilibrium. They concluded that the success of colonising species was habitat determined and the dispersal mechanisms and ecologies of individual species would play a major role in determining the succession. The arrival of species, or groups of species with similar ecologies, would be stochastic in both order and timing (Bush and Whittaker, 1991). The emergence of Anak Krakatau in 1930, and the repeated activity from this volcano, resulted in significant disturbance to the vegetation of P. Sertung and P. Rakāta Ketjil in 1952/52, 1960/61 and 1972/73 (Bush and Whittaker, 1991; Partomihardjo et al., 1992). However a large turnover of species within the succession on the Krakatau group had already been recognised (Whittaker et al., 1989) and at the same time the new island provided habitats that had not been found on the other islands for several decades (Bush and Whittaker, 1991).

On Mount St Helens recovery was initiated within 1 year of the eruption (Dale, 1989) with the arrival of *Chamerion angustifolium*. This species and other wind dispersed species were the most common early colonisers and 34 species were recorded by 1986, 17 wind dispersed, and the remainder animal or unspecified (Wood and del Moral, 1988; Dale 1989). Nitrogen fixers and several tree species had already established by this stage, there was strong clumping of species and evidence that

3 The earlier nomenclature of *Epilobium angustifolium* L. is given in the original text.
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*Lupinus* species had survived the volcanic activity and that individuals were regenerating from buried rootstocks, not seed (Wood and del Moral, 1988). However by 1996 overall diversity had stabilised (del Moral and Jones, 2002; using Shannon-Weiner index of diversity $H'$) and began to decline due to the increased cover by long-lived stress-tolerant species and the decrease in abundance of some of the pioneer species.

The overall conclusions reached in the studies of succession on Mount St. Helens are similar to those from the Krakatau group and also from the bing model. Early colonists are most likely to be wind dispersed with later colonists being better adapted to the individual habitats and longer-lived species (del Moral and Jones, 2002). The reassembly of plant species after volcanic activity is primarily stochastic, but, unlike the bings, historic events, such as the season of the eruption and the presence of any relict vegetation will play an important secondary role (del Moral et al., 1995). The studies of colonisation made on Mount Usu, (Tsuyuzaki and del Moral, 1994; Tsuyuzaki, 1996) and Myake-Jima (Kamijo, et al., 2002) in Japan, and on Long Island and Motmot (Harrison et al., 2001) in Papua New Guinea also support the models of succession described for the oil-shale bings. The dispersal mechanisms determining initial invasion are wind and animal (sea on island volcanoes), and species richness and composition is dependent on the availability and proximity of source propagules.

**6.4.3 Sand dunes**

The southern shores of Lake Michigan were the source of a series of classic studies on the plant ecology of sand dunes that was one of the first to recognise and document plant succession (Cowles, 1899a; 1899b; 1899c; 1899d). In some ways sand dunes are the closest natural site to shale bings. In common with the other primary sites, both man made and natural, that have been discussed in this chapter the dunes have a dynamic vegetation that presents opportunities to study the processes and mechanisms of plant species and how they interact with the environment (Gimingham, 1989). Like shale bings they also often have a high recreational and amenity value.
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The dunes are exposed to a high light, low nutrient environment and the substrate is very free draining, like the oil-shale bings and many of the primary sites described in this chapter. The lack of shade combined with high winds leads to extremes of surface temperature and can cause desiccation of species with short roots, although this is compensated to some degree by considerable condensation of dew from rapid night cooling (Cowles, 1899a). The dunes present an extensive chronosequence of around 450 years from primary colonisation to developed ecosystem (Lichter, 2000) in a series of spatially separated vegetation types (zones).

Cowles (1899d) comments on the similarity between the dune floras of Lake Michigan and Denmark (citing Warming between 1891 and 1896). The genera and species are often the same and when they are not related they have the same life habits. More recent works on the vegetation patterns on dune formations on Lake Michigan, (Lichter 2000) and in Holland (Grootjans et al., 2001) have concentrated on the constraints during succession that effect the transition from one step to the next, or that arrest vegetation development at a particular stage. The bing model of succession is again supported as both authors conclude that the rate of vegetation development and the establishment of individual species are dependent on the availability of suitable seed sources. Secondary factors can include seed predation and seed or seedling desiccation (Lichter, 2000), lack of dispersal agents (Grootjans, 2001) and episodic burial (Lichter, 2000).

6.4.4 Glaciers

Another classic series of papers on primary succession were produced by Cooper (1923a; 1923b; 1923c) using vegetation data from land gradually exposed by glacial retreat at Glacier Bay, Alaska. The investigations followed observations by John Muir in his diaries (published in 1915) on finding the remains of a forest that had been devastated during an earlier advance of the glacier (Cooper, 1923a). Three stages of succession are described by Cooper (1923b) based on "the increasing dominance of a new growth form".

