THE PLANT ECOLOGY OF A LIMESTONE GRASSLAND : COMPETITION AND SPATIO-TEMPORAL DYNAMICS

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"All the sweetness of nature was buried in black winter's grave,
and the wind sings a sad lament with its cold plaintive cry;
but the teeming summer will come, bringing life in its arms,
and will strew rosy flowers on the face of hill and dale"

~ Thomas Telynog Evans (1840-1865)

ABSTRACT

The research described in this thesis investigates the role of competition in the ecology of a species-rich limestone grassland in Derbyshire, England. Removal experiments demonstrated the existence of a size-based competitive response hierarchy, which may be the result of differences in below-ground foraging ability. However, despite highly plastic morphological changes observed in target plants following clearances, only a small amount of the variation in above-ground biomass of individual plants was explained by the area of neighbour-free space (<15% even for the smallest species), suggesting that short-term interference has little effect on plant performance.

Permanent plots were used to monitor the fine-scale spatio-temporal change of the community. Turnover of space occupancy was rapid among the majority of species, although the rosette-forming herbs tended to be more static, holding space for long periods of time. Differences in the spatial dynamics of species were observed between life-forms, and were strongly dependent on the dominant mode of recruitment employed. Vegetative growth led to rapid colonisation of neighbouring space and a tendency for aggregation whereas seed recruiting species were more dispersed. Despite the rapid turnover of space occupancy, changes in the species composition observed on the plots after two years of monitoring were slight. The number and identity of neighbour species had little effect on plant performance, suggesting that the spatio-temporal development of the community was primarily the product of the modular growth patterns of individual species.

In this community, short-term interference is uncoupled from the longer-term dynamics of species and within this framework potential mechanisms of coexistence are discussed. It is debated whether or not niche differentiation is necessary for species to coexist and possible methods for investigating this problem are outlined.

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AUTHOR'S DECLARATION

All of the work described in this thesis was done by me. The following parts were carried out in collaboration with other researchers.

Chapter 2 is in press in Journal of Ecology 83(1) under the title 'On decaying roots, mycorrhizal colonisation and the design of removal experiments' as a joint paper with Alastair Fitter and Richard Law.

Chapter 3 has been submitted to Ecology as a joint paper with Richard Law and Alastair Fitter titled 'Size-based competitive response of plant species in a limestone grassland'.

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Chapter One

INTRODUCTION

1.1. Summary

This chapter introduces the theory of plant competition and coexistence as a background to the research described in this thesis. The basis of plant competition is described and its effects on plant community structure are considered within the framework of plant strategy theory. In particular, the difference between short-term interference and competition for space is emphasised. The idea of competitive exclusion is introduced and equilibrium and non-equilibrium mechanisms of coexistence are discussed. Calcareous grasslands are presented as highly diverse plant communities which will be used as a model system in which to investigate competition and coexistence. In these communities the role of competition in maintaining the community structure is unclear despite a number of studies on the subject. The field site is described and the aims of the research are presented. Finally, the layout of succeeding chapters of the thesis is described.

1.2. Competition between plants

1.2.1. Defining competition

Pioneer plant communities are characterised by an overabundance of resources relative to the number of individuals present. During the course of time, these resources become more limiting as there is a net immigration of plants and species to the site. As resources become scarce, plants will compete, and classical theory predicts that those species which are more effective at obtaining and utilising light, nutrients and water, and preventing their neighbours from doing so, will be retained in the assemblage at the expense of competitively weaker species (Clements 1916).

Plants may interact directly with each other in three ways (Harper 1961): by competing for scarce resources, by secreting chemicals into the soil (allelopathy, Rice 1984), and by modifying the physical environment. Harper coined the blanket term interference for the sum of these interactions because the separate effects of each mechanism are often difficult to identify in the field, both the removal of resources and allelopathic inhibition of resource uptake will induce similar responses in a plant (Harper 1975). However, Goldberg (1990) makes a distinction between uptake (removal of resources) and non-uptake (addition to the soil e.g. allelopathy and non-additive processes e.g. modification of physical environment and microbial activity) components of interference. These components can, in theory, be isolated since uptake competition (*sensu* Harper 1961, above) will reduce the resource base whereas modifying the physical environment is unlikely to (although indirect effects mediated by microbes may be envisaged), and allelopathy may add to the chemical environment.

Keddy (1989) defines competition as "...the negative effect which one organism has on another by consuming, or controlling access to a resource that is limited in availability". This definition considers the effect rather than the mechanism of competition and is measurable in the field, but does not consider the mechanism by which competition operates. The definition of Grime (1973) of competition as "...the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, or volume of space" is more mechanistic, but it is difficult, if not impossible, to apply in practice (Grubb 1985).

1.2.2. Plant competition as a localised process

Since plants are for the most part sessile and rooted to the site where their seed germinated (Harper 1977), competitive interactions between plants are limited to neighbours whose roots or shoots are in direct contact. This is illustrated by the work of Mack and Harper (1977) who found that 77% of the variation in plant size on sand dunes could be explained by the size and proximity of

neighbouring plants within 2 cm. Interactions between plants thus occur at the level of neighbouring individuals, this contrasting with the process of competition between most animal species in which a large number of individuals from a population may interact as a result of their greater mobility.

The highly localised nature of plant competition has the consequence that the arrangement of plants in space determines the degree of contact that each plant has with member of its own and other species (Hutchings 1986; Mahdi and Law 1987) and has implications for the coexistence of species (section 1.4). Individual plants will experience interactions with a number of species, with different intensity, and this is termed **diffuse** competition (MacArthur 1972, Goldberg and Werner 1983). The result of diffuse competition is experienced as the combined loss of resources rather than species-specific effects (Fitter 1986) and the per gram competitive effect of species is often similar (Goldberg 1987).

1.2.3. Above- and below-ground interactions

Potentially limiting resources in a plant community consist of light, water and mineral nutrients. A dichotomy can thus be envisaged between the processes involved in competition occurring above-ground (for light) and below-ground (for water and nutrients).

Competition for light is based on the ability of plants to position their foliage higher in the canopy than their neighbours (Mitchley and Grubb 1986). A plant losing its place in the height hierarchy will rapidly become overtopped by such a degree that it will not recover its place and for this reason above-ground interactions are highly asymmetric (Harper 1977; Weiner 1990),. Taller plants will enjoy a disproportionate quantity of the total light resource available to the community and are likely to become dominant.

The ability to capture resources below-ground is based on an efficient root system and may be enhanced by mycorrhizal colonisation (Brundrett 1991). It

is less asymmetric than above-ground competition (Keddy 1989) and as a result will be less likely to cause competitive exclusion (see section 1.4).

It has been suggested that the ability of plants to forage effectively above- and below-ground should be negatively correlated as a consequence of resource allocation trade-offs (Tilman 1982, 1987. 1988). An alternative hypothesis is that the two should be positively correlated, more resources gained in one sphere of competition increasing the ability to forage in the other sphere (Thompson 1987; Thompson and Grime 1988), a view which is upheld by empirical evidence (Mahmoud and Grime 1976; McGraw 1985).

1.2.4. Competitive effect and response

The competitive ability of a plant comprises two components (Goldberg 1987), the capacity to suppress the growth of other plants (high **competitive effect**) and the ability to withstand suppression from other plants (low **competitive response**). The recognition of these two facets of competition is important to our understanding of how competition operates. Competitive effect is a characteristic of C-strategists (Grime 1977; section 1.3) by virtue of their fast growth which allows them to overtop their neighbours and deny them access to light. The production of a dense litter is also a trait which may lead to competitive dominance (Bergelson 1990a,b; Facelli and Pickett 1991). The ability to resist competitive suppression may be a characteristic of stress-tolerant plants (S-strategists) which may be able to survive in conditions of low light and/or nutrient availability by the efficient conservation of nutrients within the tissues (Grime 1979). However, the shade-intolerance of S-strategist seedlings may be a reason for their demise in coarse turf (Fenner 1978).

1.2.5. Competitive hierarchies

Competitive effect and response have found to be inversely correlated (Miller and Werner 1987), implying that species which are best able to suppress their neighbours are also best able to withstand suppression themselves. This relationship suggests that species can be placed in a hierarchy from high to low

competitive ability. Such hierarchies of competing species have been demonstrated to exist in a number of plant communities (Mitchley and Grubb 1986; Keddy and Shipley 1989; Shipley and Keddy 1994; Keddy, Twolan-Strutt and Wisheu 1994), a finding with important consequences for plant competition theory. It implies that competition is transitive i.e. species with a high competitive ability will always outcompete species lower in the hierarchy, and the outcome of competitive interactions is predictable from a knowledge of the position of the species in the hiearchy. The position of a species in a hierarchy may be the product of traits such as size and growth rate, factors which determine above-ground interference ability and competitive effect (Grime 1973; Gaudet and Keddy 1988).

The existence of competitive hierarchies is, however, in some dispute. It has been pointed out that the close correlation obtained by Grubb and Mitchley (1988) between field abundance and pot competitive ability could be an artefact of the dependence of both measures on plant size (Silvertown and Dale 1991) and the artificial nature of the pot experiments used by Keddy and Shipley (1989) which are biased in favour of larger plants and remove the environmental variation which may be necessary for competitive reversals to occur (Herben and Krahulec 1990).

1.2.6. Competition for space

Yodzis (1986) suggested that competition between plants could be thought of as spatial rather than consumptive since the pre-emption of space allows access to resources within that area (Harper 1977, p167). A related idea is the concept of competition for microsites, which occurs in the regenerative phase of the plant life cycle (Grime 1979; Yodzis 1986). Competition for microsites differs from resource competition because there can be only one winner. Space may be captured either by vegetative growth into neighbouring areas, or by seedling establishment in suitable microsites. The abundance of species in the field is determined by the efficiency by which space is captured and the life-span of plants. Both the reproductive potential and mortality of plants may be

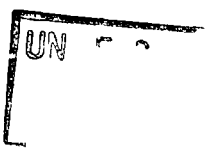
influenced by short-term interference, but this will not solely determine the outcome of spatial interactions. In order to fully grasp the role of competition in plant communities, it is necessary to separate competition into the established and regeneration phases, whilst understanding the interaction between the two processes.

Grubb (1985) makes the distinction between short-term measures of competition, by which the "yield of one plant is reduced as the result of another plant being present", which has previously been termed interference (Harper 1961), and "the relationship between two species not symbiotic with each other and capable of occupying the same landscape unit, considered over the whole life cycle" which he accepts as the true meaning of 'competition'. However, because 'competition' as a term is usually synonymous with interference (*sensu* Harper 1961; Grubb 1985), within this thesis, short-term effects on plant performance will be termed 'interference' or 'competition', and effects over the entire life-cycle of plants will be referred to as 'competition for space'.

1.3. Primary plant strategies

Grime identified two factors which would have an effect on plant community structure; stress and disturbance (Grime 1977, 1979). He defined stress as any factor limiting the production of biomass (by the removal of resources or otherwise), disturbance being those density-independent processes which act to remove biomass once it has been accumulated (herbivory is thus classed as a disturbance factor). These two factors are the principal determinants of community structure and have a large influence on the diversity of the system (q.v.).

Both stress and disturbance act to diminish the above-ground production of an ecosystem, which limits the amount of competition for light and reduces the ability of competitive species to dominate the community. As the levels of stress and disturbance in a community increase, the dominant sphere of



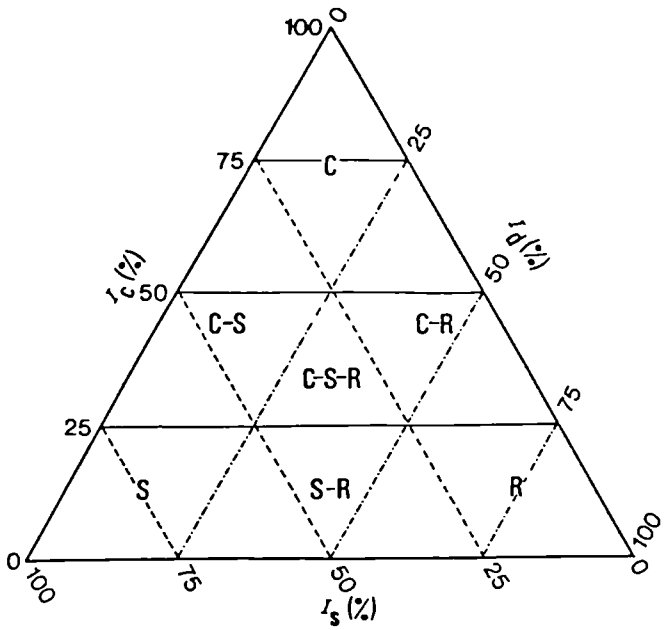


Figure 1.1. Triangular model describing the various equilibria between the intensity of stress (I_s), disturbance (I_d) and competition (I_c) in plant communities. The letters within the triangle refer to primary plant strategies (and combinations thereof) found at different intensities of these three factors. C - competitors, R- ruderals, S - stress-tolerators. (From Grime 1979, p57).

interactions will shift from being above-ground to below-ground (Weiner 1986; Wilson and Tilman 1993). This reduction in the intensity of competition with decreasing productivity (Wilson and Keddy 1986) led Grime to postulate a negative correlation between the intensity of disturbance, intensity of stress and intensity of competition within a given community (Grime 1974, 1979, 1988). This three way relationship can be visualised inside a triangle (Fig. 1.1).

Grime further recognised that the degree of stress, disturbance and competition experienced by a species was reflected in its life history traits. He thus defined three primary plant strategies (Grime 1977, 1979) of competitors (C-strategists), stress-tolerators (S-strategists) and ruderal species (R-strategists). Competitors are associated with high productivity, low stress and low disturbance environments in which competition for light is the primary determinant of plant reproductive success. These species have high growth rate, a large capacity for lateral spread and often produce an extensive litter. Stress-

tolerators are associated with nutrient-poor habitats in which a small compact growth form and conservative use of nutrients represents the best strategy for survival. Ruderals are essentially what have previously been termed r-selected species (Pianka 1970), and allocate the majority of their resources to reproduction. This life history is well adapted to environments which experience frequent episodes of disturbance. The balance of each of these three types of species in a habitat will depend on the intensity of stress and disturbance.

Tilman (1987) has a different view of competitive species. He believes that competitively dominant species are those which can tolerate a lower level of resources. This can be seen to concentrate on competitive response rather than effect and falls closer to Grime's definition of stress-tolerators than competitive species. However, while Tilman's theories may hold true for the symmetric competition for nutrients (perhaps reflecting Tilman's early work on algal communities, Tilman 1976, 1977), they are not consistent with the mechanisms above-ground interference in which rapid growth and litter production suppress smaller species (Peet *et al.* unpublished).

Grime's plant strategy theory has been criticised on the grounds that it is logically flawed (Loehle 1987), and is too general (Grubb 1985; Tilman 1987), adaptation being to particular stress and disturbance factors rather than the blanket terms used by Grime. What is stressful for one species may be beneficial for another (Harper 1982) e.g. submergence in water. However, preliminary tests of the hypotheses of the theory (such as the change in competitive intensity across stress and disturbance gradients) have been supportive (Campbell and Grime 1991; although Wilson and Tilman 1993 found no change in competitive intensity across a fertility gradient but disturbance was found to reduce competition) and strategy theory represents a useful theoretical framework in which to study plant communities.

Recently a demographic version of Grime's triangle has been devised based on empirically measurable traits of growth, reproduction and survival corresponding to C-, R- and S-strategists respectively (Silvertown, Franco and McConway 1992, Silvertown *et al.* 1993). Initial attempts to correlate Grime's community perspective and this demographic approach have proved elusive (Silvertown, Franco and McConway 1992, 1993), and it has been pointed out that correlations between the elasticities of traits cannot be directly interpreted as trade-offs (Shea, Rees and Wood 1994), but there appears to be some potential for using a demographic method to complement Grime's community level approach.

1.4. Competitive exclusion and coexistence

1.4.1. Equilibrium coexistence

A central problem of plant ecology is to explain the coexistence of plant species (Fitter 1987) since, in a community of competing plants, species higher in a competitive hierarchy would be expected to exclude those lower down (Silvertown and Dale 1991). This notion stems from the competitive exclusion principle of Gause (1934) who proposed that at equilibrium, if two species were competiting for resources, the weaker would be excluded unless the two species differed in their niche requirements for food or habitat or if resources were not limiting. From this theory, under resource-limiting conditions the number of species in a community should be equal to the number of distinct niches available for occupancy (Chesson and Case 1986).

In animal communities there are many possibilities for species to differ in their food and habitat requirements. However, since flowering plants all have similar needs for essential nutrients, light and water they are unlikely to differ in their habitat niche (Mahdi and Law 1987). The majority of species will also have similar phenology and overlap in their resource uptake. There are, however, possibilities for niche differentiation in plant communities. Tilman (1982, 1986) has suggested that species may differ in the ratio of demand for

resources, although this was found not to apply to calcareous grassland plants (Mahdi, Law and Willis 1989), and Grubb (1977) has put forward the concept of the regeneration niche in which species differ in their requirements for recruitment in time and space. It has been demonstrated that differences in the regeneration niche may allow species to coexist if there are environmental fluctuations which allow strong recruitment by species at different points in space and time (the 'storage effect', Chesson and Warner 1981; Warner and Chesson 1985; Chesson 1986).

Shmida and Ellner (1984) presented a model for the coexistence of species with identical niches competing in a homogeneous environment. They demonstrated that exclusion was prevented if species distributions were clumped which led to a prevalence of intraspecific relative to interspecific competition, each species effectively controlling its own dynamical behaviour. A similar mechanism was observed by Atkinson and Shorrocks (1981) in insect communities competing on a divided and ephemeral resource. Aggregation of the superior competitor led to an increased chance of coexistence. This mechanisms of coexistence may apply well to plant communities in which competition and dispersal are spatially limited (Czárán and Bartha 1989; Silvertown *et al.*1992).

1.4.2. Non-equilibrium coexistence

Equilibrium coexistence may be the least interesting and least likely mechanism of coexistence even if it is mathematically elegant (Keddy 1989). At competitive equilibrium (on a point attractor) the growth rates of species are zero (Huston 1979), and chance, history and environmental fluctuations have little role to play in the determination of community dynamics (Chesson and Case 1986). Such a community is an unlikely phenomenon in the real world.

Species-richness is a dynamic equilibrium between species colonisation and exclusion (Huston 1979; Tilman 1993) and thus either high rates of colonisation or high rates or low rates of extinction will lead to a diverse ecosystem. The

establishment phase is particularly important in ecological communities, "supply side ecology" (Lewin 1986) often being overlooked (Roughgarden 1988). Exclusion of a species may be prevented given an adequate supply of propagules in space and time ("spatial and temporal mass effect" Shmida and Ellner 1984, Chesson 1986) and enough disturbance to provide suitable microsites for colonisation. However, despite the dependence of species diversity on colonisation rates (Tilman 1993), the speed at which competitive exclusion occurs is likely to be the prime determinant of the number of species occurring at a particular site.

The rate of competitive exclusion is highly related to both the growth rate of the competing species (productivity) and the frequency and intensity of density-independent mortality events (disturbance). In a system with high productivity and little or no disturbance, the faster growing species will rapidly exclude those lower in the competitive hierarchy. As biomass is removed, either in terms of reduced nutrient supply or increased removal of biomass, the intensity of competition will decline (Grime 1977, 1979; section 1.3).

Frequency-dependent herbivory provides a stabilising feedback mechanism by which the dominant species in a competitive relationship will lose proportionally more biomass than the subordinate species. In this way competitive exclusion may be prevented from occurring. Herbivory is often frequency-dependent and Silvertown and Law (1987) suggested that it may maintain dominant species at a level at which they are unable to exclude other species. This effect is termed predator-mediated coexistence and has been demonstrated empirically (Paine 1966; Wells 1971) and theoretically (Caswell 1978; Pacala and Crawley 1992). Periods of density-independent herbivory may also slow the rate at which competitive exclusion occurs (Huston 1979). Unselective abiotic disturbances such as hoof prints may provide regeneration gaps for ruderal species which can escape competition by virtue of their high mobility (Slatkin 1974; Hobbs and Mooney 1985; Crawley and May 1987).

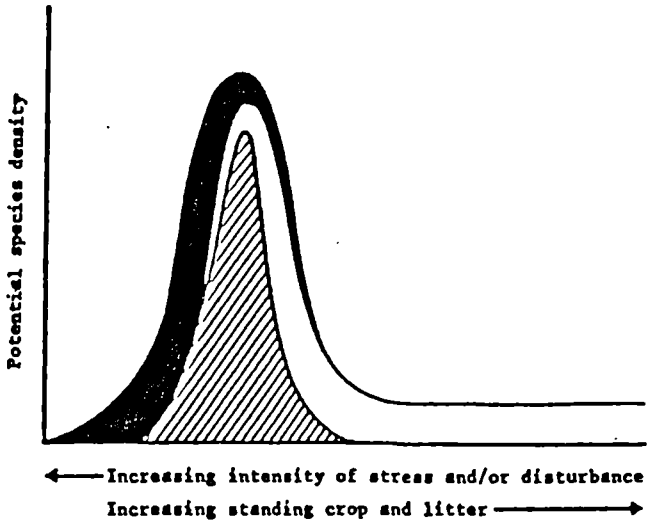


Figure 1.2. The hump-backed model of species diversity, relating the number of species in a habitat to productivity. □, potential dominants; ■, species highly adapted to stress or disturbance; ▨, species which are neither potential dominants, nor highly adapted to stress or disturbance (From Grime 1973).

Plants produce less above-ground biomass under unproductive conditions and their abiliy to suppress the growth of their neighbours by shading is reduced, thereby increasing the time taken to reach competitive exclusion. This has been termed 'slow dynamics' by Huston (1979) and is likely to result in greater diversity at a given level of disturbance. However, in extremely unproductive conditions such as desert or arctic habitats, the number of species able to tolerate the conditions will be low and an increase in productivity will enhance the diversity of the system. Similarly diversity will be low in unstable environments and shifting substrates subject to frequent disturbance episodes. At high levels of stress and disturbance there will only be S- and R-strategists respectively but at intermediate levels (represented as the central region of Grime's triangle) all three types of species will be able to persist. The dominance of competitive species will be reduced because of stress and disturbance and ruderals will be able to colonise gaps in the sward made available by disturbance episodes. The relationship of species diversity with productivity is expected to follow a hump-backed curve (Fig. 1.2; Rosenweig

and Abramsky 1993) and be greatest at intermediate levels of stress and disturbance (Grime 1979; Huston 1979).

Slow dynamics may also arise in conditions in which the adult plants are long-lived or there are small differences in the competitive ability between species (Shmida and Ellner1984). Under these circumstances, the time taken to reach competitive exclusion will be prolonged and slight disturbance episodes may prevent equilibrium, with the consequent loss of species, from being attained. Hubbell and Foster (1986a,b) observed this to be the case in stands of tropical rain forest trees. The woody species in this ecosystem are all long-lived and are competitively equivalent. Recruitment occurs through opportunistic colonisation of stochastic gap formation (lottery competition) and the species composition undergoes a random walk through time.

1.4.3. Mycorrhizal interconnections

Some 80% of all land plants are estimated to form mycorrhizal symbioses and the fungal mycelium may connect two or more plants in a network (Newman 1988). Grime (1990) has suggested that these networks may provide a route for the transfer of resources between species, there being a net movement from dominant source plants to subordinate sink plants. Such interactions may ameliorate the effect of competition between species, resources being shared rather than monopolised (Allen and Allen 1990).

Grime *et al.* (1987) observed that mycorrhizal connections may increase species diversity in herbaceous microcosms, although the mechanism by which the increased diversity occurred has been debated (Bergelson and Crawley 1988). Under certain circumstances, mycorrhiza can have a detrimental effect on diversity, actively parasitising the subordinate plants and transferring the resources to the dominants (N.K. Watkins personal communication). Since, it has yet to be demonstrated that transfer of carbon between plants is translocated to shoot material and does not just remain in the mycelial

components of the roots, the existence and operation of mycorrhizal networks as a mechanism for coexistence remains unclear.

1.5. Calcareous grasslands

Calcareous grasslands are highly diverse meadow communities occurring on the chalk and limestone geologies of north-western Europe, often containing up to 40 species m^{-2} (Grubb 1986). These grasslands were created through the Neolithic clearances which occurred as man turned increasingly to agriculture as a means of subsistence (Smith 1981). Calcareous grasslands may also have established in areas where forests failed to achieve a closed canopy following the Devensian glacial, erosion being too rapid, slopes too steep or soil too shallow for trees to root (Pigott and Walters 1954). Some grasslands may thus have their origins in the early part of the Holocene, Bush and Flenly (1987) finding evidence for Pre-Boreal origin.

Although tropical rainforests are rightly exemplified for their species richness, at scales of less than a metre, grassland communities are the most diverse communities in the world (Fig. 1.3). The high species richness of calcareous grassland communities at such a small scale poses interesting ecological questions. Since high levels of competition are expected to reduce diversity (Grime 1979), to what degree are the species in these communities interacting?, and if competition is present then what are the mechanisms maintaining the high diversity? The fundemental ecological questions raised by calcareous grasslands and the large numbers of rare species which they contain have been the cause of a wealth of literature (see for example Hillier *et al.* 1990).

The nutrient poor soils and heavy grazing characteristic of calcareous grasslands gives rise to a small and compact flora, with a relatively low growth rate (Grime 1990). Individuals can thus be packed into a small area of turf, providing a causal link between soil infertility and species richness. The plants found in such habitats are, for the most part, archetypal stress-tolerator species

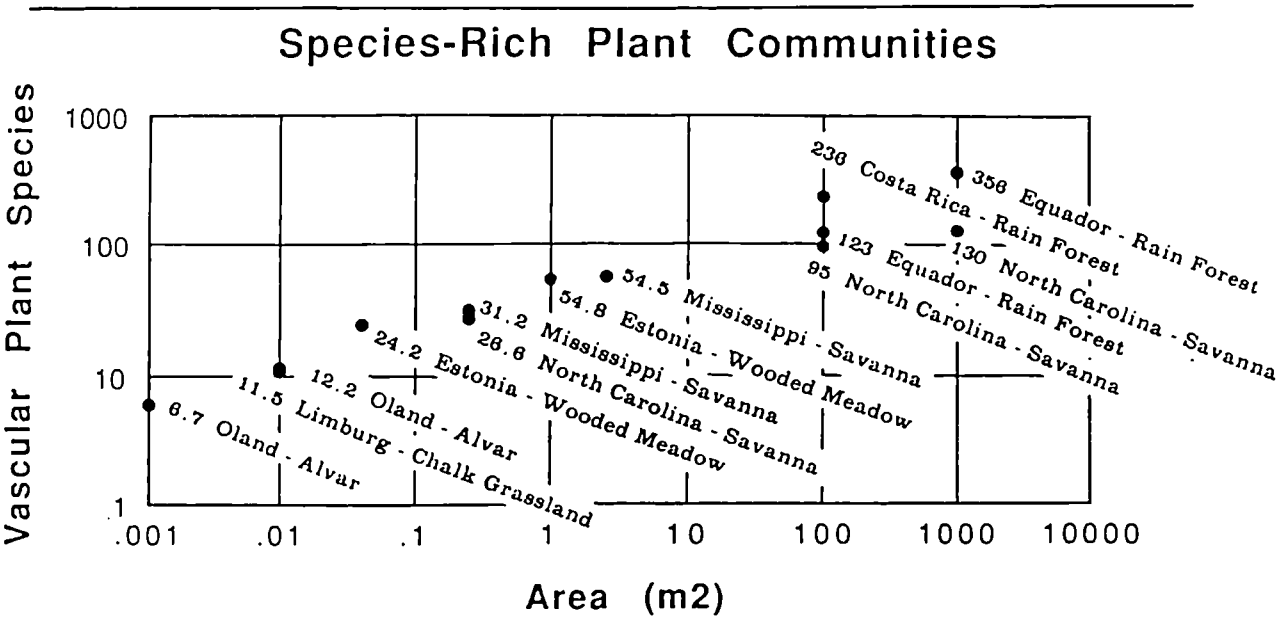


Figure 1.3. At scales of 0.001 - 10 m^2, the world's most species-rich plant communities are grasslands (from Peet *et al.* unpublished manuscript).

(*sensu* Grime 1977) and, as such, may have little influence on each others dynamics (Grime 1990). Mahdi (1988; and described in Law and Watkinson 1989) carried out small-scale ramet removal experiments in a limestone grassland in Derbyshire, England in order to simulate natural birth and death processes, and found no significant change in the density of the remaining plants. He observed no differences between species in their time of flowering and requirements for soil depth, nutrients (N and P) and soil pH (Mahdi, Law and Willis 1989) so niche differentiation could not be evoked as an explanation for the lack of competition. The results of this work suggest that the interactions between plants were not strong enough to alter the species composition of the site and thus would not determine the field abundance of a species. However, it is entirely possible that the statistical power of the experiment was too small to detect competition (Law and Watkinson 1989).

By contrast Mitchley and Grubb (1986) demonstrated the existence of a consistent hierarchy of abundance of the perennial species in chalk grassland in southern England and this ranking of species was shown to be well correlated with the competitive ability of species in pot experiments (Mitchley and Grubb

1986) and the height of leaves of species in the field (Mitchley 1988). This suggests that above-ground competition is a major determinant of plant reproductive success; such a conclusion is perhaps surprising in an ecosystem in which light is a more readily available resource than mineral nutrition (Ford 1990; Mitchley 1990). Further, the existence of a competitive hierarchy would be expected to lead to low diversity unless there are processes acting to prevent or prolong competitive exclusion (see section 1.4).

Many calcareous grassland species are highly aggregated in space as a result of local clonal growth patterns (Mahdi and Law 1987; van der Hoeven, de Kroon and During 1990), a feature which may have important consequences for the dynamics of the system (Silvertown *et al.* 1992). It has suggested earlier in this chapter that clumping often reduces the intensity of interspecific interactions and this may be a partial explanation for the coexistence of species in calcareous grassland.

1.6. Priestcliffe Lees Nature Reserve

The fieldwork part of this research was carried out at Priestcliffe Lees, a limestone grassland (Plates 1.1 and 1.2) in the Peak District National Park, Derbyshire, England (latitude 53° 15′ N, longitude 1°47′ W), at an altitude of 320m with a gently sloping south-westerly aspect. The soil is shallow (mean depth 16.8 cm), being loess overlying Carboniferous limestone (Pigott 1962), and slightly acidic (pH 6.00 ± 0.03). Levels of soil nitrogen and phosphorus are low (Mahdi and Law 1987). The flora is typical of the CG2c category of the British National Vegetation Classification (*Holcus lanatus* - *Trifolium repens* subclass of *Avenula pratensis* - *Festuca ovina* grassland; Rodwell 1993) and a complete list of species recorded at the site is presented in Table 1.1. Priestcliffe Lees has a history of rough cattle grazing for the last 65 years and is grazed naturally by rabbits.

Plate 1.1. Priescliffe Lees Nature Reserve, a species-rich limestone grassland in Derbyshire, England in October (above) and June (below).

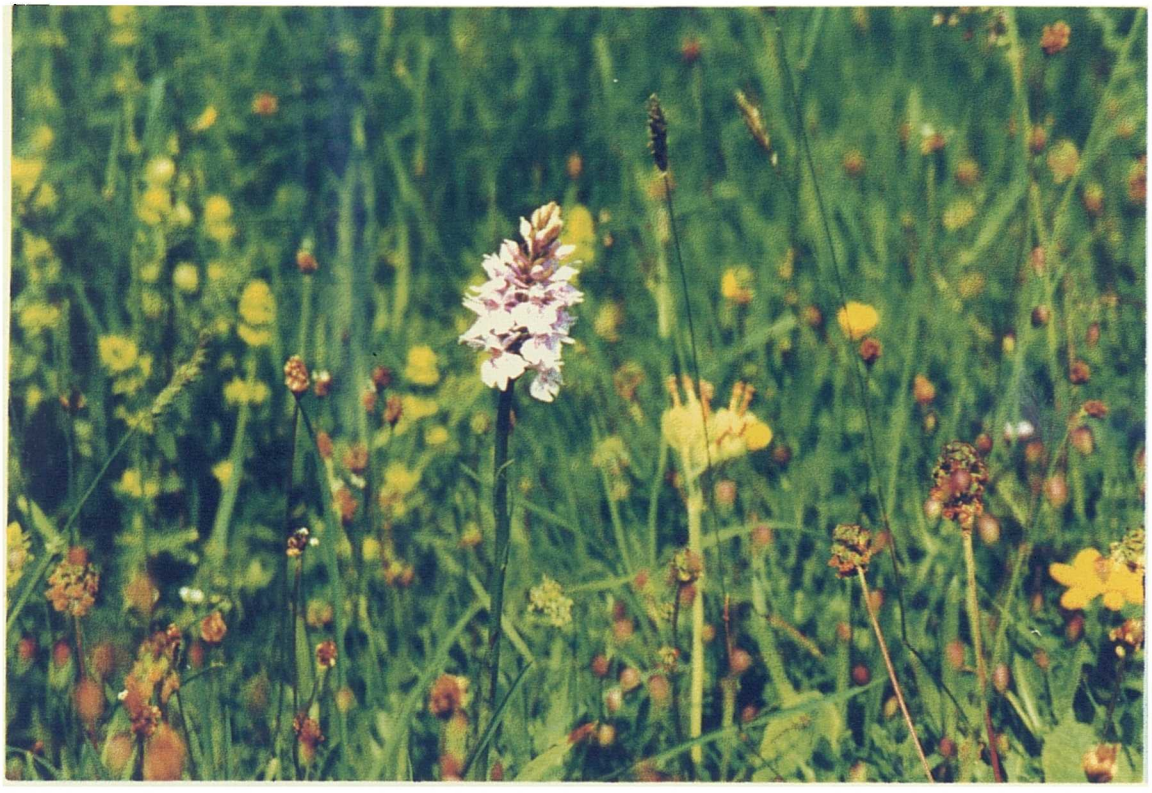


Plate 1.2. Species occurring at Priestcliffe Lees. *Rumex acetosa* and *Dactylis glomerata* (above) and *Dactylorhiza fuschii* (below).

Table 1.1. List of plant species occurring at Priestcliffe Lees Nature Reserve. Nomenclature follows Stace (1991). Two character names are abbreviations used in the text.

MONOCOTYLEDONS	
Ac	*Agrostis capilliaris*
Ao	*Anthoxanthum odoratum*
Bm	*Briza media*
Cc	*Carex caryophyllea*
Cf	*Carex flacca*
Cy	*Cynosurus cristatus*
Dg	*Dactylis glomerata*
Df	*Dactylorhiza fuschii*
Dd	*Danthonia decumbens*
Dc	*Deschampsia cespitosa*
Fo	*Festuca ovina*
Fr	*Festuca rubra*
Hp	*Helictotrichon pratensis*
Hl	*Holcus lanatus*
Km	*Koeleria macrantha*
Lp	*Lolium perenne*
Lc	*Luzula campestris*
Ph	*Phleum pratense*
Po	*Poa annua*
DICOTYLEDONS	
Am	*Achillea millefolium*
Ag	*Alchemilla glabra*
An	*Anenome nemorosa*
Bp	*Bellis perennis*
Cr	*Campanula rotundifolia*
Ca	*Carduus nutans*
Cn	*Centaurea nigra*
Ce	*Cerastium fontanum*
Co	*Conopodium majus*
Cm	*Cratageous monogyna*
Eo	*Euphrasia officinalis* agg.
Gv	*Galium verum*
Ga	*Gentianella amarella*
Hn	*Helianthemum nummalarium*
Hs	*Heracleum sphondylium*
Hr	*Hypochaeris radicata*
Lm	*Lathyrus linifolius ssp. montanus*
La	*Leontodon autumnalis*
Lh	*Leontodon hispidus*
Li	*Linum carthartícum*
Lo	*Lotus corniculatus*
Mv	*Minuarta verna*
Pi	*Pilosella officinarum*
Pl	*Plantago lanceolata*
Po	*Polygala vulgaris*
Pe	*Potentilla erecta*
Pv	*Primula veris*
Pr	*Prunella vulgaris*
Ra	*Ranunculus acris*
Rb	*Ranunculus bulbosus*
Rm	*Rhinanthus minor*
Ru	*Rumex acetosa*
Sm	*Sanguisorba minor*
Sj	*Senecio jacobea*
To	*Taraxacum sect. Ruderalia*
Th	*Thymus polytrichus ssp. britannicus*
Tp	*Trifolium pratense*
Tr	*Trifolium repens*
Vc	*Veronica chamaedrys*
Vl	*Viola lutea*
Vr	*Viola riviniana*
PTERIDOPHYTES	
Bl	*Botrychium lunaria*

Based on the primary plant strategies of the species present at Priestcliffe (as supplied by Grime, Hodgson and Hunt 1988) the intensity of stress and disturbance at the site can be estimated. This method places the community below the centre of the triangular ordination, with the greatest importance being attributed to stress (Fig. 1.4). From the position of Priestcliffe Lees in the

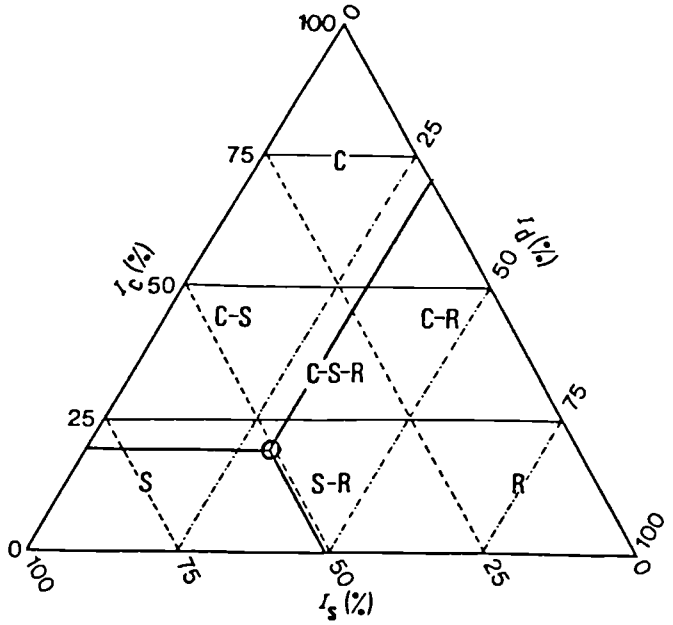


Figure 1.4. The position of Priestcliffe Lees within the Grime's triangular ordination based on the strategies of the species occurring at that site. $I_s = 51\%$, $I_d = 30\%$, $I_c = 19\%$. (After Grime 1979).

triangle it would be expected that this community would be structured more by stress and disturbance than by competitive interactions.

This site was originally chosen for study because it is rich in species and ownership by the Derbyshire Wildlife Trust ensured constancy of management. It is the same site as used by Mahdi (1988) for his work, thus allowing a continuation of the research programme which he initiated.

1.7. Objectives and the structure of the thesis

The thesis addresses the following three questions about the limestone grassland community at Priestcliffe Lees.

1. To what extent is the growth of plants determined by interactions between neighbours? This question is motivated by the conflicting results of Mitchley and Grubb (1986), whose research suggested that the relative abundance of species in chalk grassland was primarily determined by above-ground competition, and Mahdi (1988) who was unable to detect interactions between plants at Priestcliffe Lees. This question is addressed in chapters 2 and 3 by a neighbourhood removal experiment. Chapter 2 tests several alternative methods by which the experiment may be done and chapter 3 makes use of the approach in a field-based removal experiment performed on *in situ* adult plants. To investigate the scale of below-ground foraging, chapter 4 describes an experiment in which a pulse of Rubidium was released at points in the field, and the uptake into neighbouring plants was measured.

2. What are the spatio-temporal dynamics of the community? Although it may be shown that plant growth is influenced by the presence of neighbours, it does not necessarily follow that such interactions play a major role in driving the dynamics of the community. A first step in establishing this is a detailed description of the spatio-temporal changes observed on permanent plots at Priestcliffe. In chapter 5 the spatial growth patterns and turnover of each species is considered in isolation. An attempt to characterise the spatial patterns observed for each species using fractal geometry is detailed in chapter 6.

3. Are the spatio-temporal dynamics of species determined by interactions with neighbouring plants? Following a description of the dynamics of each species in isolation, chapter 7 describes the results of randomisation tests which analyse spatial interactions between species on the permanent plots. This can be seen to synthesize the results from the previous two objectives by considering the role of interactions between plants in driving the dynamics of the community.

Chapter 8 the results of the proceeding chapters are discussed in relation to the original objectives of the thesis. The role of short-term interference and competition for space in the community is considered and, within this framework, possible mechanisms which may account for the high diversity of these plant communities are presented.

Chapter Two

THE DESIGN OF REMOVAL EXPERIMENTS

2.1. Summary

Removal experiments are widely used to study competition in natural ecosystems but suffer from a number of methodological drawbacks. This chapter describes two glasshouse bioassays using field soil which were designed to test for effects of removal experiment methodology on plant growth. Soil was sieved to remove plant roots which were then added back to some samples. The presence of decaying roots in the soil did not significantly alter the performance of *Holcus lanatus* plants over the timescale of the experiment (three months). However, sieving the soil significantly reduced the mycorrhizal infection of *Holcus lanatus* roots and subsequent shoot growth over the same period of time. In the same experiment, a non-mycorrhizal species (*Cerastium fontanum*) was unaffected by soil disturbance. These findings suggest that the disturbance resulting from total plant removal will have adverse effects on the performance of plants remaining in the sward. Since the presence of roots seems to have little effect, above-ground clipping and leaving roots to decay in the soil is likely to be a better approach to removal experiments which are used in this research programme.

2.2. Introduction

Experiments involving the manipulation of plant density are widely employed in the study of competition in the field (e.g. Wilson 1993 and see reviews by Law & Watkinson 1989; Aarssen & Epp 1990; Goldberg & Barton 1992) and the selective removal of vegetation is the most commonly used method of achieving this aim (Aarssen & Epp 1990). However, it is impossible to manipulate density alone without altering other important environmental

factors and these undesired side-effects may confound the interpretation of the results if they have a significant effect on plant performance.

Removal of above-ground biomass may be achieved either by clipping, in which case active roots will remain in competition with the target plants (Evans 1971) and regrowth of shoots may occur, or by herbicide application, leaving decaying roots which may either provide a pulse of nutrients into the soil (Putwain & Harper 1970; Berendse 1983) or lead to mineral sequestration by an enhanced soil microflora (Díaz *et al.* 1993). Manual extraction of roots disturbs the soil and may disrupt the network of mycorrhizal mycelium, subsequently affecting the performance of plants not removed. The design of removal experiments therefore inevitably involves a choice between removing the roots (and disturbing the soil and the mycorrhizal network) and leaving the roots (which may subsequently affect the nutrient status of the soil).

This chapter describes the results from two bioassays designed to investigate the magnitude of two possible side-effects which may influence removal experiments carried out as part of this research project (chapter 3). The aims of the bioassays were, firstly, to determine the extent to which decaying roots left in the soil affect soil fertility over the time period of the experiment and, secondly, to determine the effect of disturbing the soil on the mycorrhizal colonisation and performance of plants. This allows an assessment of which factors have undesired effects on target plant performance and this knowledge can be used to improve the design and interpretation of field removal experiments.

2.3. Materials and methods

Two glasshouse bioassay experiments were performed; in both, the soil was obtained from Priestcliffe Lees Nature Reserve. Soil was obtained from the field by the extraction of randomly positioned cores of 5 cm radius and 10 cm depth.

2.3.1. Experiment One

In the first experiment, 30 soil cores were taken from the site and these were split into three equal sections vertically down the core such that there was no difference in the depth of the cores between treatments. Two of these sub-cores were sieved through 2 mm sieves and the roots removed, the final sub-core being left unsieved with the roots remaining. In one of the sieved soils, the roots were returned to the sample. There were thus three treatments; sieved soil (without roots), sieved soil (roots replaced) and unsieved soil (with roots). A fourth treatment in which roots were removed without sieving would have been desirable in order to have a fully factorial design but is impossible to achieve using field cores.

Each of the treatment soils were randomly placed in a compartment of a seed tray (4 cm x 4 cm cross-section and 5 cm deep), and a 5 day old *Holcus lanatus* seedling was planted in each. *Holcus lanatus* was selected as the study species since it occurs naturally at Priestcliffe Lees and is relatively fast growing, such that any differences in growth between treatments should rapidly become apparent. The seed trays were placed in a glasshouse with 16 hour sodium lighting and were watered daily. The temperature range experienced by the plants was approximately 15-25°C. Half of the plants were harvested after 65 days and the remainder were left to grow for a further 25 days to determine whether there was a difference in mineral release or sequestration of the decaying roots over time. The 90 day growing period was chosen because this was the approximate length of the field removal experiments. At each harvest, plant material was split into above- and below-ground parts, dried for four days in an oven at 100°C and then weighed. The effects of the three treatments and possible interactions with the time of harvest were analysed using a two-way analysis of variance.

2.3.2. Experiment Two

The second bioassay was designed to determine the effect of soil disturbance on mycorrhizal colonisation and plant performance for two target species,

Holcus lanatus and *Cerastium fontanum*. *Holcus lanatus* is usually found to be colonised by arbuscular mycorrhizal fungi (Harley & Harley 1987) whereas *Cerastium fontanum*, which also occurs naturally at Priestcliffe Lees, is non-mycorrhizal (Harley & Harley 1987).

Twenty-five cores were taken from Priestcliffe Lees; each was split into four subcores, two of which were sieved and had the roots replaced and two of which were not manipulated. Therefore all the subcores contained roots and differed only in the presence or absence of sieving. These subcores were placed into the same growing trays used in the first experiment. Two seedlings of each species were planted into separate sieved and non-sieved soil from each core such that both species were present in all treatments from all cores. Two seedlings were planted into each core because of the substantial mortality observed in the first experiment; the smaller seedling in each compartment was removed after two weeks. All above-ground plant material was harvested after 90 days and dried and weighed as in experiment 1. Differences in shoot dry weight between the sieved and unsieved treatments and between species were tested using a two-way anova.

