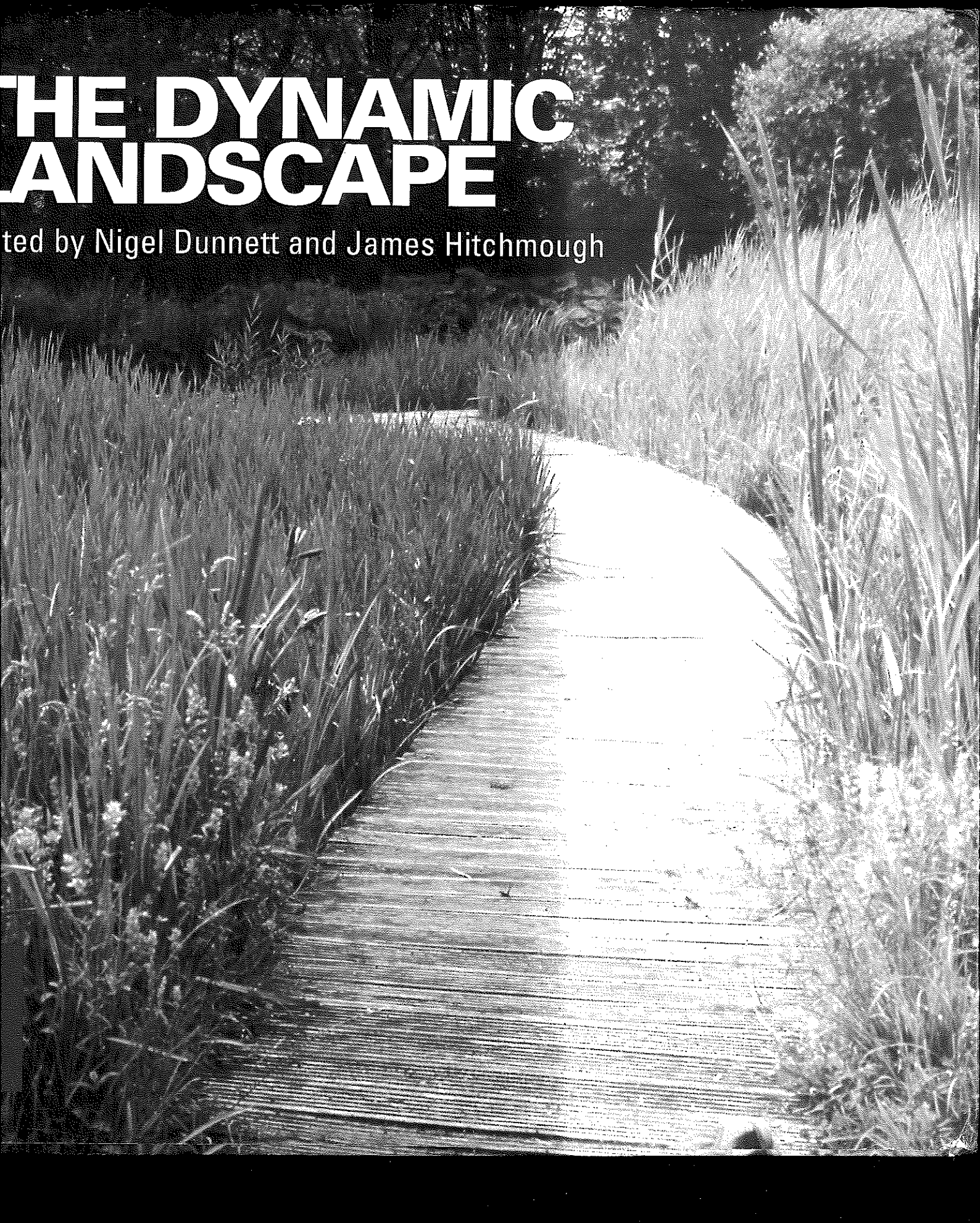


# THE DYNAMIC LANDSCAPE

edited by Nigel Dunnett and James Hitchmough



## Chapter 4

# The dynamic nature of plant communities – pattern and process in designed plant communities

*Nigel Dunnett*

All planting design, if it is to be successful, must to some extent be a compromise between what is desirable (artistic or creative vision) and what is possible (scientific reality). Of course, technology can be employed to push the boundaries of what is possible on any given site, but this is often at a considerable environmental cost. The great advantage of an ecologically-informed basis to planting is that it has the potential to achieve full creative vision with relatively little site modification. Having said that, even the terms 'ecological' or 'naturalistic' planting encompass a broad spectrum of approaches, ranging from pure restoration ecology (which aims to reproduce as closely as possible a target or reference of semi-natural plant community) through to ornamental plantings that

may be highly naturalistic but bear no resemblance to any naturally occurring plant communities. But most points on this nature ↔ art continuum (described fully in Chapter 3) can be characterised by having some degree of creativity associated with them: achieving a 'natural' quality is of great importance and they are therefore driven at least partly by visual principles. Even habitat creation approaches involve some form of species selection and arrangement to distil the essence of a plant community.

The scientific underpinning of the different approaches to planting that are described as ecological can also vary widely. At the most basic level, for most ecologically-informed schemes, scientific thinking will come in at the plant-selection

level: making plant choices based upon the 'right plant, right place' philosophy. This concept is fundamental: plants are the great interpreters of site conditions and accurately reflect and mirror what might be minute changes in soil type, topography, climate and management. Choosing plants according to *fitness to site* reduces the need for drastic and resource-intensive site manipulation. Plants from habitats that share similar environmental constraints tend to share common traits or characteristics, and this is a tendency that can be fully exploited in planting design (Dunnett 1995). At one extreme, this may involve putting together cosmopolitan mixes of plants that are adapted to certain site conditions, but with no regard to their geographical origin. At the other extreme, plant selection may have a strong geographical element to it and may aim to reproduce the character of a plant community (rather than trying to copy it completely) that is suited to particular site conditions. This 'biogeographic' approach may use very attractive reference communities from widely separated countries (for example, the contemporary 'prairie' and 'steppe' perennial planting styles in Western Europe), or be much more tied into local or regional reference plant communities.

But the value of scientific understanding goes much further than simply helping to put an appropriate plant list together. Applying scientific principles can actually guide the way that plants are arranged to achieve a fully naturalistic effect, but one that also actually works as a functioning plant community into the indefinite future. Plant communities tend to show identifiable *patterns* in the way that different species are arranged, both horizontally and vertically – these are related not only to environmental variation but also to the characteristics of the plants themselves and how they interact. As well as patterns in space, 'natural' plant communities show patterns in time: they are dynamic and change over a

range of timescales, as a result of ecological *processes*. These changes in space and over time are directly related to each other, and manifest themselves in the way that naturalistic vegetation appears and functions. In this light, it is no coincidence that one of the first ecological publications that opened people's eyes to the dynamic nature of plant communities (and one of the most influential ecological publications of the twentieth century) was titled *Pattern and Process in the Plant Community* (Watt 1947). The aim of this chapter is to identify principles that enable us to understand *patterns and processes in designed plant communities*. The aim is not to repeat standard ecological texts but instead to provide insights into how a designed ecological landscape might function over time and space. Where ecological concepts are introduced they are clearly linked to their implications in terms of how vegetation is designed, established and managed. It should also be stressed that it is assumed that readers will be familiar with basic scientific concepts relating to the requirements for successful plant growth and these will therefore not be considered here.

