

CHAPTER ONE

“The ecosystems which appear naturally on derelict land, without human assistance, are of considerable interest...they tell us about processes of ecosystem reconstruction and also about natural ecosystem development.”

A.D. Bradshaw (1983). Presidential address to the British Ecological Society, December 1982.

1 Introduction

The importance of understanding the mechanisms and processes of colonisation and vegetation dynamics has long been recognised as a major factor in interpreting the development of plant communities. Only rarely does the opportunity arise to study colonisation on a primary succession site that is previously unresearched. The oil-shale bings of West Lothian provide such an opportunity. The shale bings, like all spoil heaps and quarries, start as sterile environments, with no previous vegetation or existing seedbank; therefore colonisation by plants and the subsequent development of vegetation is a primary succession. There are few naturally occurring sites where primary succession can be studied. This rare man-made habitat offers an environment against which accepted models of colonisation and their components can be tested.

The West Lothian shale bings are vast heaps of spoil, the waste product of the paraffin industry in Scotland. From the mid -19th to the mid - 20th century crude oil was produced in West Lothian by retorting locally mined oil-bearing shale and it is the discarded, burnt shale that forms the substrate of the bings. The individual bings vary in size, age and contain examples of both managed and unmanaged sites (Chapter Two and Appendix 1). Although the oil-shale bings are man-made, the plant communities and patterns of vegetation found there represent a range of seral and temporal stages within primary succession.

1.1 Ecological Importance of the West Lothian Bings

The shale bings are of great ecological and scientific importance as examples of primary succession and vegetation dynamics. The bings are unique in the United Kingdom. Oil-shale spoil is physically and chemically different from other spoil types making predictions from research on other spoil sites difficult and unreliable (Chapter Four). Many of the sites have remained unmanaged since shale extraction ceased and are slowly being colonised by plants and animals. Others have been reshaped, seeded and planted in various ways during the 1970's and 80's when land reclamation was "fashionable". The resulting vegetation, in both instances, is unique and varied. Their heterogeneity, both between and within sites provides a wide range of habitat conditions for the study of colonisation processes and the ecology of individual species that are adapted to low competition high stress conditions.

1.1.1 Importance of the bings to West Lothian

Formal recording of plant and animal species presence has been carried out on most of the bings although there is no published data on abundance, distribution or community structure. There has been little research in any scientific discipline on the bings and many of them appear only as vague outlines on topographical maps. Despite this, the potential value of some of the sites as habitats for locally rare species has been recognised (Chapter Seven) and they now have some degree of protection. The oil-shale bings form one of the eight main habitats in West Lothian's Local Biodiversity Action Plan (Sheldon, 1997). The bing habitats vary from almost bare substrate to semi-natural grassland, heather scrub and pioneering birch woodland, providing refuges for a range of animals and plants that are under increasing pressure in surrounding agricultural and urban areas.

1.1.2 Global importance of the bings

On a global scale the recent renewal of interest in oil extraction from shale is likely to lead to an increase in the volume of oil-shale spoil, particularly in the United States of America. Public opinion and government policy in many countries now demand that sites degraded by industrial processes should be restored to acceptable levels of "naturalness". To be able to comply with this it is necessary to achieve

ecosystems on oil-shale spoil that are self sustaining, are developed economically, possess the species and structure desired, control erosion, and form a safe and socially acceptable landscape. The West Lothian shale bings provide indicators for management and reclamation best practises.

1.2 Aims

The aim of this thesis is to identify the mechanisms and processes that determine the development of plant communities during succession and explain the processes driving vegetation dynamics. This has been addressed by experimentation, investigation, enquiry and analysis of new data collected from the study of vegetation on oil-shale bings in West Lothian, Scotland. The resulting information is used to test a range of successional models from literature and to produce a succession model of vegetation dynamics on the bings. Species traits from the bing vegetation are then compared with those from vegetation in other primary sites.

In any research involving the study of biological processes in a man made environment it is important to understand the historical background to its ecological status as well as a detailed knowledge of the particular aspects being studied. The following sections of this chapter briefly review methods of analysing and describing vegetation, the theories of succession, the mechanisms and processes of succession, other mechanisms and processes effecting vegetation dynamics, and previous research on other types of spoil and natural primary succession sites. A series of questions (Section 1.7) addresses how succession models proposed in the literature might be tested using information from the bing sites. In Chapter Two the geological processes that formed the oil-bearing shale strata are described, the physical and political geography of the study area is defined and a brief history of the shale-oil industry is outlined. Individual reports on the various aspects of the research are presented in later chapters.