The level of arbuscular-mycorrhizal colonisation of plant roots was determined using the following procedure. The roots of all plants were washed in water and cleared in 10% KOH at 90°C for 5 min. The roots were then rinsed three times in water, acidified in cold 1% HCl for 15 min and stained in 1% acid fuchsin at 90°C for 15 min. The roots were mounted in lactoglycerol on a slide after destaining overnight in lactoglycerol at room temperature. The degree of colonisation of arbuscular mycorrhizal fungi in the roots was determined by epifluorescence microscopy (Merryweather & Fitter 1991) at x250 magnification using 100 intersections per slide (McGonigle *et al.* 1990).

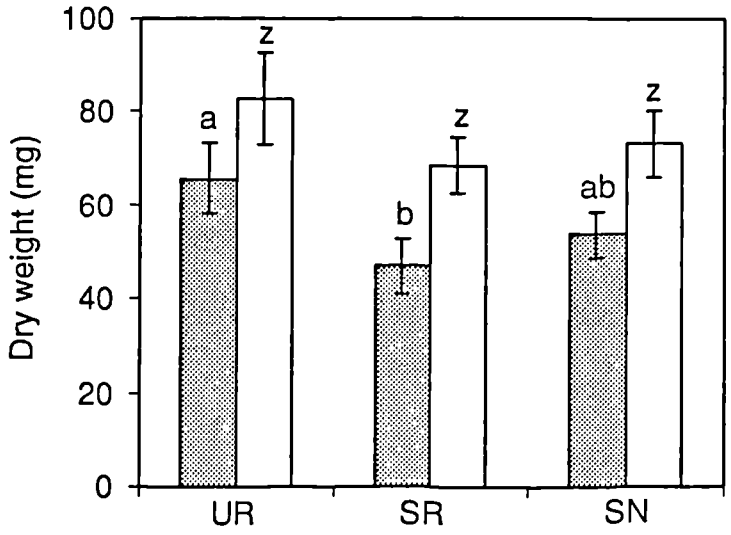


Figure 2.1. Means (± SE) of shoot ▨ and root □ dry weight of *Holcus lanatus* plants grown in field soil in a glasshouse bioassay for 90 days. Treatments are unsieved soil with roots present (UR, N=24), sieved soil with roots (SR, N=18) and sieved soil with the roots removed (SN, N=25). Two-way analysis of variance (treatment x harvest) carried out on log transformed data revealed significant differences between treatment means of shoot weights ($F_{2,61} = 3.48$, $P < 0.05$) but similar analysis of root dry weight demonstrated no treatment effect ($F_{2,61} = 0.53$, $P > 0.05$). Treatment means significantly different from each other at $P < 0.05$ were determined using Duncan's multiple range test and are denoted by different letters.

2.4. Results

2.4.1. Experiment One

Of the 90 seedlings planted in this experiment, only 67 survived to be harvested. Seedling mortality was random with respect to the treatments. Shoot weight but not root weight differed significantly between treatments (Fig. 2.1). A Duncan's Multiple Range test demonstrated that when plants were grown in the presence of roots, those in the sieved soil were smaller than those in unsieved soil ($P < 0.05$) but that restoring roots to the sieved soil had no effect on plant growth. The root/total weight ratio of plants grown in the presence of roots was less in unsieved soil than plants in sieved soil but neither was significantly different from the third treatment (soil without roots) (Fig. 2.2). The time of harvest had a significant effect on both root weight ($F_{1,61}$

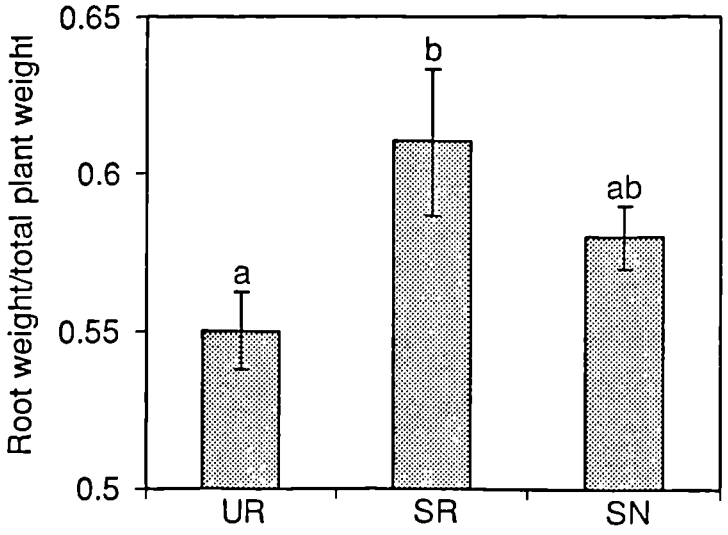


Figure 2.2. Means (± SE) of the root/total weight ratio of *Holcus lanatus* plants grown in field soil in a glasshouse bioassay for 90 days. Treatments are unsieved soil with roots present (UR, N=24), sieved soil with roots (SR, N=18) and sieved soil with the roots removed (SN, N=25). A two-way analysis of variance (treatment x harvest) performed on log transformed data revealed a treatment effect ($F_{2,61}$ = 3.35, $P < 0.05$) and a harvest effect ($F_{1,61}$ = 7.22, $P < 0.01$). The interaction term was not significant. Different letters denote treatments significantly different ($P < 0.05$) as determined by Duncan's multiple range test.

=24.65, $P < 0.001$), shoot weight ($F_{1,61}$ = 11.86, $P < 0.001$) and root/total weight ratio ($F_{1,61}$ = 7.22, $P < 0.01$) but there were no significant interactions between treatment and harvest.

2.4.2. *Experiment Two*

There was less seedling mortality in this experiment than in the first; only one *Holcus lanatus* and three *Cerastium fontanum* plants died after the first two weeks. *Cerastium* plants were smaller than *Holcus* and exhibited no response to the sieving treatment (Fig. 2.3). The roots of *Cerastium* were found to contain no mycorrhizal colonisation but structures normally associated with arbuscular mycorrhizal fungi were present in the roots of *Holcus*. By contrast *Holcus* plants were heavier in the unsieved treatment. No arbuscules were recorded in any intersection and where they were seen to be present on other parts of the slides

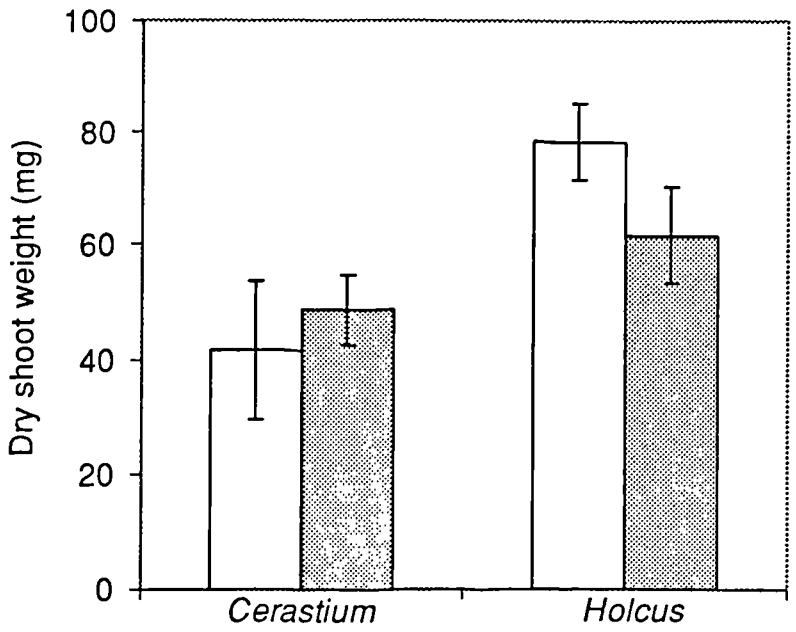


Figure 2.3. Mean shoot dry weight for *Cerastium fontanum* (a non-mycorrhizal species) and *Holcus lanatus* (a mycorrhizal species) plants grown in a glasshouse bioassay in field soil for 90 days. The two treatments are undisturbed ☐ and disturbed ⬚ soil. A two-way analysis of variance (species x treatment) performed on log transformed data demonstrated an effect of species ($F_{1,70}$ = 16.64, $P < 0.001$), no treatment effect ($F_{1,70}$ = 0.19, $P > 0.05$) and a significant interaction of species x treatment ($F_{1,70}$ = 6.16, $P < 0.05$).

they were either poorly stained or degenerate, as is often the case in old colonisation. The percentage root length colonised by hyphae, vesicles and total colonisation (the sum of hyphal and vesicular colonisation) were significantly greater in the plants grown in unsieved soil (Table 2.1), although total colonisation rates were low (<20% root length). The dry shoot weight of plants was weakly positively correlated with the percentage hyphal infection of the roots (Fig. 2.4).

2.5. Discussion

2.5.1. The effect of decaying roots on plant performance

The lack of effect of root removal on plant root and shoot growth suggests that leaving roots to decay in the soil would not significantly alter the outcome of a manipulation experiment in this system. There was no interaction between harvest and treatment which demonstrates further that roots appear to have no

Table 2.1. Analysis of variance of arbuscular mycorrhizal colonisation (as a percentage of root length) of *Holcus lanatus* plants grown in a glasshouse bioassay in unsieved (control) and sieved field soil (N = 17 and 20 respectively). The F-value is taken from a one way analysis of variance carried out on arcsine transformed data. The means of each treament are given ± SE.. * indicates $P < 0.05$, ** indicates $P < 0.01$.

Parameter	Treatment	Significance
Total infection (%)	control 7.7 ± 1.5 sieved 3.2 ± 0.7	$F_{1,35} = 6.52$ *
Hyphae (%)	control 4.8 ± 1.0 sieved 2.3 ± 0.5	$F_{1,35} = 4.62$ *
Vesicles (%)	control 2.9 ± 0.7 sieved 0.9 ± 0.3	$F_{1,35} = 8.06$ **

effect on the soil fertility within three months of above-ground removals. This conclusion is supported by that of Seastedt (1988) who reported that the release of nutrients from decaying roots in tall grass prairie is very slow, with only 10% of initial nitrogen present in roots being lost within one year. Phosphorus mineralisation was faster, but decaying roots still retained around 60% of the original nutrient concentration after one years decay. Berendse (1983) found no difference between yields in unfertilised removal and control plots after removing part of the above-ground vegetation even after the removal plot had recovered from the disturbance. If decaying roots had provided a pulse of nutrients into the soil then it would have been expected that the manipulated plot would yield greater biomass than the control plot. In these experiments microbial activity should be increased in the glasshouse relative to the field because of the higher temperature and supply of moisture in the protected environment. In addition all nutrients released would be confined to the experimental pots. It would thus be expected that both nutrient release from decaying roots and possible nutrient sequestration by the microbiota would be less important under natural conditions.

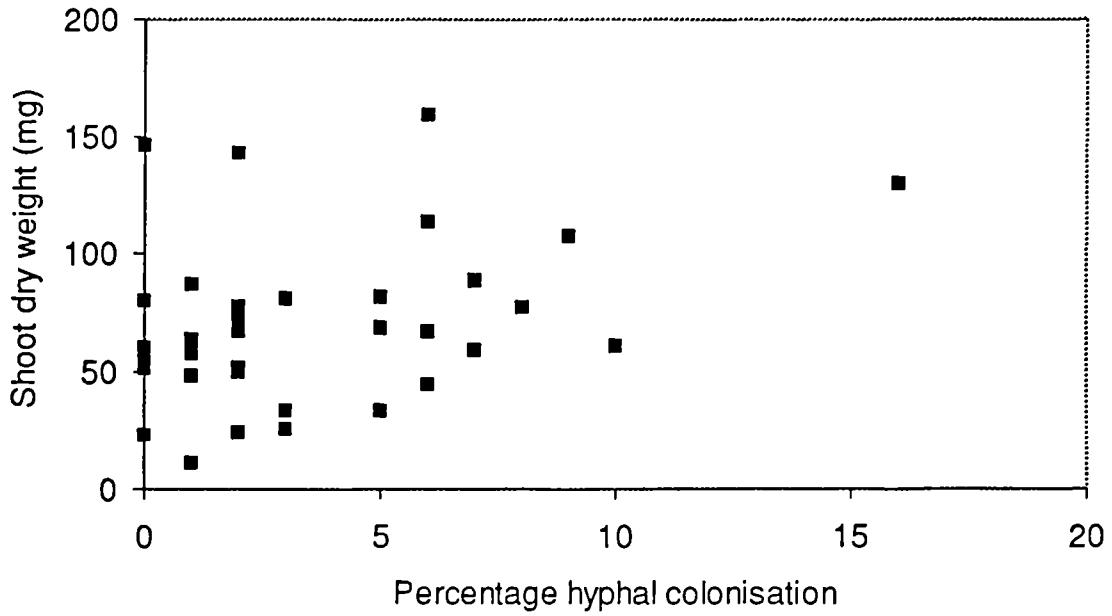


Figure 2.4. Dry shoot weight of *Holcus lanatus* plants grown in a glasshouse bioassay in field soil for 90 days as a function of the percentage of root length colonised by vesicular-arbuscuar mycorrhizal hyphae. Spearman's rank correlation coefficient, R = 0.31 (P = 0.062).

In the first experiment, the shoot dry weight of *Holcus* plants was lower in sieved than in unsieved treatments (both treatments containing roots) suggesting that sieving has a detrimental effect on plant growth (Table 2.1). However, it might also be expected that there would be a significant difference between the unsieved treatment and the sieved treatment without roots since the presence or absence of roots seemed to have little effect on shoot weight. The result that the shoot weight of plants in the sieved treatment containing roots was not significantly less than the unsieved treatment suggests that roots left in the soil may actually have a small detrimental effect on plant growth. This could arise as a result of increased numbers of pathogens present on dead roots in the soil (West, Fitter & Watkinson 1993) or slight uptake in nutrients caused by increased microbiotic activity (Seastedt 1988).

2.5.2. Mycorrhizal colonisation

The second experiment confirmed the detrimental effect of sieving soil on the biomass of *Holcus* but there was no effect of sieving on the non-mycorrhizal *Cerastium*. In a similar study, Evans and Miller (1988) observed that soil disturbance reduced phosphorus uptake of mycorrhizal maize and wheat and had no effect on non-mycorrhizal spinach and rape. Previous work has shown that soil disturbance can decrease the colonisation rate of mycorrhizal fungi by the disruption of the mycelial network (Read & Birch 1988; Jasper, Abbott & Robson 1989; Birch, Read & Rorison 1990; Fairchild & Miller 1990) and, similarly, I found decreased hyphal colonisation of *Holcus lanatus* in the disturbed soil treatment. However, there is no conclusive evidence of a causal relationship between mycorrhizal colonisation and plant performance in our study. The correlation between shoot weight and hyphal colonisation was slight, as expected with such low colonisation of the plant roots by mycorrhizal fungi. It is expected that increased mycorrhizal colonisation of the plants would increase the performance of plants because *Holcus lanatus* has been demonstrated to benefit from mycorrhizal association when grown on its own and in competition with *Lolium perenne* (Fitter 1977) and the beneficial effects of mycorrhizal symbiosis are well documented. In the first experiment the root/total weight ratio of *Holcus* was greater in plants growing in sieved soil then in unsieved soil. This is possibly because plants in disturbed soil, with lower mycorrhizal colonisation, had lower nutrient uptake per unit root mass than more mycorrhizal plants.

Extrapolation of the results of these experiments to the field is problematic. Although infection rates are likely to be greater (Read, Koucheki & Hodgson (1976) observed a mean colonisation of 55% of *Holcus lanatus* roots in a calcareous grassland close to Priestcliffe Lees), and disturbance will cause a greater loss of symbiotic connections, the amount of mycelium present in the soil will also be greater, facilitating rapid recolonisation. Jasper, Abbott & Robson (1991) found that the amount of recolonisation of plants by mycorrhizal fungi following soil disturbance was greater in pasture soil containing high

numbers of spores and mycorrhizal roots than in forest or heathland soil which contained less inoculum. The majority of species in calcareous grasslands are mycorrhizal (Read, Koucheki & Hodgson 1976; Peat & Fitter 1993) and extensive colonisation of seedling roots may occur within two weeks (Birch 1986). However, in the case of manipulation experiments with a number of different density treatments or gap sizes, different treatments will disrupt the mycorrhizal network to a different extent and the rate of recolonisation of the target plants will differ between treatments. In the nutrient poor soils of calcareous grasslands the benefit of improved access to immobile nutrients derived from the symbiosis may be crucial to some plants. This is especially true since mycorrhiza can mediate competitive interactions (Allen & Allen 1990; Hartnett *et al.* 1993) to the extent that they may increase plant species diversity in experimental microcosms (Grime *et al.* 1987). An initial advantage gained by plants as a result of earlier infection may be further increased by the effects of asymmetric competition.

Disturbing the soil has a number of ecological effects in addition to the disruption of the mycorrhizal mycelial network. These include the break-up of the crumb structure, influencing water holding potential, and redistribution of nutrients and organic matter throughout the soil horizon which may, in turn, affect plant rooting patterns and growth. However, the null effect of soil disturbance on the non-mycorrhizal species in this experiment demonstrates that these effects are likely to be of secondary importance to the disruption of mycorrhizal connections.

2.5.3. *The design of removal experiments*

The results of these bioassays suggest that the best methodology for manipulating the density of mycorrhizal plants in calcareous grasslands is to remove above-ground biomass and leave the roots to decay naturally. Soil disturbance is demonstrated here to reduce both mycorrhizal colonisation and performance of usually mycorrhizal plants and, although there may be a slight effect of decaying roots on plant growth, this is substantially less. However,

this is not to say that these results can be extrapolated to any community. The best methodology to use in manipulation experiments will differ between habitats depending on the degree of mycorrhizal infection and characteristics of the vegetation and soil. In communities in which mycorrhizal fungi are absent and/or phosphorus is not limiting e.g. strandveld in South Africa (Allsopp & Stock 1994), soil disturbance may have little effect on plant performance. By contrast, an ecosystem in which the decomposition process is rapid may not be a good candidate for leaving roots to decay in the soil, although the conditions required for high microbial activity are also likely to be associated with a high rate of nutrient leaching.

By their nature, perturbation experiments always have undesired side effects but it is possible to assess the degree to which such side effects may affect plant performance by conducting laboratory tests prior to field experiments. Manipulations of density remain one of the few ways it is possible to judge the true effects of competition in the field and the methodological flaws cause fewer problems in interpretation than does the extrapolation of the results of laboratory competition experiments to natural communities.

Chapter Three

PLANT COMPETITIVE RESPONSE

3.1. Summary

This chapter describes two removal experiments carried out at Priestcliffe. The first experiment suffered from a number of methodological flaws and produced equivocal results. In the second experiment eight sizes of gap were created around *in situ* target plants by the application of a biodegradable herbicide. Plants in larger gaps had more leaves than control plants although there was a concomitant decrease in mean leaf length. These morphological changes were exhibited by all of the study species and may be due to increased red/far-red light ratios in larger gaps. However, the different treatment sizes had no effect on the total leaf length of the target plants. Fecundity was also unresponsive to treatment. The biomass of smaller species increased in larger gaps. The variation in plant traits explained by the treatment was greater for smaller species than for larger species suggesting the existence of a size-based response hierarchy. Morphological plant characteristics (leaf number and mean leaf length) were more sensitive to gap size than performance traits (biomass, fecundity and total leaf length) and, as such, competition is expected to play a limited role in controlling plant dynamics in the field.

3.2. Introduction

The role of competition in structuring plant communities has been a matter of debate since the beginning of the century (Clements 1916; Gleason 1926). The prevalence of negative interactions in natural systems has now become generally accepted (Connell 1983; Schoener 1983) but the importance of competition in different habitats and the precise mechanisms by which it operates are still unclear (Grime 1973; Newman 1973; Tilman 1987; Thompson & Grime 1988; Grace 1990).

In relation to calcareous grasslands, there have been conflicting results concerning the capacity for interspecific competition to determine the relative abundance of species in the field (chapter 1, section 1.5). Mitchley and Grubb (1986) assert that abundance is primarily determined by the position of a species in a competitive hierarchy whereas Mahdi (1988) found no evidence for interspecific interactions. Grime's theory of primary plant strategies (1977, 1979) predicts a negative correlation between the intensity of stress, disturbance and competition in a given habitat and within this framework competitive interactions in calcareous grasslands may be less important than the other two factors. However, it is still not obvious how much the performance of plants is influenced by neighbouring vegetation.

Removal experiments have long been used in the study of competitive interactions in natural communities (e.g. Pinder 1975; Allen & Forman 1976; Fowler 1981; see also reviews by Aarssen & Epp 1990 and Goldberg & Barton 1992), and are further employed in this study. These manipulations work on the premise that if the performance of the remaining plants increases after the removal of some or all of the neighbouring vegetation then this is an indication of the presence of competitive interactions. A decrease in performance following removal suggests a beneficial association between plants.

Many perturbation experiments have been used to study species-specific competitive effects by analysing pairwise interactions of removals (e.g. Fowler 1981; Silander & Antonovics 1982; Goldberg 1987) but of these only one study (Silander & Antonovics 1982) found evidence for species-specific effects, this occurring between the two community dominants. This lack of specificity is perhaps unsurprising since plants perceive competition as the loss of resources and cannot distinguish the species causing that loss (Fitter 1987) and effects per unit biomass are likely to be similar for many species (Goldberg & Werner 1983; Goldberg 1987). With this being the case, it may be more enlightening to examine the response rather than the competitive effect of species. In this

study, it is the response to diffuse competition which is being measured. No attempt is made to investigate species-specific interactions.

This chapter describes removal experiments carried out at Priestcliffe, in which plant performance was monitored over a range of artificially created densities. The aims of the work were to determine to what degree the performance of plants is affected by the presence of neighbouring plants (objective 1, section 1.7) and if there are interspecific differences in the intensity and nature of the competitive response.

3.3. Materials and methods

3.3.1. Experiment One

Eleven species (*Achillea millefolium, Carex flacca, Carex caryophyllea, Cerastium fontanum, Dactylis glomerata, Festuca ovina, Koeleria macrantha, Plantago lanceolata, Ranunculus bulbosus, Sanguisorba minor* and *Trifolium repens*) were used in this experiment. Ramets were taken from the field and grown outside in York for one month prior to being replaced in the sward at Priestcliffe Lees. Ramets at Priestcliffe were selected randomly and removed in a core of soil down to 10cm depth. The removed soil was then replaced with soil obtained from elsewhere on the site (from a depth of 5-10 cm to minimise the amount of seeds contained in the sample) and a ramet of the same species grown at York was planted into the centre of the clearance.

Seven of the species (*Achillea millefolium, Carex caryophyllea, Cerastium fontanum, Dactylis glomerata, Festuca ovina, Koeleria macrantha* and *Ranunculus bulbosus*) were subjected to two treatments (5 mm radius clearance and 40 mm radius clearance), replicated twenty times per species. The remaining species were subjected to 6 treatments (5 mm, 10 mm, 20 mm, 30 mm, 35 mm and 40 mm radii clearances), replicated ten times per species. The number of leaves per plant and the total leaf length was measured on the placement of the plant into the soil at the beginning of April 1992 and again on 6 July and 1 September.

3.3.2. Experiment Two

Six species (*Briza media, Carex caryophyllea, Dactylis glomerata, Lotus corniculatus, Plantago lanceolata* and *Sanguisorba minor)* were used in the experiment as they were reasonably abundant in the sward and have contrasting life histories. Target ramets were selected randomly in an area of 48 m^2 and an area around them was cleared of all neighbouring vegetation using biodegradable glyphosate herbicide (Tumbleweed; Fisons Plc, Ipswich). The herbicide was applied by hand into cylinders of the required radius of clearance. The target ramets were protected for two days after weed killer application by plastic tubes which shielded the total shoot length. Controls in intact vegetation were also subjected to this two day protection. The removal of neighbours around plants *in situ* was preferred over transplant experiments (e.g. Watkinson & Harper 1978; Grace & Wetzal 1981) as it has the dual advantages of leaving intact both the above-ground structure of the community (outside the area of perturbation) and the soil (especially the mycorrhizal network). The lack of soil disturbance is particularly important in calcareous grasslands in which some 70% of species are usually mycorrhizal (Peat & Fitter 1993) and infection by mycorrhizal mycelium can greatly affect plant performance (Birch, Read & Rorison 1990; chapter 2).

Eight treatments (radii of clearance 0, 15, 20, 25, 30, 35, 40 and 50 mm) were used, replicated 12 times for each species giving a total of 576 study plants (96 per species). 50 mm was chosen as the greatest radius of clearance since it was large enough to prevent contact of the target plant with neighbouring shoots. The size of gaps were maintained by cutting back the above-ground vegetation every month during the study. Cutting vegetation below-ground was also considered as an option but rejected because the roots of target plants would also have been cut, especially in smaller gaps.

Throughout the duration of the experiment the study plots were protected from cattle grazing by an electric fence. This was done because of damage to the

target ramets by cattle trampling in experiment one. Rabbits were not excluded.

The number of leaves and total leaf length of each plant were measured at the beginning of the experiment in late March/early April 1993 and again on two successive occasions (21 June and 19 July) in the same year. The presence and number of any flowerheads was also recorded. The number and length of stems was used in the case of *Lotus corniculatus* due to the difficulty of measuring the number and length of the leaves.

On 19 July the above-ground biomass of all remaining plants was harvested, dried at 100°C for four days and weighed on a micro balance. The below-ground plant parts were left untouched because of the difficulty of separating target plant roots from neighbouring roots in the field. The time elapsed from the beginning to the end of the experiment was approximately 100 days.

The abundance of species in the field was determined by a field survey on 19 July 1994 (exactly one year after the final harvest of the experiment). 100 points were randomly located in the sward in an area close to where the removals were sited. The number of ramets of each of the target species within a 2 cm radius of each point was recorded and this data was used to calculate the density and above-ground yield of species in the field (yield being the product of density and shoot weight per ramet).

3.3.3. Data Analysis

Analysis of covariance was performed on the number, mean and total length of leaves at the end of the experiment using the initial value of each attribute as the covariate in order to remove the natural variation due to initial plant size. This analysis was also carried out on the shoot weight of plants at the final harvest using initial total leaf length as a covariate, since the total leaf length and shoot weight of a plant are highly correlated.

The analysis of covariance yielded a regression equation of the variate on the covariate (see Mead & Curnow (1983), pp145 *et seq.*) and this relationship was used to adjust the values of the variate so that the variation due to initial plant size could be removed. The variation due to the covariate was removed even when the it was not significant since there are good *a priori* reasons for believing that initial plant size should affect plant size at the final harvest. Regression was then performed on the variates after removing the variation due to initial plant size against the area of vegetation cleared by herbicide. Since there was more than one Y value for each value of X the residual sum of squares were partitioned into a 'pure error' term (sums of squares of data around the treatment means) and a 'lack of fit' term (the remaining part of the residual sum of squares). The significance of the variation explained by the regression was tested by the F-ratio of the regression mean sum of squares and the lack of fit mean sum of squares and the lack of fit was tested by the F-ratio of the lack of fit mean sum of squares and the pure error term (Sokal & Rohlf (1981), pp477 *et seq.*). If the lack of fit was significant then this means that although the regression slope may be significantly different from zero the within group variation is too large to accept with confidence the presence of a relationship between the variate and gap size.

3.4. Results

3.4.1. Experiment One

There was substantial mortality of plants during the course of the field season, the reasons for this being twofold. Firstly, the unexpected and prolonged dry weather in April subjected the newly planted ramets to drought stress before their root systems were well developed enough to forage for water further down in th soil profile. Secondly the unscheduled arrival of cattle onto the site caused ramet death by trampling and grazing. A number of species lost so many replicates that the remaining data could not be used. The species which have been analysed are *Carex caryophyllea, Dactylis glomerata, Festuca ovina, Koeleria macrantha, Plantago lanceolata, Sanguisorba minor* and *Trifolium repens.*

Table 3.1. Analysis of covariance carried out on the size of five limestone grassland plants grown in the field from April to September 1992. The treatments were two gap sizes (5mm and 40mm radius). The covariate was the initial variable size. * signifies $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Variable	Treatment	Covariate
Carex caryophyllea	Number of leaves	$F_{1,13} = 9.095$ **	$F_{1,13} = 1.661$
	Mean leaf length	$F_{1,13} = 4.084$	$F_{1,13} = 0.182$
	Total leaf length	$F_{1,13} = 20.775$ ***	$F_{1,13} = 4.270$
Cerastium fontanum	Number of leaves	$F_{1,22} = 1.471$	$F_{1,22} = 1.444$
	Number of stems	$F_{1,22} = 2.283$	$F_{1,22} = 2.104$
Dactylis glomerata	Number of leaves	$F_{1,25} = 5.531$ *	$F_{1,25} = 0.530$
	Mean leaf length	$F_{1,25} = 1.378$	$F_{1,25} = 0.649$
	Total leaf length	$F_{1,25} = 0.074$	$F_{1,25} = 2.063$
Festuca ovina	Number of leaves	$F_{1,16} = 2.398$	$F_{1,16} = 1.899$
	Mean leaf length	$F_{1,16} = 1.341$	$F_{1,16} = 0.264$
	Total leaf length	$F_{1,16} = 0.022$	$F_{1,16} = 6.717$ *
Koeleria macrantha	Number of leaves	$F_{1,18} = 14.765$ ***	$F_{1,18} = 8.677$ **
	Mean leaf length	$F_{1,18} = 11.119$ **	$F_{1,18} = 1.140$
	Total leaf length	$F_{1,18} = 0.218$	$F_{1,18} = 5.365$ *

Carex, *Koeleria* and *Dactylis* all had significantly more leaves in the large gaps than the small manipulations (Table 3.1). *Festuca* followed this general trend (Fig. 3.1) but the difference between the two treatments was not significant. Although the number of leaves of *Koeleria* plants increased in the larger gaps, these leaves were significantly shorter on average (Fig. 3.2). Both *Dactylis* and *Festuca* also had shorter leaves in the larger gaps, but this observation was not significant. The total leaf length of *Carex* was much greater in the 40mm manipulations, this being a consequence of a greater number of slightly longer leaves (Fig 3.3). All other species maintained similar total leaf lengths over both treatments.

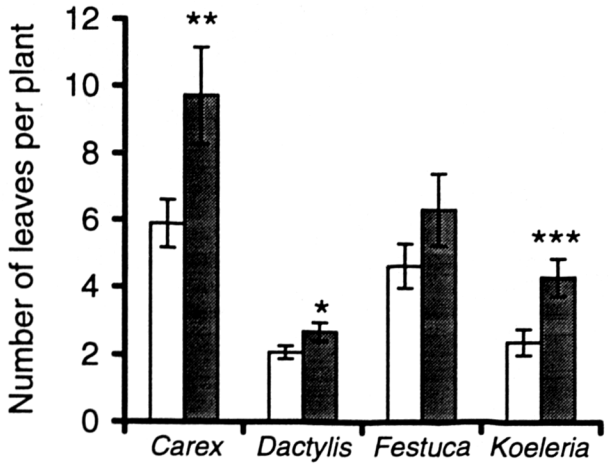


Figure 3.1. The mean number of leaves per plant (± S.E.) of four limestone grassland plants grown in small (5mm radius) □ and large (40mm radius) ▨ gaps in the field from April to September 1992. Treatments significantly different are indicated by * for $P < 0.05$, ** for $P < 0.01$ and *** for $P < 0.001$. The significance level is calculated from an analysis of covariance performed on log transformed data using the initial number of leaves as a covariate (see Table 3.1).

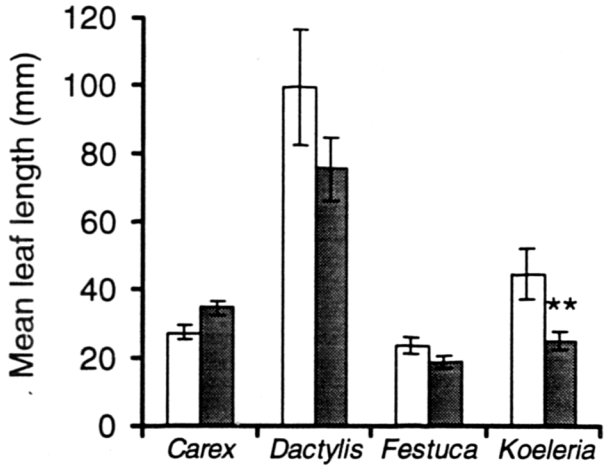


Figure 3.2. The mean leaf length (± S.E.) of four limestone grassland plants grown in small (5mm radius) □ and large (40mm radius) ▨ gaps in the field from April to September 1992. Treatments significantly different are indicated by ** for $P < 0.01$. The significance level is calculated from an analysis of covariance performed on log transformed data using the initial mean leaf length as a covariate (see Table 3.1).

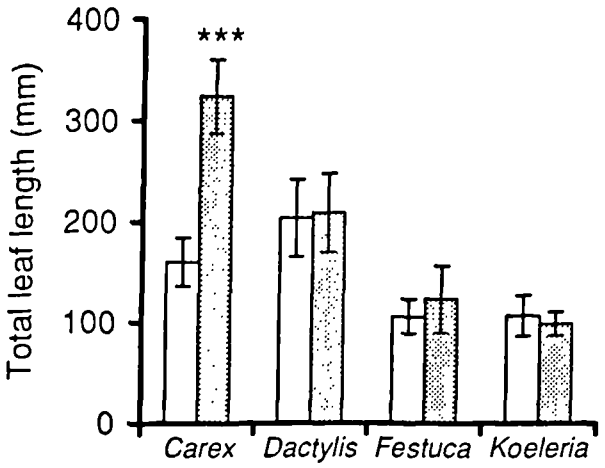


Figure 3.3. The mean total leaf length (± S.E.) per plant of four limestone grassland plants grown in small (5mm radius) □ and large (40mm radius) □ gaps in the field from April to September 1992. Treatments significantly different are indicated by *** for $P < 0.001$. The significance level is calculated from an analysis of covariance performed on log transformed data using the initial total leaf length as a covariate (see Table 3.1).

Of the three species subjected to a range of gap treatments no significant differences could be detected between any of the plant traits measured between the manipulations (Table 3.2). An important point to note from the analysis of covariance was the lack of significant relationships between the variate and covariate in the majority of cases.

3.4.2. Experiment Two

A number of the plants died within the first month of the study, possibly because of an insufficient protection period following the herbicide applications. *Dactylis glomerata* was particularly badly affected, few ramets surviving in clearances exceeding 30mm in radius. Results from this species are not included in the analysis for this reason. The other species also lost a large number of plants but this did not preclude analysis. *Carex caryophyllea* had no plants remaining in the largest treatment. The remaining plants all grew well during the season suggesting that these survivors were unaffected

Table 3.2. Analysis of covariance carried out on the size of three limestone grassland plants grown in the field from April to July 1992. The treatments were six gap sizes (5, 10, 20, 30, 35 and 40mm radius). The covariate was the initial variable size. * signifies $P < 0.05$, ** $P < 0.01$.

Species	Variable	Treatment	Covariate
Plantago lanceolata	Number of leaves	$F_{5,30} = 0.953$	$F_{1,30} = 4.882$ *
	Mean leaf length	$F_{5,30} = 1.321$	$F_{1,30} = 0.282$
	Total leaf length	$F_{5,30} = 1.308$	$F_{1,30} = 4.466$ *
Sanguisorba minor	Number of leaves	$F_{4,15} = 0.343$	$F_{1,15} = 0.000$
	Number of stems	$F_{4,15} = 1.569$	$F_{1,15} = 0.927$
	Total leaf length	$F_{4,15} = 2.870$	$F_{1,15} = 7.448$ *
Trifolium repens	Total stem length	$F_{5,31} = 1.071$	$F_{1,31} = 9.953$ **
	Number of leaves	$F_{5,31} = 0.817$	$F_{1,31} = 4.025$
	Leaves/stem length	$F_{5,31} = 1.195$	$F_{1,31} = 2.249$

by the herbicide application. The herbicide was very effective at forming gaps of the correct size (Plate 3.1).

Analysis of covariance demonstrated treatment effects on the number of leaves of *Briza*, *Carex*, *Plantago* and *Sanguisorba* and the mean leaf length of *Briza*, *Plantago* and *Sanguisorba* (Table 3.3). Again, a surprising result from this analysis is the general lack of any relationship between the variates (plant size measurements at the end of the experiment) and the covariates (measured at the beginning of the experiment) in all species except *Plantago*.

The number of leaves per plant showed the greatest response to gap size, the variation explained by the regression analysis ranging from 14-50% (Fig. 3.4). The response of *Plantago* was not significant. Although the number of leaves per plant demonstrated a tendency to increase as the gap size increased, there was a concomitant decrease in mean leaf length (Fig. 3.5) which was significant for all species except for *Sanguisorba*. These changes in plant morphology were

Plate 3.1. 50 mm clearances following herbicide application around *Sanguisorba minor* (above) and *Carex caryophyllea* (below).

Table 3.3. Analysis of covariance carried out on the size of five limestone grassland plants grown in the field from April to July 1993. The treatments were seven gap sizes (15-50cm radius) and controls. The covariate was the initial value of the variate for the first three variables and initial total leaf length in the case of dry shoot weight. * signifies $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Variate	Treatment	Covariate
Briza media	Number of leaves	$F_{6.21} = 4.984$ **	$F_{1.21} = 0.935$
	Mean leaf length	$F_{6.21} = 4.844$ **	$F_{1.21} = 5.215$ *
	Total leaf length	$F_{6.21} = 0.878$	$F_{1.21} = 0.362$
	Dry shoot weight	$F_{6.21} = 1.306$	$F_{1.21} = 0.211$
Carex caryophyllea	Number of leaves	$F_{6.18} = 3.509$ *	$F_{1.18} = 0.911$
	Mean leaf length	$F_{6.18} = 1.474$	$F_{1.18} = 0.011$
	Total leaf length	$F_{6.18} = 0.866$	$F_{1.18} = 0.005$
	Dry shoot weight	$F_{6.18} = 2.368$	$F_{1.18} = 0.003$
Lotus corniculatus	Number of stems	$F_{7.24} = 1.408$	$F_{1.24} = 3.271$
	Mean stem length	$F_{7.24} = 1.864$	$F_{1.24} = 0.367$
	Total stem length	$F_{7.24} = 0.762$	$F_{1.24} = 6.329$ *
	Dry shoot weight	$F_{7.24} = 1.196$	$F_{1.24} = 3.696$
Plantago lanceolata	Number of leaves	$F_{7.44} = 3.145$ **	$F_{1.44} = 19.162$ ***
	Mean leaf length	$F_{7.44} = 2.251$ **	$F_{1.44} = 0.354$
	Total leaf length	$F_{7.44} = 0.947$	$F_{1.44} = 15.292$ ***
	Dry shoot weight	$F_{7.44} = 1.167$	$F_{1.44} = 22.689$ ***
Sanguisorba minor	Number of leaves	$F_{7.36} = 3.465$ **	$F_{1.36} = 1.855$
	Mean leaf length	$F_{7.36} = 5.854$ ***	$F_{1.36} = 5.687$ *
	Total leaf length	$F_{7.36} = 0.843$	$F_{1.36} = 3.015$
	Dry shoot weight	$F_{7.36} = 0.541$	$F_{1.36} = 5.250$

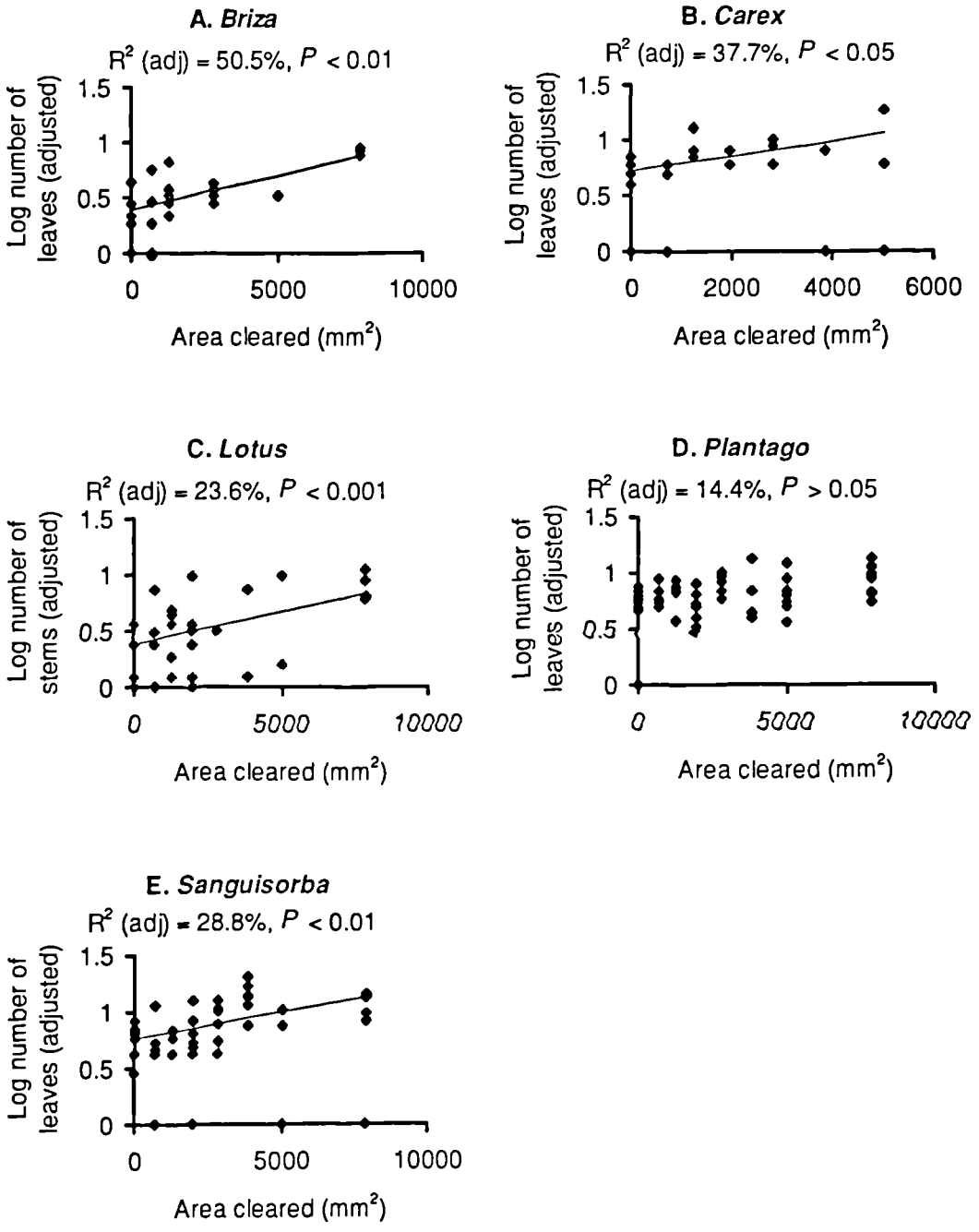


Figure 3.4. The number of leaves of five limestone grassland species measured after 100 days growth as a function of the area cleared around target ramets using herbicide. The variate has been adjusted using the regression relationship with the initial number of leaves per plant obtained from an analysis of covariance. The *P* value is the significance level of the variation explained by the linear regression line. The data were log transformed prior to the analysis.

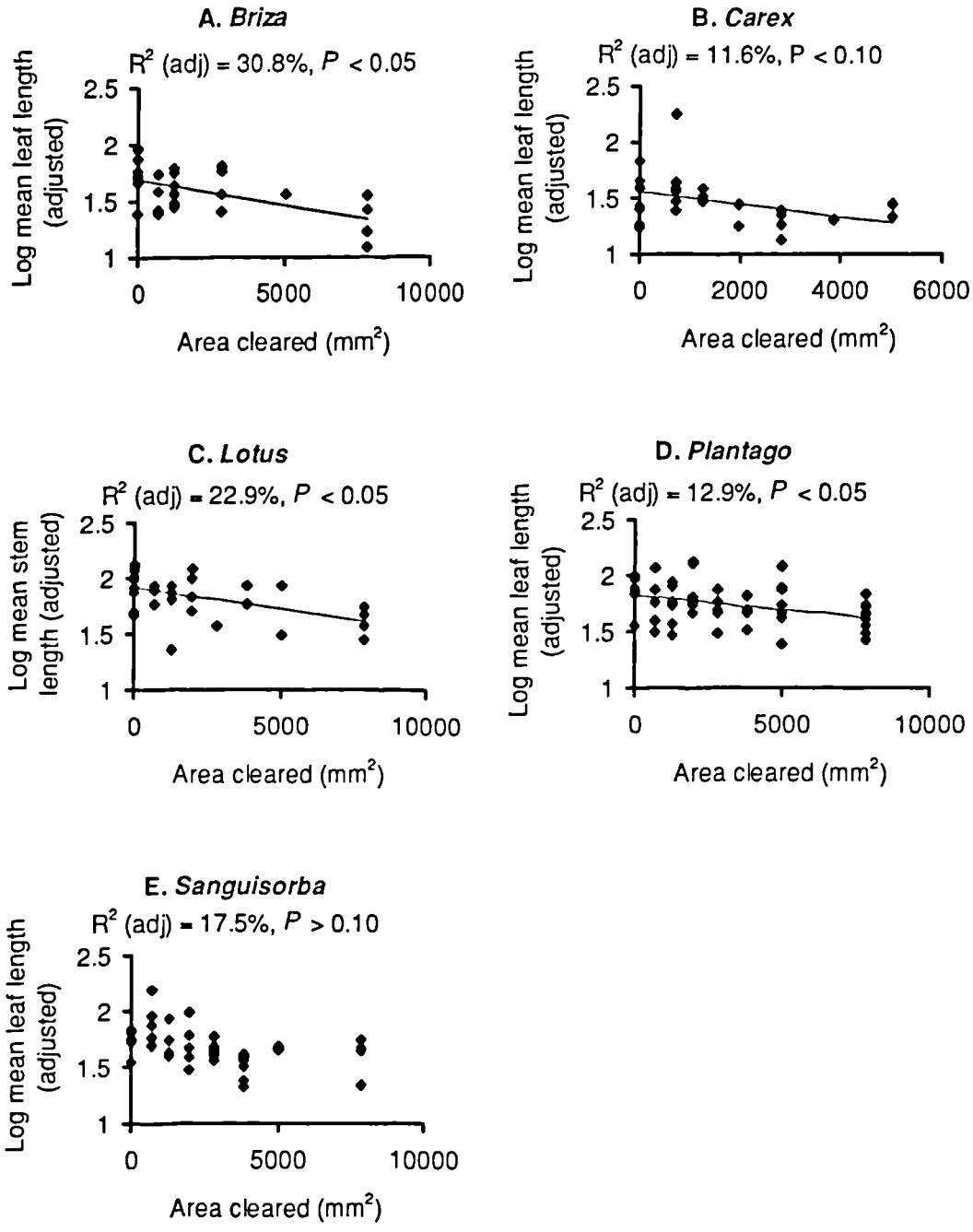


Figure 3.5. The mean leaf length of five limestone grassland species measured after 100 days growth as a function of the area cleared around target ramets using herbicide. The variate has been adjusted using the regression relationship with the initial mean leaf length obtained from an analysis of covariance. The *P* value is the significance level of the variation explained by the linear regression line. The data were log transformed prior to the analysis.