### **The dynamic nature of plant communities**

Any acceptance of an ecologically-informed approach to planting must fully embrace the concept of change. The common perception that plant communities in the wild are relatively static, with little alteration in their composition or appearance from year to year, is of course a misconception: change is fundamental to the processes that operate within semi-natural plant communities. Indeed, it could be said that every ecological principle that a designer or manager needs to be aware of is related in some way to this dynamic nature of plant communities. Change is apparent and important in all timescales, and for our purposes can be broken down into three main categories:

- changes in the way a unit of vegetation develops over a single growing season or year (processes related to the different rates of development and performance of component species, and generally referred to as *phenological* change)
- changes in the abundance, performance or visual presence of component species, or the overall biomass of the plant community between different years (generally referred to as *fluctuations* or *cycles*)
- longer-term changes in the character, composition or type of vegetation (generally referred to as *successional* change).

Change also operates at all spatial scales, whether this be at the level of two plants side by side competing with each other for space or resources, or the interaction between two plant community or vegetation types (again linked to competition), or at the largest landscape scale where the manner in which different vegetation units are linked together can affect the way that plants and animals (including humans) can move around any given area. Processes operating at all these scales manifest themselves in the vertical and horizontal structure of vegetation, and in the very survival and long-term integrity and persistence of any given vegetation type.

Vegetation change is partly driven by the obvious changes within the lifecycles of individual plants and populations of plants – establishment, growth, maturity, reproduction and regeneration, senescence and death – but is equally tied up with physical environmental factors and constraints, competition and plant-plant interactions, and, crucially, with the nature of the landscape context and the surrounding vegetation types.

Ecologically-informed or 'sustainable' planting has been defined as designed vegetation that maintains its integrity over successive generations with minimal resource inputs (Dunnett 1995). In order to disentangle this statement, we will first

consider factors that maintain the integrity of vegetation. That is, how do more than one species co-exist in any given unit of space, and continue to co-exist? The question of how biodiversity is promoted and maintained, and its importance to the functioning of ecosystems, has been one of the fundamental questions in plant ecology and is the subject of much current debate. It also has great relevance to the aesthetics and functioning of designed vegetation. We shall then consider patterns of vegetation change over different scales of time and space.

#### **Competition and co-existence – how plants interact**

The successful combination of different plant species is one of the main functions of planting design and landscape management. In traditional, horticultural-based planting design, aesthetic and functional considerations predominate: how do the different component species work together visually and how do they perform the tasks (such as dividing or filling spaces) for which they have been designed? Biological questions relating to how plants interact with each other and their surrounding environment as a community or unit of vegetation receive little or no consideration. This is mainly because the planting environment is generally modified to suit the requirements of standard landscape plants, whether this be through modification and importation of soils, fertilisation or irrigation, or through pruning and other maintenance operations, all of which entail an energy, labour and financial cost.

An ecological approach to landscape vegetation can be radically different. Aesthetic and functional considerations can be equally applicable, but questions of ecological compatibility and long-term dynamics are also a central concern. Rather than specifically arranging plants in their final desired positions, and subsequently ensuring that that is

where they remain, ecologically-informed planting can be more akin to starting and managing a successional process. However, compared to the vast bulk of ecological literature on the functioning of semi-natural plant communities in the wild, there has been surprisingly little application of ecological ideas in terms of the way plant communities function in landscape or ornamental planting: indeed, the vast majority of mainstream ecologists would probably not recognise this as a valid subject of study. Because, as discussed in Chapter 2, many so-called ecological approaches to landscape planting tend to emphasise the visual connection with naturalistic vegetation rather than the underlying processes going on in that vegetation, there is a real need to develop ecological models that address questions relevant to the way that vegetation may develop as part of human designed landscapes. At the most immediate level, these questions relate to factors that enable plants to co-exist under the wide range of potential environmental and site conditions, and to the characteristics of plants that enable them to be compatible with other plants growing in their immediate vicinity. In other words, factors that promote greater diversity and species richness in vegetation.

#### **Why is biodiversity and species richness important?**

The intrinsic value of biodiversity is a fundamental tenet of nature conservation. At a basic level, because a range of co-existing species can exploit more resources than can a single species on its own, diverse mixtures tend to out-perform any single species in terms of total biomass production. However, the greatest claim for the value of biodiversity is that diverse plant communities are considered to be more stable and resistant to change than simple systems. There are two main theoretical arguments to back this assertion (McCann 2000).

One explanation is based on the assumption that as long as species do not react in identical ways to environmental variation, the greater the number of different species present, the greater the number of different responses, and that, as a consequence, variation will be smoothed out at the total community level. The second general explanation is based upon the idea that at greater diversity there is a greater chance of having species present that are capable of functionally replacing important species that may be adversely affected by external pressures, and that can therefore maintain ecosystem functioning.

Having said this, there is remarkably little scientific research evidence to fully back these claims: theory is definitely ahead of experience. It is clear that monocultures and very simple systems of low diversity are vulnerable to environmental fluctuations. But it is also apparent that chasing high biological diversity for its own sake is also open to question – certainly the notion that the greater the number of species the better (i.e. the greater the biodiversity) is not necessarily tenable on ecological grounds. The main indicators of ecosystem health and functioning, such as productivity, carbon sequestration, water relations, nutrient cycling and storage, and resistance and resilience to environmental change, are primarily dictated by the performance of vegetation dominants (i.e. those species that contribute the greatest amount to the total biomass of the community) and these are likely to be relatively few in number (Grime 1998), perhaps only 20–25% of the total numbers in a plant community (Schwartz *et al.* 2000). So do the remaining species have any ecological value, or are they merely exploiting available niches without contributing significantly to the functioning of ecosystems? Whilst many argue that the loss of any species can have profound and unforeseen consequences, more evidence is required to answer this question fully on purely ecological grounds

(Purvis and Hector 2000).

Some of these arguments may seem rather obscure and irrelevant to designers and managers of landscape vegetation, especially when maintenance techniques can be used to remove the dynamic element from designed plantings. However, an understanding of the value of biodiversity in landscape vegetation, and the mechanisms that maintain it, become crucial if visually and ecologically-rich vegetation is to be created with reduced maintenance input. Given that promoting biodiversity is one of the often-quoted advantages of an ecological approach to landscape planting, what are the real benefits in the context of designed vegetation? These fall into a number of areas, as follows.