1.3 Analyses and Statistics

Various methods of classifying and describing vegetation and plant communities can be found in literature (Grime, 1974; Silvertown *et al.*, 1992; Harper, 1982; Peterken,

1974; Shimwell, 1971; Greig-Smith, 1983; Rees and Bergelson, 1997; Tilman, 1988; Austin 1977; Rodwell, 1991a; 1991b; 1992; 1995; 2000). Analytical and statistical methods are dependent on the types of data being used and the questions being posed.

Community ecology is studied on a wide range of temporal and spatial scales, from millimetres to kilometres and from days to centuries (Gauch, 1982). Even when studying the ecology of a single species more than one characteristic will be measured and the relationships between these characteristics need to be studied simultaneously. Community ecology field data are noisy because, although numerous species abundancies are controlled by a relatively small number of environmental and historical factors, each species is individual and each site and environmental factor is, to some degree, unique. A range of multivariate strategies have been developed, providing the ecologist with the tools required to analyse, format and present data by three basic methods depending on whether the emphasis is to be on aspects of community structure or relation to the environment.

1.3.1 Direct gradient analysis (DGA)

This is used to study the distribution of species along recognised, easily measured, environmental gradients. Plant communities are not a random assemblage of plants. Their composition is dependent on a wide range of factors, both biotic and abiotic. Classification and description methods frequently group plant species together by environmental and/or resource gradients (Ellenberg, 1988; Hodgson, *et al.*, 1995). These can be indirect environmental gradients (altitude, aspect and slope) or direct environmental gradients (pH and temperature) as described by Austin (1972; 1977), and Austin and Smith (1989). These methodologies are often based on the established phase of the life history of individual species within a community and may not be directly transferable to the developing vegetation on the bing sites being studied. The purpose of direct gradient analysis is to gather and organise community and environmental data in a quantitative way. It determines which environmental factors(s) principally affect(s) the distribution of organisms and communities within

the study area, which factors are secondary to this distribution and whether the communities are discrete and well defined or follow a continuum (Gauch, 1982).

1.3.2 Ordination

Ordination is used when the main emphasis is on community structure or when environmental data are not available. It places similar entities in proximity with each other by a range of techniques. These include weighted averages, principal components analysis (PCA), reciprocal averaging, detrended correspondence analysis (DCA), and canonical correlation analysis (CCA). Ordination is effective for showing relationships, reducing noise, identifying outliers and disjunctions, and presents the data in terms of community composition. This may or may not relate to environmental factors. Ordination is commonly used in the study of succession and other floristic analyses (Austin, 1977; Daniels, 1978; Wildi, 1988).

1.3.3 Frequentist statistics

Ecological community field data are not usually suitable for statistical methods of analysis. Standard frequentist statistics are, however, used on the results of ordination and other multivariate analyses to determine the probability of a null hypothesis (e.g. there is no relationship between vegetation communities and altitude). They can also be used to test the non-randomness of occurrence of groups of species (e.g. Monte Carlo Analysis). A wide range of frequentist statistics is recognised as standard analytical tools and is necessary to describe the results of experimental data. T-tests, Chi-squared, Mann-Whitney, Anova, Regressions, F-test and many others can be selected to show the statistical significance of the outcomes of research.

1.3.4 Bayesian statistics

The Bayesian approach to statistics is a relative newcomer to Ecology although it is based on Bayes' Rule and derived from a problem¹ expressed more than 240 years

¹ *Given* the number of times in which an unknown event has happened and failed: *Required* the chance that the probability of its happening in a single trial lies somewhere between any two degrees of probability that can be named.

ago (Bayes, 1763). Bayesian statistics were subsequently developed by, among others, Jeffreys (1934; 1937) but the theory was suppressed for most of the 20th Century by frequentist statisticians. The main problem facing the ecologist is that the Bayesian method of analysis can not just be added to the range of statistical methods already used. Bayesian statistics, or inverse probability statistics, involve substantial changes to the methods and philosophy of science and are largely untested. This type of analysis has been used to predict the outcome of plant competition experiments with some degree of success (Damgaard, 1998; Pascual and Kareiva, 1996), but its general use is very much under discussion (Dennis, 1996).