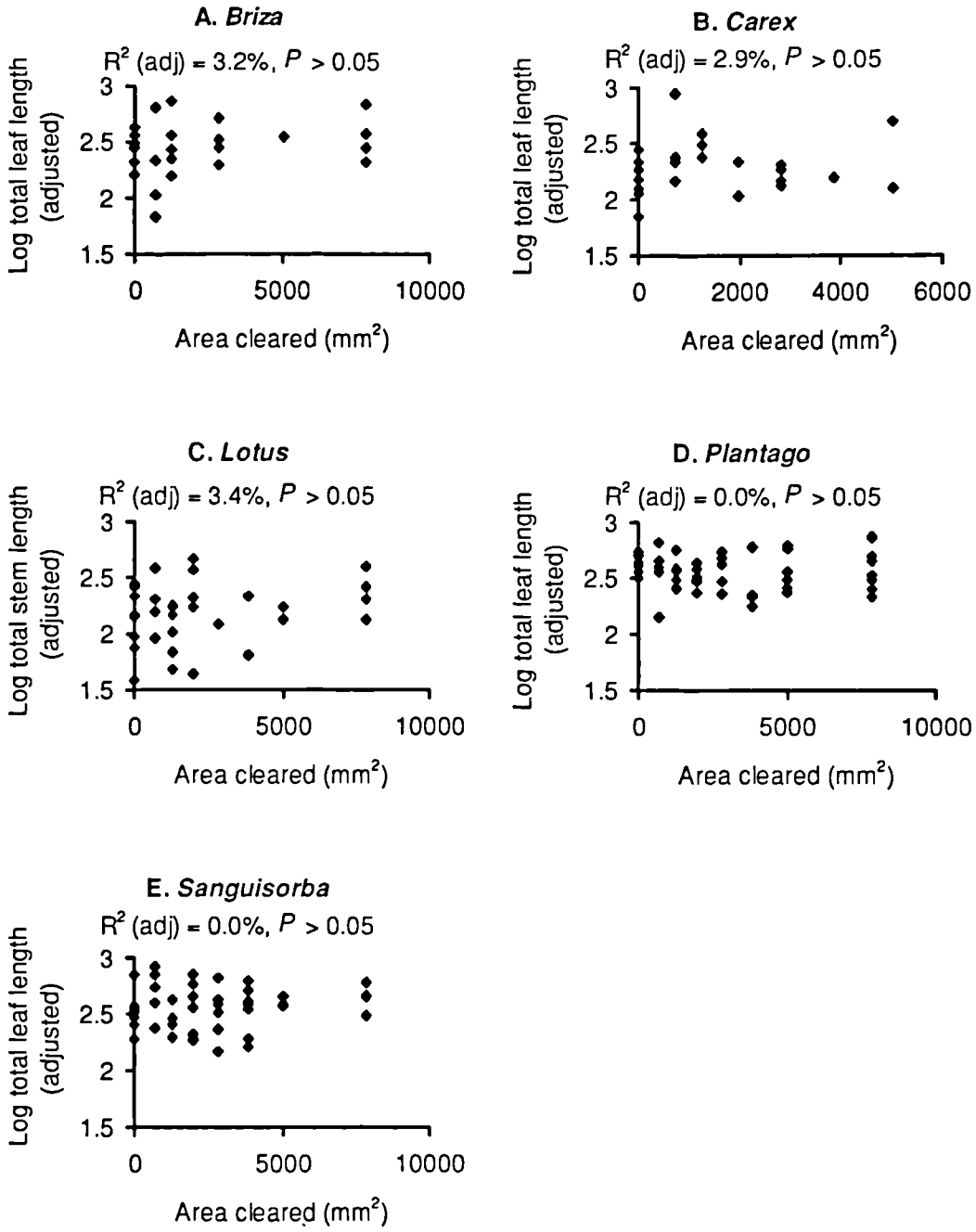


Figure 3.6. The total leaf length of five limestone grassland species measured after 100 days growth as a function of the area cleared around target ramets using herbicide. The variate has been adjusted using the regression relationship with the initial toal leaf length per plant obtained from an analysis of covariance. The *P* value is the significance level of the variation explained by the linear regression line. The data were log transformed prior to the analysis.

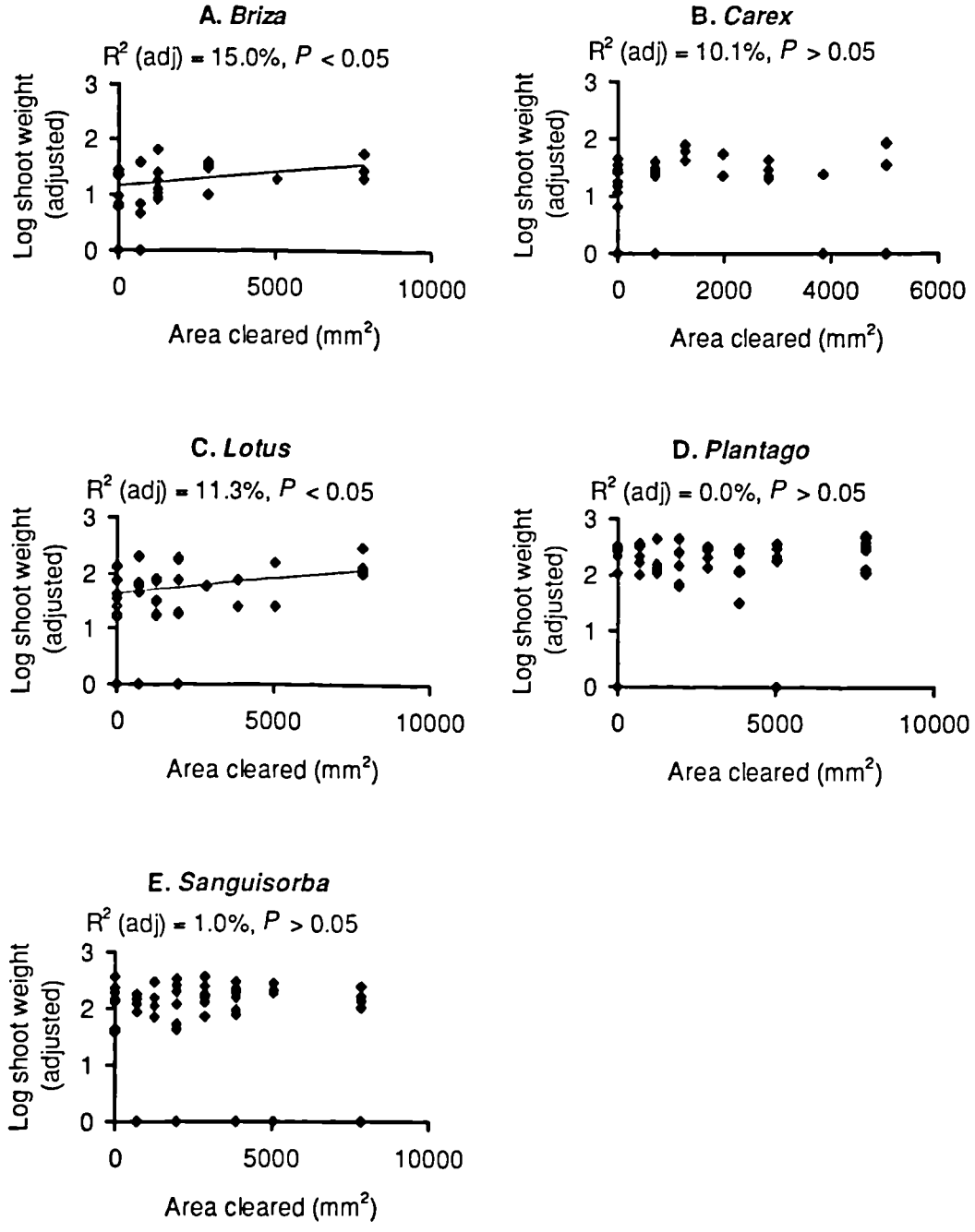


Figure 3.7. The shoot weight of five limestone grassland species measured after 100 days growth as a function of the area cleared around target ramets using herbicide. The variate has been adjusted using the regression relationship with the initial toal leaf length per plant obtained from an analysis of covariance. The *P* value is the significance level of the variation explained by the linear regression line. The data were log transformed prior to the analysis.

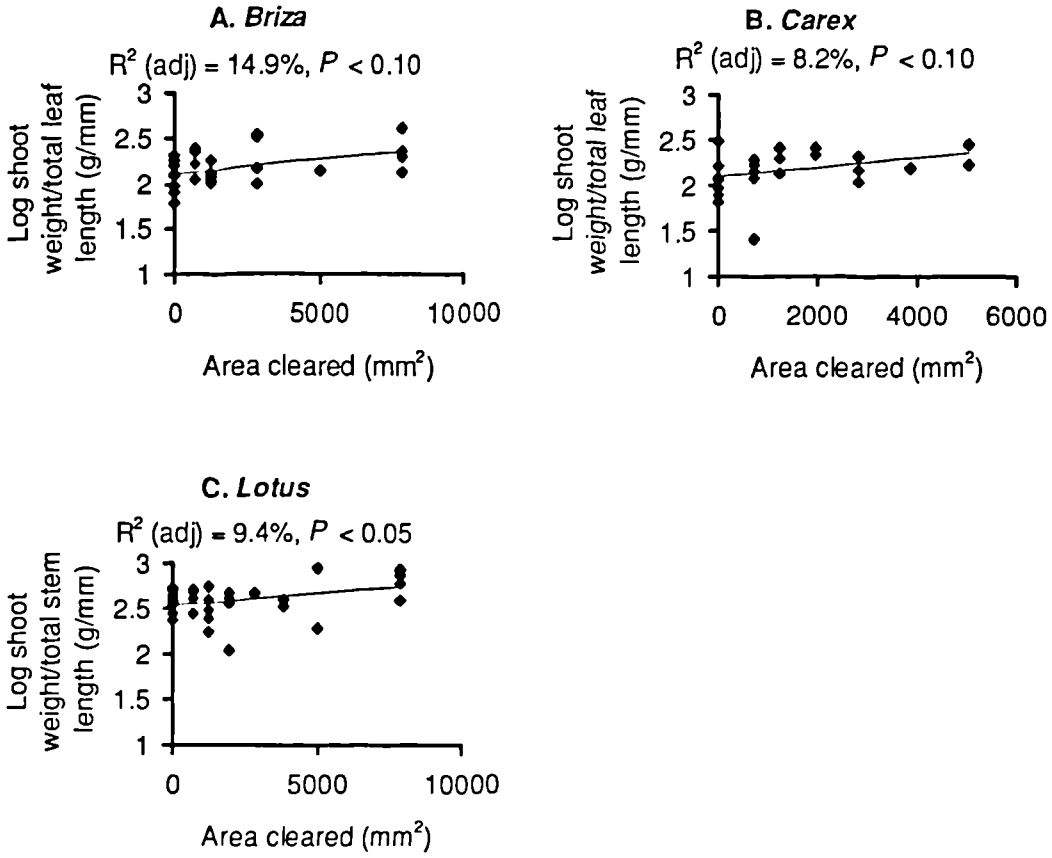


Figure 3.8. The ratio of shoot weight/total leaf length of three limestone grassland species species measured after 100 days growth as a function of the area cleared around target ramets using herbicide. The *P* value is the significance level of the variation explained by the linear regression line. The data were log transformed prior to the analysis.

opposite in direction and as a result the total leaf leaf per plant exhibited no change over the range of treatments (Fig. 3.6) in any of the species. None of the significant regression relationships had a significant lack of fit.

The shoot weight of *Briza* and *Lotus* was greater in larger gaps (Fig. 3.7). *Carex* followed a similar relationship but this was not significant at the 5% level. The increase in shoot weight observed in *Lotus* could be clearly demonstrated to be the result of increased biomass allocation per unit stem length (Fig. 3.8) and this approached significance in the case of both *Briza* and *Carex*.

Table 3.4. Ranking of species according to their shoot weight, increase in total leaf length and the variation explained in regression analysis of three plant traits against gap size. Spearman's Rank Correlation Coefficient, $r_s = -0.900$ ($P < 0.05$) between shoot weight in controls and the variation explained in leaf number and between shoot weight in controls and the variation explained in shoot weight.

	Shoot weight in controls ± SE (mg)	Increase in total leaf length in controls ± SE (%)	Variation in leaf number explained (%)	Variation in mean leaf length explained (%)	Variation in shoot weight explained (%)
Briza media	18.04 ± 3.44 (5)	177 ± 40 (4)	50.5 (1)	30.8 (1)	15.0 (1)
Carex caryophyllea	23.23 ± 4.60 (4)	120 ± 43 (5)	37.7 (2)	11.6 (5)	10.1 (3)
Lotus corniculatus	56.24 ± 12.13 (3)	433 ± 117 (2)	23.6 (4)	22.9 (3)	11.3 (2)
Sanguisorba minor	170.96 ± 37.60 (2)	454 ± 100 (1)	28.8 (3)	17.5 (2)	1.0 (4)
Plantago lanceolata	281.20 ± 56.18 (1)	367 ± 39 (3)	14.4 (5)	12.9 (4)	0.0 (5)

Of the five species analysed, only *Sanguisorba* and *Plantago* produced any flowers during the course of the study and the number of flowerheads per plant did not show any clear trend with treatment at either harvest.

The variation explained by the regression of plant traits against gap size can be taken to indicate the effect of competition on plant growth and morphology relative to other factors (Aarssen & Epp 1990). The variation explained by the regression of both the number of leaves per plant and the shoot weight against gap size was negatively correlated with the mean size of species, measured as the shoot weight of the control plants at the end of the experiment (Table 3.4). There was no such relationship between the variation explained in any of the traits and plant growth rate (measured as the increase in total leaf length of the control plants). The variation explained by the regression of plant shoot weight was negatively correlated with the yield of species in the field (measured as kg biomass m^{-2}) but not the field density of species.

3.5. Discussion

3.5.1. Limitations of removal experiments

The experimental approach of manipulating neighbour density is not without its limitations. Alteration of the density of selected species may change the micro climate around the remaining plants and the response of species may be due to these changes rather than reduced competition for resources.

The methodology used in the first experiment disturbed the soil and this disrupts the network of mycorrhizal mycelium and may reduce the performance of target plants (chapter 2). The transplants used for this experiment may also have not had sufficient time to develop their root systems before being planted into the sward and, as such, been at a disadvantage compared to the native plants. This may explain why there were few significant responses of plants to the manipulation treatments even in the case

of species which produced significant changes in morphology in the second experiment.

In the second experiment a potential problem was that the partially removed roots may provide a pulse of nutrients into the perturbed areas (Berendse 1983), although Seastedt (1988) has demonstrated that this release is either very slow, or it leads to the sequestration of nutrients by an increased microbial community involved in the decomposition process (Díaz *et al.* 1993). However, a glasshouse bioassay showed that decaying roots had little affect on soil fertility over the time period of the experiment (chapter 2). Herbicides may leave unknown residue in the soil which may affect plant peformance (Aarssen & Epp 1990) but Glyphosate, the herbicide used in the second experiment, is strongly adsorbed to the soil and is immobile. Loss from the soil is caused by micorbial degradation, the principle metabolite being aminomethylphosphonic acid (Fisons Plc., personal communication) which is unavailable to plants in the form of organic nitrogen and phosphorus.

The intensity of the manipulation carried out may affect the results obtained from the study. Allen and Forman (1976) detected large responses associated with removals which left large areas of bare ground but this result may reveal more about the capacity of individual species to colonise a site by vegetative expansion rather than the importance of competitive interactions. However, as has already been noted in reference to the work of Mahdi (1988), very small manipulations may be unable to detect the presence of competition. The experiments here were thus carried out over a range of densities.

3.5.2. Individual plant response

The general lack of correlation between the initial measures of plant size and the measurements taken at the end of both experiments in the majority of species is surprising since it is to be expected that larger plants will remain larger than smaller plants. However, the initial measurements were taken at the very beginning of the growing season and the status of the unmeasured

below-ground plant parts may play a large part in determining its subsequent performance (J.D. Graves pers. comm.). Nevertheless this result suggests that caution is needed in predicting plant behaviour in the field from data such as size hierarchies.

The mean length and number of leaves per plant in most of the study species of the first experiment and some of the first exhibited a highly plastic response to manipulated alterations in neighbour density. The observation for *Carex caryophyllea* in the first experiment of slightly increased mean leaf length in the larger gap is hard to understand, especially considering that this species displayed the opposite trend in the second experiment. The lack of response of a large number of species in the first experiments may have been a result of the bad methodology used in this study; the roots of the transplants were poorly developed and unlikely to behave as mature plants and the soil used to fill the gaps was more nutrient poor than that which was removed. The resultant changes in leaf length and number observed in all species in the second experiment and *Koeleria macrantha* in the first may well be phytochrome induced responses to changes in light quality, enhanced apical dominance and the suppression of branching being a typical reaction to the reduced red/far-red light ratio experienced by plants in smaller gaps (Hutchings & de Kroon 1994; Smith 1994). Plants in dense swards that have longer leaves will receive more light whereas plants in larger gaps may produce a number of shorter leaves as a more efficient foraging strategy. Recent work has demonstrated that potential competitors may be detected via reflected light from neighbouring vegetation prior to the onset of competition (Ballaré *et al.* 1987; Ballaré, Scopel & Sánchez 1991) and these kinds of morphological changes may be produced as an adaptive response to future shading.

3.5.3. *Sensitivity of response at the species level*

The absence of flowering in the majority of the study species in the second experiment (the number of inflorescences was not measured in the first study) is not a surprising result. *Carex* and *Briza* largely recruit vegetatively and this

is a general strategy in a habitat where pre- and post-dispersal seed predation is high (Mortimer 1993) and the low soil fertility leads to opportunistic flowering. Fecundity is usually well correlated with biomass (Harper 1977; Watkinson and White 1985; Weiner 1988; Schmid and Weiner 1993) so a significant response of the number of flowers to increasing gap size in *Plantago* and *Sanguisorba* in the absence of differences in plant biomass would not be expected.

The importance of competition, relative to other ecological factors, to each species (in terms of the R^2 value; Aarssen & Epp 1990) is negatively correlated with mean plant size in the second experiment. The larger dominants are less affected by competition than the smaller species. *Briza media* is particularly affected by gap size, over 50% of the variation in the increase in number of leaves and 30% of the variation in mean leaf length is explained by the regression of these traits against the area cleared. This size-dependent response is also consistent with the conclusions of Miller & Werner (1987) that who found that competitive response is negatively correlated with plant biomass of the species and is to be expected due to the greater level of resources required to produce new leaves in larger species. This has the consequence that the dynamics of species will tend to operate over different spatial and temporal scales (Thórhallsdóttir 1990a). Such size-based hierarchies have previously been observed in natural communities (Grime 1973; Mitchley & Grubb 1986; Miller & Werner 1987; Gurevitch *et al.* 1990) and Gaudet & Keddy (1988) found that plant size was a good predictor of the effect of one species on another.

The negative correlation between the variation in plant shoot weight explained by the treatment effect and species yield in the field is similar to the relationship between competitive ranking and field abundance (in terms of yield) observed by Miller and Werner (1987). This observation is suggestive of the importance of competition in determining the relative abundance hierarchy but cannot be taken as implying a causal relationship. The correlation may be partially a result of the close relationship between mean shoot weight of each

species and the variation of plant shoot weight explained by the treatment (species yield being the product of mean shoot weight and field density).

3.5.4. Is competition occurring?

The first experiment provides little evidence to answer this question. The final biomass of the target species was not measured and results from the second experiment have indicated that changes in total leaf length are unlikely to occur even when there is an increase in shoot biomass. However, the total leaf length of *Carex caryophyllea* was observed to increase dramatically in the larger gaps in spite of the problems associated with this experiment. The success of this species may be related to the fact that it has shallow roots which may have taken less time to develop than the other species and since it is non-mycorrhizal (Harley & Harley 1987) it would not be affected by the disturbance of the mycelial network.

Biomass is highly correlated to fecundity and survival (Harper 1977; Pacala & Silander 1985) and thus is probably the best predictor of the reproductive success of a plant in the field. The second experiment has shown that the biomass of *Briza* and *Lotus* may be negatively affected by a large density of neighbours whereas the biomass of *Sanguisorba* and *Plantago* is unresponsive over a large range of densities in the field. *Carex* seems to be responding in a similar manner to *Lotus* and *Briza* and the lack of a significant relationship between shoot weight and gap size may have been partly a result of the absence of a 50 mm gap treatment for this species. We can thus conclude that *Briza, Lotus* and possibly *Carex* are being suppressed by diffuse competition at normally observed densities.

Although the biomass of *Plantago* and *Sanguisorba* are not affected by the range of gap sizes employed in this study we cannot conclude that they are unaffected by competition. Several alternative explanations are possible. The largest clearance may have been insufficient to provide enough resources to increase biomass significantly, or the time required for an increase following

the removal of neighbours is greater than the 100 day period of this study. Both *Plantago* and *Sanguisorba* show a large increase in total leaf length from the beginning to end of the experiment and it would be thought that differences between plants grown in different gap sizes would become apparent, but it may be that extra resources are first allocated to below-ground parts (Fitter 1986) which were not studied here. It is thus impossible to say with any confidence whether these species are not experiencing competition in the field or if the space available to the plant must increase beyond 50 mm radius before any increase in plant biomass occurs. The morphological changes observed in the plants are not necessarily indicative that the plants are competing for light but may be genetically-based plant responses to fluctuations in light quality.

3.5.5. The scale of competitive interactions

The shoot weight of *Briza* and *Lotus* in the second experiment are linearly related to gap size but there must be a point at which increasing gap size will have no further affect on a plant. This point will arise at the point at which the plant is totally freed from competition. In this study the 50mm radius gap was sufficient to remove all contact of the target plant with neighbouring shoots (personal observation) but the biomass of *Briza* and Lotus is still increasing. It is possible, however, that the variability in the data is masking the non-linearity. In calcareous grasslands the ratio of fine root length to leaf area is very high (Mortimer 1992) and the range of competition may thus be greater below-ground. It is demonstrated in chapter four that roots may obtain nutrients at greater than 5cm distance from the plant. Although the gaps were maintained above ground by cutting, the roots of neighbours were free to recolonise the gap following the initial clearance. Root competition is also likely to be more important in such unproductive habitats (Weiner 1986; Ford 1990), where insufficient resources are present for plants to suppress each other above-ground, and the recolonisation by neighbouring roots will have reduced the resources available to the target plants.

3.5.6. Implications for community dynamics

Gaps larger than 50mm radius are extremely rare in grasslands (Mahdi 1988; Silvertown & Smith 1988; Hook, Lauenroth and Burke 1994; McLellan, personal observation) so the second experiment realistically covers the range of densities likely to be experienced by a plant in the ecosystem. Thus, at normally observed densities the results shown here demonstrate that the performance of the larger matrix forming perennials (Grubb 1986), *Plantago* and *Sanguisorba*, will remain unaffected by the presence of neighbouring plants whereas the smaller species, *Briza* and *Lotus*, are suppressed by diffuse competition. However, even for these species, the amount of variation in above-ground biomass explained by the manipulation treatment was low (<15%) suggesting that competitive interactions play little role in controlling the dynamics of plants in the field.

Chapter Four

ROOT FORAGING BEHAVIOUR

4.1. Summary

In nutrient poor grasslands, the prevalent sphere of competition is below-ground and the ability of plants to forage for mineral nutrients is an important component of their competitive ability. The ability of three plant species (*Briza media, Carex caryophyllea* and *Plantago lanceolata*) to assimilate mineral nutrients at different distances from a source was investigated using Rubidium as a tracer element at two times in the growing season (April and July). Rubidium concentrations were found to be greatest within 0-3 cm from the nutrient source, although uptake continued up to 6-9 cm, demonstrating that interference between the roots of neighbouring plants occurs over larger scales than shoot interference. Concentrations if Rubidium in the shoots of species followed the pattern *Plantago* > *Briza* > *Carex*. The assimilation of Rubidium by *Carex* and *Plantago* occurs almost exclusively in 0-3 cm from the source but from further distances in *Briza* which suggests that the grass has a wider spread of roots and may be able to tap resources left untouched by the more deeply rooted *Plantago*.

4.2. Introduction

The capacity to forage for mineral nutrients and water in the soil is an important component of a plant's competitive ability. This is especially true in calcareous grasslands in which the combination of nutrient poor soils and intense herbivory limits the amount of above-ground biomass (Grime 1979; Willems 1983) and interference between roots has a greater role in determining the outcome of interactions between plants than competition for light (Weiner 1986; Ford 1990).

The species characteristic of these nutrient poor grasslands are typically small, relatively slow-growing species (Grime 1990) and the distance over which shoots of neighbouring plants can influence each other can be no more than a few centimetres. In contrast the allocation of plants to root material relative to shoots in increases under moderate grazing regimes (van der Maarel & Titlyanova 1989) and calcareous grassland species will tend to have well developed root systems which are active all year round as a defence against nutrient deficiency and drought (Grime *et al.* 1991). It is therefore likely that the roots of plants will wield an influence on neighbours which are out of shoot contact. Previous studies on competition between species at this site which have demonstrated that the biomass of target plants continues to increase with the space cleared above ground, even when their shoots are not in contact with neighbours (chapter 3), suggest that this is indeed the case. The precise pattern of nutrient uptake as a function of distance will differ between species and determine how much plants are able to compete for resources with their neighbours.

Root competition is less asymmetric than shoot competition (Keddy 1989; Weiner 1990) and this leads to the prediction that the amount of nutrient uptake should be proportional to plant size. However, it is possible that the dominant species are able to deny smaller species access to certain patches and thus command a greater proportion of the resource base. Alternatively a greater precision in foraging and higher physiological plasticity of subordinate species (Crick & Grime 1987; Campbell & Grime 1989; Campbell, Grime & Mackey 1991) may result in a greater resource use efficiency (uptake of nutrients per unit plant mass) by these plants which would enhance their capacity to persist in the sward. Other factors, such as the degree of mycorrhizal colonisation will affect how efficient plants are at acquiring nutrients through their root structures (Heap & Newman 1980; Brundrett 1991) and the distance over which nutrients can be assimilated (Read, Francis & Finlay 1985).

This chapter describes the results from an experiment designed to investigate the foraging patterns of three plant species in a limestone grassland. This has two aims; firstly, to determine the distance over which plants can compete for soil resources and the degree of foraging at different distances from a target plant and, secondly, to examine interspecific differences in resource uptake efficiency.

4.3. Materials and methods

4.3.1. Field experiment

The study was undertaken in Priestcliffe Lees Nature Reserve limestone grassland (described in detail in chapter 1) between April and July 1994. On two occasions during this period (April 6 and June 15) 1.5 ml of 10.1 mg ml^{-1} Rubidium Chloride (RbCl) solution were injected into 60 points in the sward at a depth of 5 cm, the depth at which the roots of grassland plants tend to be most active (Fitter 1986), using a hypodermic syringe. These were arranged in four lines of 15 points, each point being 40 cm apart, the transects separated by a distance of 50 cm. The injections occurred in different locations some 5 m apart for the two studies in order to avoid the problem of rubidium remaining in the soil from the earlier study influencing the results of the latter. Rubidium was used since it is not naturally present in either the soil or plant tissue and acts physiologically as potassium. The use of radioactive tracers was not permitted in the nature reserve. The Rubidium technique has been successfully used by Fitter (1986b) in a similar investigation of root foraging and for studies of potassium uptake (Russell 1977).

All above-ground biomass of three target species (*Briza media, Carex caryophyllea* and *Plantago lanceolata*) was removed up to a distance of 12 cm from the injection points 14 days after the initial injections. Harvest dates were April 20 and June 29 respectively for each study. Plant material was separated into four zones: 0-3 cm, 3-6 cm, 6-9 cm and 9-12 cm distance from the injection point. The injection points were sampled consecutively along the transects until 10

replicates of each species in each zone were obtained. At the time of the second harvest points were randomly located in the sward at a distance of at least 1 m from the injection sites and all above-ground biomass of the three target species occurring within a 3 cm radius was removed. This procedure was continued until 5 replicates of each species were obtained as controls.

This methodology assumes that the Rubidium remains exactly at the point of injection unless it is moved along the plant roots. However, some diffusion will occur, although over two weeks this is likely to be a small distance compared to the distances over which the foraging patterns are being measured. The site is gently sloping so plant material was only collected uphill from the injection point since movement of Rubidium due to mass flow of water downhill could be confused with root foraging activity.

4.3.2. Atomic absorption spectrophotometry

Plant material of each species from each zone was oven dried at 100°C for five days, ground and mixed with 10 ml of deionised water. These samples were then left in a cold room (8-10°C) for a period of ten days to allow the rubidium to dissolve. This method was demonstrated to provide similar results to total acid digests of the plant material. The samples were then filtered and the total Rubidium concentration was measured using a Varian SpectrAA-20 Atomic Absorption Spectrometer (Varian Techtron Ply Ltd, Springvale, Australia). Prior to the spectral analysis 1 ml of 100 ppm KNO_3 solution was added to each sample to prevent ionisation of the Rubidium during the combustion process in the spectrometer.

4.3.3. Statistical analysis

Differences in Rubidium uptake between plants of different species and distance from the injection point were analysed using two-way analysis of variance on log transformed data for each experiment. Tukey's honestly significant difference test (Sokal and Rohlf 1981) was used to determine pairwise differences between treatments since this test has a relatively constant

Table 4.1. Results from a two-way analysis of variance performed on the concentration of rubidium (ppm) in the shoots of three limestone grassland plants at differing distances from a point into which 1.5 ml of RbCl was injected 14 days previously in April. *Carex caryophyllea* was not included in the analysis because no rubidium was detected in the samples. Treatments are distance (0-3, 3-6, 6-9 and 9-12 cm from the injection point) and species (*Briza media* and *Plantago lanceolata*). The data were log transformed.
*** indicates $P < 0.001$. Different letters denote treatment means significantly different at $P < 0.05$ as determined by Tukey's honestly significant difference test.

Factor	Significance		Treatment means	
Distance	$F_{3,62} = 3.68$	***	0-3 cm	148.28 a
			3-6 cm	32.24 b
			6-9 cm	5.89 bc
			9-12 cm	2.38 c
Species	$F_{1,62} = 0.32$		*Plantago*	61.65 a
			Briza	13.91 a
			(*Carex*	0.00)
Species x distance	$F_{3,62} = 0.86$			

error rate (equal to the level of significance) over a number of pairwise comparisons (Boardman and Moffitt 1971). The variation in Rubidium acquisition at different distances away from the point source was analysed separately for each species at each harvest also using Tukey's honestly significant difference test.

It must be pointed out that the non-random method of field sampling used in the experiment leads to errors which may not be independent and, strictly speaking, violates one of the assumptions of the analysis of variance procedure. The results from the analysis performed on the data must therefore be viewed with caution.

4.4. Results

A two-way analysis of variance performed on the first experiment (April) demonstrated significant differences in rubidium uptake between zones but not between species (Table 4.1), the majority of the absorbance occurring within the first 3 cm from the injection points, although a substantial proportion was also taken up by plants rooted 3-6 cm from the injection. Differences between species were observed in the second experiment (Table 4.2), the ranking of rubidium concentration in the shoots of species being *Plantago* > *Briza* > *Carex*. However, the use of controls in this experiment demonstrated that Rubidium was being taken up at distances of 6-9 cm from the injection point. It was not possible to test for significant differences in the concentration of rubidium of each species between the experiments, since the plots used were separated in space and significant differences could be interpreted either as plot or time differences, or a combination of both. However, the concentration of rubidium in *Plantago* shoots was less in July than April, whereas *Carex* displayed the opposite trend. The concentrations in the shoots of *Briza* were similar for both experiment.

At the first harvest none of the *Carex* samples contained enough rubidium to be within the detection range of the spectrometer. This was probably because of the extremely small weights of this species present in the samples and does not necessarily mean that no uptake of rubidium was occurring. *Briza* had over 40 ppm Rubidium present in shoots sampled from within 3 cm of the injection point, and this was significantly greater than the uptake at 6-9 cm and 9-12 cm from the source (Fig. 4.1). Concentrations of around 200 ppm and 40 ppm were observed in *Plantago* at 0-3 cm and 3-6 cm from the injection points respectively. The uptake at 0-3 cm was significantly different to that occurring at all other distances and uptake at 3-6 cm was significantly different to that occurring at 9-12 cm (effectively 0).

At the second harvest the concentration of Rubidium in the shoots of *Briza* was approximately 40 ppm at 0-3 cm from the injection point and approximately 20

Table 4.2. Results from a two-way analysis of variance performed on the concentration of rubidium (ppm) in the shoots of three limestone grassland plants at differing distances from a point into which 1.5 ml of RbCl was injected 14 days previously in July. Treatments are distance (0-3, 3-6, 6-9 and 9-12 cm from the injection point and controls) and species (*Briza media*, *Carex caryophyllea* and *Plantago lanceolata*). The data were log transformed.
** indicates $P < 0.01$, *** $P < 0.001$. Different letters denote treatment means significantly different at $P < 0.05$ as determined by Tukey's honestly significant difference test.

Factor	Significance		Treatment means	
Distance	$F_{4,101} = 9.63$	***	0-3 cm	55.94 a
			3-6 cm	16.53 b
			6-9 cm	11.32 bc
			9-12 cm	3.74 cd
			control	1.84 d
Species	$F_{2,101} = 4.39$	**	*Plantago*	25.57 a
			Briza	18.32 b
			Carex	10.88 c
Species x distance	$F_{8,1} = 0.94$			

ppm at 3-6 cm distance, both greater than observed in control plants (Fig 4.2). The concentration at 6-9 cm distance was not significantly different from either the concentration in the first two zones or the controls. *Carex* shoots had similar concentration of Rubidium to *Briza* at 0-3 cm distance but uptake in the other zones were not significantly different from the control plants (although plants from 6-9 cm distance were also not significantly different from those at 0-3 cm). Similar to the first harvest *Plantago* absorbed rubidium very strongly at 0-3 cm from the source of the nutrient but absorption in all other zones was not significantly different from the controls.

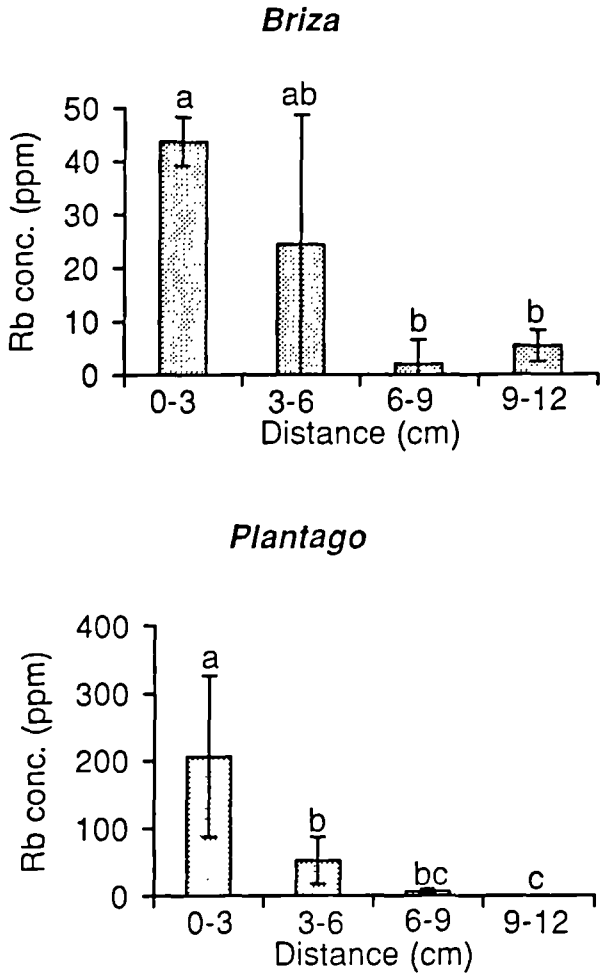


Figure 4.1. Concentration of Rubidium present (± SE) in the shoot biomass of two limestone grassland species at 4 distances from an injection point of RbCl (1.1mg ml^{-1}) made 14 days previously in April 1994. Different letters indicate treatments significantly different from each other at $P < 0.05$ as determined by Tukey's honestly significant difference test.

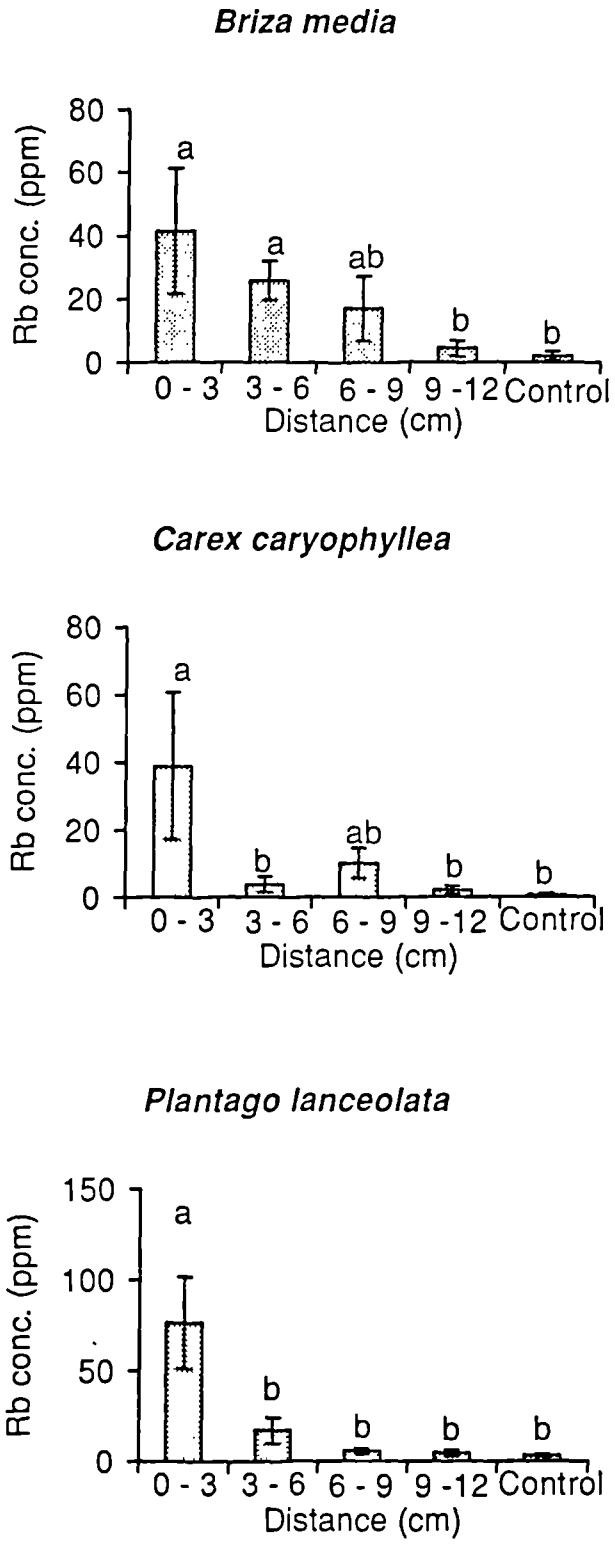


Figure 4.2. Concentration of Rubidium present (± SE) in the shoot biomass of three limestone grassland species at 4 distances (+ controls) from an injection point of RbCl (1.1mg ml^{-1}) made 14 days previously in June 1994. Different letters indicate treatments significantly different from each other at $P < 0.05$ as determined by Tukey's honestly significant difference test.

4.5. Discussion

4.5.1. Experimental design

The experiment has the drawback that the statistical errors associated with different observations are not independent. For example, two plants of *Briza* sampled at different distances from the same point source of Rubidium are subject to the same errors associated with that Rubidium source. The design was economical in terms of the use of Rubidium but, as a consequence, violates an assumption underlying analysis of variance.

For future work of this kind, an alternative experimental design would be to harvest no more than one species at one distance from the Rubidium source. Another possibility would be to ensure that in the neighbourhood of each Rubidium source each species would be present at each distance, so that the errors associated with each spatial location could be removed as a block effect. However, this would be difficult to achieve in practice.

A further complication for this type of experiment concerns the inclusion of time in the analysis of variance. Since it is impossible to use the same site for experiments undertaken at different times in the same field season, the inclusion of time as a main treatment effect can only be achieved if several randomly selected sites are used for each time the experiment is carried out.

4.5.2. The scale of root interference

The presence of rubidium in the shoots of control plants suggests that there was some degree of contamination during the laboratory preparation of samples for analysis. Slight amounts of Rubidium in a sample therefore cannot be taken to indicate that this was obtained via root uptake in the field without conducting an appropriate statistical test. Because of this contamination it is difficult to predict from these results the precise distance over which roots can acquire nutrients. However, we can be certain that foraging definitely occurs over 6 cm and this probably continues up to 9 cm away from the plant. This is much greater than the area over which shoots can interfere and suggests that the

increased biomass observed in several species following the removal of vegetation, even after target plants were no longer in shoot contact with their neighbours, was due to the reduction of root competition (chapter 3).

The uptake of rubidium at a certain distance from the source does not necessarily indicate that roots can forage at this distance. It is possible that resources are translocated between tillers in a clump of *Briza*, or between physiologically integrated ramets of *Carex*, this phenomenon having been observed in other clonal species (Hutchings & de Kroon 1994 and references contained therein), which may be confused with root activity here. A further possibility might be that nutrients are redistributed between plants through a network of mycorrhizal mycelium (Grime *et al.* 1987; Newman 1988). Since *Carex caryophyllea* does not form symbioses with soil fungi this problem can be ignored for this species at least, but both *Plantago* and *Briza* are mycorrhizal (Read, Kouchecki & Hodgson 1976; Harley & Harley 1987).

4.5.3. Interspecific differences in foraging ability

Interspecific differences in foraging patterns were most notable between *Plantago* and the two other species. *Plantago* has a pronounced tap root (Grime, Hodgson & Hunt 1988) and in a laboratory study had roots extending three times as deeply as those of *Briza* (Reader *et al.* 1993). However, although *Plantago* is more efficient at acquiring rubidium at 0-3 cm from the point source the concentration of the element in *Briza* shoots 3-6 cm away was only half as great as observed in the closest plants in contrast to a much lesser absorption at that distance by *Plantago*. *Briza* tends to be shallow rooted (Grime *et al.* 1988) and the results here suggests that the roots are spread out from the plant rather than downwards in the case of *Plantago*. *Carex* is also shallow rooted (Grime *et al.* 1988) but the this study suggests that the majority of the root activity is confined to the first 3 cm around the plant. Mortimer (1992) examined the root and shoot systems of five calcareous grassland perennials and observed that the graminoids tended to place proportionally less biomass to below-ground structures than forbs but had a greater root length to leaf area ratio. This

suggests that root placement occurs on a different scale between these two life-forms as predicted by Campbell, Grime & Mackey (1991). The greater resource uptake efficiency of *Plantago* is consistent with the view that this species is a superior competitor to the other two species, demonstrated in chapter three, and could be a result of the greater proportion of biomass allocated to the root system (Mortimer 1992). The close, deep rooting of this species also suggests a reason why it did not benefit from large clearances around selected plants (chapter 3).

4.5.4. Temporal and spatial separation of foraging

There was no marked temporal variation in the foraging patterns of *Briza* between the two studies but the null results obtained for *Carex* in the first study suggest that this species is more active in June than April. However, it is impossible to make this conclusion with certainty since the lack of detection of Rubidium in *Carex* shoots in the first experiment may have been due to the small biomass of plants of this species which were analysed on the spectrophotometer. The temporal pattern observed for *Plantago* suggests that more nutrient acquisition occurs earlier in the season for this species. Temporal separation of root activity has been suggested as a mechanism whereby coexistence may occur between species (Fitter 1986b, 1987; Veresglou & Fitter 1987) but it is the subordinate species (*sensu* Grime 1987) which are thought to be active earlier in order to escape interaction with the dominants (Fitter 1986b). This is in contrast with the results obtained here in which *Plantago* is the early forager. However, it has also been suggested that spatial separation of foraging depth may foster coexistence between grassland species (Berendse 1981, 1982; Sydes & Grime 1984; Fitter 1987) and Fitter (1976) observed that *Lolium perenne* preferentially located its roots where *Plantago* was not present. The wider spread of *Briza* coupled with its shallow root system is suggestive of this theory and may allow this species to tap resources left untouched by the deeper rooted dominants such as *Plantago*.

Chapter Five

FINE-SCALE SPATIO-TEMPORAL DYNAMICS

5.1. Summary

In this chapter the results from fine-scale monitoring of three permanent plots at Priestcliffe Lees are presented. Temporal patterns of space capture and loss are described for a number of species and changes in spatial structure through time are summarised. Differences in the rate of turnover and growth patterns between species are considered and similarities of species with the same life form and reproductive strategy are emphasised. Turnover of cell occupancy was rapid among many species, but the species composition of the plots did not alter markedly over the course of the study. It is suggested that differences in the behaviour of different life-forms might provide a partial explanation of species coexistence.