- *Aesthetics and visual pleasure.* The aesthetics of naturalistic vegetation is a complex topic and is explored in full in Chapter 11 by Anna Jorgensen. Whilst simple low-diversity plantings work well in more formal settings where there may be a requirement for neatness, order and predictability, there is little doubt that diverse naturalistic vegetation has its own beauty in other less-controlled contexts. This may partly be a result of a rich assemblage of textures, forms and colours, or that in more diverse mixtures there is a greater chance at any one time of components of the vegetation being at the height of their visual display. Diversity and richness are also one component of *complexity*: one of four key factors identified by Kaplan and Kaplan (1989) that are said to result in attractive natural landscape. Certainly, many scientists who may question the absolute ecological value of biodiversity also say that they value it purely on aesthetic grounds.
- *Stability: removing vulnerability from simple systems.* This argument has the closest affinity to pure ecological theory. Introducing greater diversity into landscape plantings could be seen as an insurance policy against the failure of one or more component species caused by environmental disturbances such as climatic extremes or disease.
- *Setting up succession.* One of the most distinctive features (and one that is often the most difficult to accept) of naturalistic or ecologically-informed plantings is their unpredictability. As illustrated later in this chapter, different species or components rise and fall in their abundance over time. This may be a result of environmental disturbance, but is also likely to be a result of differences in the length of lifecycles of different species, and a result of the outcome of competition between component species. Including a diversity of *functional groups* of plants within an initial mix, both facilitates succession and again insures continuity of the integrity of the vegetation. A functional group in ecological terms refers to organisms (that may not necessarily be related) which behave in the same way in response to environmental change, or perform the same ecological function. For example, in planting new naturalistic woodland, both pioneer and longer-term forest trees may be included in the same mix to enable long-term species replacement to occur.
- *Supporting other types of organisms.* In general, the greater the diversity of plant species in a unit of vegetation, the greater the diversity of other types of organism (e.g. birds and insects) that it supports, through the provision of a wider range of food sources or habitat opportunities (Knops *et al.* 1999). As discussed in Chapter 1, there is not necessarily any relationship between whether vegetation is composed of purely native species or a mix of natives and exotics in terms of the number of organisms it supports. What is of more importance is the vertical or horizontal structure

of the vegetation in terms of the number of layers it is composed of, or of interactions between vegetation types across boundaries or ecotones.

- *Filling up available niches.* It is a cliché that 'nature abhors a vacuum'. Bare ground rarely remains in that state for long. Most weed control in landscape plantings involves the removal of undesired plants from gaps between desired plants. These undesirable plants, or weeds, are simply filling space that is not being exploited by the intended species. This may partly be because the planted species have not expanded to fill the space, or it may be that the other species are filling ecological niches that the components of the designed system are leaving empty. For example, bare ground beneath shrubs quickly colonises with aggressive species tolerant of light shade. By filling niches at the outset through the inclusion of additional species, for example by ensuring full ground cover throughout the year, and promoting a multi-layered vegetation structure, the need for weed control in this situation is reduced.
- *Maximising the length of display: phenological change.* Filling a wide range of available ecological niches also enables the length of visual display to be increased through the exploitation of species with different phenologies (specific patterns of growth and flowering) within the same unit area of vegetation. An obvious example is that of spring flowering bulbs and herbaceous plants within a deciduous woodland that exploit the light conditions at ground level before the leaves on the dominant trees cast dense shade below. Similar principles operate in many plant communities. The idea of exploiting phenological change is discussed later in this chapter.

### **Competition between plants and promoting diversity in landscape vegetation**

Promoting diversity in vegetation is primarily about reducing the vigour of potential dominant species – it is simply not enough to include a larger number of species in a mix – that greater diversity of species has to be resistant to competition and elimination from aggressive species. Dominant species are those that, in the absence of constraining factors, tend to eliminate other species through *competition*, resulting in low diversity or mono-specific stands of vegetation. It is easy to think of plants as being essentially passive organisms, unlike animals that actively hunt and compete with each other for food resources. However, where resources are abundant, plants can be equally competitive, fighting for the same unit of water, nutrient or light, and often in an aggressive manner, moving both roots, shoots and foliage to capture those resources. In this situation, in the absence of constraining factors, the best competitor for those resources will tend also to be the winner in terms of space, eventually excluding less competitive species. This pattern holds for fertile, productive 'high energy' environments, but tends to fall apart when certain constraining factors are introduced to a habitat or ecosystem. It is therefore of great importance to understand what the constraining factors are that can increase the diversity of plant communities (through reducing the vigour of aggressive species), and equally to understand how to put together plant mixes with complementary competitive abilities so that no one species tends to eliminate all others. The most appropriate basis for our purposes to help understand how plants interact with themselves and with their environment in this context is Grime's Plant Strategy Theory (CSR theory). The CSR model has proved to be a remarkably powerful tool for predicting how plants and other organisms react to changes within their environment (Dickinson and Murphy 1998). Whilst the model has been used in

nature conservation management, there has been only very limited application to the functioning of non semi-natural vegetation (although, for example, see Hitchmough (1994)).

The basic starting point for CSR theory is that there are two fundamental sets of environmental threats that limit the growth and survival of aggressive, potentially dominant species: those that hinder the functioning of the plant, and thereby its growth rate and production of biomass, or those that physically damage or destroy plant tissues or biomass already present. The first set of threats is termed *stress* factors, involving constraints that affect the physiological processes of the plant. Such factors include extreme low or high temperatures, heavy shade, drought or low nutrient availability. The second set of threats is termed *disturbance* factors and include grazing, cultivation and trampling. Every habitat on the earth's surface can be defined by the relative combinations of stress and disturbance factors that operate on it. Over the course of evolutionary time, natural selection has resulted in plants that grow in environments subject to such pressures developing adaptations that aid their survival and regeneration in those environments. What is remarkable is that unrelated species growing in geographically separated parts of the world show very similar responses to the same sorts of environmental pressures or constraints.

Grime (1979) has identified three basic responses or 'strategies' for survival in environments that are subject to the various combinations of high and low stress or disturbance (Table 4.1)

The combination of low environmental stress and disturbance is characteristic of typical 'productive' conditions (i.e. where nutrients and water are not in limited supply and regular physical damage is rare) that encourage vigorous plant growth and the dominance of aggressive species that has been previously discussed. Such conditions may be found, for example, on abandoned fertile agricultural fields, old unworked allotments or gardens, or unmanaged productive grasslands: species that are well adapted to these environments tend to be tall herbaceous perennials, have spreading clonal growth and rapid summer growth rates. They are extremely effective *competitors* and tend to dominate vegetation, crowding out less vigorous species and resulting in low-diversity stands. Common competitors, or C-strategists, of northern Europe include rosebay willowherb, *Chamerion angustifolium*, and stinging nettle, *Urtica dioica*. In effect, the competitive strategy is to maximise the capture of resources (light, water and nutrients) and to invest these in further growth to capture still more resources.