1.4 Succession - The Mechanisms and Processes

The changing patterns of vegetation on land have been recognised from the earliest periods in human history, indeed farmers have used this knowledge to maintain cyclical crop production (slash and burn) since agriculture began. King (1685) is reputed to have presented the first scientific study of succession when he described Irish bog vegetation for Philosophical Transactions and the term "succession" was first used, in its present ecological sense, by the French biologist Dureau de la Malle (1825). A review of 21 key papers tracing the development of ecological succession theory from Cowles (1901) to Drury and Nisbet (1973), including reprints of many of them, has been published as volume five of the Benchmark Papers in Ecology series (Golley, 1977). From this it was possible to compile a generic model of the sequence of succession that the bing vegetation would be expected to follow. Succession can be divided into two main categories, primary succession and secondary, or subsequent, succession. Primary succession develops on a completely sterile environment with no previous vegetation. Secondary succession develops after disturbance on previously vegetated land. Literature suggests that the mechanics and processes of both primary and later successions follow similar overall sequences from invasion to stabilisation.

1. Invasion: In both primary and later successions invasion is the initial arrival of seeds and spores on an unvegetated substrate. These may already be in the seedbank (dispersal through time) after the loss of previous vegetation or may

arrive by dispersal from the surrounding area (dispersal through space) (Grubb, 1987). The success of invasion is dependent on seed and spore availability, dispersal characteristics, wind direction, animal activity and entrapment (surface roughness). As the bings are primary sites the vegetation is expected to reflect that found in the surrounding landscape: the nearest seed source.

2. Ecesis: Availability of a large number of seeds does not presuppose germination. Of the seed species represented only some will germinate and of these varying percentages of individual species will reach the seedling stage (Fenner, 1985). Fenner (1987), and Eriksson and Eriksson (1998) suggest that seed dormancy in some species may increase the potential for successful germination and establishment, as may seed size and morphology (Guo, *et al.*, 2000; Funes, *et al.*, 1999). It is unlikely that these will be major deciding factors in the spatial distribution of seedlings on shale bings as it is recognised that the effectiveness of these strategies is strongly linked to competition intensity (Eriksson and Eriksson, 1998). The microsites where seeds are trapped must be conducive to germination and establishment. Early colonising plants, particularly in a primary succession, must be able to acquire ample nutrients and water without mycorrhizal associations (Johnson, 1998) as sterile environments, like oil-shale bings, are depauperate in mycorrhizal propagules. Many of the germinating species will not be suited to the bing habitat and will survive only for a short time as transients (section 1.6 paragraph 1).
3. Survival: As mentioned in the previous paragraph germination and the establishment of seedlings are not synonymous with plant survival. While a continuing supply of water and nutrients is required, long-term survival is also dependent on levels of soil fertility, pH, light and moisture, falling within limited ranges for individual plant species, as described by Ellenberg (1988). Excess amounts of soluble salts, such as are reportedly found on oil-shale spoil (Bradshaw and Chadwick, 1980), and heavy metals are toxic to many species. The physiological features of individual species, like leaf size, plant height, mechanical and chemical protection against grazing, and clonal colonising ability will all be important factors contributing to survival and population growth.