5.2. Introduction

The ability to capture and hold space is crucial for a plant species to persist in a sward. Space holding is a function of longevity and spatial growth patterns reflect how efficiently plants can colonise available areas. Certain species form close aggregations and others are more loosely associated. Lovett Doust (1981) coined the terms 'phalanx' and 'guerrilla' respectively for these two growth forms. Phalanx species tend to dominate patches with monospecific stands and spread into neighbouring areas whereas the guerrilla strategy is more mobile and less tightly packed. These two strategies represent opposite ends of a continuum and most species will have spatial dynamics which fall between the two. Although these terms were originally defined with respect to clonal growth, the concept can be widened to include sexual recruitment patterns (Herben *et al.* 1993).

Species with a large capacity for clonal growth will have a spatial structure based on the length and branching pattern of rhizomes (Bell and Tomlinson 1979; Harper and Bell 1979; Bell 1984) and species recruiting from seed will be distributed according to the stochastic nature of seed fall and germination. Vegetative reproduction tends to fall closest to the phalanx strategy whereas seed production generally gives rise to a looser structure.

Since competition between plants is highly localised (Mack and Harper 1977; Pacala and Silander 1985; Silvertown *et al.* 1992), knowledge of the spatial dynamics of the interacting species is an essential prerequisite for predicting the outcome of competition (Silvertown and Wilson, unpublished). The spatial structure of plant communities measured at one point in time has been given a great deal of attention in ecological literature (Grieg Smith 1983; Kershaw and Looney 1985) and since the advent of plant demography the temporal dynamics have been well studied (Harper 1977; Silvertown and Lovett Doust 1993). However, despite an early awareness of the importance of interactions between spatial and temporal processes (Watt 1947), it was not until recently that the full spatio-temporal extent of plant community dynamics has been considered (During and van Tooren 1988; Thorhallsdottir 1990a; Herben *et al.* 1993; van der Maarel and Sykes 1993).

This chapter describes a permanent plot study which was established in order to monitor the short-term spatio-temporal dynamics of limestone grassland plants at a very fine scale. The work has three main objectives:

1. To document the spatio-temporal dynamics of the plant community at small spatial and temporal scales in order to determine the rate and direction of changes in species composition.
2. To investigate interspecific differences in turnover and spatial growth patterns.
3. To analyse the interdependence of the growth patterns of individual species.

These aims have been chosen in order to assess how individual growth patterns and local interactions between species drive the dynamics of the community. This chapter contains most of the information relating to the first two objectives, focusing on the dynamics of each species in isolation from each other. This thread is continued in chapter 6, which attempts to reduce the spatial information for each species by using fractal geometry. Finally, in chapter 7, randomisation tests are used to analyse the interdependence of interspecific spatio-temporal patterns.

5.3. Materials and methods

5.3.1. Permanent plot monitoring

Two permanent plots were established in June 1992. These were sited half a metre apart. The plots consisted of a metal point quadrat (40 x 28 points each 1 cm apart) which was bolted onto a larger quadrat (Fig. 5.1). This larger quadrat was pinned into metal sleeves which were embedded in concrete. A third quadrat, identical in all aspects to the first two but sited several metres away, was established in July 1993.

The plots were censused by dropping a pin vertically into each hole of the movable arm and then moving the arm down 1 cm on the frame and repeating the procedure. The plant species rooted closest to the pin within a 5 mm radius of the pin was recorded and if no species was present within this area the point was taken to be a gap. *Trifolium repens* was treated in a different manner to the other species. Since it is highly stoloniferous and the root system is largely adventitious (Sackville Hamilton and Harper 1989), the presence of stolons was recorded.

Censusing of the first two plots was undertaken fifteen times over a two year period (Table 5.1). The 1992 censuses were somewhat erratic but from 1993 to 1994 the plots were censused every five weeks excluding December-February.

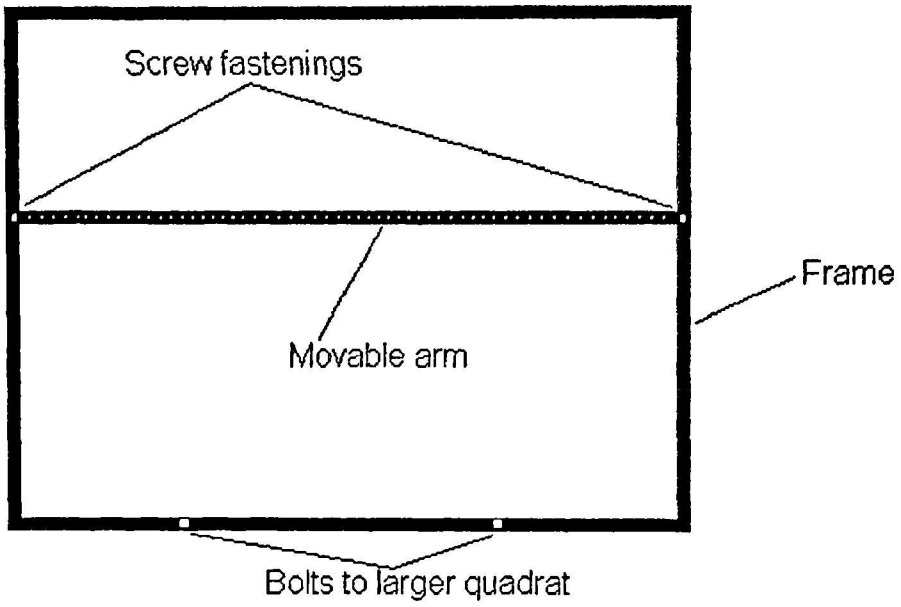


Figure 5.1. The quadrat used for permanent plot monitoring. The movable arm has 42 pin holes (precisely 1 cm apart) into which a pin was dropped vertically. The arm itself can be moved on the frame in a series of screw holes (also precisely 1 cm apart) by which it is secured. The whole quadrat can be firmly bolted onto a larger quadrat.

Table 5.1. Dates of permanent plot monitoring

Census	Date
1	22/6/92
2	19/7/92
3	24/8/92
4	19/11/92
5	29/3/93
6	3/5/93
7	7/6/93
8	12/7/93
9	16/8/93
10	20/9/93
11	25/10/93
12	28/3/94
13	2/5/94
14	6/6/94
15	11/7/94

The third plot was censused nine times over a one year period on the same dates as the first two grids (from July 1993 onwards).

The data obtained at each census consisted of a record (being either a plant species or a gap) in 1120 cells for each plot. The inclusion of only one species per cell is consistent with the format of output from cellular automata models (see chapter 7) but has the disadvantage that it does not give a complete picture of all plants present.

The grids were protected from cattle grazing and trampling during March-November, but were grazed over the winter. Rabbits and invertebrate herbivores had access to the plots all year round.

5.3.2. Quantification of errors

There are a number of possible problems of the methodology and accordingly the following tests were carried out in order to quantify the magnitude of recording errors.

Although the grid was firmly fixed into the ground, slight movements in the position of plants or of the substrate could result in recording errors. At the twelfth census (March 1994) yellow plastic markers were placed exactly where the pins fell at the corners of each grid. The movement of the grid in relation to the substrate was then recorded at successive censuses.

Possible errors in recording might arise through plants being recorded in the wrong position. At the thirteenth census the position of plants on the plots was collected in the usual way but a recensus took place on the following day. Recording errors could thus be quantified by comparing the two accounts of the same census. An error was said to have occurred when either a plant was recorded as present when it has previously been absent and vice-versa.

The method does not give a complete map of the positions of all plants present and but a complete record of all species in each grid cell, not just the species closest to the pin, was carried out at the final census.

5.3.3. Data analysis

For each census a number of summary statistics were calculated for all species with a mean abundance greater than 10 cells. Several other species were also included in the analysis which had a lower mean abundance because of strongly seasonal dynamics (*Ranunculus bulbosus, Potentilla erecta*). The population dynamics of each species were summarised by the number of cells occupied at each census and the gains and losses of cells between censuses. The spatial structure was summarised by the mean clump size of species and the fractal dimension (results presented in chapter 6).

The mean clump size was calculated as the number of cells occupied by a species on the grid divided by the number of discrete clumps. Clumps were taken to be discrete if there was no conspecific in the immediate (8 cell) neighbourhood. The mean clump size for a number of species might be underestimated as a result of clumps occurring at the margins of the grid, and

continuing outside of the recorded area. However, it is difficult to account for this problem and it is not believed to greatly affect the ranking of species.

The birth and death analysis only deals with the inner 864 cells, a margin of 2 cells deep being excluded. This was done so that the data in this chapter match exactly with that in chapter 7 in which the role of a 20-cell neighbourhood is investigated.

A principal components analysis was carried out in order to determine which species had similar dynamical properties, using the mean and coefficient of variation of the following summary statistics : mean cell gains per cell, mean cell losses per cell and mean clump size. The mean cell gains per cell were calculated as the mean number of cells being gained between each census divided by the number of cells already occupied (essentially the per cell birth rate of cells). The mean cell losses per cell were calculated in a similar manner. These statistics were thought to represent the temporal and spatial dynamics of each species and the coefficients of variation were included in the analysis as a measure of seasonality. The analysis was rotated using the VARIMAX method (Norušis 1990). This technique works by creating compound axes of the principal component factors such that the observations lie close to the axes. This eases the interpretation of the analysis since the observations will be clearly associated with particular factors.

5.4. Results

5.4.1. Species composition

Despite being closely situated, the species composition of the first two plots was very different. Plot one was diverse and dominated by the graminoids *Briza media, Cynosurus cristatus, Dactylis glomerata* and *Festuca rubra* (Fig 5.2). In contrast plot two was dominated by *Lolium Perenne, Trifolium repens* and *Dactylis glomerata* (Fig. 5.3), a composition more typical of mesotrophic than calcareous grassland (Rodwell 1993). *Plantago lanceolata* was the most abundant

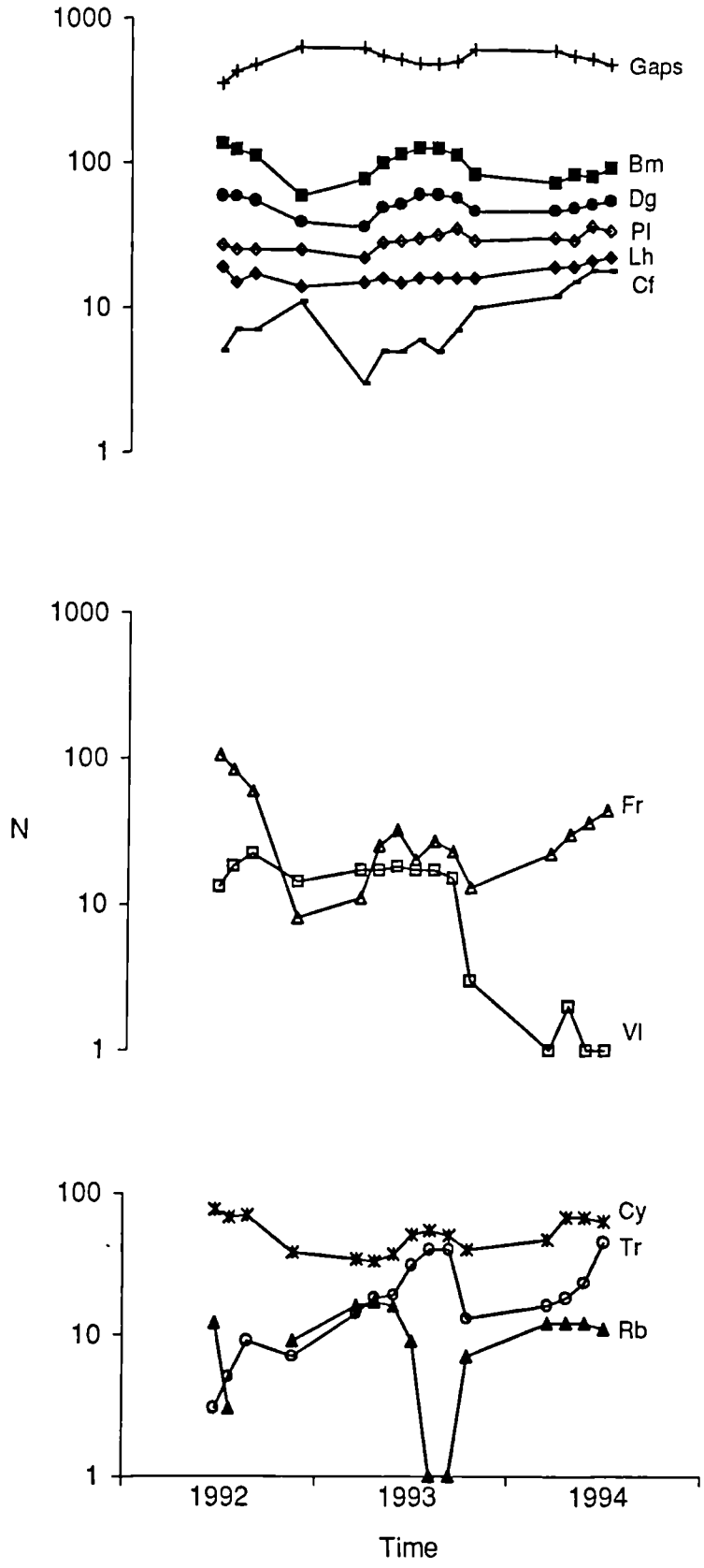


Figure 5.2. Number of grid cells (N) occupied by 10 plant species on the first permanent plot, monitored from 1992-1994. Species abbreviations follow Table 1.1.

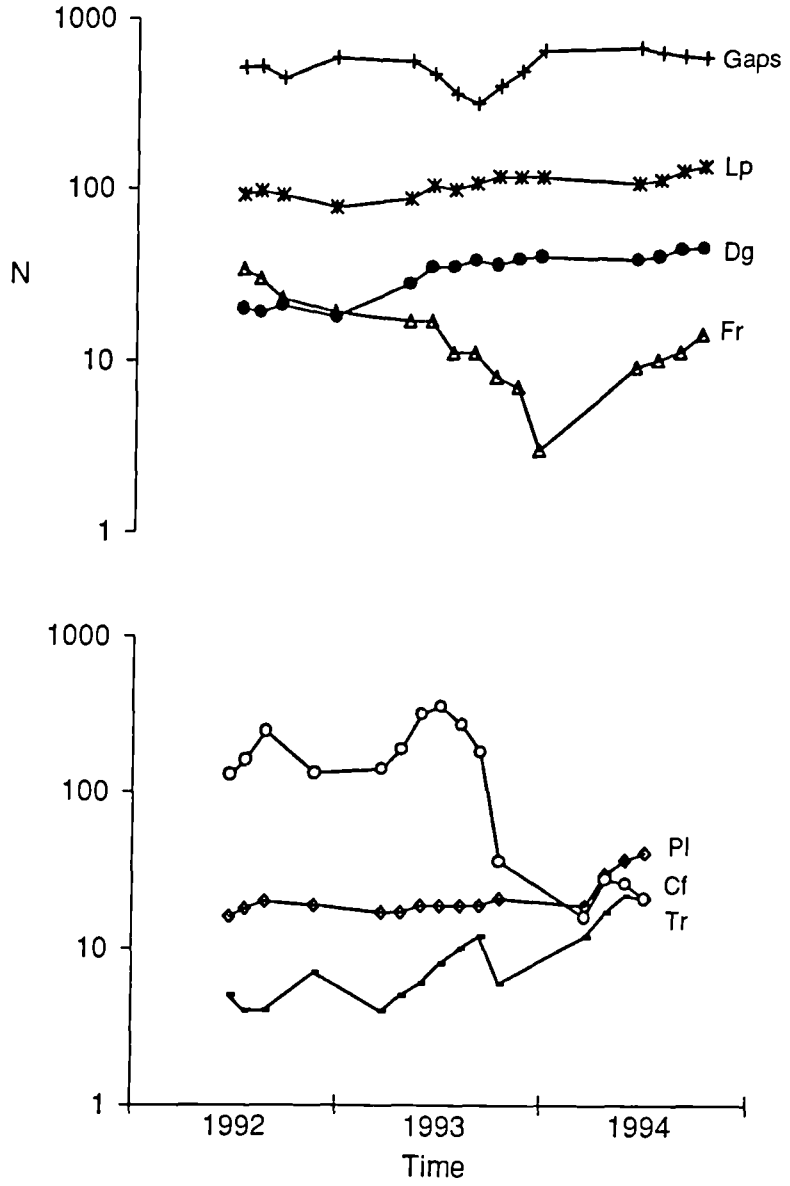


Figure 5.3. Number of cells occupied by 6 plants species on the second permanent plot, monitored from 1992-1994. Species abbreviations follow Table 1.1.

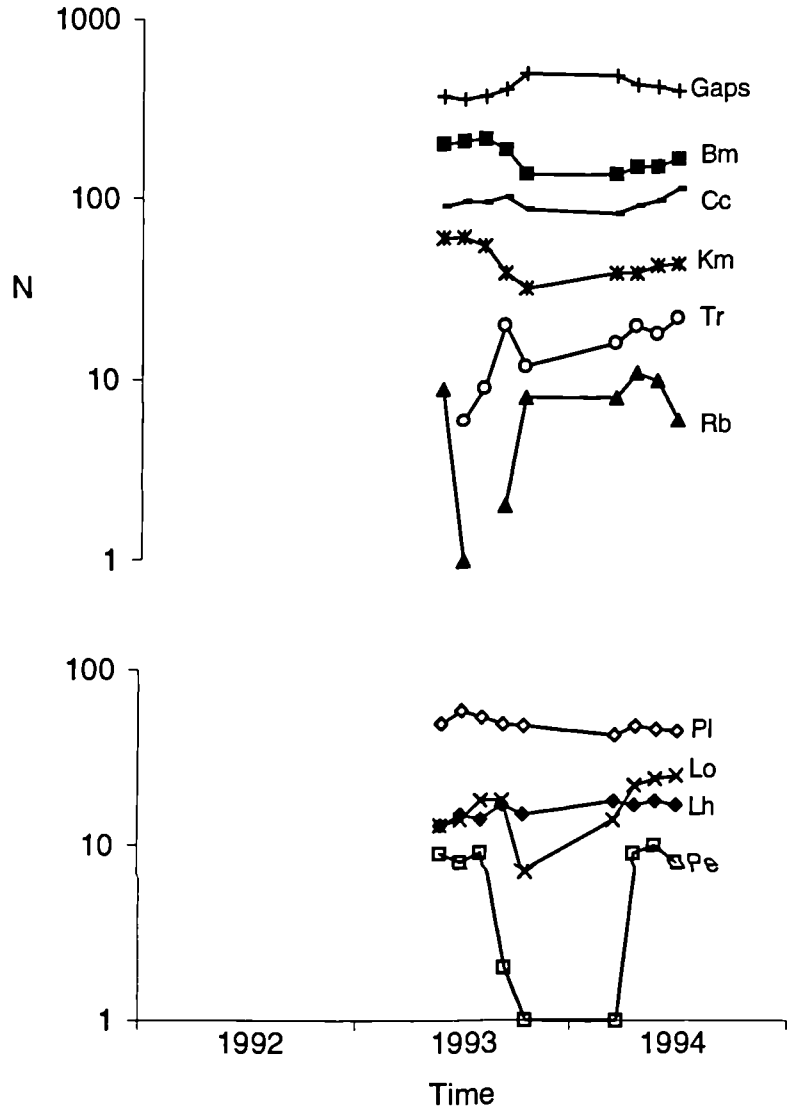


Figure 5.4. Number of cells occupied by 9 plants species on the third permanent plot, monitored from 1993-1994. Species abbreviations follow Table 1.1.

forb on both grids. Plot three was also diverse and dominated by *Briza media*, the sedge *Carex caryophyllea* was the next most abundant species (Fig. 5.4). Over 30 species were recorded on the three plots during the course of the study (Table 5.2).

5.4.2. Seasonality

Many of the species in the first plot exhibit a similar pattern of cell occupation (Fig. 5.2), this reaching a steady peak over the summer and declining over

winter. The number of unoccupied grid cells follow an opposite trend as they are colonised over the season. Several species, *Ranunculus bulbosus* and *Trifolium repens*, are more markedly seasonal and *Leontodon hispidus* appears to have little seasonal dynamics. *Carex flacca* is notable for its increase in late summer/early autumn in both 1992 and 1993. *Ranunculus* has a very different phenology to the majority of species, having a maximum cell occupancy in autumn and spring and becoming scarce by midsummer.

On the second grid, only *Carex flacca* and *Trifolium repens* exhibit marked seasonality in the pattern of cell occupancy (Fig. 5.3). *Trifolium* cover is a maximum is mid-summer, whereas *Carex* demonstrates an increase later in the season, in a similar pattern to that observed on the first grid.

The temporal dynamics of species on grid three are more difficult to interpret since they are only for a one year period (Fig. 5.4). However, within this limited data set it is possible to say that *Potentilla erecta, Ranunculus bulbosus* and *Trifolium repens* all show strongly seasonal patterns in cell occupation, *Trifolium* and *Potentilla* have high summer occupancy while *Ranunculus* displays the same early phenology as displayed on the first grid.

5.4.3. Directional changes

Certain species increased or decreased their cell occupation over the two year monitoring period. *Festuca rubra* substantially declined in abundance in 1992, but was showing a resurgence in 1994. *Carex flacca* increased in abundance over the two years, as did *Trifolium repens*. *Viola lutea* declined catastrophically between the tenth and eleventh census. This was due to rabbit disturbance by scratching of an area of the sward which was densely occupied by *Viola* rosettes. At the eleventh census very few *Viola* plants remained and in their place was a hole filled with rabbit droppings. Several other species were affected but to a lesser extent than *Viola* which lost the majority of individuals in the population. The number of gaps increased following the first census but

Table 5.2. A list of species recorded on the three permanent plots during the course of the study.

Plot	Species recorded
One	*Anthoxanthum odoratum, Briza media, Carex caryophyllea, Carex flacca, Cerastium fontanum, Cynosurus cristatus, Dactylis glomerata, Festuca rubra, Helictotrichon pratensis, Holcus lanatus, Hypochaeris radicata, Leontodon hispidus, Plantago lanceolata, Ranaunculus bulbosus, Rhinanthus minor, Trifolium repens, Trifolium pratense, Viola lutea, Viola riviniana.*
Two	*Achillea millefolium, Anthoxanthum odoratum, Briza media, Carex caryophyllea, Carex flacca, Cerastium fontanum, Dactylis glomerata, Festuca rubra, Holcus lanatus, Leontodon hispidus, Lolium perenne, Plantago lancolata, Taraxacum sect. Ruderalia, Trifolium pratense, Trifolium repens.*
Three	*Briza media, Carex caryophyllea, Carex flacca, Dactylis glomerata, Festuca rubra, Galium verum, Holcus lanatus, Hypochaeris radicata, Koeleria macrantha, Leontodon autumnalis, Leontodon hispidus, Lotus corniculatus, Luzula campestris, Plantago lanceolata, Potentilla erecta, Primula veris, Prunella vulgaris, Ranunculus bulbosus, Sanguisorba minor, Trifolium repens.*

then settled into a regular seasonal pattern. This may have been due to an initial perturbation caused by the onset of the monitoring but the system seemed to have stabilised once the more sensitive species were lost (possibly *Trifolium pratense*).

All of the species on the second grid, except *Festuca rubra* and *Trifolium repens*, increased in abundance over the two year monitoring period (Fig. 5.3). The temporal dynamics of *Festuca* are very similar to its behaviour on the first grid, showing an initial decline in 1992 followed by an increase in numbers in 1994. *Trifolium repens* increased from 1992 to 1993 reaching a peak abundance in excess of 350 cells but then the population appeared to crash in 1994, not rising above 100 cells of occupation. In contrast *Plantago lanceolata* increased in 1994. *Carex flacca, Dactylis glomerata* and *Lolium perenne* exhibit the summer growth

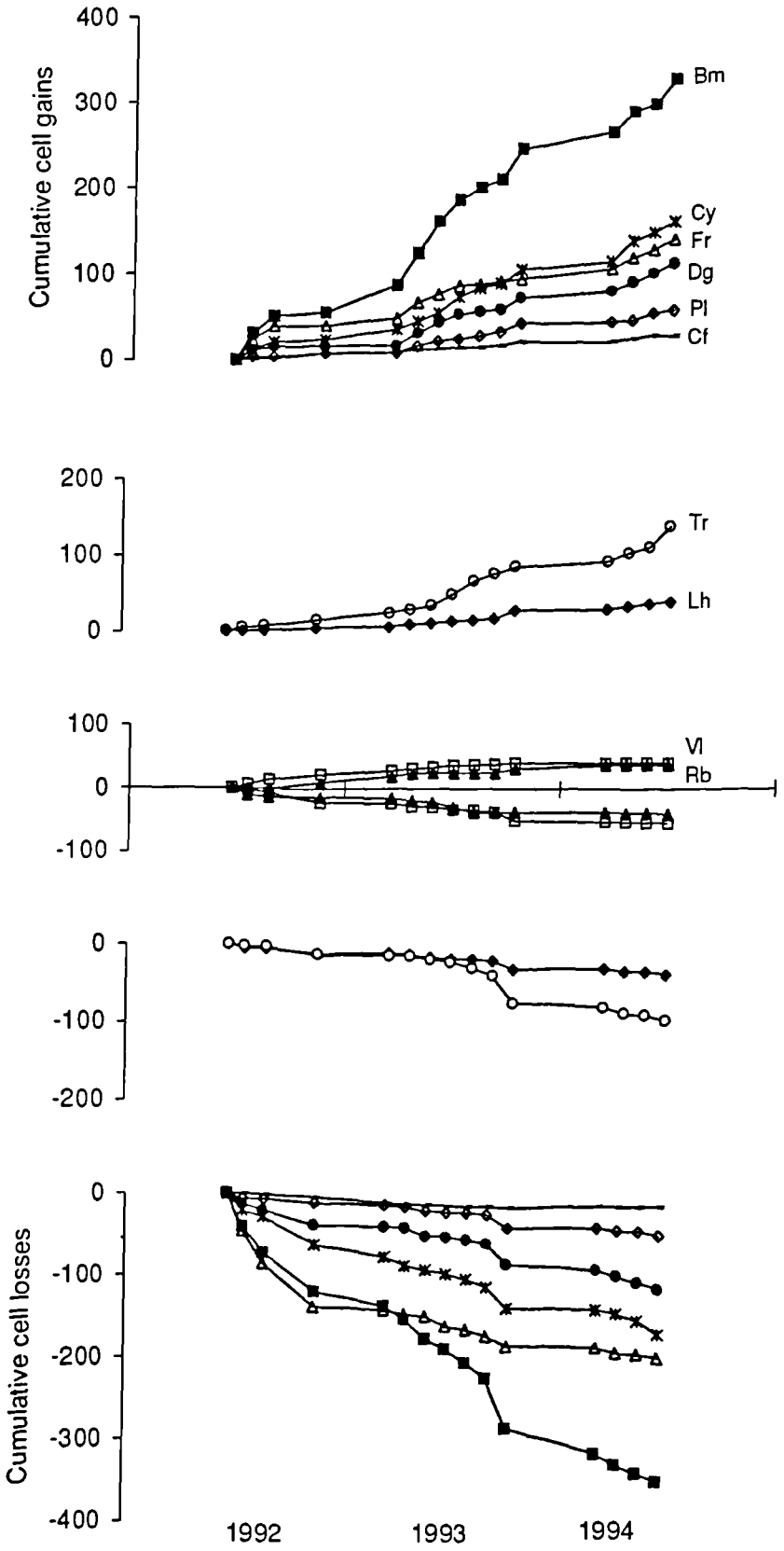


Figure 5.5. Cumulative gains and losses of grid cells of 10 plant species on the first permanent plot, monitored from 1992-1994. Species abbreviations follow Table 1.1.

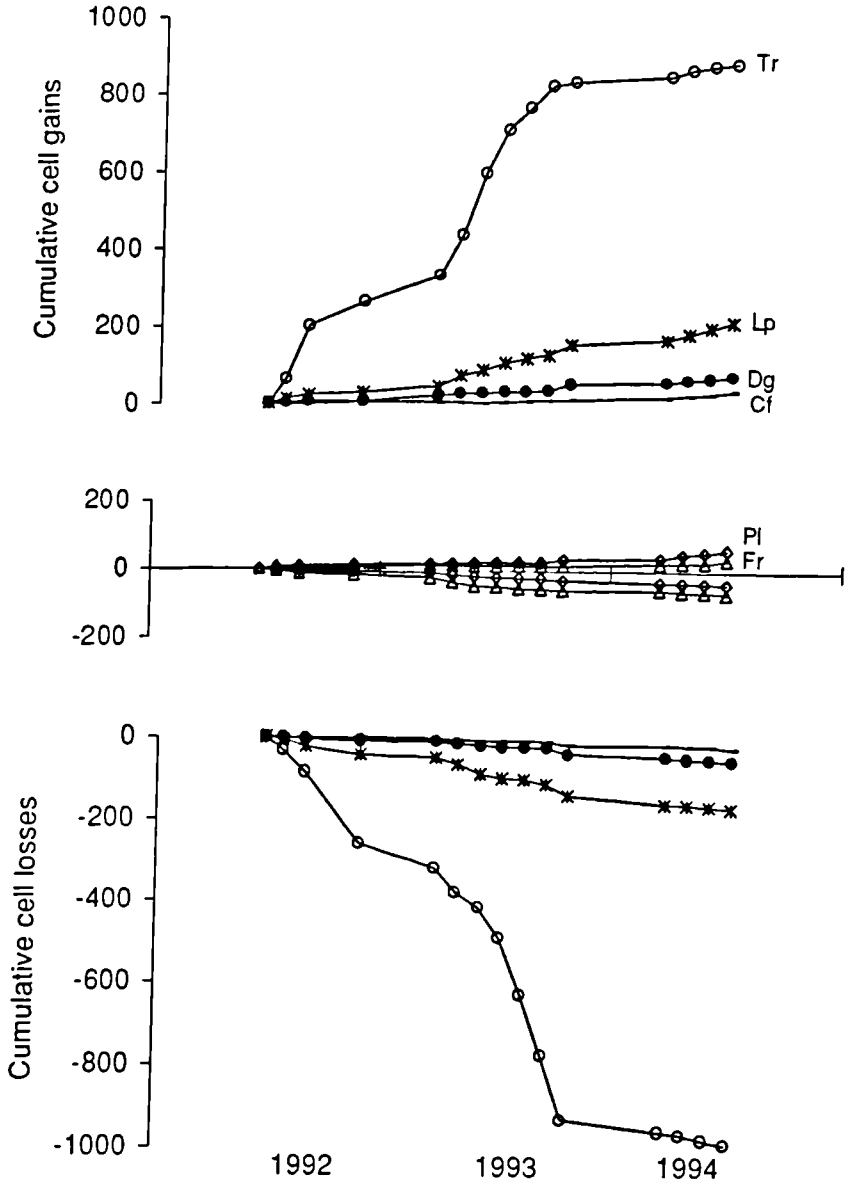


Figure 5.6. Cumulative gains and losses of grid cells of 6 plant species on the second permanent plot, monitored from 1992-1994. Species abbreviations follow Table 1.1.

and winter decline seen for grid one species, this being superimposed on the overall increase of these species.

On the third plot *Leontodon hispidus* and *Trifolium repens* increased steadily over the monitoring period whereas *Plantago lanceolata* declines. *Briza media* and *Koeleria macrantha* both experienced large losses of cell occupancy at the start of

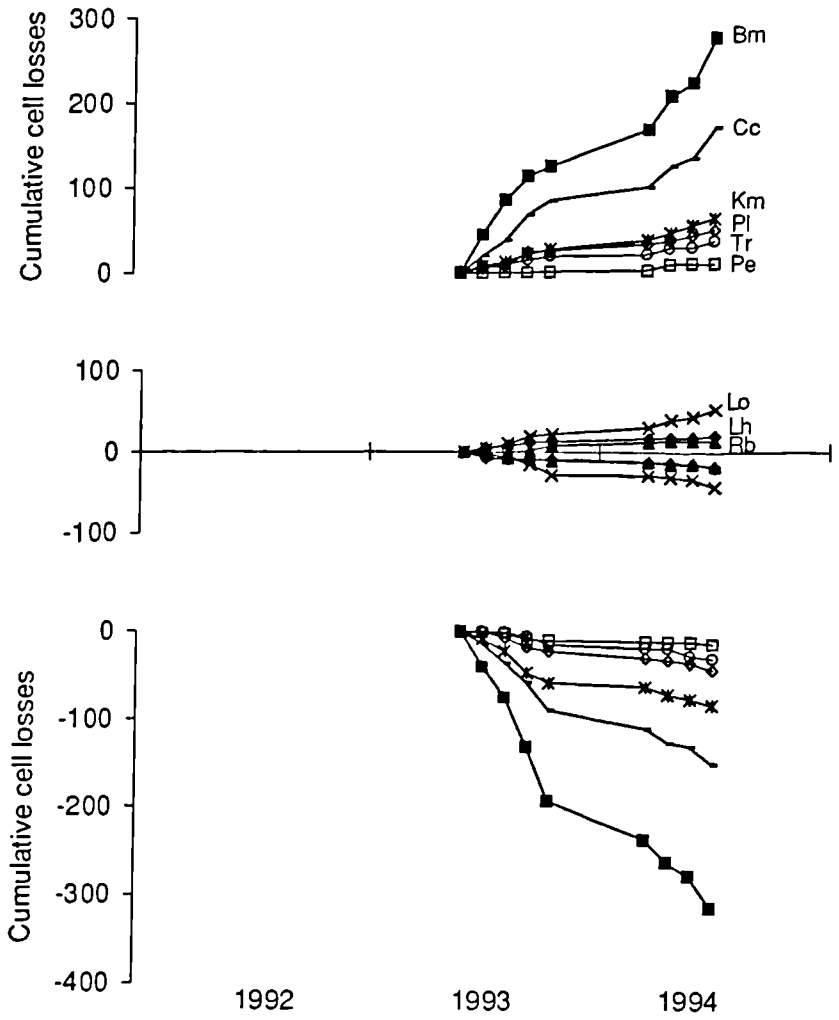


Figure 5.7. Cumulative gains and losses of grid cells of 9 plant species on the third permanent plot, monitored from 1993-1994. Species abbreviations follow chapter 1.

the monitoring period which may be disturbance related but could also be part of the natural population cycle. It is difficult to distinguish between these two possibilities in the absence of a longer run of data.

5.4.4. Turnover

On the first plot, the grasses had the greatest turnover (Fig. 5.5). *Trifolium repens* was also highly dynamic. The perennial forb species and *Carex flacca* had comparatively low turnover. *Trifolium repens* gained and lost cells rapidly on the second plot (Fig. 5.6), exhibiting much greater turnover than other species.

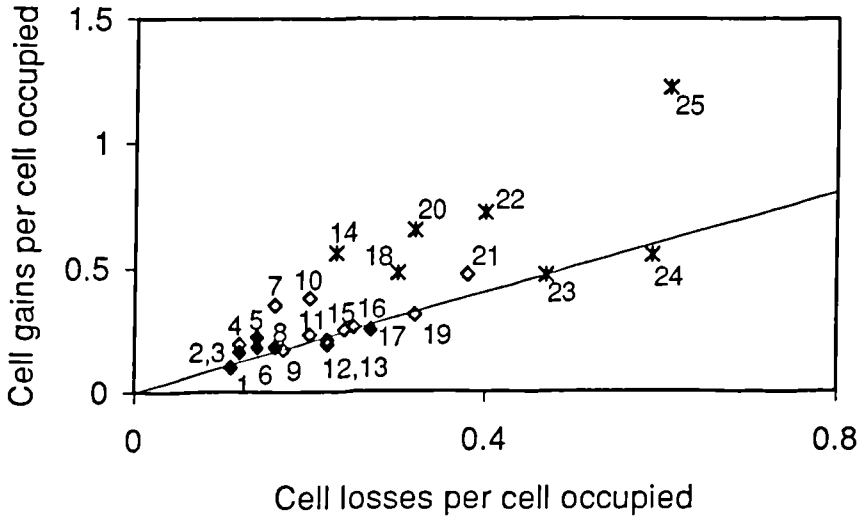


Figure 5.8. Mean cell gains and losses per cell occupied of the plant species recorded on three permanent plots. Symbols denote different life-forms: graminoids (open diamond), rosette-forming perennial forbs (closed diamond), other forbs (asterisk). The line indicates per capita losses = per capita gains.

Species (plots given in brackets): 1 - *Plantago lanceolata* (3), 2 - *Plantago lanceolata* (1), 3 - *Lolium perenne* (2), 4 - *Dactylis glomerata* (2), 5 - *Plantago lanceolata* (2), 6 - *Leontodon hispidus* (3), 7 - *Carex flacca* (2), 8 - *Leontodon hispidus* (1), 9 - *Dactylis glomerata* (1), 10 - *Carex flacca* (1), 11 - *Carex caryophyllea* (3), 12 - *Koeleria macrantha* (3), 13 - *Briza media* (3), 14 - *Trifolium repens* (3), 15 - *Cynosurus cristatus* (1), 16 - *Briza media* (1), 17 - *Viola lutea* (1), 18 - *Lotus corniculatus* (3), 19 - *Festuca rubra* (2), 20 - *Ranunculus bulbosus* (1), 21 - *Festuca rubra* (1), 22 - *Trifolium repens* (1), 23 - *Trifolium repens* (2), 24 - *Ranunculus bulbosus* (3), 25 - *Potentilla erecta* (3).

The grass species had greater turnover than the other forbs. Similar interspecific differences were observed on the third plot. The graminoids *Briza media*, *Carex caryophyllea* and *Koeleria macrantha* had greater cell gains and losses than the forb species.

On the first plot the cumulative gains lines of *Cynosurus cristatus* and *Festuca rubra* cross after the first year of monitoring. In the first year *Cynosurus* gained more cells than *Festuca*, with the reverse being true for the second period.

The mean per cell gains and losses also demonstrate the slow dynamics of the rosette-forming perennial species compared to the graminoids and other forbs (Fig. 5.8). The per cell dynamics of the seasonal species (*Trifolium repens, Potentilla erecta, Ranunculus bulbosus*) are artificially elevated since at certain periods of the year high recruitment will occur from few individuals. This is particularly noticeable in the case of *Potentilla.*

5.4.5. Spatial dynamics

The mean clump size of many of the species on the first grid seems to vary over the monitoring period (Fig. 5.9). *Briza, Dactylis* and, to a certain extent, *Festuca* all have larger clumps in the summer. *Carex flacca* has larger clumps in autumn/winter. The clump size of both *Viola* and *Cynosurus* decreases over time, whilst that of *Trifolium* increases. *Leontodon, Plantago* and *Ranunculus* have a relatively constant mean clump size independent of season. All three of these species tend to exist as solitary plants, as does *Carex* except for a slight increase in clump size late in the year. The graminoids (*Briza, Cynosurus, Dactylis* and *Festuca*) are more clumped. *Trifolium* also appears to be clumped in pattern.

The patterns on the second grid are similar to the first for *Carex* and *Plantago,* although at this location *Carex* only increases in clump size in the second winter (Fig. 5.10) although it still largely survives as isolated ramets. *Plantago* is also unclumped and largely unseasonal. *Lolium perenne* is extremely clumped, as is *Trifolium repens,* although *Lolium* is clumped irrespective of season whereas *Trifolium* has a tendency to form clumps in the summer. *Festuca* exhibits a marked seasonality in its clumping patterns, and has some degree of clumping. *Dactylis* has a tendency to aggregate and increases its clump size over the two years of study.

Temporal patterns of clumping are difficult to interpret on the third grid due to the small run of data. The patterns exhibited by *Leontodon, Lotus* and *Carex*

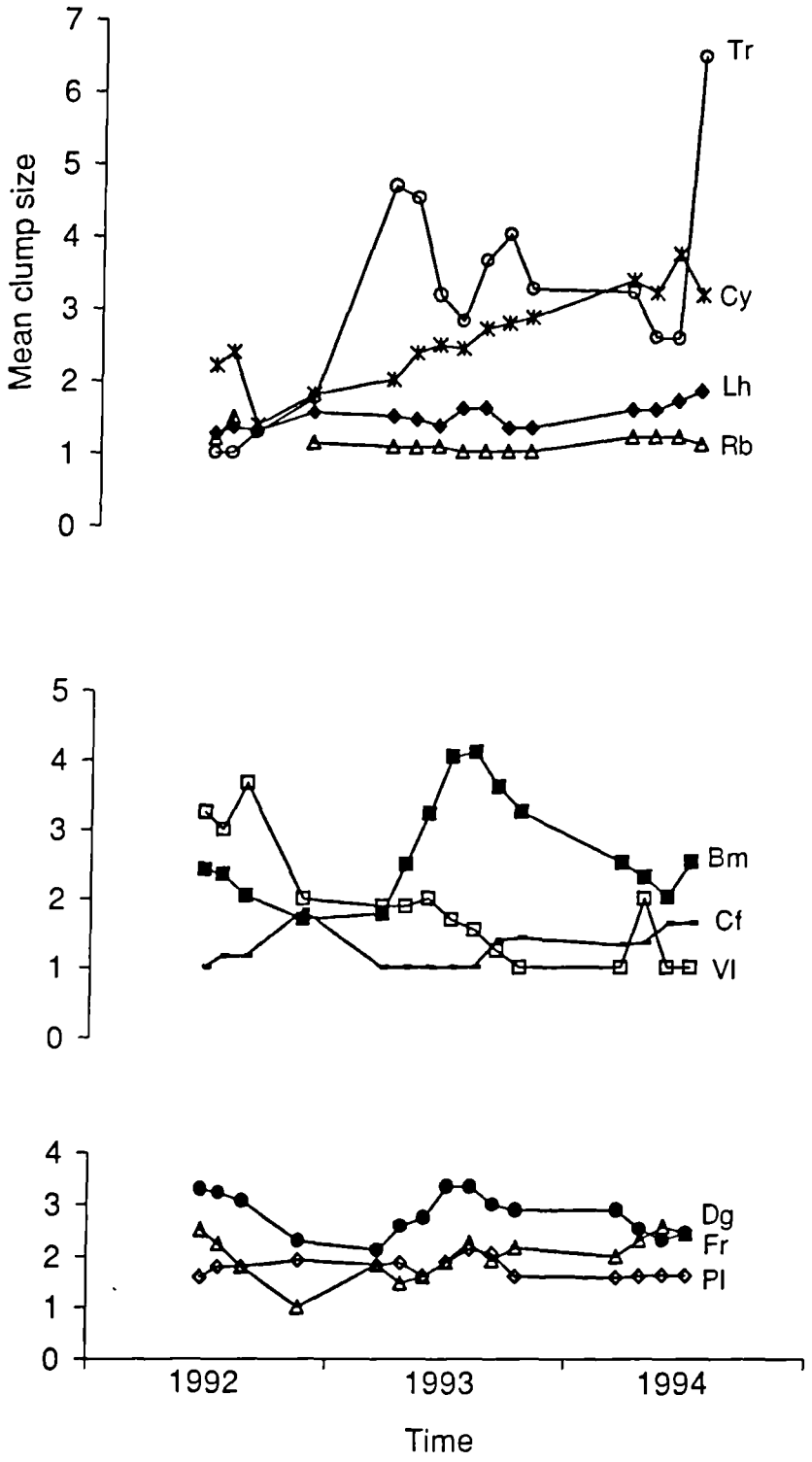


Figure 5.9. Mean clump size of plant species on the first permanent plot. Species abbreviations follow Table 1.1.

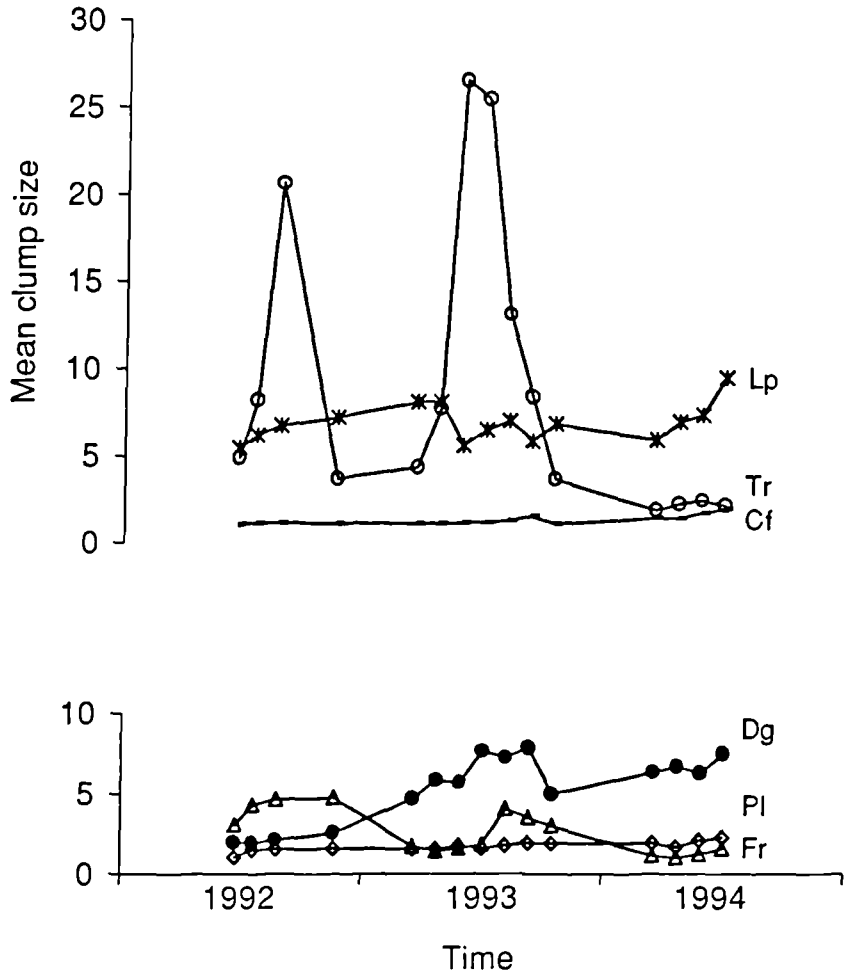


Figure 5.10. Mean clump size of plant species on the second permanent plot. Species abbreviations follow Table 1.1.

seem to have no seasonal trend (Fig. 5.11). *Ranunculus, Trifolium, Potentilla* and, to a lesser degree, *Plantago* are clearly more clumped at particular times of the year when their abundance is high. *Briza* becomes less aggregated over time. As would be expected from observations on the first two plots, *Trifolium* has a large tendency to form conspecific clumps on this grid, a trait also shared by *Potentilla. Leontodon, Plantago* and *Ranunculus* are not heavily clumped, *Briza, Carex* and *Koeleria* are intermediate in this respect.