Environmental stress and disturbance tend to limit the ability of competitive species to dominate. Restricted availability of resources (stress) prevents

Table 4.1. Combinations of environmental stress and disturbance resulting in the three basic plant response strategies

		Intensity of stress	
		Low	High
Intensity of disturbance	Low	Competitors (C-strategists)	Stress-tolerators (S-strategists)
	High	Disturbance-tolerators (R-strategists)	Uninhabitable



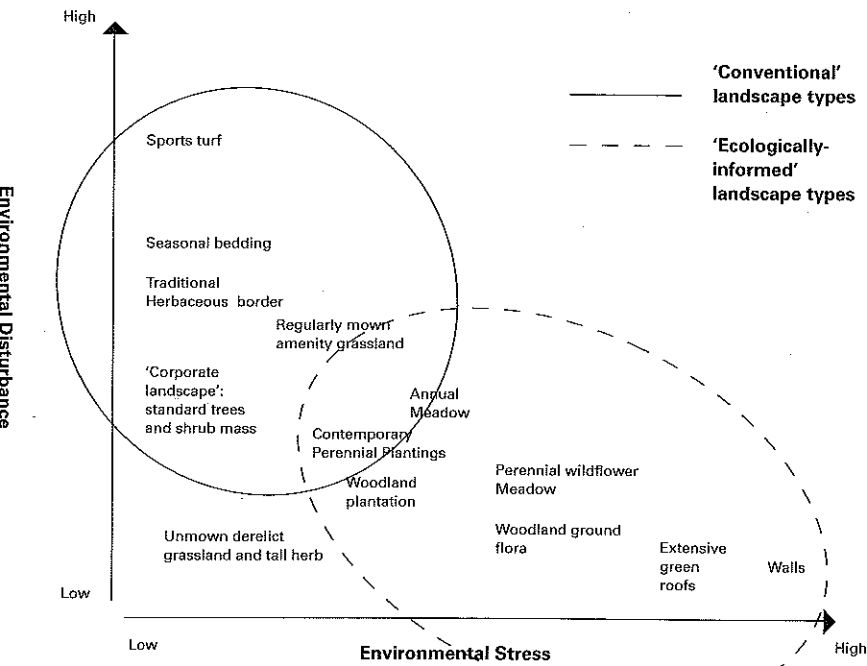
rapid growth (both in height and spread), thereby allowing species better adapted to growth under harsh conditions. Where resources are in very limited supply (i.e. in stressed environments), plants have evolved very different strategies. Rather than exhibiting rapid rates of growth, *stress-tolerant* species tend to be slow growing and evergreen, with specialised physiologies and often with modified protective tissues. Vegetation tends to be unproductive, relatively sparse and with low biomass. In such 'low energy systems' (Dickinson and Murphy 1998), plants tend to reproduce primarily through vegetative growth rather than by seed. In effect, the stress-tolerant strategy is one of thrift: to make the most of captured resources by sitting tight rather than investing in rapid growth to capture more resources. The nature of competition between plants in such environments has been the main area of controversy in the development of CSR theory. Examples of relatively stressed habitats include low-fertility acid or calcareous grasslands and the understory habitat of woodlands.

Environments where the disturbance or destruction of vegetation is a regular occurrence have given rise to plant strategies that either avoid or enable rapid recovery from that disturbance. Although naturally disturbed environments include screes and landslides, shingle beaches and sand dunes, the majority of disturbed environments are human-influenced (e.g. cultivated fields and agricultural grasslands). Plants adapted to such environments tend to show rapid growth rates and a reliance on reproduction through seed as well as vegetative expansion. For example, annuals are adapted to regular severe disturbance: their rapid growth rate enables them to take quick advantage of bare ground following a disturbance event, and copious seed production ensures their survival into future generations before another disturbance. Biennials and short-lived perennials are similarly adapted to disturbances on a longer time-cycle. In

effect, the *disturbance tolerant* strategy or *ruderal* strategy (named after the roadside habitats from which the disturbance-tolerant life-history was first described) is an insurance policy: investing resources in mechanisms that ensure a rapid response to predictable patterns of disturbance (Figure 4.1).

The three main strategies listed above are extremes. In reality, most species exhibit combinations of traits from the different strategies depending upon the exact environmental conditions to which they are adapted. The crucial point is that, in terms of the maintenance of diversity in vegetation, low stress combined with low disturbance is not good, favouring the aggressive competitor species. Equally, combinations involving high intensities of stress and/or disturbance produce hostile conditions for plant growth, restricting vegetation to a limited number of highly adapted species. In general, greatest species diversity is promoted at moderate intensities of environmental stress and/or disturbance. This is easily illustrated with reference to various grassland types. The more species-rich semi-natural grassland types tend to occur on relatively low fertility, free-draining acid or calcareous soils (moderately stressed) or, in the case of traditional hay meadows, on relatively fertile sites subject to moderate disturbance (hay cutting and after-grazing). The addition of fertilisers (reducing stress) or the removal of maintenance (reducing disturbance) will result in these grasslands becoming dominated by aggressive competitive grasses, with an associated loss of diversity.

The CSR model can be readily adapted to aid understanding of how designed vegetation functions. In the majority of landscape contexts, 'stress' generally equates to a lack of availability of resources (water, light and nutrients) and, in particular, nutrient status. Disturbance can be equated to the frequency and intensity of mechanical maintenance operations. Figure 4.1 illustrates the relationship of a range of herbaceous



4.1 The relationship of urban landscape types to the intensity of environmental disturbance (maintenance operations) and/or environmental stress (site fertility)

landscape vegetations to the intensity of environmental stress and disturbance.

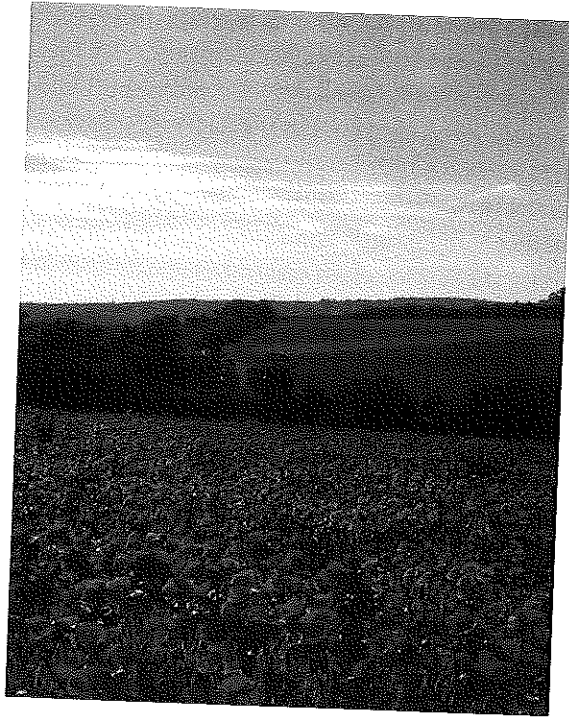
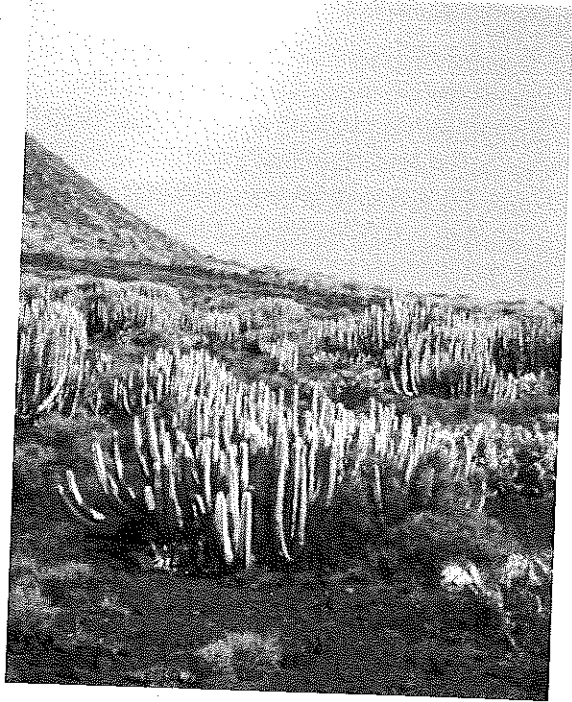
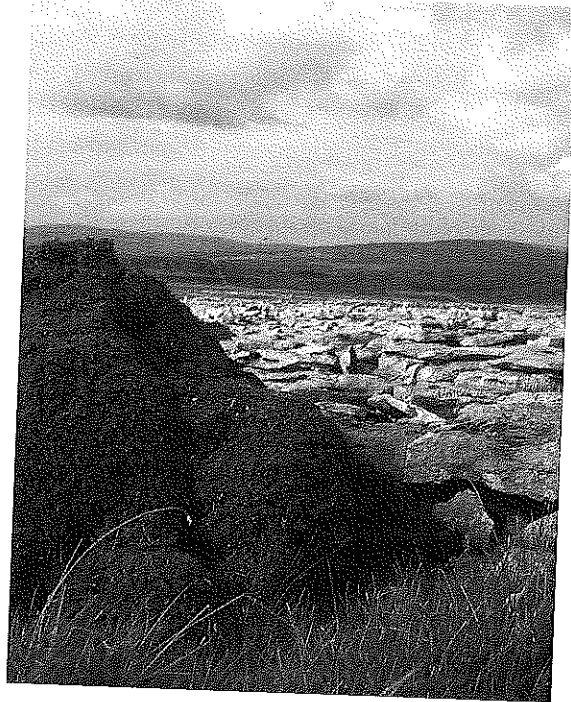
In general, the 'conventional' landscape types tend to cluster at the low-stress, high-maintenance corner of the diagram. Such landscape types prosper on sites with relatively moderate to high fertility, even though many of the component species growing in their native habitats are associated with low-moderate fertility. The desire of designers and horticulturists to achieve rapid plant growth has institutionalised the notion that highly cultivated plants 'need' fertile soils. Many stress-tolerant cultivated species will, however, grow well at very low-fertility levels. Conversely, the more ecologically-informed vegetation types tend to be suited to sites with moderate to low fertility and where maintenance input is also relatively moderate to low.