4. **Reproduction:** Continued invasion of species is by seed dispersal from locally established vegetation and from neighbouring areas and is dependent on the reproductive output of individual plants and population size. Reproduction is a function of the number of flowering heads, length of flowering time, availability of pollinators, number of seeds produced, vegetative spread, and the viability, longevity and dormancy of seeds. Varying seed production between and within individual species is a major determinant of the ratios of species within plant communities, seedbanks and seed rain. The fecundity of locally available species suited to the shale bing habitats will be a primary contributor to their colonising success, both spatially and temporally, and to the overall vegetation structure.
5. **Pre-emption:** Stochastic elements will play a large part in determining the initial floristics of the sites and any subsequent changes in community structures (Harper, 1982; Rees and Bergelson, 1997; Miles, 1973). It is a matter of chance which species arrive first in any new environment. The growth strategies of these first colonisers can inhibit or facilitate colonisation by later arrivals. Extreme pre-emption can result in an initial flora of a few species that are easily replaced or a completely non-invasible plant community. The full importance of initial floristics and transitory species in determining the outcome of competition and community structure remains an as yet unresolved question in community ecology (Rees and Bergelson, 1997). It is hoped that this study of the vegetation processes on the shale bings will begin to address the issue.
6. **Changes in resource gradients:** As mentioned earlier in this chapter (introductory paragraph) there is a wide range of variation in the height, basal area and age of the bing sites in this study (Appendix 1). The greatest distance between any two bings is 7 kilometres and all 19 lie within a 10-kilometre radius. This makes them ideal for recording changes in resource gradients, which can occur both over time and spatially. These changes can be caused by existing vegetation, by topographical and climatic components or a combination of these.
7. **Competition:** In the initial stages of succession competition is absent when pioneers are still isolated but it increases with the increase in population in successive stages. It is not expected to be a major factor in areas of the bings with low vegetation cover. Competition can be for light, moisture, air and

nutrients. Clements (1916) states that "Competition occurs whenever two or more plants make demands in excess of the supply." These plants can be from the same or different species. Competition effects are greatest between individuals or species with the same or similar requirements for resources and least between associated plants with differing demands. They are often most consequential during the stages of ecesis (section 1.4 paragraph 2) when closely dispersed seeds from one species develop into numerous seedlings, each with identical demands on the same limited resources.

8. Interactions: Inter- and intra-specific interactions are not always competitive (although competition is an interaction). Within many developing plant communities, like those found on the bing site, species and individuals in a mixed population will survive better than those growing in a single species stand. Pioneers often act as nurse plants to other invading species, with much benefit to the latter but at no cost to the former. The relation between trees and herbs in a community is non-competitive because species in lower layers of vegetation are adapted to the conditions imposed on them and in many cases benefit from shading or other factors.

1.5 Other Mechanisms and Processes

Mechanisms and processes that do not fall into any one of the succession categories will have varying degrees of influence on the overall patterns and dynamics of developing vegetation at both species and community level.

1. Plasticity: Plasticity and intra-specific variation play an important part in the ability of individual plants to compete within a population or community. This is particularly true of weed species (Harper, 1960; Harper, 1977; Gray, 1993) and is likely to be a predominant factor in the early successional vegetation of the shale bings. The significance of relative growth rate and plasticity in relation to competition has been recognised by many as an important element of ecophysiology (Burdon and Harper, 1980; Jefferies *et al.*, 1981; Parsons, 1968; Tilman, 1985; Shipley and Parent, 1991; Marañón and Grubb, 1993; Peltzer, 1999).

2. Climate: Annual and seasonal changes in temperature, rainfall and hours of solar radiation all have a direct effect on seed production, germination, establishment and growth in plants. Even minor changes of climate can cause large-scale increases or decreases in the populations of individual species. The possible affects of global warming on Scotland are the subject of fierce debate making the consequence of any subsequent climate change on the succession patterns of the shale bings unpredictable and completely outwith the remit of this study.

1.6 Other Influences Affecting Plant Community Structures

Several factors that determine plant community structure are external or temporary influences and do not fall into the categories of mechanisms or processes. These are animal behaviours or plant strategies that directly govern the efficacy of elements of the succession process. Transient, transitory and uncommon species from surrounding landscapes are constituents of the earliest stages of all successions. Their effect on a new landscape and the advantages that such a site offers them are frequently ignored in the investigation of colonisation.

1. Transients: These are plant species (sometimes called ephemerals) that are not lasting or durable, whose seeds invade an ecosystem, germinate and establish but only rarely survive to reproduce. Transients are often relatively abundant species from nearby ecosystems that are unsuited to the physical and/or chemical conditions in their new environment. They are likely to be important in the development and maintenance of the ecosystem (Grime, 1998) by adding more nutrients and organic matter to the soil than they extract. They are representative of the assortment of potential later colonisers and are important to the continuing biodiversity of a community in subsequent successional stages.
2. Transitory species: Transitory species are species that form an integral part of one or more of the early stages of succession. These are species whose ecological niche is to move from one disturbed site to another. They reproduce and are well adapted to the initial conditions of the new environment. However as the ecosystem develops they are less able to compete with new invaders, or are unable to adapt to the physical and chemical changes in the developing substrate.