The mean per capita cell gains of graminoid species is inversely correlated with mean clump size (Fig. 5.12). *Carex flacca* is the most solitary graminoid species

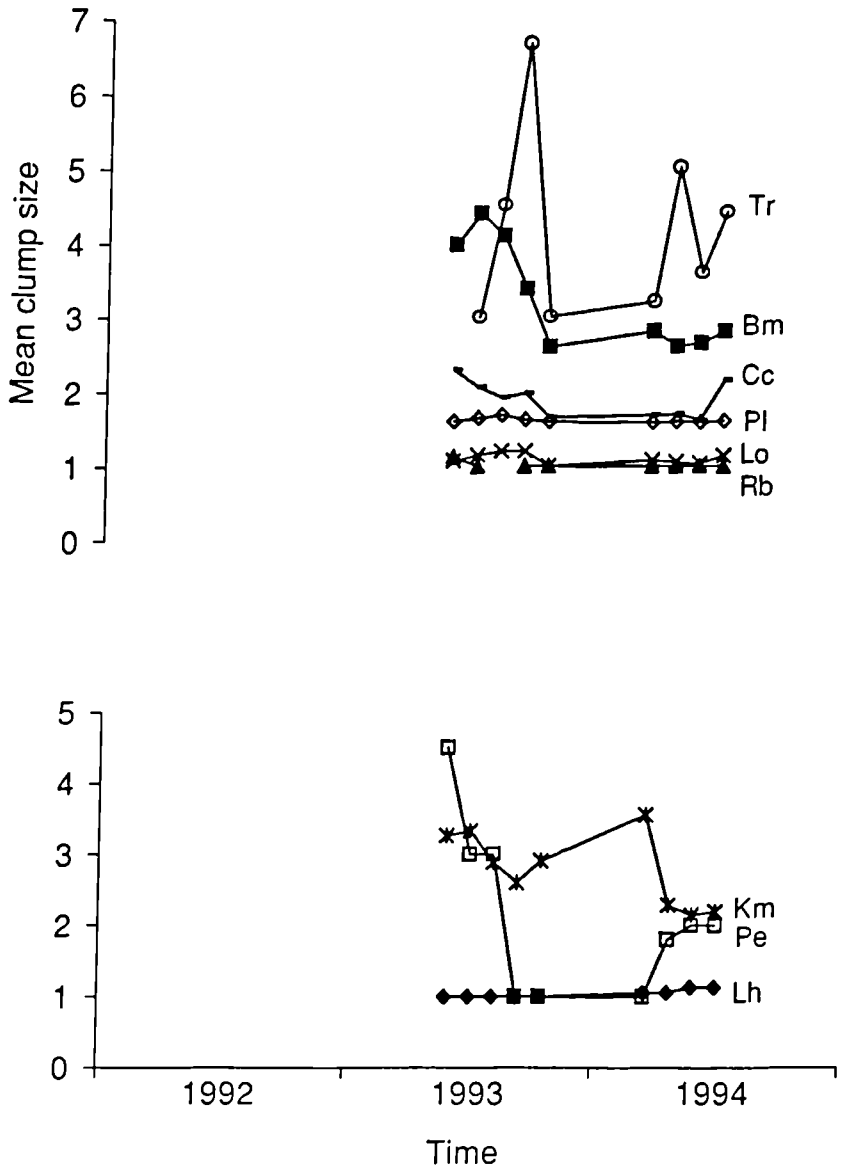


Figure 5.11. Mean clump size of plant species on the third permanent plot. Species abbreviations follow chapter 1.

and has one of the highest mean per cell gain. *Lolium perenne* and *Dactylis glomerata* are the most clumped species and have correspondingly lower mean per cell gains.

5.4.6. Ordination

The ordination of 25 'species' (some of these are the same species on different grids) with respect to the first two factors of the principal components analysis

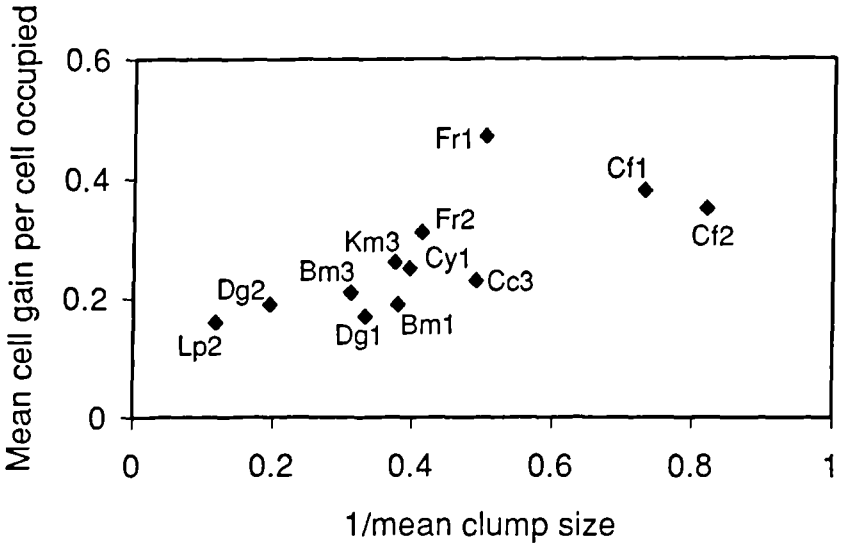


Figure 5.12. The relationship between 1/mean clump size and the per capita rate of cell gain of the graminoid species occurring on three permanent plots. Pearson's correlation coefficient, $R = 0.733$ ($P < 0.01$). Species abbreviations follow chapter 1.

is represented in Figure 5.13. The first factor is highly correlated with the per capita birth and per capita death rates and coefficient of variation of the birth rate (Table 5.3). This first principal component is also related to the coefficient of variation of mean clump size but this itself is correlated to birth rate ($R = 0.459$, $P < 0.05$) and death rate ($R = 0.597$, $P < 0.01$). The second factor is correlated with the mean clump size and the coefficient of variation of clump size. It is negatively correlated with the coefficient of variation of both per capita birth and death rates. The graminoid species are largely confined to the lower right quadrant (with the exception of *Festuca rubra* and *Carex flacca*), whereas the rosette-forming perennial forbs tend to lie in the lower left quadrant. Other perennial forb species occur largely in the top half of the ordination, *Trifolium repens* in the right quadrant, *Ranunculus bulbosus* on the left.

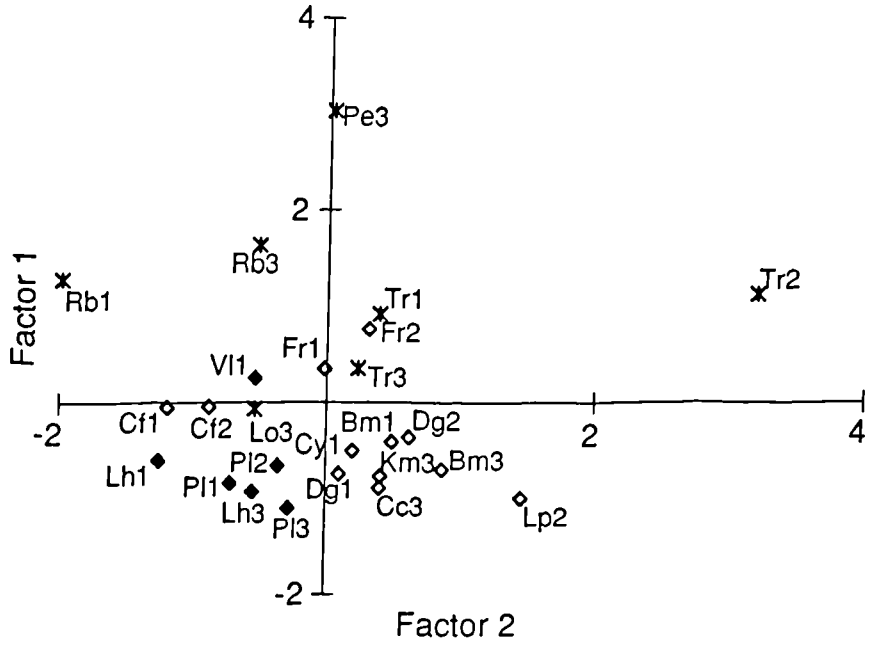


Figure 5.13. Plot of the first two factors from a principal components analysis carried out on 25 data sets of species occurring on the three permanent plots. Symbols denote different life-forms: graminoids (open diamond), rosette-forming perennial forbs (filled diamond), other forbs (asterisk). Species abbreviations follow chapter 1.

5.4.7. Quantification of errors

Both of the first two grids moved 1 mm from census 11 to census 12 and then remained in this position for the remainder of the study. This movement could well be due to the early growth of vegetation moving the position of the grid. The third grid did not move at all from census 11 to 15.

Recensusing of plots led to a number of errors which were separated into misrecording of forbs and graminoids (Table 5.4). The error as a percentage of the number of 'live' cells (being the sum of graminoid and forb cells) was around 5% for all three grids. Ramets of *Plantago lanceolata* and *Leontodon hispidus* were never wrongly recorded.

The complete census of all species present in cells of the plots demonstrated that for the most part, cells were only occupied by a single species (80-90% of

Table 5.3. Correlation of plant traits with the first two factors of the principal components analysis.

Plant trait	Factor 1	Factor 2
Per capita birth rate	0.91755	0.05158
CV per capita birth rate	0.78901	-0.39452
Per capita death rate	0.90830	0.17052
CV per capita death rate	0.15451	-0.69779
Mean clump size	0.04797	0.86279
CV mean clump size	0.62716	0.63015

Table 5.4. Recording errors made in a recensus of the three plots.

Cell type	Number of cells	Number of errors	Percentage error (%)
GRID ONE			
Forbs	111	4	3.60
Graminoids	308	18	5.84
Live cells	419	22	5.25
Total cells	1120	22	1.96
GRID TWO			
Forbs	128	7	5.47
Graminoids	240	8	3.33
Live cells	368	15	4.08
Total cells	1120	1	1.34
GRID THREE			
Forbs	178	7	3.93
Graminoids	377	15	3.98
Live cells	555	22	3.96
Total cells	1120	22	1.96

cells excluding gaps, Table 5.5). The additional species in cells were generally graminoids.

Table 5.5. Number of cells in each plot with more than one species present

Cell type	Number of cells	Extra graminoids (% of total cells)	Extra forbs (% of total cells)	Extra plants (% of total cells)
GRID ONE				
Graminoids	352	64 (18.2%)	1 (0.3%)	65 (18.5%)
Forbs	154	23 (14.9%)	2 (1.3%)	25 (16.2%)
Live cells	506	77 (15.2%)	3 (0.6%)	80 (15.8%)
Total cells	1120	77 (6.7%)	3 (4.5%)	80 (7.1%)
GRID TWO				
Forbs	131	11 (8.4%)	1 (0.8%)	12 (9.2%)
Graminoids	277	24 (8.6%)	1 (0.4%)	25 (9.0%)
Live cells	408	35 (8.6%)	2 (0.5%)	37 (9.1%)
Total cells	1120	35 (3.1%)	2 (0.2%)	37 (3.3%)
GRID THREE				
Forbs	166	55 (33.1%)	0 (0.0%)	55 (33.1%)
Graminoids	423	44 (10.4%)	8 (1.9%)	52 (12.3%)
Live cells	589	99 (16.8%)	8 (1.4%)	107 (18.2%)
Total cells	1120	99 (8.8%)	8 (0.7%)	107 (9.5%)

5.5. Discussion

5.5.1. Limitations of the study

Movement on the grid was slight over the period that it was monitored and it would seem reasonable to assume that it was equally as well fixed during the remainder of the study. Recording errors were also small (approximately 5% of non-empty cells).

In addition to this, the recording technique used has a number of limitations:

1. The exact population size of species could not be calculated since the presence of a species in a cell could indicate a single ramet or a large number of ramets. However, for larger species such as *Plantago lanceolata* the population and number of cells occupied are almost identical.

2. No differentiation was made between adults, seedlings and vegetative offspring.

3. The detailed monitoring of plants at such small intervals will cause some degree of disturbance to the community. Care was taken to minimize this disturbance but it is impossible to determine how great an effect the sampling itself had on the dynamics of individual species.

4. This monitoring programme has been undertaken over smaller spatial and temporal scales than have previously been considered. The intensity of such monitoring by a single individual means that only small areas can be sampled which may be unrepresentative of the whole community.

The complete census of grid cells demonstrates that the majority of cells (80-90%) contain only one species but this still leaves a number of uncounted plants. The graminoids are likely to have been most underestimated in terms of the number of cells occupied since a single grass tiller could easily share a cell with another species. The dynamics of graminoid species presented here can be only seen as an indication of the actual behaviour of species in the field for this reason. The turnover of such species is likely to have been underestimated because there is often more than one tiller occupying a grid cell and tiller turnover in such circumstances may pass unnoticed.

The abundance and dynamics of forbs will be relatively accurate since plants of species such as *Plantago* and *Leontodon* occupy whole grid cells and were rarely wrongly recorded in location. However, one problem in the interpretation of results from these and other herbaceous species is that no differentiation is made between adult plants and seedlings. Seedling turnover was observed to be substantially greater than that of adults but this was not quantified. Turnover estimates for these species will therefore be an overestimate. However, within the plots recruitment from seed was a rare phenomenon relative to clonal expansion, so this should not present a great problem.

This study is not, nor was ever intended to be, a complete demographic record of all the species studied. However, it does give an indication of the spatio-temporal dynamics of the community in terms of space capture which would be very difficult to achieve using detailed demographic recording of species.

5.5.2. Community dynamics

Grime (1990) suggested that calcareous grasslands comprise plants with a slow-turnover of leaves and roots. He further suggested that the 'slow-dynamics' of the community (Huston 1979) was partially responsible for coexistence of species since competitive exclusion would occur over a prolonged period of time. From the results presented here and from other studies (Herben *et al.* 1993; Rusch and van der Maarel 1992; van der Maarel and Sykes 1993) it is apparent that there is a marked degree of turnover in species-rich grasslands even over short time-scales. Around 20% of graminoid cells will not be occupied by the same species after five weeks and for certain species such as *Trifolium repens* the rate of cell loss and gain is much greater. However, the rosette-forming perennial species conform to the idea of typical calcareous grassland plants envisaged by Grime (1990), long-lived and with slow turnover (Grubb 1990).

The number and turnover of gaps within the community are important since they provide microsites for colonisation, whether by clonal growth or seed dispersal. There is a greater number of gaps (cells containing no rooted species) on the plots than would be expected by superficial examination of the sward, a finding also reported by Silvertown and Smith (1988) and Thórhallsdóttir (1990a) in mesotrophic grasslands. However, the absence of rooted plants in a cell does not preclude the possibility of above-ground cover and the vegetation cover at Priestcliffe was almost totally continuous. The existence of gaps was a seasonal phenomenon; plants died in the autumn leaving a space and these were progressively recolonised by new plant growth over the following growing season. Gaps were a minimum of 40-50% of total grid area in July and a maximum of up to 75% of total grid area in November,

in comparison to 25% gap cover in summer and 60% in March observed by Thórhallsdóttir (1990a) in cells of the same size.

The majority of recruitment on the grids occurred through clonal growth of the species involved. Seedlings were observed on the grid but tended to be short-lived. It is possible that the high mortality of seedlings was a direct result of intrusion by the plot recording but other studies have also reported the low survival rate of seedlings in calcareous grassland (Silvertown and Dickie 1980; Verkaar and Schenkeveld 1984; Hillier 1990). Seedlings of *Cerastium fontanum* in particular were observed to appear and disappeear very quickly, this species known to recruit from a substantial seed bank (Salisbury 1964).

A high proportion of the species monitored over the course of the study demonstrated no clear change in abundance in the absence of seasonal fluctuations but there were several species which lost or gained a large number of cells. *Trifolium pratense* was initially an abundant species on the first plot but rapidly declined after the onset of the study and became locally extinct. Disturbance caused by the censuses could have possibly been the cause of the rapid decline of this species. *Festuca rubra* also exhibited a dramatic decline in the first year on both the first and second plots but was increasing in abundance towards the end of the study. The synchronous behaviour of this species on two grids suggests that the dynamics of *Festuca* might be strongly influenced by climatic factors.

Viola lutea suffered a catastrophic decline which was caused by rabbit disturbance. This may have been because this species is particularly palatable to rabbits or alternatively the result of stochastic disturbance which may, by chance, have equally have affected other species which tended to occur in tight clumps.

Many of the species which exhibited a marked increase in the number of cells occupied, *Carex flacca, Dactylis glomerata, Leontodon hispidus, Lolium perenne* and

Plantago lanceolata, are large species which may be competitive dominants. The reduction of grazing throughout the study may have benefited these species which are normally suppressed by herbivory.

Trifolium repens increased in abundance on the first and third plot, which may again have been caused by the lack of summer grazing, this species is very palatable to stock (Grime, Hodgson and Hunt 1988; Sackville Hamilton and Harper 1989), and demonstrated interesting behaviour on the second grid. It was the one of the most abundant species at the beginning of the recording programme (148 cells) and rapidly increased to a high of 450 cells in the midsummer of 1993. However, in 1994 there were very few stolons to be seen. This would appear to be part of a boom/bust cycle although it is hard to conclude this with confidence with such a short run of data. An alternative explanation would be a climatic induced population decrease but this hypothesis is hard to substantiate since the same species is increasing on both the other grids. Interspecific competition might be another possible cause of the decline but the abundance of gaps on the second grid which were previously occupied by *Trifolium* lend little support to this suggestion. Other species of *Trifolium* have been demonstrated to suffer in yield if grown in the same plot over a number of years (Katznelson 1972), a possible mechanism for this being the production of secondary chemicals which are autoallelopathic in this species (Newman and Rovira 1975; McFarlane, Scott and Jarvis 1982a,b). Nitrogen is well known to have a detrimental effect on the performance of *Trifolium repens* (Burdon 1983; Sackville Hamilton, personal communication), so the nitrogen-fixing habit of this species may have an adverse effect on its own environment. The growth rate of modules in *Trifolium repens* is strongly dependent on the temperature at the shoot apex (Sackville Hamilton and Harper 1989) which gives rise to the highly seasonal patterns observed in this and other studies (Fig. 5.14).

The lack of any clear trend in abundance for the majority of species with such a high turnover rate of cell occupation suggests that the system is stable at large

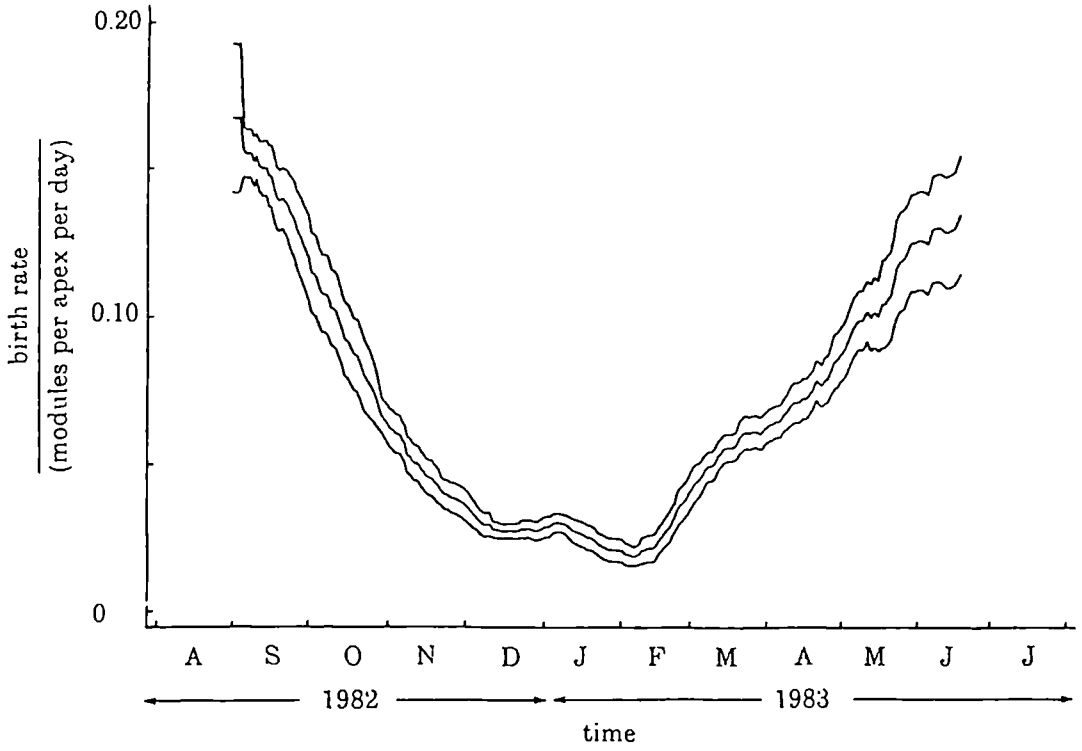


Figure 5.14. Variation in the birth rate of modules per shoot axis of *Trifolium repens* during the course of one year in a permanent pasture. The lines represent the running means of 32 consecutive estimates ± two standard deviations. The seasonal patterns of growth are very similar to those observed in *Trifolium repens* populations at Priestcliffe. (From Sackville Hamilton and Harper 1989).

spatial scales but unstable at small spatial scales. This uncoupling of fine- and large-scale dynamics was also noted by Herben *et al.* (1993) and may be a characteristic of self-organising systems in which small-scale fluctuations may enhance large scale stability (Chesson and Huntly 1989; Prigogine and Stengers 1992).

The fluctuating fortunes of *Cynosurus cristatus* and *Festuca rubra* on the first plot suggest that competitive reversals may occur between years, a phenomenon which has been observed in other grassland communities (Herben and Krahulec 1990). This may be related to environmental factors, such as climate, or maybe the result of stochastic recruitment patterns. Nonetheless, reversals in the ability of species to capture space will tend to prolong the process of

competitive exclusion and promote coexistence between species with similar competitive ability.

5.5.3. Interspecific differences in spatial dynamics

An immediate feature of the ordination diagram (Fig. 5.13) is that the same species from different grids are generally clustered together. In addition to the clustering of the same species, species of the same growth form tend to be located together on the axes. The rosette-forming herbs *Plantago lanceolata* and *Leontodon hispidus* are in the lower-left quadrant while the majority of the graminoids (*Briza media, Carex caryophyllea, Cynosurus cristatus, Dactylis glomerata, Koeleria macrantha* and *Lolium perenne*) are in the lower-right quadrant. These groupings show that the major difference between the two groups is that the graminoids have a tendency for clumping as a result of their recruitment through the production of vegetative tillers or short stolons (*Carex caryophyllea*). Neither *Plantago* or *Leontodon* have a large capacity for clonal expansion in this kind of habitat and recruit largely from seed (Grime, Hodgson and Hunt 1988). The slightly higher placing of the graminoids on the y axis points to the greater turnover of these species (see also Fig. 5.8). This difference is likely to be underemphasised because of the seedling dynamics of the forbs and the within cell turnover of the graminoids which has already been discussed. Grubb (1990) suggests that may of the dicotyledonous species in calcareous grassland are very long-lived and Dickie (1977, cited in Grubb 1990) recorded half-lives of 18 and 56 years for populations of *Sanguisorba minor* and *Plantago media* respectively. The rosette forming perennials may be considered analogous to the 'fortress' species of Herben *et al.* (1993) since these species are longed lived and recruit occasionally through seed (Grubb 1990). Seedling mortality is high but once a site is gained it is held for a long period of time.

Within the graminoids themselves *Lolium perenne* tends to be more clumped, due to intravaginal tillering (Turkington and Harper 1979), and less dynamic. *Festuca rubra* and *Carex flacca* fall well outside within the main graminoid

grouping. *Carex flacca* occurs on the margins of the upper and lower left quadrants. It is reasonably dynamic but tends to occur as solitary plants rather than clumps, relatively long stolons (some 3cm in length) leading to an overdispersed pattern at small-scales (Mahdi and Law 1987; van de Hoeven, de Kroon and During 1990). *Festuca rubra* is both highly dynamic and aggregated. The behaviour of this species is complicated since it may change from having a low turnover to being highly mobile in swards of different density (Herben *et al.* 1993; Skalová and Krahulec 1992). Grubb (1990) separates the graminoids into species which form compact tufts with no or short rhizomes (*Dactylis glomerata, Festuca ovina*) and those with spreading rhizomes which may 'wander through the turf' (*Carex flacca*, certain *Festuca rubra*). The former group has the potential to form matrices of monospecific clumps in the sward and are typical of the phalanx strategy. These species are suppressed by diffuse competition and clumping is a possible mechanism by which interspecific interactions are reduced (Shmida and Ellner 1984). The clumping patterns of the graminoid species minimise the degree of interspecific contact thus affording a partial escape from competition (Silvertown *et al.* 1992). Tillers dying in the centre of clumps are likely to be swiftly replaced by vegetative growth of the same species and the dynamics of these species will occur around the gap margins. The negative correlation between clump size and per capita birth rate is almost certainly due to this situation and shows that these species are distributed along a continuum between the phalanx and guerrilla strategies. There appears to be a trade-off between the size of monospecific stands (which enhances the likelihood of self-replacement) and mobility (allowing fast colonisation of ephemeral gaps).

Trifolium repens is highly mobile and moves rapidly through the sward (Leith 1960; Thórhallsdóttir 1990a,b), this ability based on spreading stolons and adventitious rooting (Sackville Hamilton and Harper 1989). *Trifolium repens* is a characteristic guerrilla species which is reflected by its high placement on the y axis. This species grows in lines and its apparent clumping tendency is a result of the sampling of stolons since it must have at least one neighbouring stolon.

The *Trifolium* on the second plot appears by its ordination to be extremely clumped and this is a result of its high abundance. Lines of *Trifolium* grow adjacent to each other and thus form solid blocks of cell occupation. *Trifolium repens* has been found to be positively associated with *Lolium perenne* (Turkington and Harper 1979) and that is possibly also the case here. These may coexist together because of different phenology and growth form (Leith 1960) and because the nitrogen fixing habit of *Trifolium* has a beneficial effect on the grass.

Both *Potentilla erecta* and *Ranunculus bulbosus* have a high turnover of cell occupancy as a result of their highly seasonal recruitment patterns but *Ranunculus* corms are very long-lived. In a study on chalk grassland at Castle Hill Nature Reserve the mortality of *Ranunuculus* plants was roughly 10% over three years (Grubb 1990), this being a much slower rate of turnover than observed by Sarukhán and Harper (1973) for the same species on more fertile soil. *Ranunculus* usually retreats underground in mid-July and regenerates in the autumn from underground corms. The flowering shoots of *Potentilla* die back in the winter and are replaced in the late spring from basal reserves (Grime, Hodgson and Hunt 1988). These two species differ greatly in their spatial pattern. *Ranunculus* occurs as isolated rosettes whereas *Potentilla* forms discrete clumps.

Viola lutea seems to have been badly placed in the ordination. *Viola* plants are long-lived but the rosettes moved on the plots and thus gave the impression of having a higher turnover. The death rate was also increased by the density-independent mortality caused by rabbits and occasional presence of seedlings. This species should probably be included in the *Plantago-Leontodon* cluster, as a long-lived rosette-forming perennial herb. However, the clonal growth patterns of this species separate it from the other members of this group.

5.5.4. Implications for coexistence

Coexistence in species-poor communities can be almost totally explained in terms of complementary of life-forms (Grubb 1977) since the dominant species will not be able to capture all of the resources in an ecosystem and subordinate species will utilise the gaps left by these species (Grime 1987). In reference to calcareous grasslands it is clear that there are too many species for this explanation to hold, but competition for space between species of similar life-form is likely to be more intense than those with distinct and complementary growth patterns. It may thus be enlightening to investigate mechanisms which permit coexistence between plant species with similar ecologies (e.g. Werner 1979; Shmida and Ellner 1984) in addition to those which differ in their niche requirements.

Chapter Six

THE FRACTAL GEOMETRY OF PLANT SPATIAL PATTERN

6.1. Summary

Fractal geometry was used to provide a measure of the spatial structure of plant species recorded on permanent plots. The fractal dimension of a species was taken to be indicative of the ability of species to colonise space at a fine-scale. Species recruiting largely through clonal growth tended to have greater fractal dimensions than seed-recruiting species, reflecting local growth patterns. Temporal changes in the fractal dimension demonstrated that certain species had highly dynamic spatial structure whereas the fractal dimension of other species remained relatively constant over the period of study. The use of applying fractal geometry in plant ecology is discussed.

6.2. Introduction

The occupation of biological space is essential for all organisms since it allows access to resources within the vicinity. In the context of sessile plants, space capture is particularly important since they are unable to forage more than a short distance from the site at which they are rooted (Harper 1977).

Plants may occupy new sites by two processes, vegetative expansion and seed dispersal. The spatial pattern of any particular species will be dependent on the relative allocation to sexual and asexual recruitment and the scale over which the two processes operate. In relation to clonal expansion a continuum has been envisaged between phalanx and guerrilla growth forms (Lovett Doust 1981; Schmid and Harper 1985). Phalanx growth is characterised by compact genet architecture and leads to the formation of tight monoclonal patches (Schmid 1986). In contrast, species typifying the guerrilla strategy tend to have long wandering rhizomes and a looser spatial structure. Whereas phalanx

species monopolise space in a small area, guerrilla species are better adapted to invade new sites.

6.2.1. Fractal geometry

Many natural spatial patterns are complex and difficult to measure using Euclidean geometry. As an example, imagine measuring the length of the coast of Britain with a pair of dividers. This is an almost impossible task since the length of the coastline increases indefinitely as the distance spanned by the dividers decreases. Richardson (1961, and described in Mandelbrot 1967) found that the length of coastline increased as a power relationship of the divider length (Fig. 6.1) which demonstrated the scale-dependence of the measurement. This power relationship is the scaling dimension of a set and applies well to many of the fragmented and disjointed structures occurring in nature. Mandelbrot (1977, 1982) coined the term 'fractal' for this kind of pattern.

Fractals have the property of being self-similar (or self-affine[1]), that is they can be seen to comprise the same essential form independent of the scale at which they are observed. This is exemplified by the von Koch curve or snowflake which is assembled out of different sized equilateral triangles (Fig 6.2). Magnifying this structure reveals an identical pattern. Since the process for generating the von Koch curve is potentially endless, the shape has a finite area but infinite perimeter. This property has already been observed in relation to the length of Britain's coastline. Whereas Euclidean geometry uses very simple building blocks (lines) and often requires complex construction, fractal geometry consists of more complex building blocks but simpler construction rules (Hastings and Sugihara 1993).

[1] A self-similar object can be constructed out of rescaled copies of itself and the rescaling is uniform in all dimensions (isotropic). In self-affine objects the rescaling can be anisotropic (Hastings and Sugihara 1993). Natural objects are almost always self-affine rather than self-similar.

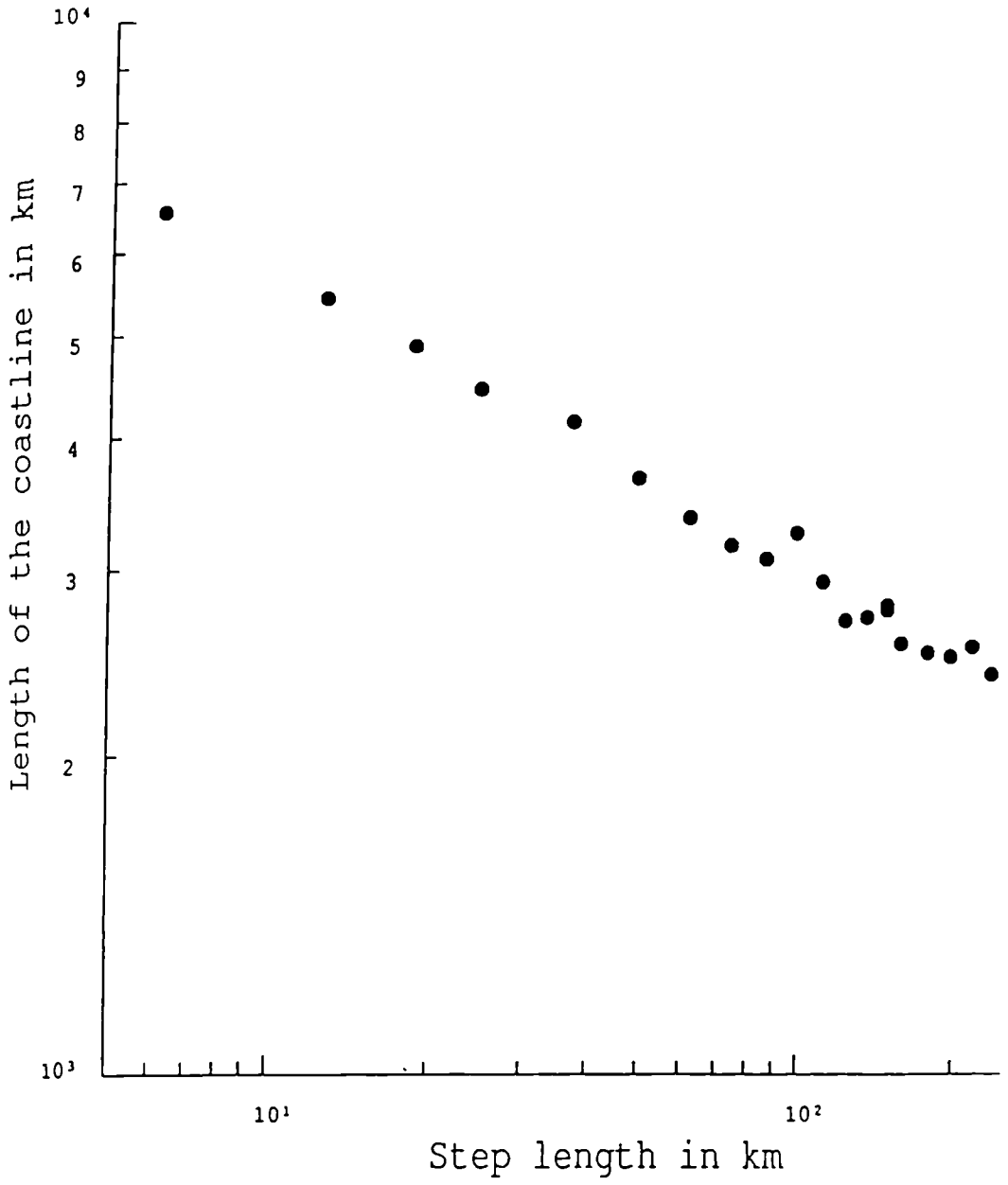


Figure 6.1. The estimated length of the coastline of mainland Britain as a power function of the step length of dividers used for the measurement. (from Morse 1988).

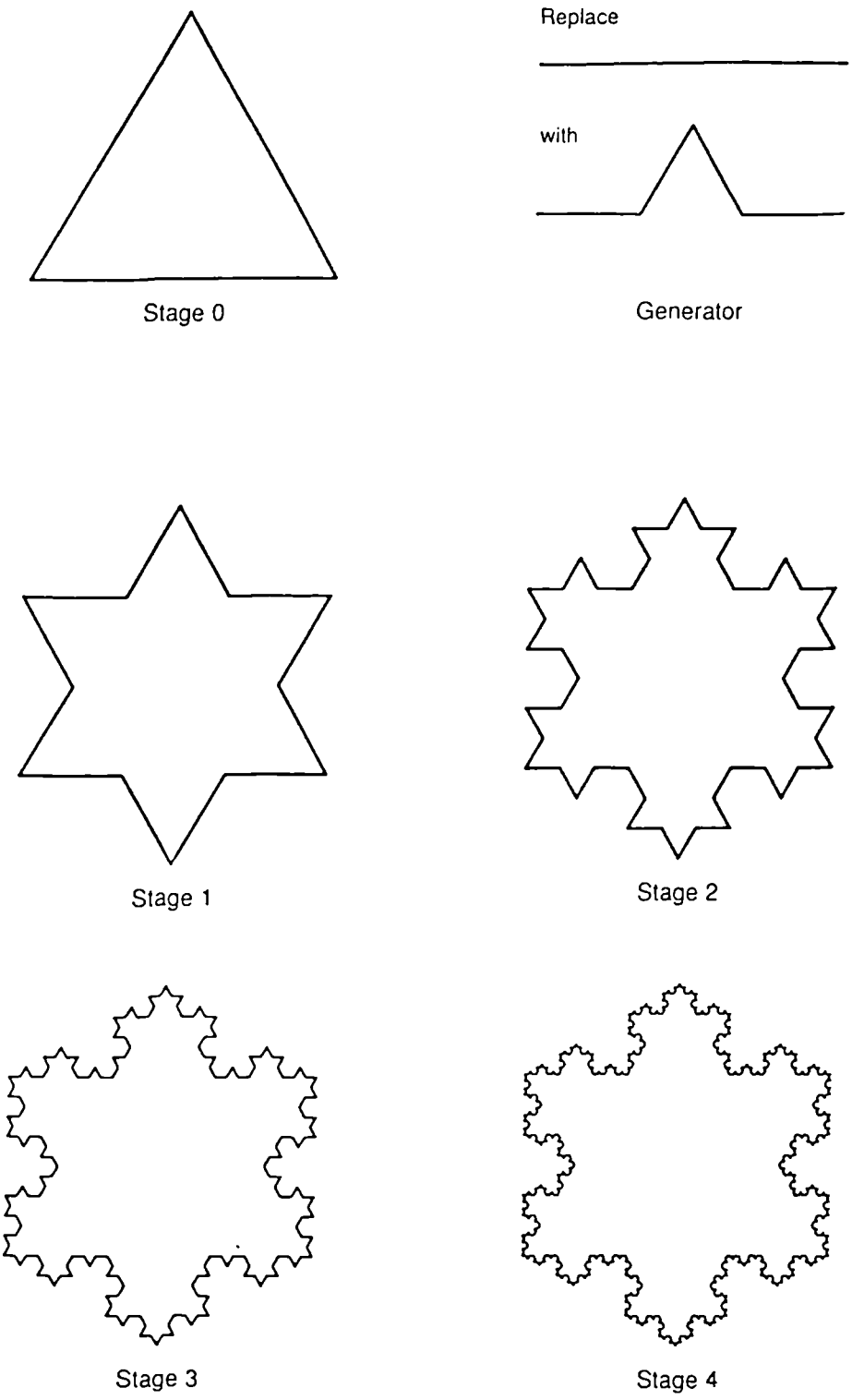


Figure 6.2. The steps in constructing a Koch curve or snowflake. Beginning with an equilateral triangle (stage 0), the middle third of each outer line segment is replaced by a similar triangle of one third of the size. This fractal has dimension log 4/log 3 = 1.26. (from Hastings and Sugihara 1993).

6.2.2. Applications of fractals in ecology

As a result of the difficulties in measuring natural patterns using Euclidean methods, fractals have become increasingly widely used in ecology (Sugihara and May 1990; Williamson and Lawton 1991; Field 1992; Hastings and Sugihara 1993). Examples include the characterisation of leaf geometry as the habitat space available to arthropods (Morse *et al.* 1985), root architecture (Fitter and Stickland 1992), soil microtopography (Armstrong 1986), landscape structure (Milne 1992) and plant spatial pattern (Palmer 1988).

The modular growth form of plants leads naturally to a self-similar form (Fig. 6.3) and Astrid Lindenmayer has constructed convincing fractal plants using simple growth rules (L-systems, Lindenmayer and Prunsinkiewicz 1990). A similar approach has been utilised for modelling the development of clonal plant genets based on branching rules (Harper and Bell 1979; Bell 1984; Bell 1986). This inherent self-similarity in the growth form of modular plants allows the characterisation of plant morphology using fractal geometry. Since a line has topological dimension 1 and a filled box has dimension 2, a solid object occurring in a two-dimensional plane will have a fractal dimension between 1 and 2 depending on its space filling capacity. Species which form tight clumps (phalanx species) might therefore be expected to have a fractal dimension close to 2, whereas those species which grow in lines (guerrilla species) e.g. *Carex arenaria* (Noble, Bell and Harper 1979) are likely to have a fractal dimension close to 1. Species which occur as isolated individuals (a possibility for species which recruit from seed) will have a fractal dimension of less than 1, termed 'dust' by Mandelbrot (1982) and this value will approach zero for widely dispersed plants.

As part of a larger objective to investigate interspecific differences in spatio-temporal dynamics of species in a limestone grassland (see introduction to chapter 5), this chapter describes an attempt to elucidate the fractal dimension of the spatial pattern of a number of herbaceous plant species. The aim of the work was to determine the usefulness of the fractal dimension as a measure of

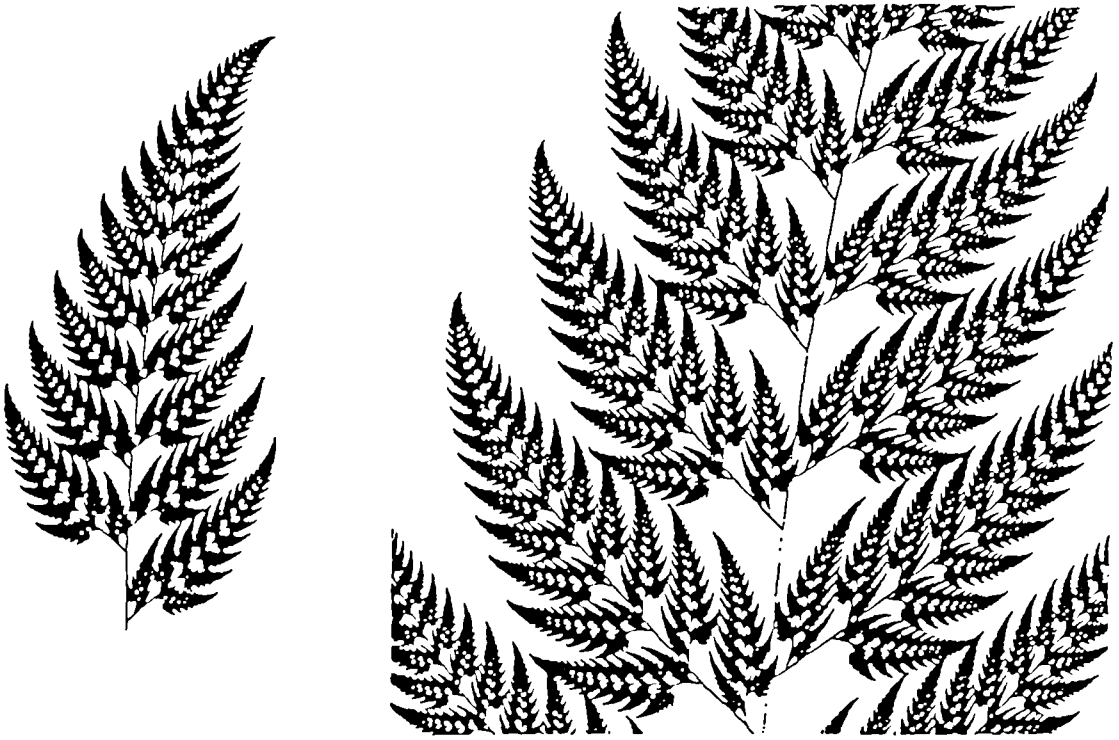


Figure 6.3. The self-similar black spleenwort fern which can be simply generated through an iterative process. (from Barnsley 1988).

plant spatial pattern and to describe the temporal variation in the fractal dimensions of a number of herbaceous plant species.

6.3. Materials and methods

6.3.1. Mapping of plant spatial pattern

The distribution of organisms are often mapped in 10 x 10 km squares or similar regular grids. Williamson and Lawton (1991) observe that many of these maps of organisms have the appearance of being self-similar and suggest that distributions can be characterised by fractal geometry. This procedure would allow the use of patterns of distribution at one scale to predict patterns at larger or smaller scales. It also provides an insight into the ability of the species to capture space.

The permanent plot data (detailed in chapter 5) is essentially a fine-scale species distribution map. The data are in the form of species occurrence on a regular grid of 40 x 28 of 1 cm square cells and consists of three such grids censused over a two year period (although the record for the third grid is only one year). The permanent plot records comprise distribution patterns for a number of species of differing abundance and life-form and thus provide an adequate set of data for characterising the fractal dimension of plant spatial pattern and how this changes in the course of time.

6.3.2. Fractal dimensions

Mandelbrot (1977) defined fractals as 'a set for which the Hausdorff-Besicovitch dimension strictly exceeds the topological dimension'. The Hausdorff dimension (D) can be calculated by determining the number of spheres of topological dimension n required to cover a set X in n dimensional Euclidean space. Where $N(r)$ is the smallest number of spheres of radius r it can be demonstrated that the limit

$$D = \lim_{r \to 0} (-\log N(r)/\log r)$$

exists. Given that X is a subset of Euclidean space with scaling dimension D, the value of D is the Hausdorff dimension of X (Hastings and Sugihara 1993). Since the Hausdorff dimension is equivalent to the scaling dimension in Euclidean space it is an important concept used in calculating the fractal dimension of a set.

6.3.3. The box dimension

Whereas the Hausdorff dimension is defined in terms of the number of spheres required to cover a set in Euclidean space, an equivalent calculation can be performed using $N(r)$ cubes of side length r. The box dimension, D, is computed as the negative slope of a plot of $\log N(r)$ against $\log r$ (Hastings and Sugihara 1993).