The value of CSR theory for ecologically-informed planting design lies in two areas:

- 1 **Plant selection.** Matching species with the same ecological strategies is one aspect of ensuring ecological compatibility with site conditions. For example, creating meadow-like herbaceous communities on fertile productive sites using stress-tolerant species from plant communities typical of low-nutrient free-draining calcareous soils (as is often recommended in the UK) will be unsuccessful without high management intervention. However, more vigorous species with a higher competitive element may be a far better option. As well as matching species to site, the CSR system also enables species matching within a planting mix so that competitive elimination with planted material is diminished and co-existence enhanced. A range of British native herbaceous species have been classified according to the CSR system (Grime *et al.* 1988). However, apart from some preliminary suggestions by Hitchmough (1994), there has been no attempt to date at classifying non-native species for landscape planting purposes.
- 2 **Vegetation management.** The CSR model provides an elegant framework for predicting the effect of different management regimes on the performance and diversity of vegetation. Again, there has to date been little application of the model away from semi-natural rural vegetation, although O. Gilbert (1989) has classified a range of urban vegetation types according to their predominant vegetation strategies. We return to this matter at the end of this chapter.

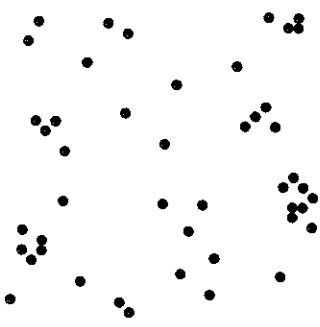
### Patterns

We have seen how diversity can be maintained, through the promotion of the co-existence of species within a given area of space, but how does this actually work out on the ground? What is the visual and physical manifestation of diversity? Whilst the distribution of plants within more diverse



4.2

Examples of plants that exhibit different 'strategies':  
(a) rosebay willowherb, *Chamerion angustifolium*, an aggressive, vigorous 'competitor';  
(b) Juniper, *Juniperus communis*, a slow growing, evergreen 'stress tolerator', growing in thin, free-draining soil and exposed conditions on a limestone pavement in North Yorkshire;  
(c) vegetation adapted to hot arid conditions on Tenerife – a very different climate but the vegetation is also evergreen and slow growing; and  
(d) Poppies, a typical 'ruderal' species, flowering on an abandoned cultivated field



4.3  
**Aggregated plant distribution: hypothetical distribution of a species across an area of space showing patches of higher density imposed on a general distribution of lower density (modified from Greig-Smith (1964))**

communities may, at first glance, appear to be random, ecological studies indicate that this is rarely the case. The distribution of a particular species may respond to (often small-scale) spatial changes in environmental factors such as soil moisture, concentration of particular nutrients, pH and so on, and the growth form of the plant (whether it spreads vegetatively or clonally by stolons or rhizomes, or how its seed is distributed), but it is also dependent upon competitive interactions with its neighbours. For example, a walk through a semi-natural woodland or forest reveals that many species occur in clumps or groups rather than as scattered individuals. This can be a result of many factors: some species form suckering clumps, others may have established at the same time as a result of some disturbance, such as a mature tree falling down to open up a glade. The main point here is that the plants are usually distributed in *patterns* and these

patterns can be used as a basis for the design of diverse naturalistic plantings. The detection of patterns of plant distribution has been an area of scientific study as well as for design inspiration. At the most basic level, distribution patterns within mixtures of plants can be described according to how *aggregated* and *segregated* the component species are (Pielou 1961). The degree of aggregation of a species is an indication of the amount of association of individuals or groups of individuals of that species. In effect, it is a measure of the non-randomness of the distribution of the species. In general, most species show some form of aggregation or clumping (see Figure 4.3). This may vary from a very loose association to a dense massing.

There has been a tendency to invest these naturalistic patterns with an almost mystical quality, presenting them as a set of rules that, if plants are

Table 4.2. Possible causes of plant distribution patterns

Distribution pattern	Possible cause
Singly or small clusters	Exact requirements for regeneration from seed rarely met in the habitat. Spread by rhizomes is strictly limited. May indicate sensitivity to intense herbivory. Surrounding species may suppress expansion. Possible allelopathic effects
Larger cluster and groups	Species exhibit limited rhizomatous growth from initial colonisation or establishment centres. Indication of competitive balance within a habitat. Possible artefact of early successional stages, reflecting distribution patterns when habitat was originally more open to invasion
Patches	Potential reflection of patchiness of the environment, for example fluctuations in soil characteristics, or previous disturbance patterns. Possible early successional stage, indicating phase of expansion of competitors
Extensive stands	Species generally have rhizomatous growth habit, stoloniferous spread, competitively excluding other species. Possible artefact of low disturbance and environmental stress. Very common in competitors and stress-tolerant competitors

laid out in these patterns, ecologically-functioning vegetation will automatically result. This is by no means the case because these patterns are, in the first place, largely a reflection. Planting according to these patterns will result in a naturalistic *appearance* in the short to medium term, but a long-term maintenance of these patterns will be dependent on an understanding of the underlying causes of the patterns. Table 4.2 indicates potential causes for observed plant distribution patterns. The table shows a gradient, moving from top to bottom, from individuals and small clusters through to extensive monocultural stands. A distinction is made between cluster-based distributions, whereby it is still possible to identify individual plants or clones through to more extensive patches and stands. The latter are generally associated with higher productivity systems. The distinction also reflects clonal versus non-clonal growth morphology (again this is linked to productivity). Secondly, there is an indication that some patterns may be ephemeral points within successional development.