1. The pioneer community: evident in areas closest to the glacier front and in patches within the other stages. Vegetation varies in density from scattered
individuals to close cover. This is synonymous with the earlier description in this chapter of vegetation on the steep middle slopes of the shale bings

2. The willow alder community: generally occupies the steep middle slopes. The thickets are larger and closer together with distance from the receding glacier front.

3. The conifer forest: in 1923 this was an almost pure stand of young *Picea sitchensis* with occasional *Tsuga* spp.

Jones and Henry (2003) described a similar directional succession on the glacier foreland of Ellesmere Island in the Canadian High Arctic. Using Twinspan and canonical correspondence analysis they identified four main stages of dominance over a 44 year chronosequence, moving from moss dominated vegetation, to graminoid-forb, to deciduous shrub-moss and culminating in evergreen-dwarf shrub-moss (Jones and Henry, 2003).

The overall conclusions from research and description of glacier foreland suggest that, in this habitat, primary succession follows the classical deterministic model of Clements (1916) as new, denuded land is revealed by the retreating glacier. This is in contrast to the bings and other primary succession habitats, both natural and man-made, where distance from suitable seed sources and regular physical disturbance of the substrate leads to delay or arrestment of vegetation development.

### 6.5 Discussion and Conclusions

It is doubtful if any single model can effectively represent the mechanisms and processes of succession and Clements’ (1916) six sub-processes, with the possible exception of stabilisation, are a useful way of dividing the process. When succession is considered, either temporally or spatially, the vagaries within each stage that pertain to individual sites and conditions can be described and discussed in relation to the original model. Succession is not a single process and its direction, or lack of direction, is determined by a large number of interrelated causal factors. Cause and determination imply that the process is not random (Lawton, 1987). If the process is not random then the assemblage of a new community should be predictable and comply to set of rules (Odum, 1969). In a mini-review of assembly rules, using
examples from a wide range of literature on both plants and animals, Belyea and Lancaster (1999) proposed that three main factors influence the formation of communities; dispersal constraints, environmental constraints and internal dynamics. Succession is a gradual assemblage of species into communities within an environment that will ultimately evolve into an ecosystem. The main factors that influence the outcome of vegetation successions are also dispersal constraints, environmental constraints and internal dynamics. The mechanisms and processes governing succession therefore comply with assembly rules.

6.5.1 Model comparisons

The bing model presented in this chapter was based wholly on observations made in the field, analysis of vegetation data collected in the field and from simple glass house trials as described in earlier chapters. These observations provided fundamental information supplying the answers to 'which species are present on the bings?', 'how abundant are they?', 'where are they?', 'how did they get there?' and 'what vegetation patterns, if any, can be found?' thus allowing direct comparison with literature from other sources that was not previously possible.

The successional model of the bing followed the general patterns and early stages of vegetation development outlined in the broad descriptive models of succession (e.g. Watt, 1947). The patterns of vegetation recorded in the individual positions within the bings (top, middle and base) represented chronosequences pertaining to the succession and were comparable with models of the internal dynamics of seral stages described in the literature (e.g. Connell and Slayter, 1977). The bing model of succession follows the early stages of succession described by Clements (1916) and these stages are influenced internally by (at least) three, concurrent, processes that influence small-scale patterns in vegetation and make each succession unique: within species variation in physiology, seed production and the ability to establish within the new community. Pattern at low level intensity, as is found in most of the bing vegetation, is controlled by small numbers of factors and Kershaw (1963) confirms that these can usually be attributed to the morphology of individual species (Kershaw, 1963).
Sociological patterns are the product of interrelated causal factors: partly the properties of the plants, the interaction of species on species, individuals on individuals, partly reflecting the microenvironment. The patterns can be modified by the microenvironment and are dependent on the competitive ability of individual species. The age of individuals can affect competitive ability, the physical or chemical environment may be modified by one species thus affecting the distribution of another species and allelopathic interactions between species can either inhibit or enhance establishment. There was no evidence of species competition from analysis of the bing data but the consistent grouping of particular species with similar habitat requirements demonstrates strong sociological patterns (Chapter Three). Under contrasting conditions the outcome of interaction between the same two species might be different. For example *Leucanthemum vulgare* and *Fragaria vesca* form an almost exclusive association on large areas of the steep middle slopes of the bings, yet each of the species is an individual and major component of the more species-rich, grassland community of the tops and plateaux.