This can be visualised by imagining a square of side length 2 in Euclidean space. This can be covered by 1 box of side length 2 or 4 boxes of side length 1. The box dimension is thus

$$D = \frac{\log 4 - \log 1}{\log 2 - \log 1}$$

$$= \frac{0.602}{0.301}$$

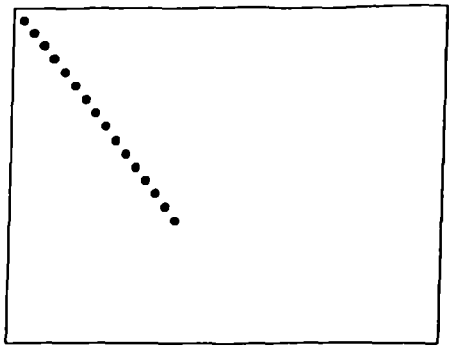
$$= 2$$

This is the value which would be expected for a solid square, exactly equal to its topological dimension in Euclidean space. This is logical since as the scale of measurement is halved the number of boxes needed to cover the square is 2^D. Repeating this procedure with a line of length 2, we can find the scaling (box) dimension is 1. The line can be covered with 2 box of side length 2 and two boxes of side length 1. The number of boxes required to cover the set is doubled as the scale of measurement is halved.

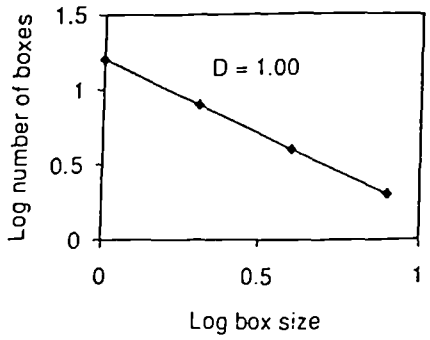
6.3.4. Calculation of the box dimension

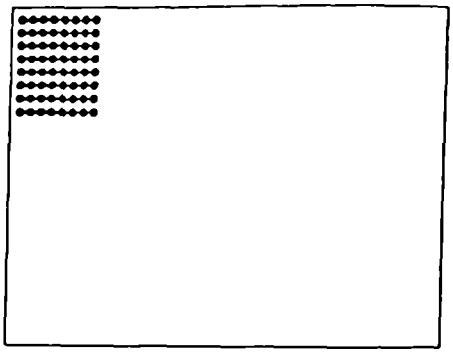
A program to calculate the fractal dimension was coded in C on a Sun Sparc 2 workstation (see appendix). This involved splitting each plot into a number of square boxes of side length (r) 1, 2, 4 and 8 cells. The number of boxes in which a species occurred ($N(r)$) was calculated for each of the four box sizes. The box dimension could then be computed as the negative slope of a linear regression performed on log $N(r)$ against log r. In order that the boxes would fit exactly over the grid data the data set was truncated into 24 x 40 cells. This was achieved by removing the bottom 4 rows of cells from the analysis. In the case of *Potentilla erecta*, in which the majority of the abundance was located in the bottom of the grid, the top 4 rows of cells were removed before the analysis.

Tests of the algorithm demonstrated that the box dimension of a filled square and a line were 2 and 1 respectively (Fig. 6.4). The fractal dimension of *Carex flacca* on the first census of the second permanent plot was exactly 0, indicating

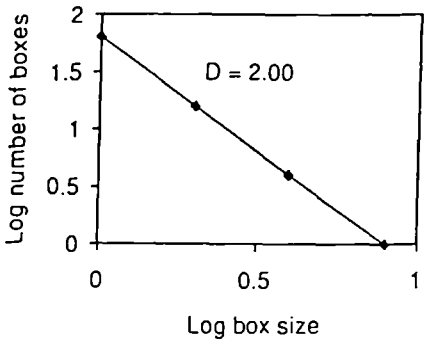


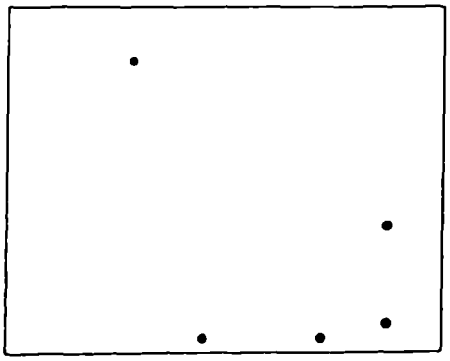
Diagonal line (16 cells)



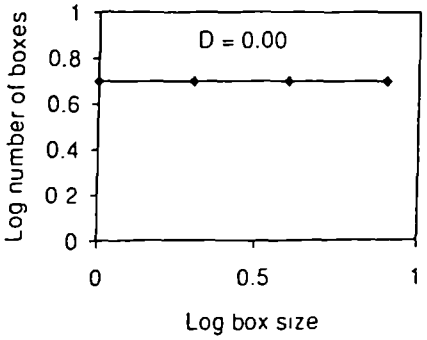


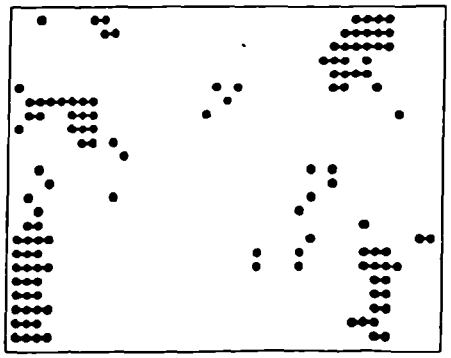
Box (8 x 8 cells)





Carex flacca, Grid 2/1





Lolium perenne, Grid 2/1.

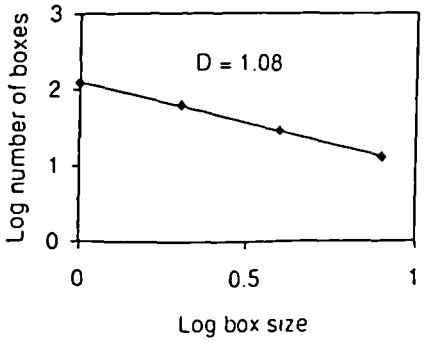


Figure 6.4. The box dimension (D) of two hypothetical and two actual plant distributions. The diagonal line has dimension 1 and the filled box, dimension2, exactly equal to their topological dimensions. *Carex flacca* occurs as a series of isolated points and thus has dimension 0.

that this species occurs as a number of isolated plants, and the box dimension of the distribution of *Lolium perenne* on the same grid was estimated as 1.08. The closeness of the dimension of *Lolium perenne* to 1 does not necessarily indicate that this species grows in straight lines as is clearly not the case (Fig. 6.4). A patchy distribution can also have dimension 1 (Gautestad and Mysterud 1994). The combination of clusters and isolated points leads to a fractal dimension between 0 and 2 depending on the relative occurrence of both.

Although the box dimension of a square and line was correctly estimated as their topological dimension this was only because both were in units of 8. Estimates of the box dimension for lines and squares of different size would not give so precise an estimate since it measures space-filling ability of the largest box. Similarly, a square of side length 8 which fell across the boundary of two or more boxes would return an incorrect fractal dimension. However, in this study such regular patterns are unlikely to occur, and tests involving slight movement of the squares over the grid returned similar fractal dimensions for the same distribution.

6.4. Results

6.4.1. Observed patterns

The fractal dimension of the spatial pattern of species on the three permanent plots ranged from 0 (*Carex flacca* (plot 2), *Potentilla erecta* (plot 3), *Ranunculus bulbosus* (plot 3)) to 1.5 (*Briza media* (plot 3), *Trifolium repens* (plot 2)) (Figs 6.5, 6.6 and 6.7). The fractal dimension of *Trifolium repens* was highly seasonal on all three plots, the same being true of *Festuca rubra* on plots 1 and 2 and *Potentilla erecta* on the third grid. *Ranunculus bulbosus* exhibits seasonal fluctuations in its fractal dimension on plot 1 but is stable at a value close to 0 on plot 3. The fractal dimension of *Cynosurus cristatus* (plot 1) was observed to increase throughout the time series. *Viola lutea* has a fractal dimension between 0.5 and 1 until the eleventh census when it drops to 0.

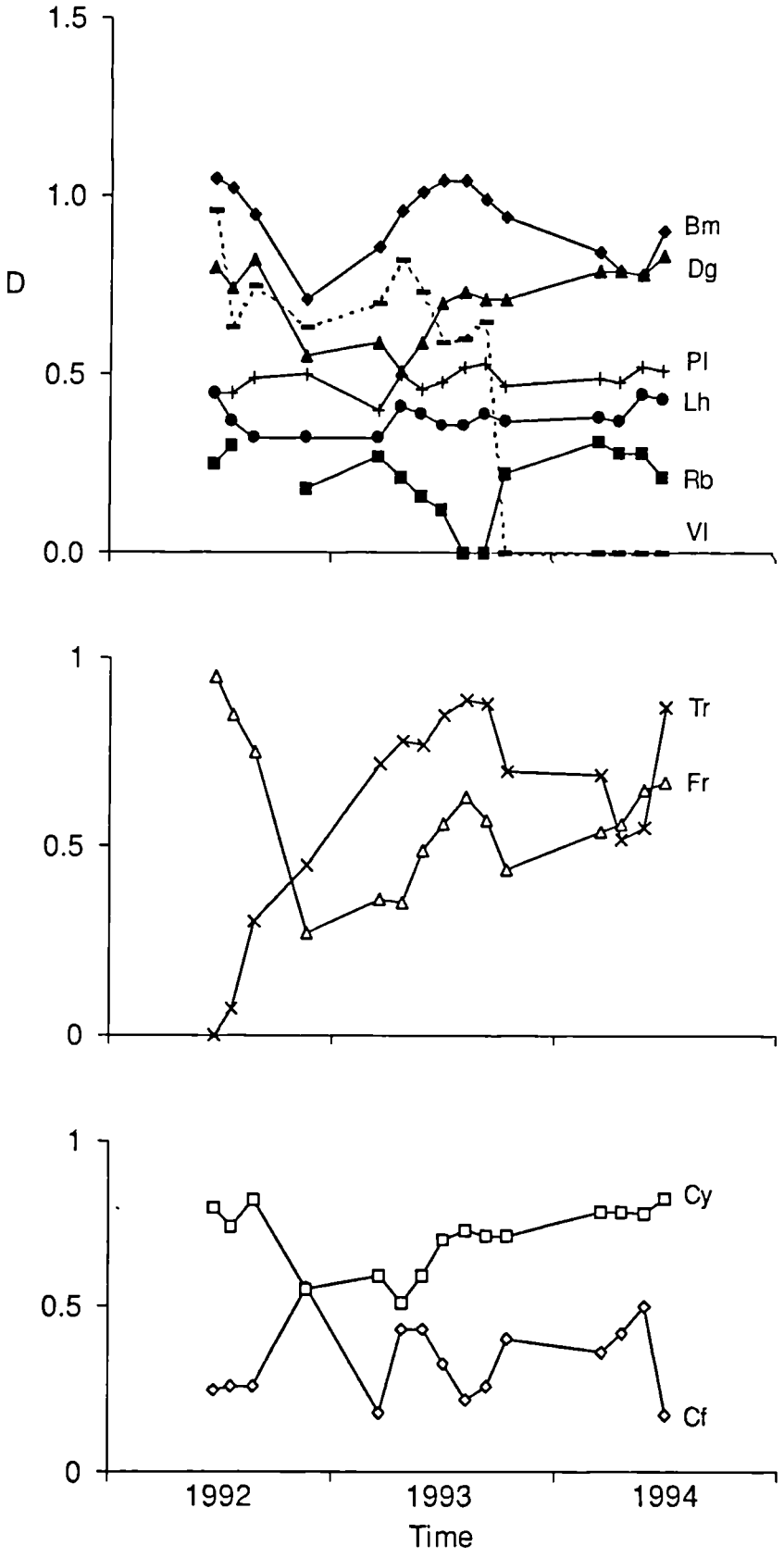


Figure 6.5. The fractal dimension (D) of the spatial layout of nine plant species occurring on the first permanent plot. Species abbreviations follow Table 1.1.

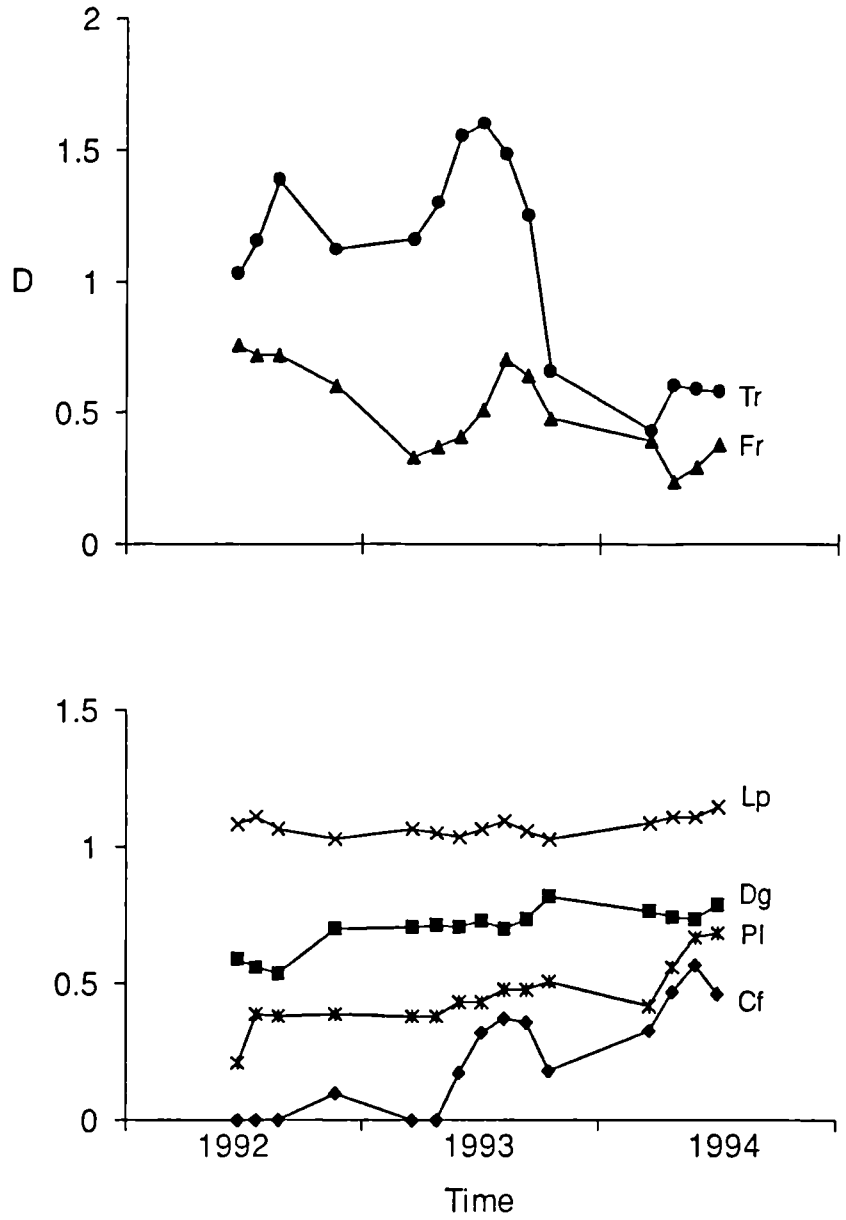


Figure 6.6. The fractal dimension (D) of the spatial layout of six plant species occurring on the second permanent plot. Species abbreviations follow Table 1.1.

Species with fractal dimensions below 0.5 can reasonably be expected to be those which do not have a tendency to clump. Species falling into this category in include *Carex flacca, Leontodon hispidus, Lotus corniculatus, Ranunculus bulbosus* and *Potentilla erecta*. Those species with a fractal dimension greater than 1 are likely to have a distribution consisting of clumps and a few isolated plants.

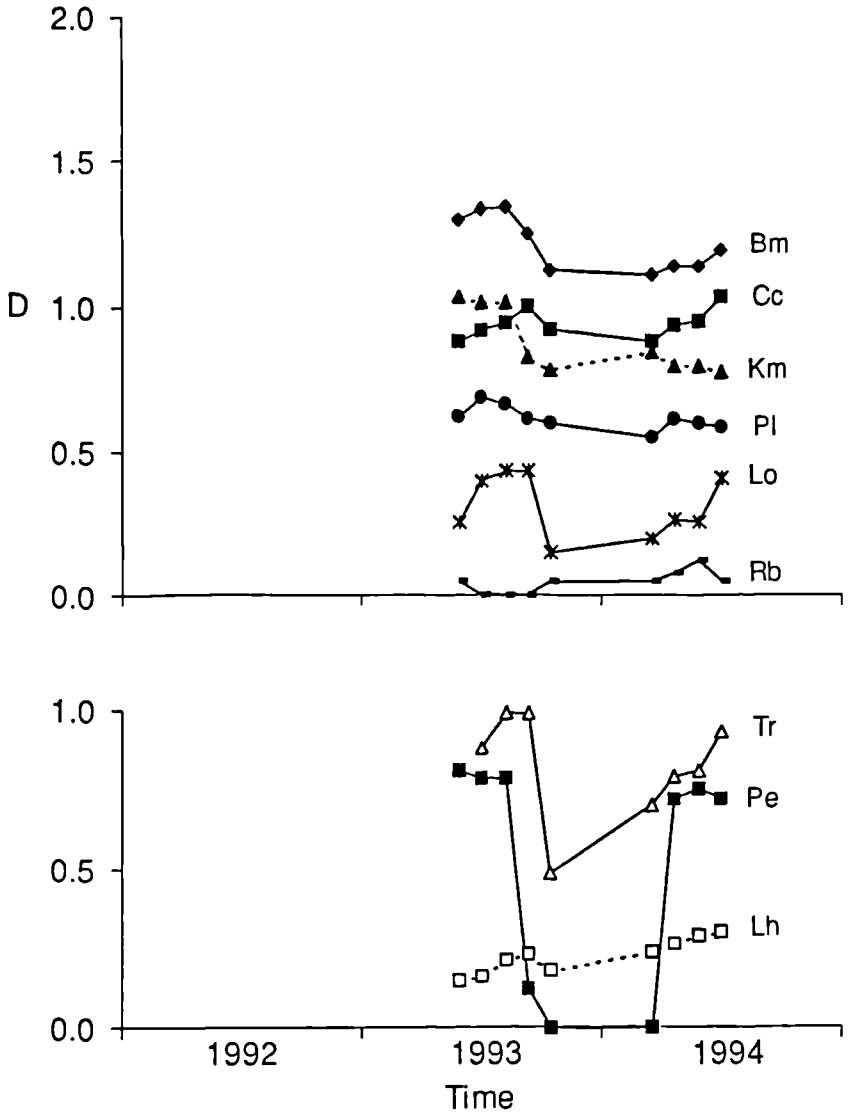


Figure 6.7. The fractal dimension (D) of the spatial layout of nine plant species occurring on the third permanent plot. Species abbreviations follow Table 1.1.

These clumping species include *Lolium perenne* and *Briza media*. The majority of graminoid species, with the exception of *Carex flacca*, have a fractal dimension approaching 1 whereas the forb species tend to have a dimension less than 0.6, although both *Viola lutea* and *Trifolium repens* have fractal dimensions rising above this value. *Dactylis glomerata* has a generally low fractal dimension compared to the other graminoid species.

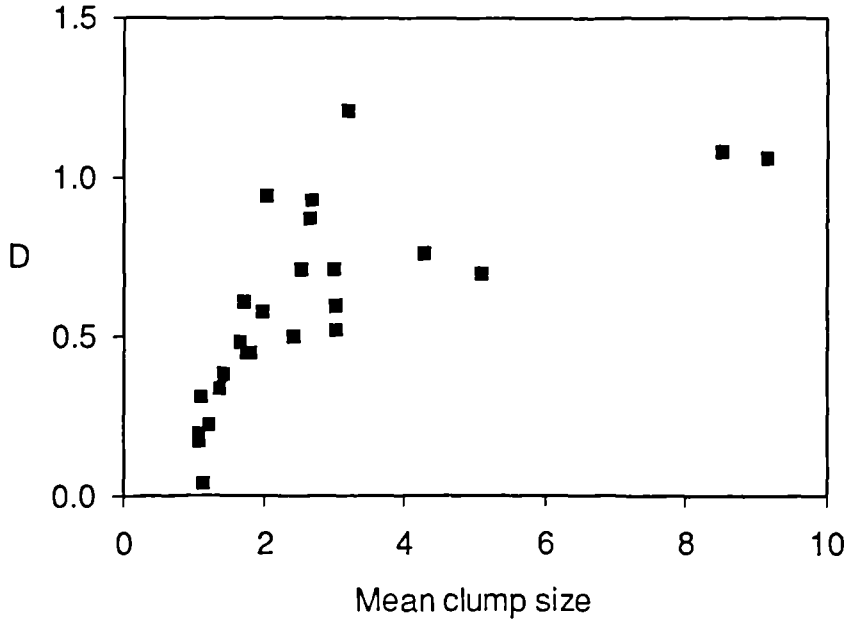


Figure 6.8. A scatterplot of the fractal dimension (D) and mean clump size (averaged over the time series) of plant species occurring on the three permanent plots. Pearson's correlation coefficient, $r = 0.705$, $P < 0.001$.

6.4.2. The correlation of fractal dimension with abundance

The ranking of species by fractal dimension was highly related to the ranking of species by cell occupancy (Spearman's rank correlation coefficient, $r_s = 0.891$, $P < 0.001$) and mean clump size (Figure 6.8). The mean abundance and clump size of species are themselves significantly correlated ($r = 0.616$, $P < 0.001$).

The large dependence of fractal dimension on the abundance of each species complicates the interpretation of the results. However, the number of occupied cells did not completely determine the fractal dimension of a species (Fig 6.9). In an attempt to remove the relationship between D and abundance, a randomisation test was used to determine if the fractal dimension of species was significantly different from that which would be expected from a random distribution of occupied cells with the same abundance. A dimension significantly greater than would be expected by random suggests an aggregated distribution of occupied cells whereas a dimension significantly less

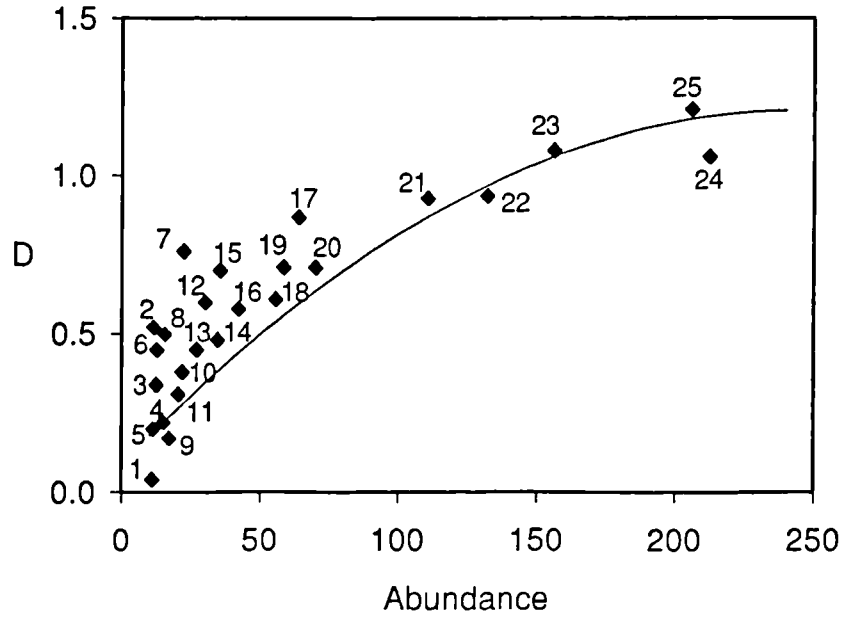


Figure 6.9. The mean fractal dimension (averaged over the time series) of the 25 plant species on the three permanent plots as a function of their abundance. (Pearson's correlation coefficent, r = 0.858, P < 0.001). The regression line illustrates the fractal dimension which would be expected at each abundance given a random distribution of occupied cells.

Species (plots given in brackets) : 1 - *Ranunculus bulbosus* (1), 2 - *Potentilla erecta* (3), 3 - *Carex flacca* (3), 4 - *Ranunculus bulbosus* (1), 5 - *Carex flacca* (2), 6 - *Viola lutea* (1), 7 - *Trifolium repens* (3), 8 - *Leontodon hispidus* (3), 9 - *Festuca rubra* (2), 10 - *Leontodon hispidus* (1), 11 - *Lotus corniculatus* (3), 12 - *Trifolium repens* (1), 13 - *Plantago lanceolata* (2), 14 - *Plantago lanceolata* (1), 15 - *Dactylis glomerata* (2), 16 - *Festuca rubra* (1), 17 - *Koeleria macrantha* (3), 18 - *Plantago lanceolata* (3), 19 - *Dactylis glomerata* (1), 20 - *Cynosurus cristatus* (1), 21 - *Carex caryophyllea* (3), 22 - *Briza media* (1), 23 - *Lolium perenne* (2), 24 - *Trifolium repens* (2), 25 - *Briza media* (3).

suggests an overdispersed distribution of cells. 1000 randomisations were used for each two-tailed test.

The randomisation tests demonstrated that no species had a fractal dimension significantly less than would be expected by random (Table 6.1) and a number of species consistently exhibited significantly greater dimension than would be expected. The results for *Viola lutea*, indicate that the observed fractal

Table 6.1. The results from randomisations carried out to test whether the fractal dimension of the species occurring on the three permanent plots were significantly different from that expected from a random distribution of cell occupancy with the same number of occupied cells. The significance levels all refer to observations significantly greater than would be expected by random. * signifies $P < 0.01$, ** signifies $P < 0.001$. Species abbreviations followTable 1.1.

	CENSUS														
Year:	---------1992------				----------1993----------							-------1994-------			
Month:	6	7	8	11	3	5	6	7	8	9	10	3	5	6	7
Grid One															
Bm				*	**	**	**	**	**	**	**	**			
Cf				**		*	*	*			**	*	*	*	*
Cy	*				**		**	**	**	**	**	**	**	**	**
Dg											*			**	**
Fr			*		*				**	**	**	**	**	**	**
Lh						*									
Pl			*	*											
Rb															
Tr				**	**	**	**	**	**	**	**	**	**	**	**
Vl	**	**	**	**	**	**	**	**	**	**					
Grid Two															
Cf									**	*			*	**	
Dg	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
Fr	**	**	**			**	**	**	**	**	*	*			*
Lp	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
Pl							*		*	**	**		*	**	**
Tr						**		**			**		*	*	
Grid Three															
Bm									*	*	*	*			
Cc								**	**	*					
Km								**	**	**	**	**	**	**	**
Lh															
Lo											*				
Pl															
Pe								**	**	**			**	**	**
Rb															
Tr									**	**	**	**	**	**	**

dimension was significantly greater than a random distribution ($P < 0.001$) at census 1-10 and then no longer significant, and *Festuca rubra* on the first plot had a consistent significantly greater dimension than random after census 8 but

little evidence of this before that time. *Trifolium repens* (plot 1) and *Cynosurus cristatus* were also species which had fractal dimensions greater than that expected under randomness at later censuses. *Potentilla erecta* exhibits a pattern consistent with its seasonal formation of clumps from below-ground parts (see chapter 5), the fractal dimension for this species being much greater than would be expected from random during the middle of the year (May to October). The graminoid species had consistently greater fractal dimensions than would be expected by a random distribution of cells on the grids, with the exception of both sedge species. The herbaceous species did not exhibit this consistency and on occasion did not differ from that expected from a random distribution (*Plantago lanceolata* on plot 3). Exceptions to this generalisation were *Trifolium repens* which had significantly greater dimensions from random on plots 1 and 3, but less so on the second plot, and *Potentilla erecta*, which showed evidence of an aggregated spatial distribution.

6.5. Discussion

6.5.1. Problems with the fractal dimension

Virkkala (1993) measured the fractal dimension of the spatial distribution of passerine birds in Finland and this was highly correlated with the number of grid cells occupied by the species (M.H. Williamson, personal communication). However, he erroneously measured the fractal dimension of the boundary of the range rather than using the actual points of distribution (Gautestad and Mysterud 1994). The fractal dimension of the boundary can only take values $1 < D < 2$, which may be inappropriate if the number of grid cells occupied is small and widely dispersed.

In this study, there is also a very close correlation between cell occupancy and the box dimension. This is to be expected since species which are better able to fill space at a fine-scale are likely to be more abundant in the sward whereas species which occur as isolated plants are less likely to achieve dominance. Fine- and coarse-scale abundance are positively correlated (Virkkala 1993) but

this is not a tautological relationship. It is possible that species may have a high tendency for clumping but have a low frequency of clump occurrence e.g. *Potentilla erecta* and *Viola lutea* which both have high fractal dimensions in spite of their low abundance.

Since the fractal dimension is measuring the ability to fill space at fine-scales we would expect a correlation between mean clump size and fractal dimension. However, the size of the clump does not alone determine the fractal dimension. Species which grow in lines would have smaller dimension than species with the same number of occupied cells in a clump but form solid blocks; this difference reflects the ability to colonise local space.

6.5.2. The relationship between fractal dimension and growth form

Species with a tendency to grow clonally tend to have both higher fractal dimension and significantly greater dimensions than would be expected from a random distribution of cell occupancy, than those which recruit from seed. This group of phalanx species encompasses the majority of the graminoids aside from *Carex flacca* and their close modular growth form enable them to efficiently capture space. *C. flacca* has longer rhizomes (approximately 3 cm) which gives rise to a more dispersed distribution of ramets (Law and Mahdi 1987; van de Hoeven, de Kroon and During 1990). *Trifolium repens* is a typical guerrilla species and the fractal dimension of this species exhibits a highly seasonal pattern. As a result of the linear growth patterns of *Trifolium* the fractal dimension is greater than would be expected at low density but less at high density (Table 6.1). This species effectively captures space through the rapid production of stolons and at high density can form large areas of conspecific occupation as occurred on plot 2 during 1992/93. The rosette-forming herbs, *Plantago lanceolata* and *Leontodon hispidus* are of intermediate abundance on the plots but have low fractal dimension, consistent with the knowledge of their recruitment from seed and existence as isolated plants.

Potentilla erecta has a high fractal dimension in spite of its low abundance on plot 3 during the summer months. This is because of the phenology of this species in which the shoots die back in late autumn and are replaced the following spring by the mobilisation of below-ground resources (Grime, Hodgson and Hunt 1988). Although, *Ranunculus bulbosus* also has a highly seasonal phenology (Mahdi, Law and Willis 1989; chapter 5), this is not reflected in the fractal dimension in plot 3. This species regenerates from below-ground corms but tends to occur as isolated individuals. The fractal dimension is correspondingly low, approaching 0. The population of *Viola lutea* on the first plot was subjected to intense density-independent mortality caused by rabbit scratching in late 1993. The fractal dimension of this species displays the change from the clumped distribution of the species in censuses 1 to 10 followed by the shift to isolated rosettes for the remainder of the time series.

The fractal dimension of plant spatial pattern on the permanent plots is not solely a product of species growth forms. Spatial heterogeneity in the environment, interspecific interactions (see chapter 7) and herbivory will also shape the distribution patterns. However, the observed trends do seem to be consistent with the life-history characteristics of species presented in the last chapter. The data used here demonstrated interesting trends in the fractal dimension of species but was limited by its discretised form and small area. The use of both a larger area of mapping and continuous rather than discrete records will permit a more detailed evaluation of the usefulness of fractal geometry in the characterisation of plant spatial pattern and its variation through time.

Chapter Seven

CELLULAR AUTOMATA RULES FOR PLANT INTERACTIONS

7.1. Summary

Cellular automata are a class of discrete models in which the change in state of a particular cell is dependent on its current state, and the state of cells in the immediate neighbourhood. This conceptual framework applies well to the process of competition between plants in which the future growth and survival of an individual may be influenced by neighbouring plants. Data of spatial pattern recorded from the permanent plots were discrete in time and space and thus analogous to the output from a cellular automata. This chapter derives cellular automata type rules for the changes observed on the permanent plots. Randomisation tests were used in order to test the null hypothesis that the patterns of cell capture and loss observed for species on the permanent plots (see chapter 5), were independent of the identity of species in the immediate neighbourhood. In general the null hypothesis was supported by the analysis, but species with a large capacity for clonal growth showed a tendency to grow into cells in neighbourhoods with elevated numbers of conspecifics. Based on these results, the community appears to be only weakly interactive and the spatio-temporal patterns observed on the permanent plot can be interpreted primarily as the product of the modular growth patterns of individual species.

7.2. Introduction

Interactions between plants occur within small neighbourhoods (Mack and Harper 1977; Weiner 1982; Pacala and Silander 1985), restricted to the area over which roots and shoots can interfere which each other. In species-rich grassland communities the compact growth form of plants (Grime 1990) may limit this distance to a few centimetres. As a result of the highly localised nature of plant processes, the spatial layout of each species assumes a large

importance in influencing the outcome of interactions, since it determines how much contact species have with each other (Turkington and Harper 1979; Hutchings 1986; Mahdi and Law 1987). Without a knowledge of the spatial distribution of plants it is often impossible to predict the future dynamics of the system (Silvertown *et al.* 1992). However, the spatial structure of the community is constantly changing, causing further changes in the population dynamics of individual species, so a snapshot picture of spatial pattern may be of little help in this context. The community is a dynamic entity and changes in the spatial structure and species composition is a self-organising process arising from local interactions between neighbouring plants.

This intercoupling of spatial dynamics in the field has recently been simulated using cellular automaton models (CAM). These models consist of cells arranged on a regular lattice, the state of each cell being a discrete value (Tamayo and Hartman 1988). Time advances in discrete steps. Subsequent states of each cell are calculated as a function of the current cell state and the state of other cells in the neighbourhood. All of the cells are updated synchronously and this generates a global map and dynamical evolution of the system (Wolfram 1984). Cellular automata were developed by John von Neumann and Stanlis Ulam (von Neumann 1966; Ulam 1970) in order to investigate theoretical ideas of universal computation and self-reproduction in computational systems, and have subsequently been popularised by John Conway's 'Game of Life' simulation (Gardner 1970, 1971). Further ground-breaking work on characterising the properties of cellular automata was taken up by Stephen Wolfram (Wolfram 1984, 1986) and Chris Langton (Langton 1984, 1986), and they are now widely used in research on adaptive complex systems and artificial life (Langton 1989).

In a plant ecological context the lattice can be thought of as a two-dimensional surface and each cell may be assigned a state corresponding to occupation by a particular species. In this artificial community, "plants" may be born and die based on biologically realistic rules. Birth and death processes of plants in the

field may be strongly dependent on the number and identity of species in the neighbourhood around a plant (Mack and Harper 1977; Weiner 1982; Pacala and Silander 1985) and similarly, the rules base of a CAM may include interactions with species in neighbouring cells. Cellular automata can thus be seen to combine both the spatial and temporal components of plant communities, albeit in a simplified discretized manner. These models generate global population and community dynamics based on local interactions between individuals.

The inherent spatial component of cellular automata and their strength of integrating the hierarchy of ecological processes of individuals, populations and communities (Huston *et al.* 1988) has led to an increase in the use of this kind of modelling framework in ecology since the early 1980s (Hogeweg 1988; Czárán and Bartha 1992, Judson 1994). Examples of research problems in plant ecology which have been investigated in this spatially explicit framework are the effect of forest fires on tree distribution patterns (McGlade 1993, Green 1989), the coexistence of species in patchy and disturbed environments (Hobbs and Hobbs 1987; Czárán 1988; Czárán and Bartha 1989; Inghe 1989; Colosanti and Grime 1993), and the influence of the spatial distribution of species on their coexistence (Weiner and Conte 1981; Crawley and May 1987; Herben 1992; Silvertown *et al.* 1992).

The models which have usually been developed to simulate community dynamics so far have been based on an abstract rule base derived from a knowledge of plant processes rather than real data. The exception to this is Silvertown *et al.* (1992) which uses probabilities of invasion from grasses in a simulated mosaic sward based on observations from Thórhallsdóttir (1990b). These invasion probabilities were essentially non-spatial but were placed in a spatial context in the model constructed by Silvertown *et al.* (1992).

The permanent plot data from Priestcliffe Lees (chapter 5) is a record of the change in spatial structure of small areas of a limestone grassland community

over a two year period. The temporal and spatial dynamics of the abundant species on these plots have been described in the two proceeding chapters by considering each species in isolation. In this chapter I investigate whether the birth and death processes of each species are neighbourhood dependent and, by doing this, attempt to derive cellular automata type rules for the dynamics of a natural plant community.

7.3. Materials and methods

7.3.1. Permanent plot data

Two permanent plots of 28 cm x 40 cm were monitored over a two year period (1992 to 1994) and a third was monitored for one year (1993 to 1994). The presence or absence of species at points 1 cm apart were recorded at intervals of five weeks on each plot over the growing season (March to November). In the majority of cases only one species occurred at each point (chapter 5, Table 5.5) and thus a species at a point could be said to have captured an area of 1 cm by 1 cm. In this way the grid can be divided into cells of 1 cm squares in a similar manner to a cellular automata lattice. For further details and limitations of the methodology used in the recording of this data see chapter 5.

The grid data from each census is analogous to the output from a cellular automata model, being a discrete representation of plant spatial distribution on a two-dimensional plane (Fig. 7.1), and represents the spatio-temporal development of the system. From this time series of spatial pattern it can be determined which cells on the lattice change state between censuses and if these changes in cell state are dependent on the number and identity of species in the surrounding neighbourhood.

7.3.2. Changes in cell state

There are two possible changes in state for a cell on the grid, it may either cease to contain a species which was previously present (being replaced by another species or a gap), or it may contain a species which was previously not present

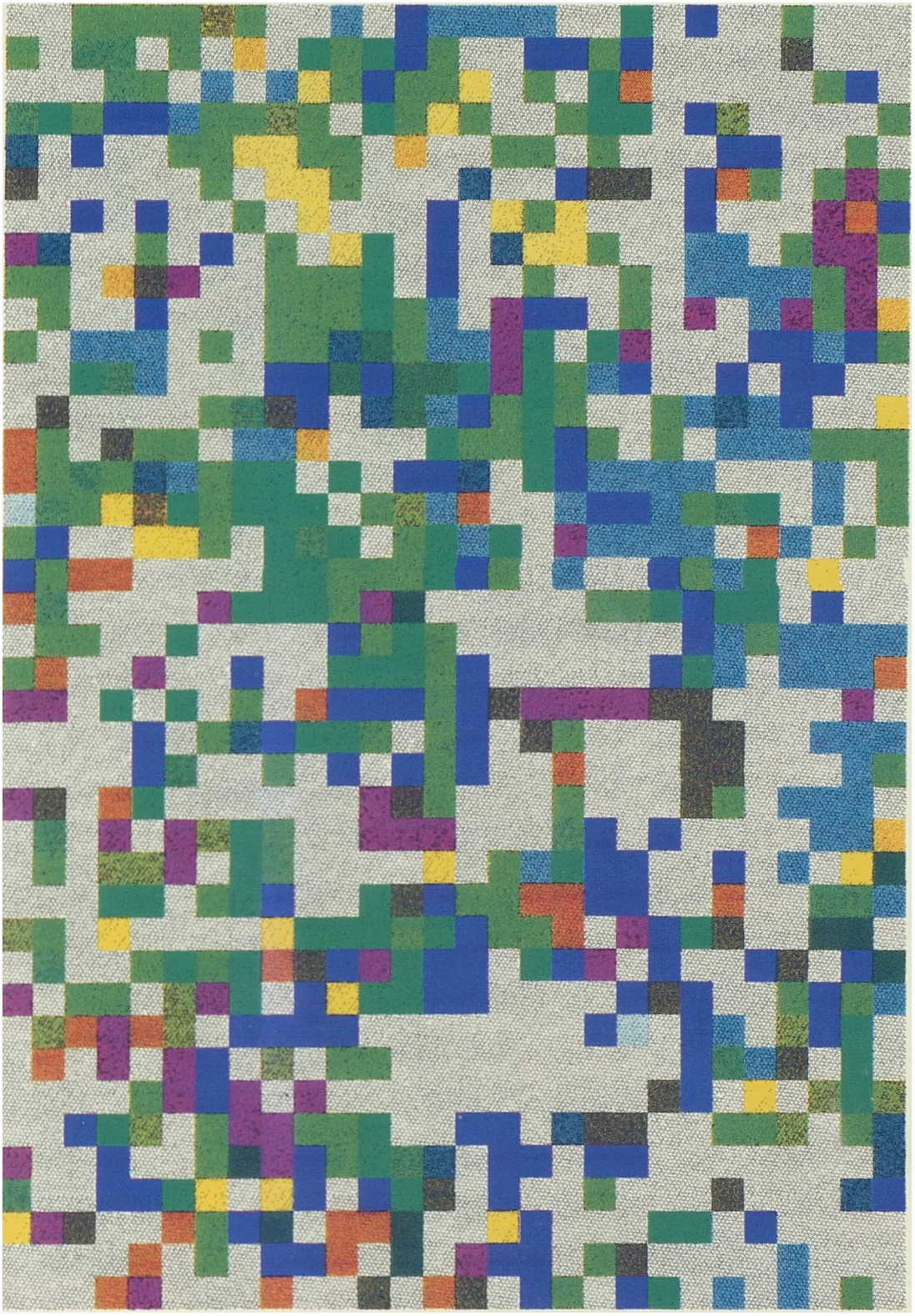


Figure 7.1. A discretized representation of the spatial layout of limestone grassland species on the first permanent plot at the first census. Obvious species are *Ranunculus bulbosus* (yellow), *Leontodon hispidus* (orange), *Plantago lanceolata* (brown), *Trifolium pratense* (pink), *Festuca rubra* (dark blue) and *Dactylis glomerata* (light blue).

in that cell. The first process equates with the loss of space and will be termed a 1→0 transition. The second event concerns the capture of space and is termed a 0→1 transition when referring to a particular species. The other possible transition types for a cell between censuses is a 0→0 transition (a gap remaining unoccupied) and a 1→1 transition (successful holding of space by the resident species).

7.3.3. Defining the neighbourhood

For the principle of cellular automata models, it is necessary to define the neighbourhood over which interactions are likely to have an effect on the performance of target plants. The neighbourhood used in most cellular automata models is the 8 cells adjacent to the target cell (Fig. 7.2a), known as the 'Moore neighbourhood' (Durrett and Levin, unpublished). The area which this incorporates depends on the size of the cells. Here it would represent roughly 1 cm distance from the target cell. Mack and Harper (1977) found that the number, identity and angular dispersion of plants within 2 cm explained 77% of the variation in biomass of a target individual in a sand dune community. Weiner (1982) explained over 80% of the variation in seed production in *Polygonum spp.* by the number and distance of conspecific neighbours in a 15 mm radius from the target plant. Although these results cannot be directly extrapolated to calcareous grasslands, the scale of plant size in these two studies is similar to that found at Priestcliffe, and data on root interference demonstrates that it is greatest at 0-3 cm from the target plant (chapter 4), suggesting that plants in a neighbourhood extending in a 2 cm radius would have the greatest influence on the behaviour of a target plant. A neighbourhood of 2 cm radius includes 20 neighbour cells (Fig. 7.2b).

7.3.4. Randomisation tests

The neighbourhood state experienced by any target cell can be characterised by the number of neighbouring cells in which each species is present. It is thus possible to make a comparison between the neighbourhoods of cells which undergo a particular transition and those which do not and determine if there

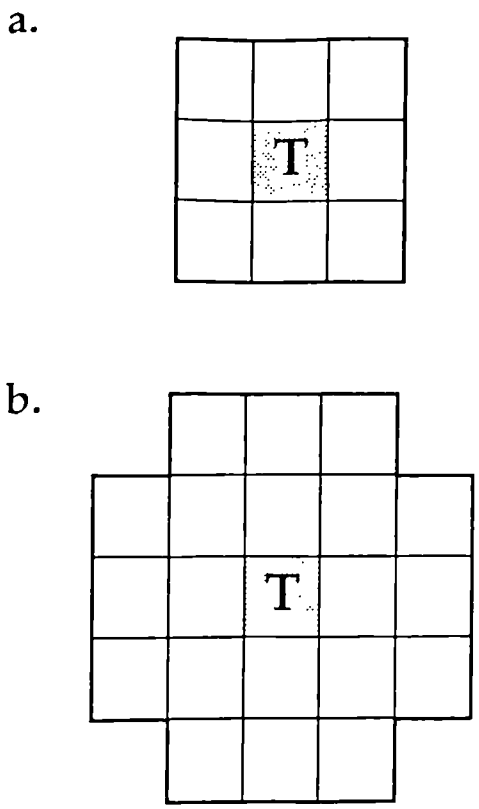


Figure 7.2. The cell regions used for analysis of the neighbourhood dependence of plant processes. The 8 cell 'Moore neighbourhood' (a), and the 20 cell neighbourhood (b) corresponding to a 2 cm radius. T represents the target cell.

are significantly greater or less numbers of a particular species present in the neighbourhood. For example, if there are significantly greater numbers of species j present in the neighbourhood when species i undergoes a 1→0 transition (cell loss) then this suggests that species j has a negative effect on the survival of species i. It has already been pointed out that the outcome of plant-plant interactions are strongly dependent on the spatial layout of species and that this spatial layout is rapidly changing, a fact which will cause problems for any attempt to use any one spatial pattern as a baseline for plant contact. It can thus be seen that by updating the spatial pattern every five weeks and using this as the neighbourhood state for cell transitions we are getting closer to an accurate description of the system dynamics.

Consider a species present in N cells at census t, k cells of which undergo a 1→0 transition by census t+1. If this transition was independent of the neighbourhood state then this would be equivalent to taking k cells at random from the set of N cells present at time t, i.e. there is no *a priori* reason why any of the cells in particular should go 1→0. The number of ways in k cells can be taken at random from N cells is given by the combinatorial formula

$$C(N, k) = N!/\{k!(N - k)!\}$$

This provides a sample space in which to carry out a statistical test of the null hypothesis that the mean number of a particular species in the neighbourhood of cells undergoing a particular transition is the same as occurs in the neighbourhood of cells taken at random. By taking a sample of k cells from the population we can generate a null model for the neighbourhood state of the target species and in iterating this procedure many times establish a distribution of the expected neighbourhood state to compare against the observed value from the transient cells. If the observed value lies far enough out in the tail of this distribution then the hypothesis can be rejected. This test was performed by calculating the distribution of the expected neighbourhood state from 1000 samples where $C(N, k) > 1000$, but where $C(N, k) < 1000$, the neighbourhood state of every point in the sample space was computed (a permutation test).