Many designers, who may not have a great deal of ecological understanding, view patterns as a means by which 'stability' can be achieved, independent of previously mentioned factors, such as fitness to site – i.e. if you have the pattern of a semi-natural stereotype then somehow stability will emerge inherently. As indicated in Table 4.2, this is a somewhat naïve view, given that observed patterns may be ephemeral points in a longer-term developmental sequence, and that patterns are an outcome of competitive interactions and environmental pressures rather than a factor that dictates how vegetation performs into the future.

The characteristic patterns that different degrees of aggregation lead to lies at the basis of the so-called German Plant Sociability school of planting design, whereby different species are assigned a sociability score according to the degree of massing that the species may typically display in the wild.

Hansen and Stahl (1993) list five sociability scores (Figure 4.4):

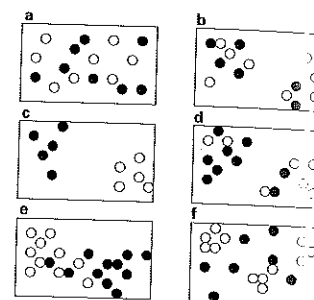
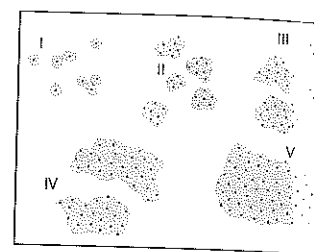
- i singly or in small clusters
- ii small groups of 3–10 plants
- iii larger groups of 10–20 plants
- iv extensive planting in patches
- v extensive planting over large areas.

The degree of segregation of two or more species gives an indication of how 'mingled together' or intimately associated they are. The lack of distinct boundaries between plant groups is another key characteristic of a naturalistic approach to planting. Figure 4.5 indicates a range of possible patterns for two-species mixtures.

In essence, the ecologically-informed detailed planting plans described in Chapter 9 are based upon interactions between the segregation and aggregation of the component species. The German Plant Sociability school of planting design was itself based upon detailed studies of the way plants are distributed in the wild, such as those carried out by Willy Lange (see Chapter 2). Vegetation mapping of this sort enables us to detect just how a diverse mix of species is able to co-exist. It not only provides a sense of how designers can arrange plants to achieve a naturalistic effect, but it can also indicate how mixtures can be put together to produce an extended season of display, using information both about their competitiveness and vigour, but also their growth form (degree of aggregation, as discussed above) and growth pattern through a season.

### Phenology

The concept of the ecological niche has already been mentioned as one means by which greater biodiversity is achieved, with species co-existing as close neighbours but not directly conflicting because they exploit different aspects of the environment. This can be viewed in terms of the relative

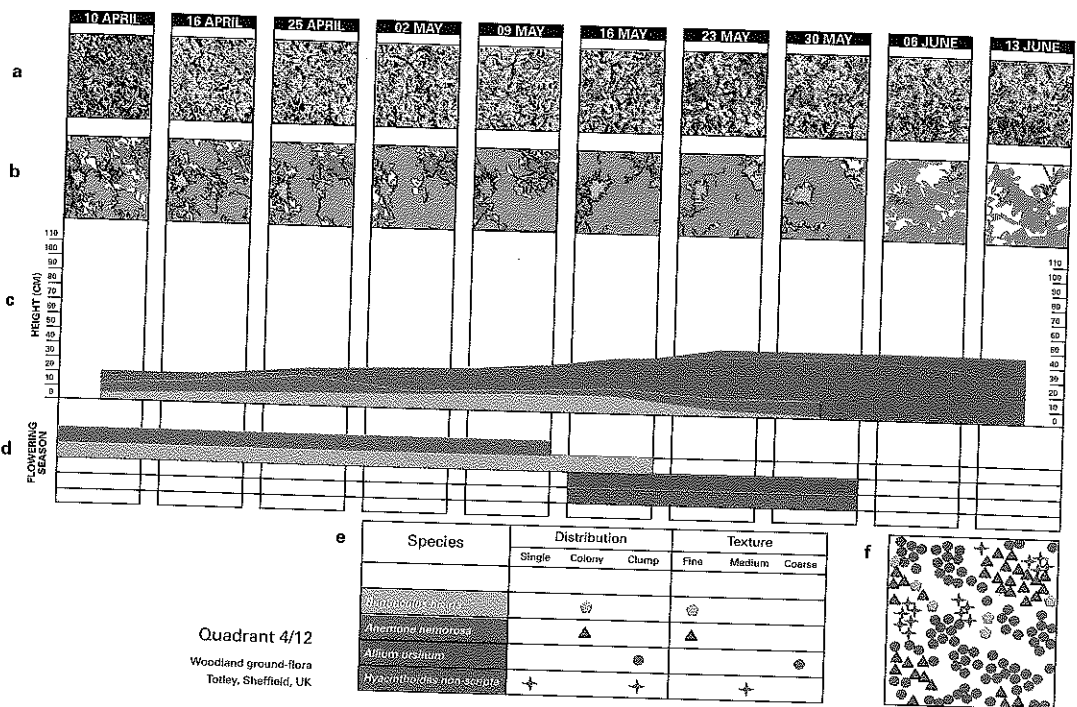


4.4 Different degrees of massing shown by plant species in the wild (from Hansen and Stahl (1993))

4.5 Six possible patterns for two-species populations: (a) and (b) not segregated; (c) fully segregated; and (d), (e) and (f) partly segregated (adapted from Pielou (1961))

4.6

Phenological change in a woodland ground flora community in Totley Wood, Sheffield. (a) Photographs of the same area over the period 10th April – 13th June 2001; (b) Diagrammatic representation of the area occupied by each species; (c) The relative heights of different species over the time period; (d) Flowering times for each species; (e) Characteristics of each species; (f) Plan showing the locations of clumps or individuals of each species in the studied area. Figure drawn from unpublished data by Cruz Garcia Albarado



abundance of different species, with dominant species (usually small in number in any plant community) grabbing most of the resources, and a larger number of sub-dominant species fitting in around the dominants. Figure 4.6 illustrates change in a woodland floor plant community over a period of three months or so in the spring.

One of the most important points from this detailed study is that a diversity of species gives a long period of display within a small unit of space. This is very different from the sort of display obtained from more standard horticultural block planting, where continuity of display might occur over larger distances. In Figure 4.6, the dominant species, *Myrrhis odorata*, which occupies the majority of the space at the end of the sequence, comes into growth relatively late and effectively hides the dying back remains of the earlier flowering species. The *phenology* of a species, i.e. its growth

pattern through the growing season, can therefore be a crucial factor in creating compatible mixtures of species that have a long season of display.