3. Uncommon species: These are usually native plant and animal species that are living at the edge of their preferred habitat range and are out competed by other, better suited species. An island refuge, like a shale bing, that provides a new habitat can potentially be of great importance to these species by providing a more amenable environment. Plant species that struggle to survive on the surrounding arable land may be the best adapted for the physical and chemical conditions found on shale bing substrate. They can also become an integral part of plant communities in later stages of succession as conditions suitable for their establishment, survival and reproduction develop (Grime, 1998).
4. Animal behaviours: Plant parasites, herbivores, predators and symbionts make ecosystem impact by vegetation less predictably related to abundance. Their effects are not investigated in this thesis, but any relevant observations resulting from survey and experimental data sets has been recorded and discussed.

1.7 Previous Research on Primary Succession Sites

There has been considerable research on primary substrates of various types throughout the United Kingdom and the rest of the World. The processes and mechanisms producing patterns of vegetation are generally accepted as being the same for all primary succession sites (Section 1.4), both natural and man-made. The physical properties of their substrates are similar (Chapters Three and Seven), although the chemical properties are more diverse (Chapter Four). Climate reflects the different geographical locations of sites, and plant species and communities will vary accordingly, but the growth traits and characteristics of many species should be comparable between distinct types of site.

1.7.1 Man made primary succession sites

These are many and varied. The most obvious are often the result of mining and quarrying for minerals. In the United Kingdom such sites were largely ignored until the 1960's and 70's when a nation wide, demolition, reclamation and restoration plan attempted to reproduce varying degrees of "naturalness" to the devastated landscapes. It was only when sites were surveyed to determine management strategies that their scientific and ecological importance was fully recognised

(introductory paragraph). The information collected from studies made on the oil-shale bings for this thesis will be compared with findings from other studies in primary succession sites in Chapter Six.

1. Oil-shale waste: There has been little research on succession, vegetation dynamics or plant communities on oil shale spoil, or on the mechanisms and processes determining the structure of the resulting vegetation in these communities. There are descriptive accounts of the vegetation (Maka, 1995; Martin 1992) and the development of both soil and vegetation (Russell, 1971) on some of the West Lothian oil-shale bings. West Lothian Council archives have a range of reports and documents relating to Drumshoreland, Seafield, Oakbank, Addiewell south and Mid Breich bings; including details of any remedial work that have been carried out from 1967 onwards (West Lothian Council, various dates). A detailed description of the physical and chemical structure of shale spoil is included in Chapter Five and a brief history and description of each bing has been compiled in Appendix 1.
2. Coal spoil: The plant communities, physics and chemistry of coal spoil, from both strip and deep mining, have been studied in many parts of the world (Allen and Allen, 1980; Jefferies *et al.*, 1981; Fyles *et al.*, 1985; Palmer and Chadwick, 1985). For example, Allen and Allen (1980) demonstrate that the earliest successional plants in reclaimed strip mines (coal) do not form mycorrhizal associations, as the acid substrate of coal spoil is low in mycorrhizal inoculum. They suggest that the lack of mycorrhizal inoculum is likely to inhibit later colonisation by mycotrophic species. It is not known if a similar range of species forms the basis of early successional vegetation on shale substrate, which is more alkaline.
3. China clay: Ecosystem development on reclaimed china clay waste in southern England has been researched and reported in a series of papers from the University of Liverpool (Marrs, Granlund and Bradshaw, 1980; Marrs and Bradshaw, 1980; Roberts *et al.*, 1980; Marrs, Roberts and Bradshaw, 1980). In these studies sixty-eight sites were surveyed to assess the vegetation and to quantify the cycling of nutrients (with emphasis on nitrogen): particularly capture

by, compartmentation in and leaching from the above ground plant material. The works concentrated on the importance of resource acquisition in the invasion by and development of vegetation. Is this a more significant factor than the proximity of seed sources and their dispersal mechanisms in determining the development of plant communities on spoil?