The null hypotheses used in the randomisation and permutation tests differed depending on the type of transition in question. The null hypothesis corresponding to a 1→ 0 transition was that the neighbourhood state of cells taken at random from the species i were the same as the neighbourhood state of the cells of i which are no longer occupied that species at the next census. The null hypothesis used in the case of the 0→1 transition was that the neighbourhood state of cells into which species i was born at the next census was the same as the neighbourhood state of all cells not containing species i. The statistical space for the 0→1 transition is given by $(C - N)!/\{k!\ (C - N - k)!$ where C is the total number of cells on the grid in which the test is being

applied. Because of the neighbourhood size used for the randomisation tests in this study, the bordering two cells of the grid cannot be analysed in terms of transitions since there is incomplete information about their neighbourhood state. The total number of cells used on each grid is thus:

$$(28 - 2 \times 2) \times (40 - 2 \times 2) = 24 \times 36 = 864 \text{ cells.}$$

The species used both for analysis as target and neighbour species were the same as those described in chapters 5 and 6. In addition the gaps were also used as a neighbour state since the amount of free space in a neighbourhood may affect plant behaviour. The randomisation tests were carried out for the species on each plot with 20 cell neighbourhoods for both 0→1 and 1→0 transitions. In addition, since clonal growth may occur over very small scales (Hutchings and Mogie 1990) the number of conspecifics in the 8 cell neighbourhood was tested for the 0→1 transition.

It must be noted that the results from these tests refer to the sample space of the plots and may not be representative of the community as a whole.

7.3.5. Type I errors

The number of tests carried out was large. For example, on the first grid, the 0→1 transitions of 10 target species were investigated will 10 kinds of heterospecific neighbour over 14 time intervals giving 1400 tests. In a substantial number of cases the null model can be incorrectly rejected (Type I error). The expected number of such errors, E, can be calculated as:

$$E = s \times N$$

where s is the level of significance and N is the number of tests performed. So for 20 tests carried out at the 0.05 significance level (5%), we would expect 1 type I error.

In each table of analysis (Tables 7.1 to 7.7) the number of type I errors expected for each significance level (5%, 1% and 0.1%) was calculated independently for interspecific and intraspecific interactions. If the number of significant results

was less than the expected number of type I errors then they were considered to be spurious and removed from the table.

7.4. Results

7.4.1. Positive and negative interactions

For a 0→1 transition, a greater than expected number of cells of a particular species in the neighbourhood suggests a positive interaction, the target species being more likely to arise given the presence of the neighbour species. Conversely, a lesser number of cells than expected for a particular neighbour suggests a possible negative interaction, the target species not growing into areas where the neighbour species has a high density. In the case of 1→0 transitions a greater than expected number of cells of the neighbour species suggests a competitive interaction, the neighbour species increasing the chances of mortality in the target species. A lesser number of individuals suggests a positive interaction. A positive interaction does not mean that having greater numbers of a particular species being present in the neighbourhood increases the performance of the target plant. It merely points to the fact that the negative effect of such a species is less than the combined effect of species in the average neighbourhood.

7.4.2. 0→1 transitions in conspecific neighbourhoods

A large number of species on all three grids have greater numbers of conspecific neighbours than would be expected in the 8 cell neighbourhood around cells which undergo a 0→1 transition (Table 7.1). In particular, the graminoid species (with the exception of both *Carex caryophyllea and C. flacca*) have elevated numbers of conspecifics in the neighbourhood as does *Trifolium repens*. *Lolium perenne* cells always undergo 0→1 in the presence of greater numbers of conspecifics. Species which generally do not have greater than expected numbers of conspecifics are *Carex caryophyllea, Carex flacca, Leontodon hispidus, Plantago lanceolata, Potentilla erecta* and *Ranunculus bulbosus*.

Table 7.1. The results of randomisation tests to determine if 0→1 transitions (births) are more likely to occur where there are greater or less than expected numbers of conspecific neighbours in an 8 cell neighbourhood. Census refers to the time at the start of a transition, so 1 represents the transition from census 1 to 2.
Species abbreviations follow table 1.1.
* greater than expected conspecifics ($P < 0.01$)
** greater than expected conspecifics ($P < 0.001$)

SPECIES	CENSUS													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
GRID 1														
Bm	*			**	**	**	**	**	**	**	**			**
Cf														
Cy														
Dg	**					**	**	*		**	**	**	**	**
Fr	*	*		**			**		**	*	**	**	**	**
Lh										**	*		*	**
Pl	*				**				**	**				**
Rb														
Tr				**		*	*	**	*	**	**	**		**
Vl	**	**	**				*							
GRID 2														
Cf												**	*	**
Dg			**	**	**		**		**	**	**	**	**	**
Fr	**		*		**									**
Lp	**	**	**	**	**	*	**	**	**	**	**	**	**	**
Pl					**	*				**			**	**
Tr	**	**	**	**	**	**	**	**	**	*		**	**	
GRID 3														
Bm							**	*			**			*
Cc														**
Km							**	**		*	**			**
Lh													*	
Lo														
Pl									*			**		**
Pe														
Rb														
Tr								**	**	*	*		*	**

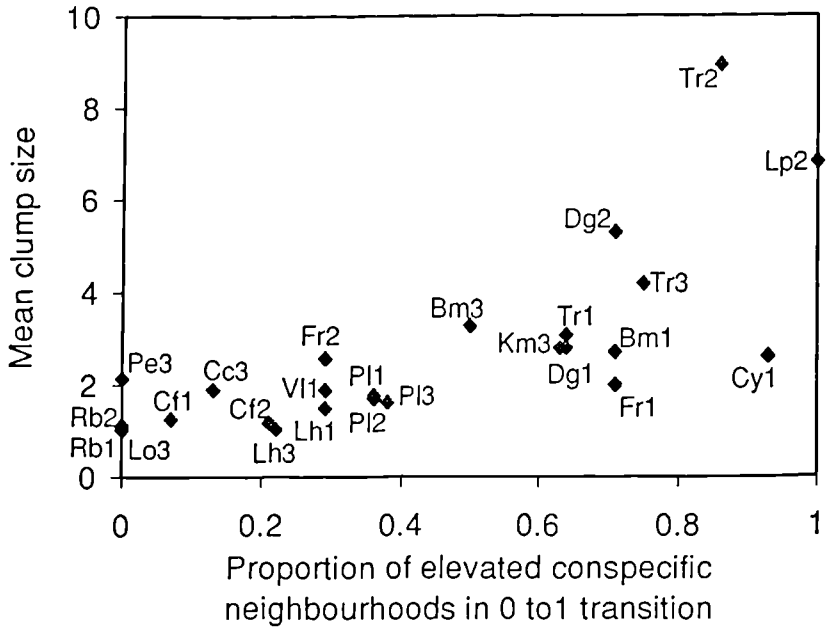


Figure 7.3. The relationship between the mean clump size of some of the plant species occurring on permanent plots and the proportion of neighbourhoods in which the number of conspecifics were elevated above that of the null model given an 8-cell neighbourhood. Spearman's rank correlation coefficient, r_s = 0.811 ($P < 0.001$). Species abbreviations follow Table 1.1.

There is a significant positive correlation between the proportion of significantly elevated conspecific 8 cell neighbourhoods in the 0→1 transition and the mean clump size of species (Fig. 7.3).

Similar patterns are evident for conspecific neighbours in 20 cell neighbourhoods (Tables 7.2-7.4), although the significance levels of many species are reduced. However several species have more significantly elevated conspecific neighbourhoods than they did at a smaller scale. These species include *Plantago lanceolata* and *Viola lutea*.

In no target species did the 0→1 transition occur more when conspecific neighbours are rare (Tables 7.1-7.4).

Table 7.2. The results of randomisation tests carried out on the first permanent plot to determine if 0→1 transitions (birth) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 0→1 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded. Census numbers given in the leading diagonal represent transitions significant at $P < 0.01$.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES										
	Bm	Cf	Cy	Dg	Fr	Lh	Pl	Rb	Tr	Vl	Gap
Bm	4-11										
Cf											
Cy			1,4-12, 14								10***
Dg				1,5-7, 11-14							
Fr		12***			4-11, 13-14						
Lh						10,14					
Pl							1,3,5, 8-10				
Rb											
Tr		14***	7,10***						7-12,14		8,9***
Vl										1-5, 7	

Table 7.3. The results of randomisation tests carried out on the second permanent plot to determine if 0→1 transitions (birth) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 0→1 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded. Census numbers given in the leading diagonal represent transitions significant at $P < 0.01$.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES						
	Cf	Dg	Fr	Lp	Pl	Tr	Gap
Cf	12,14						
Dg		3-5,7,10-14					4,5***
Fr			1,5,14				
Lp		10**		1-14		2**	3-5,7,10, 12,14*** 2,,11,13**
Pl					1,5-6,10-14		
Tr		5, 6** 8***		1,7,9*** 2**		1-9,11-13	3, 7 **

Table 7.4. The results of randomisation tests carried out on the third permanent plot to determine if 0→1 transitions (birth) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 0→1 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded. Census numbers given in the leading diagonal represent transitions significant at $P < 0.01$.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES									
	Bm	Cc	Km	Lh	Lo	Pl	Pe	Rb	Tr	Gap
Bm	7,14									
Cc		14								
Km			7,8,10,11							10***
Lh				14						
Lo					12					
Pl						9,12,14				
Pe							13			
Rb								11		
Tr									9,11,13, 14	

7.4.3. 0→1 transitions in heterospecific neighbourhoods

There is little evidence of interactions between species on the first plot (Table 7.2), although *Trifolium repens* tend to undergo 0→1 transitions in regions of the grid with a greater than expected numbers of *Cynosurus cristatus*. On the second plot, *Trifolium repens* is negatively affected by both *Dactylis glomerata* and *Lolium perenne* (Table 7.3). The third plot is almost entirely devoid of interactions.

Some of the species on all three plots exhibit a tendency to undergo the 0→1 transition in areas which contain less gaps in the neighbourhood than on average, *Lolium perenne* being typically notable in this context.

7.4.4. 1→0 transitions

The species on the first plot demonstrate little evidence of strong pairwise interactions (Table 7.5), the only significant interspecific effect was a negative interaction between *Briza* and *Viola* at the tenth census. Both *Briza* and *Dactylis* have a tendency to undergo a 1→ 0 transition in neighbourhoods with less than expected numbers of conspecifics whereas the converse is true for *Festuca*.

The second plot has a greater prevalence of effects (Table 7.6). *Trifolium repens* is positively affected by *Dactylis glomerata* and, on occasion, by *Carex flacca*. It is negatively affected by *Lolium perenne, Plantago lanceolata* and gaps. All three of the grass species (*Dactylis, Festuca* and *Lolium*) and *Trifolium* have a tendency for losing cell occupancy where there are fewer conspecifics in the neighbourhood, a trait which is especially pronounced in *Lolium*. Two of these species, *Lolium* and *Trifolium* tend to be negatively affected by gaps.

Species on the third plot (Table 7.7) appear to undergo the 1→0 transition largely at random.

Table 7.5. The results of randomisation tests carried out on the first permanent plot to determine if 1→0 transitions (death) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 1→0 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES									
	Bm	Cf	Cy	Dg	Fr	Lh	Pl	Rb	Tr	Vl	Gap
Bm	10** 12**									10***	
Cf											
Cy											
Dg				9** 10***							
Fr					6** 7**						
Lh											
Pl											
Rb											
Tr									12**		
Vl											

Table 7.6. The results of randomisation tests carried out on the second permanent plot to determine if 1→0 transitions (death) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 1→0 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES						
	Cf	Dg	Fr	Lp	Pl	Tr	Gap
Cf							
Dg						10**	
Fr							1**
Lp				1** 2* 3** 4** 5** 6*** 8* 9* 10** 11-12***			1** 3** 4** 5** 6** 10** 11*** 12**
Pl							
Tr	11***	4** 10***		1** 7** 10**	1** 13***	1* 3** 8* 14*	2*** 8*** 9**

Table 7.7. The results of randomisation tests carried out on the third permanent plot to determine if 1→0 transitions (death) of a particular target species were occurring at random with respect to neighbour species in a radius of 2 cm around the target cell (20 neighbours).
Asterisks represent a deviation from the neighbourhood expected from the null model that 1→0 transitions are independent of neighbourhood. Numbers refer to the census at the start of a transition; thus 4-11 refer to the intervals 4-5,...,11-12: ** $P < 0.01$, *** $P < 0.001$.
Underlined text indicates that the number of neighbours of a particular species is less than would be expected, normal type indicates that the number of neighbours is greater than would be expected by random.
The leading diagonal represents intraspecific interactions and is shaded.
Species abbreviations follow Table 1.1.

TARGET SPECIES	NEIGHBOUR SPECIES								
	Bm	Cc	Km	Lh	Lo	Pl	Pe	Rb	Tr	Gap
Bm	9*									
Cc		13*								
Km			11**							
Lh										
Lo										
Pl										
Pe										
Rb										
Tr										

7.5. Discussion

7.5.1. Limitations of the data and analysis

There are several limitations of the data which may influence the results of the randomisation tests to a greater or lesser degree. Firstly, a cell in which a species is present may contain one or many ramets or individuals of that species. Therefore the number of cells of a species around a target cell may not be representative of the density of the neighbour species. For certain species, however, which will only contain one individual per cell e.g. *Leontodon hispidus*, *Plantago lanceolata*, the number of cells occupied approximates well to the density of these species.

A limitation of the analysis is that a significant test does not imply any causality of interactions between species. If species A tends to go 1→0 in the presence of greater than expected numbers of species B, this does not necessarily mean that species B has a negative effect on species A. An alternative explanation could be that the environmental conditions optimal for species B are suboptimal for species A. In this community, little evidence of differentiation in the habitat niche has been demonstrated (Mahdi, Law and Willis 1989) so this environmental hypothesis is unlikely but this does not preclude explanations such as neighbour-dependent herbivory.

The 2 cm area over which the plants are thought to interact may be too small to determine the effect of neighbouring plants on the target cell. A related problem is that all cells are given equal weighting, whereas the closest plants will have a greater effect (Weiner 1982). However, given this problem, we would expect the plants in the 2 cm area to explain a large amount of the variation in plant performance. There may appear to be a contradiction between the area chosen over which plants are likely to interact and the results of the removal experiments described in chapter 3. These removals demonstrate that the biomass of certain species continued to increase following removals up to and including 5 cm from the target ramet, suggesting that all plants within this radius have a negative influence. However, the experiment

did not preclude the regrowth of roots into the area and this may complicate the interpretation of the sphere of influence (see discussion to chapter 3 and chapter 4).

7.5.2. Intraspecific growth patterns

A large number of species undergo 0→1 transitions in neighbourhoods which have elevated numbers of conspecifics. This suggests that the presence of conspecific neighbours is required for growth into a new cell and is a trait associated with those species with a high capacity for clonal growth. These include the majority of the grass species which propagate through the production of daughter tillers from existing plants (Langer 1979) and *Trifolium repens* which moves through the sward by the production of plagiotropic stolons (Sackville Hamilton and Harper 1989) (Fig. 7.3). The small-scale modular growth patterns of these species tends to lead to clumped distributions of individuals in space. By contrast, it has already be demonstrated in chapters 5 and 6 that the sexually reproducing dicotyledonous species tend to be more dispersed over the plots and these have less of a tendency for growth in neighbourhoods with greater than expected numbers of conspecifics.

The results for *Festuca rubra* in this context suggest that it is reproducing clonally on the first plot and less so on the second (Fig. 7.3). However, despite the increased clonality on the second plot, it has a lower mean clump size, possibly as a result of 1→0 transitions in this species sometime being more likely to occur in elevated conspecific neighbourhoods on the first plot (Table 7.2), suggestive of density-dependent behaviour, with a slightly beneficial intraspecific effect on the second plot (Table 7.3).

The results for 0→1 transitions in neighbourhoods of conspecifics were similar for tests carried out for both 8 and 20 cell neighbourhoods. This is to be expected since the larger neighbourhood includes the species contained in the first. However, the significance level of the tests was generally found to be

reduced for the grasses further pointing to the fine-scale over which these species propagate. *Plantago lanceolata* had greater significance of cell capture in elevated conspecific neighbourhoods in the larger scale test. This may be because this species has a rather limited capacity to grow clonally (Grime, Hodgson and Hunt 1988) but may do so slowly in a dense sward (Sagar and Harper 1964).

The results also suggest that there is a reduced chance of undergoing a 1→0 transition in neighbourhoods in which more conspecifics are present. This will have the result that isolated individuals will tend to die whereas clumps will tend to persist. A possible mechanism for this effect is the reduction in interspecific relative to intraspecific competition in clumps which may be beneficial to competitively weak species. This behaviour is demonstrated by a large number of the grass species, particularly *Lolium perenne* and *Dactylis glomerata*, species which have a tendency to form large monospecific stands.

7.5.3. Interspecific interactions

In comparison to the frequency of intraspecific interactions, there is little evidence for strong pairwise interactions between species. This may be expected because of the high degree of intraspecific contact in limestone grassland communities (Mahdi and Law 1987) and the infrequency by which other species encounter each other, since the majority will be sparse (Grubb 1986; Mahdi and Law 1987). In addition, competition is experienced as a diffuse effect from all neighbouring species on a per biomass basis (Goldberg and Werner 1983; Fitter 1987; Goldberg 1987; Miller and Werner 1987) rather than in the form of species-specific interactions.

On the first and third plots, interspecific interactions had little effect on the behaviour of species. The negative effect of *Viola lutea* on the survival of *Briza media* at census 10 (Table 7.5) is a result of the density-independent mortality of *Viola* due to rabbit scratching at this time (see chapter 5). Other species in the neighbourhood of this species would be affected by this impact. *Trifolium*

repens has a tendency to grow into neighbourhoods with a high density of *Cynosurus cristatus*. This may demonstrate that *Cynosurus* is easily invaded by the guerrilla growth form of *Trifolium*.

The second plot has a higher preponderance of pairwise interactions than the first or third plot; the lower diversity of this plot means that species will tend to contact each other with a greater regularity. The survival of *Trifolium repens* is negatively affected by *Lolium perenne* and *Plantago lanceolata* and positively affected by *Dactylis glomerata*. Its lateral spread is affected negatively by *Dactylis* and *Lolium*. *Trifolium repens* has a greater number of pairwise interactions than other species, a result of the rapid mobility of the stoloniferous growth form which may encounter many different neighbourhoods as it wanders through the sward (Turkington and Harper 1979). The greater negative effect on the spread and survival of *Trifolium* by both *Dactylis* and *Lolium* than the reciprocal effect may point to the benefit of a clumping phalanx lifestyle against invasion by this guerrilla species. Both *Dactylis* and *Lolium* form matrices in the sward of the second plot which may be difficult for *Trifolium* to penetrate.

Gaps appear to have a largely negative effect on both the capture and loss of cells. However, this may be an artefact because of the beneficial effect of conspecific neighbourhoods on many species. If there is greater birth and survival in elevated conspecific neighbourhoods then there may well be less gaps in those neighbourhoods.

The lack of significant species-specific effects does not mean that such effects are not present. Both the data and analytical methods may be incapable of detecting small underlying trends. However, more sophisticated analysis on the relationship between target tiller survival and the number, identity and proximity of neighbouring grasses in a mesotrophic grassland similarly found no significant effects (Silvertown 1994), suggesting that the results from this study are not atypical.

7.5.4. Community dynamics

As has been demonstrated in the previous two chapters, there seems to be a close correlation between the behaviour of species and their life-form here. The rosette-forming perennials (*Plantago lanceolata, Leontodon hispidus, Viola lutea, Ranunculus bulbosus*) die and reproduce in a manner which is largely independent of their neighbourhood. *Carex flacca* exhibits a similar neighbourhood independent behaviour, although this species reproduces largely by the production of daughter ramets. However, because the length of the connecting rhizomes is generally greater than 2 cm (Mahdi 1988; van der Hoeven, de Kroon and During 1990) the number of conspecifics in either the 8 or 20 cell neighbourhood is unlikely to improve the chance of a 0→1 transition. Other perennial species on the plots, *Lotus corniculatus* and *Potentilla erecta* have largely neighbourhood independent dynamics.

The grass species show a large tendency for cell capture adjacent to elevated conspecific neighbourhoods. However, despite the similar tendency for aggregation, the results presented here suggest that these species differ in their competitive ability. *Dactylis glomerata* and *Lolium perenne* tend to form tight clumps which are difficult to penetrate whereas *Cynosurus cristatus* seems to be easily invaded and competitively weak.

The sedges, *Carex caryophyllea* and *C. flacca* appear to have similar dynamics, both having neighbourhood independent growth and death. However, *Carex caryophyllea* reproduces clonally and has shorter rhizomes than *C. flacca* (Middleton 1989; van der Hoeven, de Kroon and During 1990) and the apparent neighbourhood independence of the dynamics of this species is surprising.

7.5.5. Deriving cellular automata rules for plant interactions

Although it is possible to demonstrate that cell gains and losses are neighbourhood dependent, these do not represent cellular automata rules. More than one rule could be consistent with the data. The statistical

significance of the deviation from the expected neighbourhood has been given but not the actual numbers of species involved in each case.

The work presented in this chapter is a first step in the process of building an empirical foundation for a cellular automata model. In order to derive probabilistic rules it is necessary to take this work a step further. I have shown that for a number of species the observed transitions are neighbourhood independent and for these species, the probability of cell capture and loss can be derived directly from the data. For those species which do have neighbourhood dependent transitions, the probability of cell capture and loss for particular neighbourhoods can be calculated from the data and included in the model. Future work may take these steps in order to construct a model of the spatio-temporal dynamics of a limestone grassland. From the results presented here, however, it seems that the community dynamics are largely a function of the modular growth patterns of the constituent species, and a model based on these growth forms, together with rules for the positive effects of conspecifics on clumping species, would be a reasonable starting point.

Chapter Eight

GENERAL DISCUSSION

8.1. Summary

The results of the previous chapters are summarised and implications for the structure of limestone grassland communities and the coexistence of species are discussed in relation to the objectives laid out in chapter 1. The evidence for competitive hierarchies is evaluated and it is considered that the ranking of species by short-term interference ability is not incompatible with longer-term competitive reversals given that the community is weakly interactive. Changes in plant morphology are considered in terms of competition between neighbours and their adaptive value is discussed. In this community, short-term interference is uncoupled from the longer-term dynamics of species and based on this a hypothetical model is presented for the development of the community. Within this framework, differences in the spatio-temporal dynamics of species and regeneration niches, represent possible, but not mutually exclusive, mechanisms of coexistence. The evidence for specific mechanisms is presented, and suggestions are made for distinguishing between the presence and absence of niche differentiation in plant communities.

8.2. The effect of neighbours on plant performance

8.2.1. Competitive hierarchies and reversals in rank order

The removal experiments detailed in chapter 3 provide evidence of the effect of neighbours on plant performance. Large species (*Plantago lanceolata, Sanguisorba minor*) were unaffected by removals around randomly selected individuals whereas smaller species (*Briza media, Carex caryophyllea, Lotus corniculatus*) had greater biomass in larger gaps. The ranking of plant competitive response, based on the amount of variation in above-ground biomass explained by the treatments, was negatively correlated with the mean

biomass of species. This ranking suggests the existence of a competitive hierarchy, a finding in common with other studies on calcareous grasslands (Mitchley and Grubb 1986).

If ranking in a transitive competitive hierarchy was the sole determinant of field abundance then the top-ranked species would exist as a monoculture. Given that monocultures rarely occur in nature, and if the position of a plant in a hierarchy determines its field abundance (Mitchley 1988) then this suggests that there are processes which prevent exclusion from occurring but which keep the abundance hierarchy correlated with the competitive hierarchy (Silvertown and Dale 1991). One such mechanism might be reversals in the rank order of plant competitive ability (intransitive competition), which may occur as a result of the dependence of competitive ability on plant age and size (Grace 1985; 1988) and environmental conditions (Goldsmith 1973) such that no one species is a superior competitor over all life stages and environmental conditions.

The majority of evidence for the existence of competitive hierarchies comes from laboratory-based experiments (Mitchley and Grubb 1986; Keddy and Shipley 1989) which produce artificially deterministic outcomes and remove the environmental variation which may be responsible for reversals in competitive ranking (Herben and Krahulec 1990). However, this study and others (Miller and Werner 1987; Goldberg 1987; Wilson, Twolan-Strutt and Keddy 1994) have demonstrated the existence of hierarchies in the field, although only the present work used *in situ* plants rather than transplanted seedlings. These field studies, too, could be criticised, on the grounds that the environmental variation which is responsible for competitive reversals would operate over longer timescales than the majority of field experiments (Herben and Krahulec 1990; Gurevitch and Collins 1994).

If reversals in interference ability were occurring at Priestcliffe then it would be expected that these would be detected by randomisation tests performed on the

permanent plot data (chapter 7). Intransitive competition would be demonstrated by changes in negative affects of one species on another. For instance, at one time species A would suffer in neighbourhoods with species B present (1→0 transitions increased or 0→1 transitions decreased), and at other times species B would suffer from the presence of species A. This was not found to be the case, and in fact few significant interspecific effects of any kind were detected.

The study of competition as short-term interference ability may be ecologically misleading (Grubb 1977) since the abundance of species in the field is based on interactions over the whole life-cycle of plants rather than just interference between established plants or seedlings (Silvertown, Lines and Dale 1994). Herben and Krahulec (1990) observed reversals in space capture between species in a Czech mountain grassland with certain species increasing in abundance at the expense of other species with the converse being observed at other times and on other plots. Some of the grass species on the permanent plots at Priestcliffe were observed to increase in abundance whilst other species decreased (chapter 5, Fig. 5.5) so the concept of temporally and spatially variable space capture is not inconceivable in this study. Fluctuations in the ability of grass species to invade and replace each other has also been observed in other British pastures (Thórhallsdóttir 1990; Silvertown, Lines and Dale 1994) and the existence of intransitivities in spatial competition is not inconsistent with the view that there may be a strict, size-based (Goldberg 1987), hierarchy of species based on their short-term interference ability. Short-term interference ability is one measure of dominance but will not, on its own, always allow accurate predictions to be made about the long-term dynamics of species (Silvertown, Lines and Dale 1994).

8.2.2. The role of short-term interference

The importance of competition in the determination of the reproductive success of plant species will depend on the amount of stress and disturbance in a community (chapter 1; Grime 1973, 1977, 1979). In productive conditions

neighbours are likely to have a large effect on plant performance and short-term interference ability will be the prime determinant of longer-term space capture. However, in less productive conditions neighbourhood competition may have only a small effect on plant performance and the relationship between competitive ability and the long-term success of plant species will be less clear.

At Priestcliffe the results from the removal experiments (chapter 3) demonstrate that although the biomass of some species increases following the removal of vegetation around target individuals, relatively little of the variation in plant biomass is explained by the area of neighbour-free space up to 5 cm (a maximum of 15% in the case of *Briza media*). By comparison, in a sand-dune community, Mack and Harper (1977) found that 77% of the variation in plant size was explained by the identity, distance and angular dispersion of species within 2 cm of target plants. The result that the number of gaps present in the neighbourhood of target plants had few negative effects on space capture (chapter 7) further suggests that competitive interactions are not strong enough to influence plant behaviour, at least at normally observed densities, and within this weakly interactive the position of a species in a competitive hierarchy will have little bearing on its field abundance.

8.2.3. Adaptive plant morphology

Plants may adapt to external stimuli and as such can be said to be capable of behaviour (Silvertown and Gordon 1989). One such example of plant behaviour is the ability for plants to alter their morphology in response to changes in the environment (Slade and Hutchings 1987a,b; Birch and Hutchings 1994, Wijesinghe and Handel 1994). The results from the removal experiments demonstrate that a number of limestone grassland species can plastically alter the allocation of resources to old and new leaves, thereby causing a change in the quantity and mean length of their foliage (chapter 3).

These morphological alterations are thought to be a phytochrome mediated responses to the red/far-red ratio experienced by a plant (Smith 1994). A plant under dense canopy will receive less red light than an unshaded conspecific and will react by elongating its leaves (Björkman 1981; Hutchings and de Kroon 1994) and thus push above the canopy and capture more light. This behaviour will effectively reduce the amount of competition (in terms of resource denial) experienced by the plant, which will be modifying how it perceives the environment by altering its structural development. The observation that nearby plants may be detected and reacted to by the reflection of light (Ballaré *et al.* 1987; Ballaré, Scopel & Sánchez 1991) further suggests that this kind of morphological adaptation may be a response to competition.

The species used in the removal experiments differed in their sensitivity of response to a changing light environment as measured by the variation explained by gap size in the mean leaf length and number of leaves (chapter 3, experiment two). This sensitivity was generally positively correlated with the amount of variation in above-ground biomass explained by gap size. This can be interpreted as the greater plasticity of smaller, competitively weaker species to fluctuations in light but equally as the result that species lower in the canopy will experience greater fluctuations in the incident light. Whichever interpretation is taken, the end result is that the species which are affected most by competition are more sensitive to changes in the light environment and alter their morphology which has the effect of ameliorating suppression from neighbours. This is suggestive of a trade-off between the scale and precision of foraging for light (*sensu* Campbell, Grime and Mackey 1989). In the low grazed turf of limestone grassland, the ability to etiolate leaves when shaded may allow photosynthetic material to be placed above the canopy, and competitive stress can be ameliorated. However, in more productive or ungrazed ecosystems, slight increases in leaf or stem length will be ineffective in the face of a taller sward, and rapid overtopping and competitive suppression of the competitive subordinates will result.

8.3. Spatio-temporal dynamics

8.3.1. The influence of neighbours on spatio-temporal behaviour

The results from chapter 7 indicate that the spatio-temporal dynamics of most of the plant species monitored at Priestcliffe occur independently of the presence and identity of heterospecific neighbours. *Trifolium repens* represents an exception to this rule, and may be negatively affected by clump forming grasses which are hard to invade. However, the ability of a number of species to capture and hold space was influenced by the presence of conspecific neighbours in the neighbourhood. Species with a well developed capacity for clonal expansion (the majority of the graminoids and *Trifolium repens*) were more likely to capture space in regions dominated by conspecifics, reflecting local growth patterns, and species with a tendency to form monospecific stands also tended to experience greater mortality in the absence of conspecifics (*Dactylis glomerata, Lolium perenne*). Species which recruit from seed (*Leontodon hispidus, Plantago lanceolata, Potentilla erecta, Ranunculus bulbosus*) and those with rhizomes longer than the radius of the neighbourhood considered (*Carex flacca*) had spatio-temporal dynamics which occurred independently of both conspecific and heterospecific neighbours.

The null effect of heterospecific neighbours on plant performance is consistent with the view that the community is weakly interactive (section 8.2) and demonstrates that short-term interference has no detectable effects on the longer-term dynamics of species. The spatio-temporal dynamics of the community can thus be interpreted as primarily the result of the modular growth patterns of individual species.

8.3.2. A model of calcareous grassland dynamics

Based on the results obtained from the work contained within this thesis it is possible to construct a hypothetical model of the dynamics of the plant community at Priestcliffe Lees. Given that the performance of plants is independent of the number and identity of other species in the immediate

neighbourhood a dynamically sufficient description (*sensu* Lewontin 1974) of the community dynamics can be taken to include only intraspecific interactions.

Since few interspecific effects of neighbourhood competition were observed it seems likely that species are not able to invade already occupied space and must a site must be empty prior to colonisation. If it were possible for species to colonise already occupied sites then we would expect to detect this in the randomisation tests, because the invaded species would be more likely to lose space in the presence of the coloniser. This has the consequence that the dynamics of the community will take place on the slower time scale of patch colonisation and extinction rather than the faster scale of invasions and replacement. The effect of this will be to prolong the time necessary for competitive exclusion (Huston 1979).

This view of calcareous grassland dynamics emphasises the importance of the availability of gaps and the ability of species to reach and hold spatially and temporally stochastic openings in the sward. The relative abundance of a species in the community will depend on the availability of suitable microsites for colonisation, the ability of a species to reach those microsites and the potential to hold the site once it is colonised (Grubb, Kelly and Mitchley 1982), this including both interference ability and its interaction with herbivory. Species which have few available microsites may persist provided that they are better able to reach those microsites or have a greater potential for short-term interference.

At Priestcliffe, the rosette-forming herbs recruit from seed and seedlings of those species are rarely observed in undisturbed vegetation, suggesting that they are ineffective at colonising microsites. However, they may hold space for long periods of time (chapter 5). By contrast, the grass species have a rapid turnover but their large capacity for clonal expansion leads to the rapid colonisation of local space and the high reproductive potential of seed

recruiting annuals gives them an advantage in colonising empty microsites and large areas of bare ground which may be inaccessible to clonal species.

These observations suggest that no individual species may be superior at all stages of the life cycle and that trade-offs exist between survival, reproduction and growth (Grime 1979; Law 1979; Tilman 1988; Silvertown, Franco and McConway 1992). However, a central question is whether differences between the spatio-temporal dynamics of species alone may be a sufficient explanation for the coexistence of plants in calcareous grasslands or if niche differentiation must exist if competitive exclusion is to be avoided?

8.4. Can plants with identical niches coexist?

8.4.1. Coexistence without niches

The results from this thesis are suggestive of a community in which interference has little effect on space capture, and mechanisms which act to reduce the intensity of short-term competition are of little importance. The dynamics of the system occur on the longer time-scale of patch colonisation and extinction rather than the invasion of species into already occupied sites, and species will persist if they have a non-negative growth rate at low density (Chesson 1986; Chesson and Case 1986).

The concept of niche differentiation stems from Gause (1934) but it has been suggested that differences in the ecological requirements of plant species are unnecessary in order to explain coexistence (Silvertown and Law 1987). However, recent models which claim to permit coexistence between essentially similar species based on stochastic factors provide further support for the fact that species must be ecologically distinct in order to coexist (Chesson 1991) and it has been suggested that niche differences forms an "integral part of the assembly rules of species-rich calcareous grasslands" (Grime 1990).

It is possible to test whether plants can coexist in the absence of niche differentiation by the construction of a cellular automata model in a homogeneous environment. Within this framework, all cells are open to colonisation to every species, an assumption which may be realistic in relation to calcareous grassland communities (van der Maarel and Sykes 1993), and probabilities of cell capture and loss are based on the spatio-temporal dynamics of individual species. If species manage to coexist then this is due to any one or a combination of three processes:

1. Differences in the spatial growth patterns of species

The ability to colonise microsites is largely a function of reproductive output but if species have identical reproductive output then differences in spatial growth patterns will have an influence on the capacity to reach available microsites. Clonal plants will have an advantage in colonising local space, but there will be differences between species depending on the length of spacers between ramets ('guerrilla' or 'phalanx' strategies; Schmid 1986; Inghe 1989), and seed dispersing species will be able to colonise more distance and open sites. The species at Priestcliffe Lees display contrasting spatial growth patterns (chapters 5-7) but it has yet to be tested whether growth patterns alone may be sufficient to promote coexistence. In my opinion it is unlikely that differences in patterns of growth alone may explain the persistence of a large number of species but this may operate as a mechanism of coexistence in concert with differences in the ability of species to capture and hold space.

2. Trade-offs in the ability of species to capture and hold space

It has been demonstrated that a species which is always inferior in competition for microsites (a strict competitive hierarchy) may continue to persist provided that it is a better coloniser and that sufficient microsites become available (Crawley and May 1987). In an undisturbed community competitive species will always tend to exclude the other species but within calcareous grasslands openings in the sward may be frequently created (Grime 1990), through hoof prints and rabbit scratching, providing a potential refuge for ruderal species.

At Priestcliffe, species can be separated based on their ability to colonise and hold space (chapter 5) and these are highly correlated suggesting that trade-offs may exist (chapter 5; Fig. 5.8). However, whereas two species may coexist if one is a superior competitor, the other a superior coloniser, it has yet to be tested if this mechanism will hold for a multispecies community.

3. Temporal and spatial fluctuations in the space capture of species due to stochastic processes of gap colonisation and extinction.

The space capture of a species at any one time step will depend on how many microsites become open which it can colonise and the number of other species in the vicinity which may also be able to colonise the sites. Competition for microsites will thus be a lottery and space capture will thus be temporally and spatially variable. In relation to tropical forests Hubbell and Foster (1986a,b) concluded that the regeneration of trees species was based on a lottery process and the community trajectory followed a random walk as the result of stochastic colonisation and extinction of gaps. The problem with such a 'random-walk' model is that there is no mechanism preventing species from going extinct since there is not a tendency to have positive growth rates at low density. However, the tree species in this circumstance were long-lived and it is not inconceivable that over long time periods, reversals in reproductive ability due to climatic variation (due to niche differences between species) may also act to maintain the diversity of species.

Within a cellular automata model the role of each of these mechanisms and combinations thereof in preventing competitive exclusion from occurring can be tested. The third mechanism alone can operate if species in the model have identical birth and death rates and spatial dynamics and by creating interspecific differences the first two mechanisms can be brought into being. The role of stochastic fluctuations can be removed by simulating the birth and death of species in cells as a deterministic rather than stochastic process.

8.4.2. Possibilities for niche differentiation

If it is demonstrated that species are unable to coexist in a homogeneous environment (or equivalently in a heterogeneous environment in which all species have identical niches) then is a logical necessity that coexistence must arise as a direct result of ecological differences between species. Under certain environmental conditions one species may have a greater positive growth rate, another species being dominant under different conditions. This does not preclude the operation of mechanisms discussed in *8.4.1.* and these may act simultaneously and reduce the amount of niche differentiation required for species to coexist.

Grubb (1977) defines a plant's niche in terms of four components; the habitat niche (environmental requirements in the established phase), the phenology niche (timing of life history events), the life-form niche (growth form) and the regeneration niche (requirements in the regenerative phase). However, the niche is usually defined as the resource needs, habitat requirements and environmental tolerances of species (Hutchinson 1957), which is compatible with ideas of the habitat, phenology and regeneration niche but the life-form niche tends to be synonymous with the spatial dynamics of a species. The life-form of a species may influence the niche requirements along other axes but since it does not alone refer to difference in species tolerance or habitat requirements, I will confine my definition of a plant's niche to the remaining three components.

Evidence from studies other than this thesis suggest that limestone grassland species occupy similar habitat niches. In a permanent plot study van der Maarel and Sykes (1993) observed that species in Swedish alvar grassland could occupy any microsite and Mahdi, Law and Willis (1987) found little difference in the soil pH, depth or nutrient status around nine different limestone species, although *Potentilla erecta*, usually a calcifuge, occurred in areas of greater soil depth and lower pH. There was also no difference in the ratio of limiting nutrients required by these species, failing to provide support

for Tilman's resource-ratio hypothesis of species diversity (Tilman 1982, 1986). One possibility for differentiation in the habitat niche which has been suggested is rooting depth (Fitter 1986b, 1987; Veresglou and Fitter 1987) and chapter 4 lends some support to this hypothesis for limestone grassland species. It seems feasible that the competitively dominant species have large and deep penetrating root systems and subordinate species by virtue of more precise foraging ability (Campbell, Grime & Mackey 1991) may be able to exploit the interstices of this below-ground matrix much as they do above-ground (Grubb 1986).

Mahdi, Law and Willis (1989) also considered the phenology niche and found that the majority of species could not be separated along this axis of niche space. There are, however, several species which appear to compete little with other species by the timing of their life-cycle. Among these is *Ranunculus bulbosus* which retreats below-ground in early summer and emerges again in the autumn. Differences in the timing of leaf expansion between limestone grassland species have been observed (Grime, Shacklock and Band 1985) but it is hard to envisage this as a mechanism whereby, for example, 40 species m^{-2} could have sufficiently complementary niches in order to coexist.

Whilst differences in the habitat and phenology niche may reduce the intensity of short-term interference competition, differences in the regeneration niche may allow coexistence in the longer term. Since the introduction of this idea (Grubb 1977) the notion that differences in the reproductive requirements of species may foster coexistence has been gaining support in recent years in studies of calcareous grasslands (Hillier 1984; 1990; Grime 1990; Rusch 1992; Rusch and van der Maarel 1992). The regeneration niche was originally defined with reference to sexual reproduction (Grubb 1977) but can be expanded to include asexual methods of recruitment. Vegetative expansion is a general strategy in calcareous grassland because the limited availability of mineral nutrients leads to infrequent flowering and pre- and post- seed dispersal predation is high (Mortimer 1993). However, plants of many species

occurring at Priestcliffe are dependent on sexual reproduction for successful recruitment into the next generation e.g. *Cerastium fontanum, Conopodium majus, Danthonia decumbens, Deschampsia flexuosa, Euphrasia officinalis agg., Leontodon autumnalis, Linum carthartícum, Lotus corniculatus, Polygala vulgaris, Rhinanthus minor, Rumex acetosa, Ranunculus bulbosus* and *Trifolium pratense* (Grime, Hodgson and Hunt 1988) and Hillier (1984) observed the germination of seeds of a number of species in undisturbed vegetation in a limestone grassland very close to Priestcliffe.

Clonal growth allows rapid colonisation of adjacent space and the edges of gaps (Bullock, Clear Hill *et al.* 1994), although some guerrilla species such as *Trifolium repens* are highly mobile, whereas recruitment from seed allows patches to be colonised from a further distance, such as the middle of large gaps which are inaccessible to many clonal species (Bullock, Clear Hill *et al.* 1994), the range of dispersal of seeds in chalk grassland being estimated at 0.3 to 3.5 m (Verkaar, Schenkeveld and van de Klashorst 1983).

Regeneration in calcareous grasslands is propagule rather than microsite limited (Mortimer 1993) and successful seedling establishment may depend on opportunistic germination in gaps when climatic conditions are favourable (Grime 1990). Differences have been observed between species in the microclimatic conditions required for successful germination which has led to spatial and temporal separation of recruitment episodes (Hillier 1984, 1990; Rusch and van der Maarel 1992; Rusch 1992).