### Dynamic change in time and space

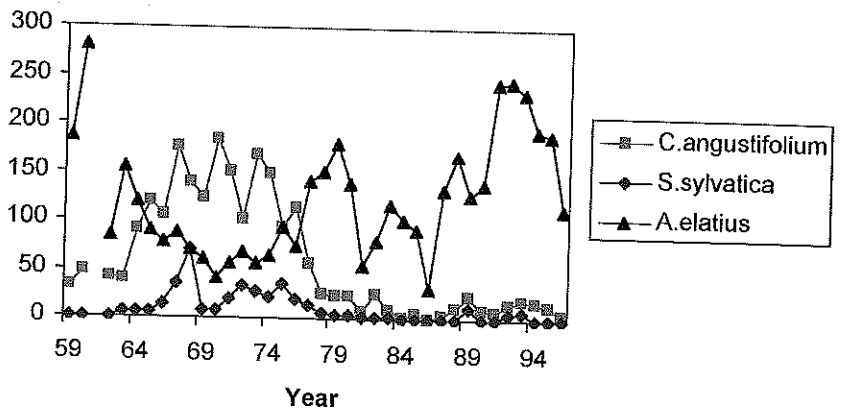
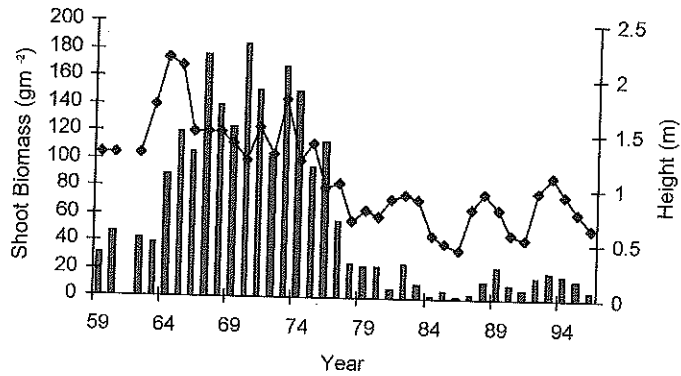
Even the seemingly most stable types of 'natural' vegetation will be subject to change. Whilst most people will assume that most of the wild vegetation they see around them (for example roadside verges and woodlands) stays pretty much the same from year to year, there may in fact be dramatic changes in the composition of that vegetation or the relative abundance of the component species. For most of us, these changes take place on a sufficiently long timescale (even if it is just from year to year) for us not to register that change is taking place. We have already discussed short-term changes that occur through a growing season, as one species takes over

from another in terms of visual display. But other changes take place over periods of more than one growing season. These are of direct relevance to the design and management of naturalistic vegetation, partly because they affect the way that the vegetation may be managed, and partly because they highlight again the point that ecologically-informed design and management of vegetation is about setting up a system that is inherently dynamic and to some extent unpredictable into the long term. We can recognise two types of longer-term dynamic change: *fluctuations* or cycles, whereby species composition may change but the overall character of the vegetation remains relatively constant, and *successional* change, whereby the actual character and type of vegetation may change over time.

**Cycles and fluctuations**

There have been surprisingly few long-term studies that have monitored changes in the composition of plant communities over more than three to five years. As can be seen from Figure 4.7, the performance of a species over such a period really gives very little information about what it is actually doing over periods of decades. Those longer studies that have been carried out tend to confirm what most gardeners know by experience: plants tend to have good years and bad years, determined primarily by weather conditions, and perennial plants (both woody and herbaceous) tend to become over-mature and require rejuvenation in due course.

Figure 4.7 is taken from the Bibury dataset, one of the longest continuous studies of herbaceous vegetation in the wild, which is taken from productive grassland vegetation on a roadside verge in the south of England. The figure shows the yearly performance of a large stand of rosebay willowherb (*Chamerion angustifolium*), a vigorous tall perennial 'competitor' that forms large spreading clumps that tend to exclude other species, and which makes a



dramatic display of tall pink flower spikes in mid to late summer.

Figure 4.7 indicates that there is considerable variation in both the height and bulk (biomass) of this species from year to year. The main factor determining these changes (in the absence of changes in management) is yearly differences in weather patterns. But there is also dramatic longer-term change, with a period of peak performance over the 12 years from 1964 to 1976. This rise and fall (which may be cyclical) is typical of the behaviour of many herbaceous perennials. Such processes in vegetation are again generally the result of the influence of dominant species going through four distinct phases (Watt 1947): pioneer (establishment of a species), building (growth to peak biomass),

4.7 Comparison of maximum shoot height (♦) and shoot biomass of rosebay willowherb over the period 1959–1996 in the Bibury road verges. No measurements were made in 1961 (from Dunnett and Willis (2000))

4.8 Comparison of the performance of *C. angustifolium*, *Arrhenatherum elatius* and *Stachys sylvatica* over the period 1959–1996 in the Bibury road verges. No measurements were made in 1961 (from Dunnett and Willis (2000))



4.9  
Succession on railway  
sidings abandoned in  
Sheffield – grassland is  
being invaded by scrub  
and birch woodland

mature and degeneracy (breakdown of dominance and invasion by other competing species).

Whilst the increase in biomass and the lateral extent of the stand can be readily explained in terms of rapid clonal extension and elimination of subordinate species – *C.angustifolium* has a high potential for dominance (Grime 1973) – the sudden decline and break-up of the stand are less easy to interpret. One explanation for the change in performance of perennials in this way may be a progressive decline in vigour of the stand as resources are accumulated in living and dead components of the biomass, resulting in reduced

nutrient supply (Watt 1947). Other explanations may include responses to extreme weather (such as drought), herbivory, allelopathy or disease.

The influence of such fluctuations is not limited to the individual species, but is played out through interactions with other species in the same community. Figure 4.8 illustrates the interplay of *C.angustifolium* with other components of the system at Bibury. *Arrhenatherum elatius* (False Oat Grass) is another ‘competitor’ and clearly benefits from the collapse in vigour of *C.angustifolium*, but the performance of *Stachys sylvatica* (Hedge Woundwort), which grows on the shady edges of the



stand of *C. angustifolium* mirrors the performance of the willowherb.

There are very few such studies that demonstrate interactions between species over extended periods, but they generally indicate the major influence of dominant species on the behaviour of subordinates, and the overriding effect of climatic factors in causing yearly fluctuations in the abundance of different species (Watt 1971).