Microtopography causes patterning in vegetation as a result of several environmental factors. The physical and chemical character of the substrate, drainage, water availability, leaching, nutrient supply and pH, will reflect the non-uniformity of the soil surface. Extremely small changes in pH or ion concentration will result in a vegetation pattern (either directly or indirectly). Chemical analysis of samples from the bing substrate (Chapter 4) demonstrated that there was considerable variation in pH, calcium, phosphorus and potassium concentration both within and between sites and Snaydon (1962) recorded that the same nutrients can vary by a factor of three within a distance of only 0.6 m in soil sampled from sites in Hampshire and Wales.

Succession is also influenced externally. The models from literature identify the main factor determining the rate and direction on succession as the availability and suitability of invading propagules from local sources. They also agree that the large-scale physical environment, altitude, latitude, isolation and climate, can impose constraints on the invasibility of a site. These are the same mechanisms and processes of succession described in the bing model therefore information collected from the bing sites can be used to formulate general hypotheses on succession.
6.5.2 Primary comparisons

The comparison of the bing vegetation with other primary sites, as opposed to general models of succession, introduced some interesting implications regarding the influences of rate of development and spatial pattern that may be unique to primary successions.

There is a major point of discussion regarding year zero of a primary succession. Bush and Whittaker (1991) consider that the recurring volcanic activity and associated vegetation setbacks should be part of a single successional model of the Krakatau group, but Partomihardjo et al. (1992) argue that the succession restarts after every major volcanic activity. On the studies of post-industrial sites year zero is usually considered to be the date of cessation of tipping unless there is documented evidence to suggest that some parts of a site have been undisturbed for longer than others. Much has been made in literature of the long-term, continuous study of primary succession on the Krakatau group. Perhaps this should be challenged and a case made for reviewing each additional disturbance as a new primary event.

A likely influence on the developing vegetation in primary successions that has not been investigated in this study is the "founder effect" that can limit the genetic variation of species arriving as early colonisers especially if a population is formed from the progeny of one, self-pollinating individual. Gray (1987) attempted to ascertain whether perennial pioneer species change genetically during succession but the results were inconclusive because of the intrinsic impossibility of untangling the temporal and spatial influences of successional environments from the inherent phenotypic variation of plants. However he does suggest that succession "is a potent force retaining plasticity for many traits in plants" that enable them to adapt to unpredictable resource levels in new habitats. I have been unable to find any published research on the influence of succession on possible genetic changes in annual pioneer species. It seems likely that the ability of some individuals to reduce their growing time, and set large amounts of seed when conditions are sub-optimal, would result in rapid selection for a particular genotype, however, a high proportion
of ruderal and pioneer species are apomictic and therefore retain the genotype of the original invading individual(s).

The proximity of seed sources to the succession site is recognised as important to the rate of recruitment and extinction on all sites. On primary sites however there is the additional constraint that the available seed has to be from species suited to the, usually, very different conditions on a new substrate. When suitable sources are a great distance from the site there can be a long period of invasion by local, short-lived, generalist species before longer-lived, better-adapted species establish. This has the effect of slowing the succession, but also increases the possibility of greater diversity within plant communities on the site in the long term. The situation is further complicated when there is a suitable seed source nearby as was exemplified in volcanic succession. The close proximity of source species to Mount St. Helens compared with the more distant sources after the initial eruption in the Krakatau group was a restraining factor in the rate of species turnover as there will always be continued immigration by the same species into the site. Wood and del Moral (1987) suggest that there should be a clear distinction made between the source pool, defined as the total species in the immediate vicinity, and the immigrant pool, which is limited to those species from the source that are actually colonising the site. On the shale bings, the lack of suitable species in the surrounding landscape has led to a diverse combination of species from various external sources forming unusual assemblages. Each site has its own unique communities because the individual bing sites stand alone, surrounded by different types of agricultural land and are continually being showered by a diverse seed rain. Conversely the massive heaps of sand produced by the china clay industry (Section 6.3.2) were species poor and the vegetation homogeneous because the sand heaps form a single continuous mass covering a vast area (Bradshaw et al., 1977; Roberts et al., 1981). The initial, successful colonisers are self-perpetuating and contribute almost all of the propagules in the seed rain, except around the periphery of the sites.

The physical size and shape of primary sites varies hugely. The individual height and area of each site determines the potential heterogeneity of habitats within the site and also their distance from potential seed sources. In the study of the shale bing
vegetation in this thesis it was possible to establish that the height of the bings had a strong correlation with the dispersal mechanisms of species that established. Higher and steeper areas had a larger proportion of wind and bird dispersed species than lower slopes and the surviving species were often not representative of the surrounding landscape.