4. Derelict land sites: Considerable research has also been documented on succession and vegetation development in quarries and gravel pits (Davis, 1982; Gray, 1982; Borgegård, 1990; Myster and Sarmiento, 1998). The general processes of vegetation on derelict land have been described many times (for example Tandy, 1975; Greenwood and Gemmell, 1978; Bradshaw and Chadwick, 1980 and others).

1.7.2 Natural primary succession sites

Volcanoes, sand dunes and glacier moraines are some of the naturally occurring substrates where primary succession has been studied. Bradshaw (1983) describes spoil left after mining as similar to that formed by these natural processes and Cadell (1925) compares the West Lothian bings to volcanoes. In contrast to the man made primary sites, many of these natural sites have been the subjects of studies over many decades, even centuries, and large, comprehensive, descriptive, data sets have been published.

1. Volcanoes: There have been several long-term studies on the development of vegetation in the aftermath of volcanic activity on the Krakatau island group, Indonesia (Ernst, 1908; van Borssum Waalkes, 1960; Bush et al., 1983; Bush and Whittaker, 1991; Partomihardjo et al., 1992; Whittaker et al., 1989; Whittaker and Bush, 1993). More recently studies have been made on the mechanisms of primary succession on Mount Vesuvius, Italy (Mazzoleni and Ricciardi, 1993) and Mount St. Helens, United States (del Moral, 1993).
2. Glaciers: Similar studies have described the development of vegetation on the forelands of receding glaciers from all over the world. Long term studies in Glacier Bay, Alaska by Cooper (1923a; 1923b; 1923c) relate 20th century vegetation patterns to tracts of land uncovered during the early stages of long term glacier retreat, starting before 1794. These studies compare the primary

succession patterns of plant communities in areas more recently (sic) uncovered by the same glacial retreat. Crouch (1993) documented the species composition of 190 sites in, and alongside, forelands in Southern Norway, recording both cryptogams and higher plants. The effects of species of willow on the establishment and survival of indigenous plants was tested on Lyman Glacier forefront in Washington (Jumpponen et al., 1998). Schlag and Erschbamer (2000) conducted experiments on seedling germination and establishment on a glacier foreland in the Austrian Alps.

3. Sand dunes: Cowles (1899a; 1899b; 1899c; 1899d) studied the plant ecology of the sand dunes on Lake Michigan in one of the first, documented examples of vegetation succession. In this series of four papers he describes, among many other mechanisms, the positive effects of facilitation by early successional species on the establishment of later colonisers. The rates of succession on the same sand dune systems were investigated by Olson (1958) and used in experimental studies to develop ecological knowledge of primary and secondary succession (Lichter, 2000).

1.8 The Questions

The following questions relate to the bing vegetation and to models of successional mechanisms and processes that have been proposed by various authors. Each of these will be addressed in more detail in later chapters, both in the context of the literature and in the light of current research.

1. Vegetation structure: Are there recognisable patterns in the bing vegetation? Do species invade from the immediately surrounding plant communities? Does species diversity increase with the age of the bings? Will the first colonisers be cryptogams, followed by grasses and herbs? Will the species composition be dictated by stochastic events or as a result of deterministic processes? Are the resulting species associations representative of recognised plant communities in the United Kingdom? (Chapter Three)
2. Environmental gradients: Are vegetation patterns associated with environmental gradients? How limiting is the absence of soil, in the biological sense, to the

- colonisation process on shale bings? Does species composition reflect gradients in either the chemical or physical environment? (Chapter Four)
3. Seed dynamics and interspecific plasticity: How great a determining factor in the establishment of vegetation is the availability of seeds and spores in seed rain and the seedbank? Is phenotypic plasticity a major contributor to vegetation dynamics at individual species level? Will local site conditions have a direct effect on the size of individual plants, measured as height above ground, and hence on the number of flower heads and seeds produced? Is any variation in seed production within a species correlated with either height or number of flower heads? (Chapter Five)
 4. Succession and other primary sites: 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? (Chapter Six)
 5. Ecological value: what is the ecological value of the study of colonisation on shale-bings? Can indicator species be used to identify the physical and chemical structure of the substrate? How important are transient species to the establishment of plant communities? Are the examples of both assisted and natural colonisation processes and mechanisms on bings relevant to the restoration and management of other spoil sites? What effect do spoil sites have on local biodiversity? (Chapter Seven)