### Succession

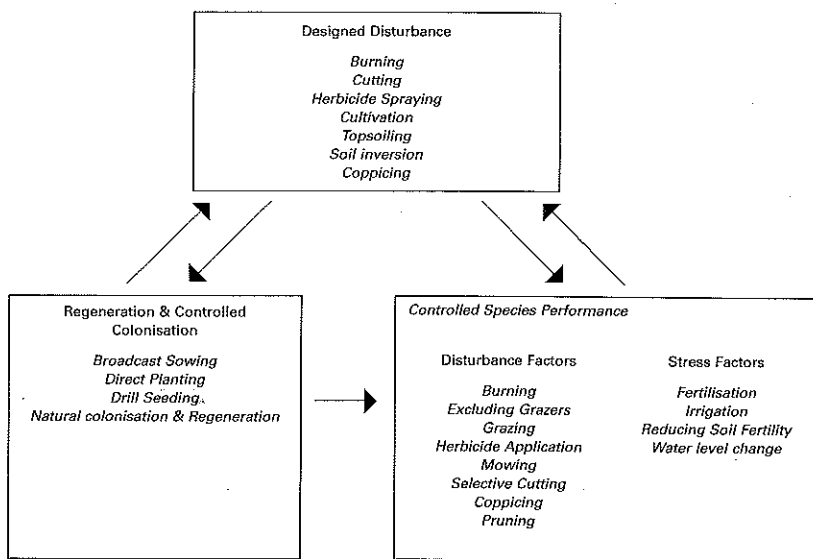
Succession is one of the fundamental concepts in ecology that is highly relevant to landscape design and management; indeed, it could be argued that a large proportion of landscape management operations are about preventing, promoting or diverting succession (although they are not often described in such terms). Succession differs from the cyclical changes and fluctuations described above in that it involves *directional* change in vegetation. Whilst cycles and fluctuations imply some sort of change within a defined vegetation type (i.e. although the precise species composition may change within a grassland, the vegetation remains as grassland), successional change implies a change not only in species composition, but also in vegetation character (i.e. grassland changes to woodland) (Figure 4.9).

In landscape terms, succession can be regarded as a force, constantly driving vegetation to alter its state, both in character but also species composition from the initial starting point. But just what is the end point? Classic succession theory suggests that in any given site, the progress of successional change can be predicted to a more or less predetermined outcome or 'climax' vegetation that is suited to a particular climate zone, with increasing species diversity, and structural complexity of vegetation as succession proceeds. However, this concept has been largely discredited and most ecologists recognise

that 'mature' vegetation is far more dynamic, with many different mature species assemblages occurring in any climatic region, and that the mature vegetation is in a constant state of flux, subject to cycles and fluctuations caused by external disturbances (Burrows 1990). For our purposes, a far better model for succession is to consider that vegetation reaches an equilibrium over time with the balance of environmental stress and disturbance factors that are operating on that site. The further away from that equilibrium that the vegetation is, the greater is the energy input required to keep it in that state. For example, maintaining short amenity grassland in lowland England requires far greater inputs of energy than maintaining deciduous woodland. This model has important implications because it suggests that the outcome of succession can be manipulated by altering the intensity of stress and disturbance operating on the system. It also suggests that succession itself can be used to guide vegetation to a state that is 'sustainable' (i.e. on any given site it can be maintained with minimal resource inputs).

Although succession has been researched and discussed in depth for many decades, the application of this knowledge has been limited in natural conservation management (Luken 1990), and has certainly been rarely discussed in urban amenity landscape management. However, for ecologically-informed landscape vegetation, a succession-based approach provides a rational basis for creative and informed management. Luken (1990), summarising succession-based management models developed in the context of restoration ecology, proposed three main components of succession management: *designed disturbance*, *controlled colonisation* and *controlled species performance*. These terms are equally applicable to the management of naturalistic landscape plantings.

Designed disturbance refers to those factors that initiate new successions and vegetation



4.10  
**A succession-based model for the management of designed urban vegetation (arrows indicate sequential operations). Adapted from Luken, 1990**

development, set back or slow down succession, or maintain cyclical change, i.e. periodic rejuvenation. In essence, designed disturbance is an artificial or human-induced operation that promotes suitable conditions for the establishment of new species or individuals on to a site. In most instances this will involve the removal of competition from existing vegetation and probably the creation of patches or areas of bare ground for seeding or planting. Some operations that can be used to create designed disturbance are listed in Figure 4.10. In effect, designed disturbances create or eliminate sites where succession can be initiated.

Controlled colonisation involves the manipulation of plant species' availability and establishment. Figure 4.10 lists operations that either directly introduce propagules of desired species, or selectively encourage certain species to establish or regenerate from species and propagule pools already present. It is clear that where non-native or ornamental species are to be included in a planting scheme, then artificial introduction is necessary. But even where vegetation is to be based

on common native species, natural colonisation on its own is rarely satisfactory, partly because of the timescales involved and also because the resultant vegetation is likely to be composed predominantly of weedy ruderal species, at least in the short to medium term. Controlled colonisation and establishment increases or decreases the availability of plant species, according to whether they are desirable or not.

Controlled species performance includes techniques that increase or decrease the growth and reproduction of plant species to shape both the composition and form of the vegetation over time. We can relate the operations listed in Figure 4.10 that differentially control species performance to Plant Strategy Theory, discussed earlier in this chapter. Some of these factors, such as increasing or reducing soil fertility, or controlling water availability, differentially affect the rate of growth of species and can be termed *stress factors*, whilst others, such as grazing, mowing and pruning, selectively remove or damage plant biomass and, therefore, can be termed *disturbance factors*.

Figure 4.10 illustrates these three components as an integrated model for the management of landscape and garden plantings. Examples of applications of this model are given in James Hitchmough's chapter on herbaceous plantings (Chapter 6) and also more specifically in Hein Koningen's chapter on the creative management of ecological plantings (Chapter 10). The arrows in Figure 4.10 indicate direct sequential steps. Each component may also be repeated through time (for example, regular coppicing of woody plants or annual hay cutting of perennial meadows).

References

- Burrows, C. J. (1990). *Processes of Vegetation Change*. Unwin Hyman, London.
- Dickinson, G. and Murphy, K. (1998). *Ecosystems*. Routledge, London.
- Dunnett, N. (1995). Harnessing Anarchy. *Landscape Design*, Nov., 25-29.
- Dunnett, N. and Willis, A. (2000). The dynamics of *Chamaenerion angustifolium* over a 38-year period in road verges at Bibury, Gloucestershire. *Plant Ecology*, 148, 43-50.
- Greig-Smith, P. (1964). *Quantitative Plant Ecology*. Butterworths, London.
- Grime, J. P. (1987). Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds) *Colonisation, Succession and Stability*. Blackwell Scientific Publications, Oxford, pp. 413-428.
- Hansen, R. and Stahl, F. (1993). *Perennials and their garden habitats*. Cambridge University Press, Cambridge.
- Hitchmough, J. D. (1994). Natural Neighbours. *Landscape Design*, 229, 16-24.
- Kaplan, R. and Kaplan, S. (1989). *The Experience of Nature*. Cambridge University Press, Cambridge.
- Knops, J. M. H. et al. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundance and diversity. *Ecological Letters*, 2, 286-294.
- Luken, J. (1990). *Directing Ecological Succession*. Chapman & Hall, London.
- McCann, K. S. (2000). The diversity and stability of ecosystems. *Nature*, 405, 228-233.
- Pielou, E. C. (1961). Segregation and symmetry in two-species populations as studied by nearest neighbour relationships. *Journal of Ecology*, 49, 255-269.
- Purvis, A. and Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405, 212-219.
- Schwartz, M. W. et al. (2000). Linking biodiversity to ecosystem functioning: implications for conservation ecology. *Oecologia*, 122, 297-305.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300-1302.
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, 35, 1-22.
- Watt, A. S. (1971). Factors controlling the floristic composition of some plant communities in Breckland. In *The scientific management of animal and plant communities for conservation*. Blackwell Scientific Publications, Oxford.