The peaks of the bings range from 100 - 240 m above sea level (a.s.l.) making them comparable in height with the lower lying islands in the Krakatau group. None of the studies of this group of islands associates possible variation in vegetation between these sites with altitude, although the highest point of P. Rakáta is 735 m a.s.l. compared with less than 200 m a.s.l. on the other islands. The larger size and height of the main island has possibly resulted in a wider range of habitats for individual species and Van Borssum Waalkes (1960) notes vegetation zones in his description of P. Rakáta. He continues, however, that they are not primarily caused by altitude (and therefore temperature) but suggests that they are attributable to differences in humidity that increase with altitude. There is no consideration of the physical problems of up-hill propagule dispersal that must be prevalent, even on the lower islands, because of the steep slopes. Recent landscape-scale analysis of the vegetation cover on Mount St. Helens by Lawrence and Ripple (2000), however, established the importance of slope gradient for revegetation in primary sites that had not been recorded in any of the other field studies on volcanoes.

So far only the effects of macrotopography have been discussed; the significance of the large-scale physical factors, altitude, angle of slope and site area, on the assembly of species during primary succession. Smaller-scale patterning, over several metres, is more likely to be caused by differences in topography, drainage, soil composition, or a combination of these (Kershaw, 1963). Weigleb and Felinks (2001) suggest that "unfavourable starting conditions" could result in grass-dominated communities persisting indefinitely in coal spoil heaps, although they do not define what these conditions are. The underlying assumption of the paper is that the succession must progress to woody, climax vegetation yet no evidence for this has been recorded in studies of many other primary sites, both natural and man-made, even after a century. On the bings there is extensive grassland on the well established larger sites that
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shows little sign of evolving into woodland, despite there being little or no grazing pressure that might prevent tree establishment.

Another underlying implication that occurs throughout the literature is that lack of available nutrients (particularly nitrogen), or extremes of variation in particular elements in the substrate prevent or delay successional processes. Results of artificial manipulation of nutrients in sites have shown that their availability, when matched to optimum species requirements, can accelerate the process of colonisation (Williams, 1975; Marrs et al., 1980; 1981; Palmer and Chadwick, 1985). These manipulative experiments normally also include artificial seeding or planting making it difficult to determine which factor is actually responsible for any increases in biomass productivity. The analysis of variance in nutrients from substrate samples from the shale bings in this study showed no significant correlation with either increased growth of individuals (measured as plant height) or with increased abundance of species. Similarly Haddock (1997) found no significant correlation of improved growth of tree species with improved nutrient availability under naturally occurring vegetation in china clay overburden.

Small-scale patterning can be based on plant morphology (Kershaw, 1963). Variance in abundance of individual species will depend on the overall vegetation cover in an area. The individuality of the vegetation recorded in primary succession sites has been evident throughout this chapter. The stages of succession may not always be directional, some stages will not develop, others may be arrested but the primary successions all follow the general succession models.

The most invasible plant communities are those with a large proportion of bare ground or with frequent disturbance (Crawley, 1987). Early colonisation in all primary habitats is stochastic, but dependent on the availability of suitable propagules, and is followed by a combination of vegetative spread, or internal seed production from random centres and continued external recruitment, producing small-scale pattern. Barnes and Stanbury (1951) presented evidence suggesting that there will be an overall reduction in pattern as a community stabilises following initial succession of colonisers. Grubb (1987) expects "primary succession to lead to
a type of vegetation that is relatively constant in composition” but continues "over a sufficient area and through sufficient time.” Theoretically a constant association of species is climax vegetation. Increasing stability of plant communities is also linked with decreasing intensity of pattern and should ultimately result in homogeneity of vegetation and very boring landscapes. There is little evidence of homogeneity developing in many of the primary sites discussed in this chapter, despite their all following similar assembly rules, suggesting that climax vegetation is some time off.

6.5.3 Summary

The mechanisms and processes producing the developing vegetation patterns on the West Lothian shale bings recorded in this investigation have been used to formulate a model of bing succession that has been compared with successional models from literature and with the vegetation dynamics of succession in other primary sites, both natural and man-made, thus establishing bings as acceptable models of primary succession that follow previously identified stages or sub-processes. The succession patterns on shale bings follow the same trends as those recorded on other primary sites. The development of vegetation on the bings at all scales, from macro- to micro- topographical, displays strong similarities to other primary habitats and is analogous to the development of island vegetation, particularly those communities found on volcanoes and oceanic islands. This leads me to conclude that observations of vegetation patterns and species data collected from oil-shale bings can be effectively used to predict the mechanisms and processes of succession on other primary sites.