It has been demonstrated that occasional periods of strong recruitment in time or space when conditions are favourable will maintain plant populations through periods in which environmental conditions are unfavourable, such that species at will have a positive mean growth rate, even at low densities (the 'storage effect' Warner and Chesson 1985; Chesson and Case 1986). This buffering effect arises from a non-linearity in the dynamics of the system and may occur in situations in which the mortality of adult plants is less variable

APPENDIX

Source code for vegetation grid data analysis programs

The source code for the vegetation grid analysis programs was written in the C programming language on a Sun Sparc 2 workstation. There were a total of three progams used for the analysis:

VGRID1	analysis of cover (number of cells occupied) and cell transitions.
VGRID2	fractal analysis
VGRID3	mean clump size

The code is shown in the `courier` *typeface. Reformatting of the code has* caused some lines to run on, not a feature of the original program.

```
/*********************************************************/
/*                                                       */
/*   VGRID Mk1                                           */
/*                                                       */
/*   Analysis of vegetation grid data                    */
/*   Abundance, spatial structure and                    */
/*   transition analysis                                 */
/*                                                       */
/*   Andrew McLellan, University of York                 */
/*                                                       */
/*   Last revised 20/9/94                                */
/*                                                       */
/*********************************************************/


#include <math.h>
#include <stdio.h>
#include <stdlib.h>
#include <string.h>
#include <curses.h>

#define maxX   100
#define maxY   100
#define MAXSTRING   100
#define MAXSPECIES  100
#define XX      40
#define YY     28              /* grid dimensions  */
#define GAP    0               /* defines Gap as species 0
*/

char string[MAXSTRING];

char speciesname[MAXSPECIES][MAXSTRING];

char file[MAXSTRING];
char filename[MAXSTRING];
char filename2[MAXSTRING];

int numberspecies;

int value;       /* for scancheck function  */

int gridtype;
int speciesplottype;

int grid[XX+1][YY+1];     /* actual grid bitmaps  */
int firstgrid[XX+1][YY+1];
int secondgrid[XX+1][YY+1];

long xdir[20] = {-2,-2,-2,-1,-1,-1,-1,-
     1,0,0,0,0,1,1,1,1,1,2,2,2};
long ydir[20] = {-1,0,1,2,1,0,-1,-2,2,1,-1,-2,2,1,0,-1,-
     2,1,0,-1};          /* neighbourhood directions  */

int border=0;       /* number of cells discounted  */

int number[MAXSPECIES];
```

```
int numbers[MAXSPECIES];                    /* species
                                             abundances  */

int neighbours[MAXSPECIES][2] = {0};

int transition[MAXSPECIES][3] = {0};

char neighbourtype[2][MAXSTRING];

char transitiontype[3][MAXSTRING];


void setstrings()

{
     strcpy(neighbourtype[0],"conspecifics");
     strcpy(neighbourtype[1],"heterospecifics");
     strcpy(transitiontype[0],"1->1");
     strcpy(transitiontype[1],"1->0");
     strcpy(transitiontype[2],"0->1");
}



void checkforfilename()

{
     if (filename2[0]=='\0') strcpy(filename2,"temp.dat");
     printf("\n\nResults stored in file temp.dat by
default\n\n");

}




void getgriddata()              /* takes grid input from
file (when it works)  */

{
     int i,j,k,l;
     int data;
     FILE *ifp;


     getchar();
     printf("\n\nFilename : " );
     gets(file);
     strcpy(filename,file);

     if ((ifp=fopen(filename,"r"))==NULL) {
          printf("\nFile error - specified file does not
exist\n");
          getgriddata();
          }
     for (i=1;i<=YY;++i)
          for (j=1;j<=XX;++j) {
```

```
          fscanf(ifp,"%d",&data);
          grid[j][i]=data;              /* puts data into
bitmap  */
          }


     fclose(ifp);

}

void coveranalysis()  /* analyses species abundance  */

{
     int h,i,j;

     for (h=0;h<numberspecies;++h)
          number[h]=0;


/*   for (i=1+border;i<=(YY-border);++i)
          for (j=1+border;j<=(XX-border);++j)
               number[grid[j][i]]+=1;   */

     for (i=1;i<=YY;++i)
     for (j=1;j<=XX;++j)
          number[grid[j][i]]+=1;


}



void cover()          /* companion function to coveranalysis
*/

{

     int k;
     double percent,abundance;
     FILE *ofp;

     printf("\n\n\n\n\n");
     printf("\nCover analysis");
     getgriddata();
     strcpy(filename2,"temp");
     printf("\nResults will be stored in file
%s\n\n",filename2);
     ofp=fopen(filename2,"w");
     fprintf(ofp,"\nCover analysis for file
%s\n",filename);

     coveranalysis();                              /* calls
math part of function */

     printf("\nSpecies abundance\n\n");           /* prints
results */
     for (k=0;k<numberspecies;++k)
          if (number[k]>0) {
```

```
                abundance=number[k];
                percent=(abundance/((XX-4)*(YY-4)))*100.0;
                printf("\n%3d. %3s    %5d
(%5.2f%)",k,speciesname[k],number[k],percent);
                fprintf(ofp,"\n%3d. %3s    %5d
(%5.2f%)",k,speciesname[k],number[k],percent);
                }
     printf("\n\n");
     fprintf(ofp,"\n\nEnd of file\n\n");
     getchar();
     fclose(ofp);
}


void convertgriddata()   /* converts grid into spans
readable format  */

{
     int i,j,k;
     int counter;
     FILE *ofp;

     printf("\n\n\n\n\n\nConvert grid data");
     getgriddata();
     strcpy(filename2,file);
     strcat(filename2,".out");
     printf("\n\nOutput to file %s\n\n",filename2);
     ofp=fopen(filename2,"w");

     for (j=1;j<=YY;++j)
     for (i=1;i<=XX;++i) {
          counter=((j-1)*40)+i;
          fprintf(ofp,"%4d %4d
%3d\n",counter,counter,grid[i][j]);
          }
     fclose(ofp);
     getchar();

}


void gridcoordinates()

{
     int i,j;
     int target;
     FILE *ofp;

     printf("\n\n\n\n\n\nGrid data for plotting");
     getgriddata();

     printf("\nSpecies for plotting: ");
     scanf("%d",&target);
     coveranalysis();
     printf("\nSpecies %s (N =
%d)\n\n",speciesname[target],number[target]);
     getchar();
     printf("File for output: ");
```

```
     gets(filename2);
     ofp=fopen(filename2,"w");

     for (i=1;i<=XX;i++)
     for (j=1;j<=(YY-4);++j)
          if (grid[i][j]==target) fprintf(ofp,"%2d
%2d\n",i,25-j);

     fclose(ofp);

}



void listgriddata()    /* produces hard copy of grid data
to file */

{
     int m,n,q;
     FILE *ofp;

        printf("\n\n\n\n\n");
     printf("\nGrid data");
     getgriddata();
     printf("\n\nName of file to store first half of grid?
");
     gets(filename2);
     ofp=fopen(filename2,"w");
     fprintf(ofp,"Grid data 1/2 for file
%s\n\n\n",filename);
     fprintf(ofp,"    ");
     for (q=1;q<=20;++q)  /* first half of grid */
          fprintf(ofp,"%3d",q);
          fprintf(ofp,"\n");
     for (m=1;m<=YY;++m) {
          fprintf(ofp,"\n%3d ",m);
          for (n=1;n<=20;++n)  {
               if (grid[n][m] == 0) fprintf(ofp,"    ");
     /* prints gap as a space */
               if (grid[n][m] != 0) fprintf(ofp,"%s
",speciesname[grid[n][m]]);
               }
          }

     fprintf(ofp,"\n\n\n");
     fclose(ofp);

     printf("Name of file to store second half of grid? ");
     gets(filename2);
     ofp=fopen(filename2,"w");
     fprintf(ofp,"Grid data 2/2 for file
%s\n\n\n",filename);
     fprintf(ofp,"    ");
     for (q=21;q<=XX;++q)     /* second half of grid  */
          fprintf(ofp,"%3d",q);
          fprintf(ofp,"\n");
```

```
      for (m=1;m<=YY;++m) {
           fprintf(ofp,"\n%3d ",m);
           for (n=21;n<=XX;++n) {
                if (grid[n][m] == 0) fprintf(ofp,"    ");
                if (grid[n][m] != 0) fprintf(ofp,"%s
",speciesname[grid[n][m]]);
                }
           }

      fprintf(ofp,"\n\n\n");
      fclose(ofp);
      printf("\n\nCompleted saving\n");
      getchar();

}



void spatialstructure()                    /* neighbour contact
analysis  */

{
      int h,i,j,k,l,m,n,p,x,y;
      double meanhetero,meanconspec,abundance;
      double q=0,lines=8;
      int targetspecies,neighbourspecies;
      FILE *ofp;

         printf("\n\n\n\n\n\n");
      printf("\nNeighbourhood analysis");
      getgriddata();

      printf("\n\nName of file to store results in? ");
      gets(filename2);
      checkforfilename();
      ofp=fopen(filename2,"w");
      fprintf(ofp,"\nNeighbour analysis for file
%s\n\n\n",filename);

      coveranalysis();

      for (h=0;h<numberspecies;++h)
           numbers[h]=0;

      for (i=0;i<2;++i)
           for (j=0;j<numberspecies;++j)
                neighbours[j][i]=0;

      for (k=1+border;k<=(YY-border);++k) {
           for (l=1+border;l<=(XX-border);++l) {
                targetspecies=grid[l][k];
                numbers[targetspecies]+=1;
           for (m=0;m<20;++m) {          /* looks at
neighbourhood  */
                x=l+xdir[m];
                y=k+ydir[m];
                neighbourspecies=grid[x][y];
```

```
                if (neighbourspecies==targetspecies)
                     neighbours[targetspecies][0]+=1;
                if ((neighbourspecies!=targetspecies) &&
                (neighbourspecies>GAP))
                     neighbours[targetspecies][1]+=1;
                }

          }
     }

     for (n=0;n<numberspecies;++n) {
                if (number[n]>0) {
                meanconspec=neighbours[n][0];
                meanhetero=neighbours[n][1];
                abundance=numbers[n];
                meanconspec=(meanconspec/abundance);
                meanhetero=(meanhetero/abundance);
                printf ("\n%3d %3s  %15s
%4.2f",n,speciesname[n],neighbourtype[0],meanconspec);
                printf ("\n        %15s
%4.2f\n",neighbourtype[1],meanhetero);
                fprintf (ofp,"\n%3d %3s  %15s
%4.2f",n,speciesname[n],neighbourtype[0],meanconspec);
                fprintf (ofp,"\n        %15s
%4.2f\n",neighbourtype[1],meanhetero);
                q+=1;
                if (fmod(q,lines)==0) getchar();
/* pauses after data of 7 species  */
                }
          }
          fprintf(ofp,"\n\nEnd of file\n\n");
          fclose(ofp);
          getchar();
}


void transitioncalculate()    /* non-spatial transition
calculations */

{
     int i,j,k,l,m,n,p,r,t;
     int change;
     int firstspecies,secondspecies;
     double prob,counts;
     FILE *fp;

     printf("\n\n\n\n\n");
     printf("\nTransition probabilities\n\n\n");
     printf("\nPlease input second grid first\n");

     for (i=0;i<numberspecies;++i)
          for (j=0;j<3;++j)
               transition[i][j]=0;

     getgriddata();

     for (i=1;i<=YY;++i)
```

```
          for (j=1;j<=XX;++j)
               secondgrid[j][i]=grid[j][i];

     printf("\nNow enter first grid");
     getgriddata();
     coveranalysis();

     for (i=1;i<=YY;++i)
          for (j=1;j<=XX;++j)
               firstgrid[j][i]=grid[j][i];

     printf("\n\nName of file to store results? ");
     gets(filename2);
     checkforfilename();
     if ((fp=fopen(filename2,"w"))==NULL)
printf("\n\ncannot open file for writing\n\n");
     fprintf(fp,"\nTransition anaylsis for file %s to time
t+1\n\n",filename);
     for (k=1+border;k<=(YY-border);++k)
          for (l=1+border;l<=(XX-border);++l) {
               firstspecies=firstgrid[l][k];
               secondspecies=secondgrid[l][k];
               if (firstspecies==secondspecies)
transition[firstspecies][0]+=1;
               if (firstspecies!=secondspecies)
transition[firstspecies][1]+=1;
               if (firstspecies!=secondspecies)
transition[secondspecies][2]+=1;
               }

     for (m=0;m<numberspecies;++m) {
          counts=number[m];
          if (counts>0) {
               printf("\n%3d. %s   (population at time t
%d)\n",m,speciesname[m],number[m]);
               fprintf(fp,"\n%3d. %s  (population at time t
= %d)\n",m,speciesname[m],number[m]);
          for (n=0;n<3;++n)  {
               prob=transition[m][n];
               if (number[m]>0) {
                    if (prob>0) {
                         prob=(prob/counts);
                         /* if (n==2) prob=(prob/((XX*YY -
counts)); */
                         }
                    printf("\n    %s      %3d
%7.5f",transitiontype[n],transition[m][n],prob);
                    fprintf(fp,"\n    %s      %3d
%7.5f",transitiontype[n],transition[m][n],prob ;
                    }
               }
          }
          change=transition[m][2] transition[m][1]
          if (counts>0) {
               printf("\n  change      %3d n',change -
               fprintf(fp,"\n  change      %3d n',change
               getchar();
               }
```

```
          }
          fprintf(fp,"\n\nEnd of file\n\n");
          fclose(fp);
}



void terminate()          /* exits program structure and
beeps! */

{
     printf("\n\nGoodbye.\n\n\007");
     exit(1);

}



void choice()              /* allows functions from menu
to be selected */

{
     char c;

     c=getchar();
     switch (c) {
          case 'a':
               listgriddata();
               break;
          case 'b':
               cover();
               break;
          case 'c':
               spatialstructure();
               break;
          case 'd':
               transitioncalculate();
               break;
          case 'e':
               convertgriddata();
               break;
          case 'f':
               gridcoordinates();
               break;
          case 'g':
               terminate();
               break;
          default:
               choice();
               break;

     }

}
```

```
void menu()             /* displays list of available
functions */

{
     printf("\n\n\n\n\n\n\n\n\n");
     printf("            ANALYSIS OF VEGETATION GRID DATA
I\n\n");
     printf("                        Basic
functions\n\n\n\n");
     printf("            a           save grid to file\n\n");
     printf("         b              abundance
analysis\n\n");
     printf("         c              spatial structure\n\n");
     printf("         d              transition
analysis\n\n");
     printf("         e         covert to spans format\n\n");
     printf("         f         grid coordinates for
plotting\n\n");
     printf("         g              end\n\n\n");

     choice();
     menu();
}


void speciesnames()      /* speciesnames stored here  */

{
     numberspecies=58;
     strcpy speciesname[0],"Gp");
     strcpy(speciesname[1],"Ac");       /*Agrostis
capillaris*/
     strcpy(speciesname[2],"Ao");  /*Anthoxanthum
odoratum*/
     strcpy(speciesname[3],"Ap");  /*Avenula pratensis*/
     strcpy(speciesname[4],"Bm");  /*Briza media*/
     strcpy(speciesname[5],"Cc");  /*Carex caryophyllea*/
     strcpy(speciesname[6],"Cf");  /*Carex flacca*/
     strcpy(speciesname[7],"Cy");  /*Cynosurus cristatus*/
     strcpy(speciesname[8],"Dg");  /*Dactylis glomerata*/
     strcpy(speciesname[9],"Df");  /*Dactylorhiza fuschii*/
     strcpy(speciesname[10],"Dd"); /*Danthonia decumbens*/
     strcpy(speciesname[11],"Dc"); /*Deschampsia
cespitosa*/
     strcpy(speciesname[12],"Fo"); /*Festuca ovina*/
     strcpy(speciesname[13],"Fr"); /*Festuca rubra*/
     strcpy(speciesname[14],"Hl"); /*Holcus lanatus*/
     strcpy(speciesname[15],"Km"); /*Koeleria macrantha*/
     strcpy(speciesname[16],"Lp"); /*Lolium perenne*/
     strcpy(speciesname[17],"Lc"); /*Luzula campestris*/
     strcpy(speciesname[18],"Pa"); /*Poa annua*/
     strcpy(speciesname[19],"Am"); /*Achillea millefolium*/
     strcpy(speciesname[20],"Ag"); /*Alchemilla glabra*/
     strcpy(speciesname[21],"An"); /*Anenome nemorosa*/
     strcpy(speciesname[22],"Bp"); /*Bellis perennis*/
```

```
     strcpy(speciesname[23],"Cr"); /*Campanula
rotundifolia*/
     strcpy(speciesname[24],"Ca"); /*Carduus nutans*/
     strcpy(speciesname[25],"Cn"); /*Centaurea nigra*/
     strcpy(speciesname[26],"Ce"); /*Cerastium fontanum*/
     strcpy(speciesname[27],"Cm"); /*Conopodium majus*/
     strcpy(speciesname[28],"Cr"); /*Cratageous monogyna*/
     strcpy(speciesname[29],"Eo"); /*Euphrasia
officinalis*/
     strcpy(speciesname[30],"Gv"); /*Galium verum*/
     strcpy(speciesname[31],"Ga"); /*Gentianella amarella*/
     strcpy(speciesname[32],"Hs"); /*Heracleum sphodylium*/
     strcpy(speciesname[33],"Hp"); /*Hieracium pilosella*/
     strcpy(speciesname[34],"Hr"); /*Hypochoeris radicata*/
     strcpy(speciesname[35],"Lm"); /*Lathyrus montanus*/
     strcpy(speciesname[36],"La"); /*Leontondon
autumnalis*/
     strcpy(speciesname[37],"Lh");      /*Leontodon
hispidus*/
     strcpy(speciesname[38],"Li"); /*Linum catharticum*/
     strcpy(speciesname[39],"Lo"); /*Lotus corniculatus*/
     strcpy(speciesname[40],"Pl"); /*Plantago lanceolata*/
     strcpy(speciesname[41],"Po"); /*Polygala vulgaris*/
     strcpy(speciesname[42],"Pe"); /*Potentilla erecta*/
     strcpy(speciesname[43],"Pr"); /*Primula veris*/
     strcpy(speciesname[44],"Pv"); /*Prunella vulgaris*/
     strcpy(speciesname[45],"Ra"); /*Ranunculus acris*/
     strcpy(speciesname[46],"Rb"); /*Ranunculus bulbosus*/
     strcpy(speciesname[47],"Rm"); /*Rhinanthus minor*/
     strcpy(speciesname[48],"Ru"); /*Rumex acetosa*/
     strcpy(speciesname[49],"Sm"); /*Sanguisorba minor*/
     strcpy(speciesname[50],"Sj"); /*Senecio jacobea*/
     strcpy(speciesname[51],"To"); /*Taraxacum officinale
agg.*/
     strcpy(speciesname[52],"Th"); /*Thymus praecox*/
     strcpy(speciesname[53],"Tp"); /*Trifolium pratense*/
     strcpy(speciesname[54],"Tr"); /*Trifolium repens*/
     strcpy(speciesname[55],"Vc"); /*Veronica chaedrys*/
     strcpy(speciesname[56],"Vl"); /*Viola lutea*/
     strcpy(speciesname[57],"Vr"); /*Viola riviniana*/

}


void main ()

{

     setstrings();
     speciesnames();
     menu();
}
```

```
/*********************************************************/
/*                                                       */
/*   VGRID Mk2                                           */
/*                                                       */
/*   Vegetation grid analysis                            */
/*   Fractal analysis and association coefficients       */
/*                                                       */
/*   Andrew McLellan, University of York                 */
/*                                                       */
/*   Last revised 9/9/94                                 */
/*                                                       */
/*********************************************************/


#include <math.h>
#include <stdio.h>
#include <stdlib.h>

enum bool {false, true};
typedef enum bool bool;

#include <string.h>
#include <curses.h>



#define maxX   100
#define maxY   100
#define MAXSTRING   100
#define MAXSPECIES  100
#define XX      40
#define YY      28              /* grid dimensions  */
#define GAP     0               /* defines Gap as species 0
*/


char string[MAXSTRING];

char speciesname[MAXSPECIES][MAXSTRING];

char file[MAXSTRING];
char filename[MAXSTRING];
char filename2[MAXSTRING];
char firstfile[MAXSTRING];
char secondfile[MAXSTRING];

int numberspecies;

int value;        /* for scancheck function  */

int counter;

int target;     /* target species in fractal analysis */

int grid[XX][YY];
int firstgrid[XX][YY];
```

```
int secondgrid[XX][YY];                    /* actual grid
bitmaps  */

int xcoord[300],ycoord[300];          /* 300 is maximum
species abundance  */

int border=2;

long xdir[8] = {-1,-1,-1,0,0,1,1,1};
long ydir[8] = {-1,0,1,-1,1,-1,0,1};            /*
neighbourhood directions  */

int number[MAXSPECIES];
int numbers[MAXSPECIES];                   /* species
abundances  */

int neighbours[MAXSPECIES][MAXSPECIES] = {0};
/* neighbour abundances */

double distance [500][500];          /* distance between two
points */
double frequency[10000];         /* frequency of different
distances */
double finalfreq[10000];
double distancevalue[10000];         /* actual distances */
double logfreq[10000];
double logdist[10000];

int box_size[4]={1,2,4,8};           /* box counting sizes */
int box_freq[4];                 /* box counting frequency */
int number_of_boxes=4;

bool euclidean=true;                 /* distance measuring
technique
                                 false = metric spaces
                                 true  = euclidean */

/* end of global variable declarations  */


/* beginning of function declarations */


void scancheck()            /* checks that entry of species
is valid  */

{
     scanf("%d",&value);
     if (value>=numberspecies) {
          printf("\nGreater than species number please re-
enter: ");
          scancheck();
          }
}
```

```
void getgriddata()              /* takes grid input from
file (when it works)  */

{
     int i,j,k,l;
     int data;
     FILE *ifp;

     printf("\n\nFilename: " );
     getchar();
     gets(filename);
     printf("\nFile for opening: %s\n\n",filename);
     if (ferror(ifp=fopen(filename,"r"))) {
          printf("\n** No such file **");
          getgriddata();
          }
     for (i=1;i<=YY;++i)
          for (j=1;j<=XX;++j) {
          fscanf(ifp,"%2d",&grid[j][i]);
          }

     fclose(ifp ;

}



void coveranalysisii()

{
     int h,i,j;

     for (h=0;h<numberspecies;++h)
          number[h]=0;

     for (i=1;i<=(YY-border*2);++i)
     for (j=1;j<=XX;++j)
          number[grid[j][i]]+=1;

}



void coveranalysis()  /* analyses species abundance  */

{
     int h,i,j;

     for (h=0;h<numberspecies;++h)
```

```
          number[h]=0;


      for (i=1;i<=YY;++i)
      for (j=1;j<=XX;++j)
           number[grid[j][i]]+=1;


}



void cover()

{

     printf("\n\nAbsolute cover analysis\n\n");
     getgriddata();
     printf("\nTarget species: ");
     scanf("%d",&target);
     coveranalysis();

     printf("\n nN (species %d):
%d\n\n",target,number[target]);
     getchar();
     getchar();

}



void spatialstructure()                    /* neighbour contact
analysis  */

{
     int h,i,j,k,l,m,n,p,x,y;
     int expect;
     double expected,abundance,abundances,numberofcells;
        double assoc,adjassoc;
     int targetspecies,neighbourspecies;
     FILE *ofp;

     numberofcells=XX*YY;

        printf("\n\n\n\n");
     printf("Neighbourhood analysis\n\n\n");
     getgriddata();

     strcpy(filename2,file);
     strcat(filename2,".acs");
     printf("\n\nResults will be saved into file
%s\n\n",filename2);

     ofp=fopen(filename2,"w");
     fprintf(ofp,"Association coefficients for file
%s\n",filename);
```

```
        fprintf(ofp,"-------------------------------------
----------\n");


      coveranalysis();

      for (h=0;h<numberspecies;++h)
           numbers[h]=0;


      for (i=0;i<numberspecies;++i)
           for (j=0;j<numberspecies;++j)
                neighbours[i][j]=0;


      for (k=2;k<YY;++k) {
           for (l=2;l<XX;++l) {
                targetspecies=grid[l][k];
                numbers[grid[l][k]]+=1;
           for (m=0;m<8;++m) {           /* looks at
neighbourhood  */
                x=l+xdir[m];
                y=k+ydir[m];
                neighbourspecies=grid[x][y];

      neighbours[targetspecies][neighbourspecies]+=1;
                }

           }
      }

/*    printf("\nSp1    Sp2    N1     N2     Contact    Expected
Ca         Ca(adj)");
      printf("\n---    ---    --     --     -------    --------
--         -------");
*/    fprintf(ofp,"\nSp1    Sp2    N1     N2     Contact
Expected     Ca         Ca(adj)");
      fprintf(ofp,"\n---    ---    --     --     -------    -----
---      --         -------");
      for (n=1;n<numberspecies;++n)
           for (p=1;p<numberspecies;++p) {
                if (number[n]>=5 && number[p]>=5) {
                abundance=numbers[n];
                abundances=number[p];

      expected=((abundance*abundances*8.0)/(numberofcells));
                expect=(int)(expected);

      assoc=((neighbours[n][p]*numberofcells)/(abundance*abu
ndances*8));

adjassoc=((neighbours[n][p]*numberofcells*numberofcells)/(2
.0*(4.0*numberofcells-number[n]-
number[p])*number[n]*number[p]));
 /*             printf ("\n %s     %s    %3d  %3d         %3d
%3d     %6.3f
%6.3f",speciesname[n],speciesname[p],number[n],number[p],ne
ighbours[n][p],expect,assoc,adjassoc);
```

```
 */             fprintf (ofp,"\n %s    %s   %3d  %3d
%3d        %3d    %6.3f
%6.3f",speciesname[n],speciesname[p],number[n],number[p],ne
ighbours[n][p],expect,assoc,adjassoc);
                }
          }
          getchar();
          fclose(ofp);
}


regression_analysis()

{
     int i;
     int N=0;
     double sigmaXY=0,sigmaX=0,sigmaX2=0,sigmaY=0;
     int flag=0;
     double numerator,denominator;
     double slope;

     for (i=0;i<counter;++i) {
          if (logdist[i]<0.7) {
               N+=1;
               sigmaX+=logdist[i];
               sigmaX2+=(logdist[i]*logdist[i]);
               sigmaY+=logfreq[i];
               sigmaXY+=(logdist[i]*logfreq[i]);
               }
          if (logdist[i]<0.2)
               flag=1;
          }


     numerator=(sigmaXY-((sigmaX*sigmaY)/N));
     denominator=(sigmaX2-((sigmaX*sigmaX)/N));

     slope = numerator/denominator;

     printf("\n\nFRACTAL DIMENSION (calculated from linear
regression on %d points)\n\n\n",N);
     if (flag==0) {
          printf("A collection of points not a cluster\n");
          printf("D (cluster dimension) = 0\n\n\n");
          }

     if (flag==1) {
          printf("D (cluster dimension) =
%5.3f/%5.3f\n\n",numerator,denominator);
          printf("                      =
%5.2f\n\n\n",slope);
          }

     getchar();


}
```

```
box_regression_analysis()

{
      int i;
      int N=0;
      double sigmaXY=0,sigmaX=0,sigmaX2=0,sigmaY=0;
      double numerator,denominator;
      double slope;

      N=number_of_boxes;

      for (i=0;i<N;++i) {
                sigmaX+=logdist[i];
                sigmaX2+=(logdist[i]*logdist[i]);
                sigmaY+=logfreq[i];
                sigmaXY+=(logdist[i]*logfreq[i]);
                }



      numerator=0-(sigmaXY-((sigmaX*sigmaY)/N));
      denominator=(sigmaX2-((sigmaX*sigmaX)/N));

      slope = numerator/denominator;

      printf("\n\nFRACTAL DIMENSION (calculated from linear
regression on %d points)\n\n\n",N);

            printf("D (scaling dimension) =
%5.3f/%5.3f\n\n",numerator,denominator);
            printf("                              =
%5.2f\n\n\n",slope);

      getchar();

}


calculate_fractal_dimension()

{

      int i;
      int smallest=0,nextsmallest=1;
      double height,width,slope;

      if (logdist[0]>logdist[1]) {
            smallest=1;
            nextsmallest=0;
            }

      for (i=2;i<counter;++i) {
            if (logdist[i]<logdist[smallest]) {
                  nextsmallest=smallest;
                  smallest=i;
```

```
                }
            if
((logdist[i]<logdist[nextsmallest])&&(logdist[i]>logdist[sm
allest]))
                nextsmallest=i;
            }

      height=logfreq[nextsmallest]-logfreq[smallest];
      width=logdist[nextsmallest]-logdist[smallest];
      slope=(height/width);
      printf("\n\nsmallest distance = %6.4f, frequency =
%6.4f",logdist[smallest],logfreq[smallest]);
      printf("\n\nnext smallest distance = %6.4f, frequency
= %6.4f",logdist[nextsmallest],logfreq[nextsmallest]);
      printf("\n\nheight = %6.4f, width =
%6.4f",height,width);
      if (logdist[smallest]<0.2)
      printf("\n\nFRACTAL DIMENSION = %6.4f\n\n",slope);
      if (logdist[smallest]>0.2)
      printf("\n\nFRACTAL DIMENSION = 0 (collection of
points not a cluster)\n\n");
      getchar();

}



void write_to_file()

{
      FILE *ofp;
      int i,j;
      double occupied_cells;

      occupied_cells=number[target];


/*    printf("\n\nFile for results: ");
      gets(filename2);  */
      strcpy(filename2,"temp");
      ofp=fopen(filename2,"w");

      printf("\n\nResults saved into file %s\n",filename2);

      for (i=0;i<counter;++i) {
            logdist[i]=log10(distancevalue[i]);
            logfreq[i]=log10(finalfreq[i]);
            fprintf(ofp,"\n%6.4f  %6.4f
",logdist[i],logfreq[i]);
            }
      fclose(ofp);

}



void write_boxes_to_file()
```

```
{
     FILE *ofp;
     int i,j;
     double size,freq;


/*   printf("\n\nFile for results: ");
     gets(filename2);    */
     strcpy(filename2,"temp");
     ofp=fopen(filename2,"w");

     printf("\n\nResults saved into file %s\n",filename2);

     for (i=0;i<number_of_boxes;++i) {
          size=box_size[i];
          freq=box_freq[i];
          logdist[i]=log10(size);
          logfreq[i]=log10(freq);
          fprintf(ofp,"\n%6.4f  %6.4f %3d %3d
",logdist[i],logfreq[i],box_size[i],box_freq[i]);
          }
     fclose(ofp);

}


void analyse_data()

{
     int i,j,k,l,m,n,p,q,r;
     int sorted;

     counter=0;

     for (i=0;i<number[target];++i)
     for (j=0;j<number[target];++j)
          if (i>j) {
          if (distance[i][j]>0) {
          sorted=0;
          if (counter==0) {
               distancevalue[0]=distance[i][j];
               counter+=1;
               }
          if (counter!=0) {
          for (k=0;k<counter;++k)
          if (distance[i][j]==distancevalue[k]) sorted=1;
          if (sorted==0) {
               distancevalue[counter]=distance[i][j];
               counter+=1;
               }
          }
     }
     }


     for (l=0;l<10000;++l) {
          frequency[l]=0;
          finalfreq[l]=0;
```

```
          }

     for (m=0;m<counter;++m) {
     for (n=0;n<number[target];++n)
     for (p=0;p<number[target];++p)
          if (n>p) {
          if (distancevalue[m]==distance[n][p])
frequency[m]+=1;
          }
     }

     for (q=0;q<counter;++q)
     for (r=0;r<counter;++r)
          if (distancevalue[q]>=distancevalue[r])
finalfreq[q]+=frequency[r];

     if (number[target]==0) {
          printf("\n\nTarget species not found\n\n");
          getchar();
          }

     if (number[target]>0) {
     write_t _file();
     /* calculate_fractal_dimension(); */
     regression_analysis();
     }

}



void box_counting()

{
     int h,i,j,k,l,m;
     int xloc,yloc;
     int xstep,ystep;
     bool presence;


     printf("\n\n\n\nFractal analysis\n");
     printf("\n(uses box counting)\n\n\n");

     getgriddata();
     coveranalysisii();
     printf("Species to analyse: ");
     scanf("%d",&target);
        printf("\n\nTarget species: %d.%s
(N=%d)\n",target,speciesname[target],number[target]);
        getchar();

     printf("\nCalculating....");



     for (h=0;h<number_of_boxes;++h)
          box_freq[h]=0;
```

```
     for (i=0;i<number_of_boxes;++i) {
          xstep=XX/box_size[i];
          ystep=(YY-(2*border))/box_size[i];
          for (j=0;j<xstep;++j)
          for (k=0;k<ystep;++k) {
               presence=false;
               for (l=1;l<=box_size[i];++l)
               for (m=1;m<=box_size[i];++m) {
                    xloc=j*box_size[i]+l;
                    yloc=k*box_size[i]+m;
                    if (grid[xloc][yloc]==target)
presence=true;
                    }
               if (presence) box_freq[i]+=1;
               }
          }


     write_boxes_to_file();
     box_regression_analysis();


}









void fractalanalysis()

{
     int i,j,k;
     int current=0;
     double xdist,ydist;
     double xval,yval;
     double boundary_distance;
     double boundary[4];


        printf("\n\n\n\n");
     printf("Fractal analysis\n");
     if (euclidean) printf("\n(using euclidean
distance)\n\n");
     if (!euclidean) printf("\n(using metric space
distance)\n\n");
     getgriddata();
        coveranalysis();
     printf("Species to analyse: ");
     scanf("%d",&target);
        printf("\n\nTarget species: %d.%s
(N=%d)\n",target,speciesname[target],number[target]);
        getchar();

     printf("\nCalculating....");
```

```
      for(i=1;i<=XX;++i)
            for(j=1;j<=YY;++j) {
                  if (grid[i][j]==target) {
                              current+=1;
                        xcoord[current]=i;
                        ycoord[current]=j;
                        }
                  }

      for(i=0;i<number[target];++i)
            for(j=0;j<number[target];++j) {
                  if (i>j){
                        xval=xcoord[i];
                        yval=ycoord[i];

      boundary[0]=sqrt((xval*xval)+(yval*yval));
                        boundary[1]=sqrt((xval*xval)+((yval-
YY)*(yval-YY)));
                        boundary[2]=sqrt(((xval-XX)*(xval-
XX))+(yval*yval));
                        boundary[3]=sqrt(((xval-XX)*(xval-
XX))+((yval-YY)*(yval-YY)));
                        boundary_distance=boundary[0];
                        for(k=1;k<=3;++k)
                              if (boundary[k]<boundary_distance)
boundary_distance=boundary[k];
                        xdist=xcoord[i]-xcoord[j];
                        ydist=ycoord[i]-ycoord[j];

            if (euclidean)
distance[i][j]=sqrt((xdist*xdist)+(ydist*ydist)); /*
calculates euclidean distance

      using pythagoras */
            if (!euclidean) {
                  if (ydist>=xdist) distance[i][j]=ydist;
                  /* calculates metric distance */
                  if (ydist<xdist) distance[i][j]=xdist;

                  }

                  if (distance[i][j]>boundary_distance) {
                        distance[i][j]=0;
                        }
                  }
                   }
                  analyse_data();

}


void terminate()           /* exits program structure and
beeps! */

{
      printf("\n\nGoodbye.\n\n\007");
      exit(1);
```

```
}



void choice()                /* allows functions from menu
to be selected */

{
     char c;

     c=getchar();
     switch (c) {
          case 'a':
               spatialstructure();
               break;
          case 'b':
               fractalanalysis();
               break;
          case 'c':
               box_counting();
               break;
          case 'd':
               cover();
               break;
          case 'e':
               terminate();
               break;
          default:
               choice();
               break;

     }

}



void menu()             /* displays list of available
functions */

{
        printf("\n\n\n\n\n\n\n\n\n\n\n\n");
     printf("                    ANALYSIS OF VEGETATION GRID
DATA II\n\n");
        printf("              Fractal analysis and
association coefficients\n\n\n\n");
     printf("            a           Association
coefficients\n\n");
     printf("            b        Fractal analysis
(correlation dimension)\n\n");
     printf("       c        Fractal analysis (box
counting)\n\n");
     printf("       d        Absolute cover analysis\n\n");
     printf("       e        End\n\n\n");

     choice();
```

```
     menu();
}


void speciesnames()      /* speciesnames stored here  */

{
     numberspecies=58;
     strcpy(speciesname[0],"Gap");
     strcpy(speciesname[1],"Ac");       /*Agrostis
capillaris*/
     strcpy(speciesname[2],"Ao");  /*Anthoxanthum
odoratum*/
     strcpy(speciesname[3],"Ap");  /*Avenula pratensis*/
     strcpy(speciesname[4],"Bm");  /*Briza media*/
     strcpy(speciesname[5],"Cc");  /*Carex caryophyllea*/
     strcpy(speciesname[6],"Cf");  /*Carex flacca*/
     strcpy(speciesname[7],"Cy");  /*Cynosurus cristatus*/
     strcpy(speciesname[8],"Dg");  /*Dactylis glomerata*/
     strcpy(speciesname[9],"Df");  /*Dactylorhiza fuschii*/
     strcpy(speciesname[10],"Dd"); /*Danthonia decumbens*/
     strcpy(speciesname[11],"Dc"); /*Deschampsia
cespitosa*/
     strcpy(speciesname[12],"Fo"); /*Festuca ovina*/
     strcpy(speciesname[13],"Fr"); /*Festuca rubra*/
     strcpy(speciesname[14],"Hl"); /*Holcus lanatus*/
     strcpy(speciesname[15],"Km"); /*Koeleria macrantha*/
     strcpy(speciesname[16],"Lp"); /*Lolium perenne*/
     strcpy(speciesname[17],"Lc"); /*Luzula campestris*/
     strcpy(speciesname[18],"Pa"); /*Poa annua*/
     strcpy(speciesname[19],"Am"); /*Achillea millefolium*/
     strcpy(speciesname[20],"Ag"); /*Alchemilla glabra*/
     strcpy(speciesname[21],"An"); /*Anenome nemorosa*/
     strcpy(speciesname[22],"Bp"); /*Bellis perennis*/
     strcpy(speciesname[23],"Cr"); /*Campanula
rotundifolia*/
     strcpy(speciesname[24],"Ca"); /*Carduus nutans*/
     strcpy(speciesname[25],"Cn"); /*Centaurea nigra*/
     strcpy(speciesname[26],"Ce"); /*Cerastium fontanum*/
     strcpy(speciesname[27],"Cm"); /*Conopodium majus*/
     strcpy(speciesname[28],"Cr"); /*Cratageous monogyna*/
     strcpy(speciesname[29],"Eo"); /*Euphrasia
officinalis*/
     strcpy(speciesname[30],"Gv"); /*Galium verum*/
     strcpy(speciesname[31],"Ga"); /*Gentianella amarella*/
     strcpy(speciesname[32],"Hs"); /*Heracleum sphodylium*/
     strcpy(speciesname[33],"Hp"); /*Hieracium pilosella*/
     strcpy(speciesname[34],"Hr"); /*Hypochoeris radicata*/
     strcpy(speciesname[35],"Lm"); /*Lathyrus montanus*/
     strcpy(speciesname[36],"La"); /*Leontondon
autumnalis*/
     strcpy(speciesname[37],"Lh");      /*Leontodon
hispidus*/
     strcpy(speciesname[38],"Li"); /*Linum catharticum*/
     strcpy(speciesname[39],"Lo"); /*Lotus corniculatus*/
     strcpy(speciesname[40],"Pl"); /*Plantago lanceolata*/
     strcpy(speciesname[41],"Po"); /*Polygala vulgaris*/
```

```
      strcpy(speciesname[42],"Pe"); /*Potentilla erecta*/
      strcpy(speciesname[43],"Pr"); /*Primula veris*/
      strcpy(speciesname[44],"Pv"); /*Prunella vulgaris*/
      strcpy(speciesname[45],"Ra"); /*Ranunculus acris*/
      strcpy(speciesname[46],"Rb"); /*Ranunculus bulbosus*/
      strcpy(speciesname[47],"Rm"); /*Rhinanthus minor*/
      strcpy(speciesname[48],"Ru"); /*Rumex acetosa*/
      strcpy(speciesname[49],"Sm"); /*Sanguisorba minor*/
      strcpy(speciesname[50],"Sj"); /*Senecio jacobea*/
      strcpy(speciesname[51],"To"); /*Taraxacum officinale
agg.*/
      strcpy(speciesname[52],"Th"); /*Thymus praecox*/
      strcpy(speciesname[53],"Tp"); /*Trifolium pratense*/
      strcpy(speciesname[54],"Tr"); /*Trifolium repens*/
      strcpy(speciesname[55],"Vc"); /*Veronica chaedrys*/
      strcpy(speciesname[56],"Vl"); /*Viola lutea*/
      strcpy(speciesname[57],"Vr"); /*Viola riviniana*/

}


void main ()

{
      speciesnames();
      menu();
}
```

```
/*********************************************************/
/*                                                       */
/*   VGRID Mk3                                           */
/*                                                       */
/*   Vegetation grid analysis                            */
/*   Mean clump size                                     */
/*                                                       */
/*   Andrew McLellan, University of York                 */
/*                                                       */
/*   Last revised 15/7/94                                */
/*                                                       */
/*********************************************************/


#include <math.h>
#include <stdio.h>
#include <stdlib.h>
#include <string.h>


#define MAXSTRING   100
#define MAXSPECIES  100
#define XX      40
#define YY     28        /* grid dimensions  */
#define GAP    0         /* defines Gap as species 0  */


/*  Global variable definitions  */

char string[MAXSTRING];

char speciesname[MAXSPECIES][MAXSTRING];

char filename[MAXSTRING];

int number_species;
int target_species;
int clump_number;
int target_clump;
int error_clump;
int frequency[500];
double mean,variance;

int grid[XX][YY];
int clump[XX][YY];
int presence[XX][YY];

long xdir[8] = {1,-1,0,-1,1,1,-1,0};
long ydir[8] = {-1,-1,-1,0,1,0,1,1};          /*
neighbourhood directions  */

int border=2;


/*  Begin function declaration  */
```

```
void get_grid_data()              /* takes grid input from
file (when it works)  */

{
     int i,j,k,l;
     int data;
     FILE *ifp;

     getchar();
        printf("\nfilename: ");
     gets(filename);
     if((ifp=fopen(filename,"r"))==NULL) {
          printf("\nFile not found\n");
          }


     for (i=1;i<=YY;++i)
          for (j=1;j<=XX;++j) {
          fscanf(ifp,"%d",&data);
          grid[j][i]=data;              /* puts data into
bitmap  */
          }


     fclose(ifp);

}



void zero_grid(

{
     int i,j;

     for (i=1;i<=XX;++i)
     for (j=1;j<=YY;++j) {
          clump[i][j]=0;
               presence[i][j]=0;
          }
}




void adjust_clump_structure(clump_error_number)

{
     int i,j;

     for (i=1+border;i<=(XX-border);++i)
     for (j=1+border;j<=(YY-border);++j)
          if (clump[i][j]==clump_error_number)
clump[i][j]=target_clump;
          if (clump[i][j]>clump_error_number)
clump[i][j]=clump[i][j]-1;
```

```
}


void check_track_clumps()

{
     int i,j,k;
     int x_coord,y_coord;
     int clump_error=0;

     for (i=1+border;i<=(XX-border);++i)
     for (j=1+border;j<=(YY-border);++j) {
          if (clump[i][j]>0)
               for (k=4;k<8;++k) {
               x_coord=i+xdir[k];
               y_coord=j+ydir[k];
               if ((x_coord<=XX)&&(x_coord>=1))
               if ((y_coord<=YY)&&(y_coord>=1))
                         if (clump[x_coord][y_coord]>0)
                    if
(clump[x_coord][y_coord]!=clump[i][j]) {
                          clump_error=1;
                          if
(clump[i][j]<clump[x_coord][y_coord]) {
                                target_clump=clump[i][j];

     error_clump=clump[x_coord][y_coord];
                                                }
                           if
(clump[i][j]>clump[x_coord][y_coord]) {
                                error_clump=clump[i][j];

     target_clump=clump[x_coord][y_coord];
                                                }

     adjust_clump_structure(error_clump);
                          }
                    }
               }

     if (clump_error==1) check_track_clumps();

}




void track_clumps()

{
     int i,j,k;
        int x_coord,y_coord;
     int neighbours;
```

```
        clump_number=0;

      for (i=1+border;i<=(XX-border);++i)
      for (j=1+border;j<=(YY-border);++j) {

              neighbours=0;
          if (grid[i][j]==target_species) {
               presence[i][j]=1;
               for (k=0;k<4;++k) {
                   x_coord=i+xdir[k];
                   y_coord=j+ydir[k];

                   if((x_coord>=1) && (y_coord>=1))
                   if((x_coord<=XX) && (y_coord<=YY)) {

                   if (clump[x_coord][y_coord]>1) {
                    clump[i][j]=clump[x_coord][y_coord];
                    neighbours=1;
                    }
                   }
               }

                   if (neighbours==0) {
                    clump_number+=1;
                    clump[i][j]=clump_number;
                    }
               }
          }

      check_track_clumps();

}



void print_clump_distribution()

{
      int i,j;
      FILE *ofp;


      ofp=fopen("clump.txt","w");

         fprintf(ofp,"\nClump distribution for species %s,
file %s\n\n",speciesname[target_species],filename);

      for (j=1;j<=YY;++j) {
      for (i=1;i<=XX;++i)
           fprintf(ofp,"%3d",clump[i][j]);
           fprintf(ofp,"\n");
           }

         fclose(ofp);
```

```
}

void print_species_distribution()

{
     int i,j;
     FILE *ofp;


     ofp=fopen("dist.txt","w");

        fprintf(ofp,"\nDistribution of species %s, file
%s\n\n",speciesname[target_species],filename);

     for (j=1+border;j<=(YY-border);++j) {
     for (i=1+border;i<=(XX-border);++i)
          fprintf(ofp,"%3d",presence[i][j]);
          fprintf(ofp,"\n");
          }

        fclose(ofp);

}



void draw_hist gram(max_clump)

{
     int i,j;

        printf("\n\nHistogram for clump distribution of
species %s\n\n",speciesname[target_species]);
     for (i=1;i<=max_clump;++i) {
          printf("\n%3d  ",i);
          if (frequency[i]>0) {
          for (j=1;j<=frequency[i];++j)
               printf("*");
               }
          }

                printf("\n\nMean = %6.4f\nS.D. =
%6.4f\n\n",mean,variance);

}
```

```
void calculate_statistics()

{

     int clump_size[500];
     double number_of_clumps=0,count=0,squared_count=0;

     int max_clump_size=0;
     int h,i,j,k;
     double temp;

     for (h=0;h<500;++h) {
          clump_size[h]=0;
          frequency[h]=0;
          }

     mean=0,variance=0;

     for (i=1+border;i<=(XX-border);++i)
     for (j=1+border;j<=(YY-border);++j)
          clump_size[clump[i][j]]+=1;


     for (k=1;k<=clump_number;++k) {
          if (clump_size[k]>0) number_of_clumps+=1;
          count+=clump_size[k];

squared_count+=(clump_size[k]*clump_size[k]);
          if (clump_size[k]>max_clump_size)


max_clump_size=clump_size[k];
                frequency[clump_size[k]]+=1;
          }

     mean=(count number_of_clumps);

        temp=(( squared_count)-
((count*count)/number_of_clumps))/(number_of_clumps-1));

        variance=sqrt(temp);

     draw_histogram(max_clump_size);
     getchar();
     getchar();

}




void select_species()

{
     printf("\nSpecies for analysis: ");
     scanf("%2d",&target_species);
```

```
     if (target_species>57) select_species();

}



void clump_analysis()

{

        printf("\n\nClump analysis\n--------------\n\n");
     get_grid_data();
     select_species();
        zero_grid();
     track_clumps();
     print_clump_distribution();
     print_species_distribution();
     printf("\n\nResults stored in file clump.txt\n\n");
        calculate_statistics();

}



void terminate(              /* exits program structure and
beeps! */

{
     printf(" 007");
     exit(1);

}



void choice()                /* allows functions from menu
                                to be selected */

{
     char c;

     c=getchar();
     switch (c) {
          case 'a':
               clump_analysis();
               break;
          case 'b':
               terminate();
               break;
          default:
               choice();
               break;

     }
```

```
}



void menu()             /* displays list of available
                           functions */

{

        printf("\n\n\n\n");
     printf("                    ANALYSIS OF VEGETATION GRID
DATA III\n\n");
     printf("                              Clump size
analysis\n\n\n\n");
     printf("            a           Clump analysis\n\n");
     printf("            b         End\n\n\n");

     choice();
     menu();
}



void set_species_names()      /* speciesnames stored here
*/

{
     number_species=58;
     strcpy(speciesname[0],"Gp");
     strcpy(speciesname[1],"Ac");       /*Agrostis
capillaris*/
     strcpy(speciesname[2],"Ao");  /*Anthoxanthum
odoratum*/
     strcpy(speciesname[3],"Ap");  /*Avenula pratensis*/
     strcpy(speciesname[4],"Bm");  /*Briza media*/
     strcpy(speciesname[5],"Cc");  /*Carex caryophyllea*/
     strcpy(speciesname[6],"Cf");  /*Carex flacca*/
     strcpy(speciesname[7],"Cy");  /*Cynosurus cristatus*/
     strcpy(speciesname[8],"Dg");  /*Dactylis glomerata*/
     strcpy(speciesname[9],"Df");  /*Dactylorhiza fuschii*/
     strcpy(speciesname[10],"Dd"); /*Danthonia decumbens*/
     strcpy(speciesname[11],"Dc"); /*Deschampsia
cespitosa*/
     strcpy(speciesname[12],"Fo"); /*Festuca ovina*/
     strcpy(speciesname[13],"Fr"); /*Festuca rubra*/
     strcpy(speciesname[14],"Hl"); /*Holcus lanatus*/
     strcpy(speciesname[15],"Ko"); /*Koeleria macrantha*/
     strcpy(speciesname[16],"Lp"); /*Lolium perenne*/
     strcpy(speciesname[17],"Lc"); /*Luzula campestris*/
     strcpy(speciesname[18],"Pa"); /*Poa annua*/
     strcpy(speciesname[19],"Am"); /*Achillea millefolium*/
     strcpy(speciesname[20],"Ag"); /*Alchemilla glabra*/
```

```
      strcpy(speciesname[21],"An"); /*Anenome nemorosa*/
      strcpy(speciesname[22],"Bp"); /*Bellis perennis*/
      strcpy(speciesname[23],"Cr"); /*Campanula
 rotundifolia*/
      strcpy(speciesname[24],"Ca"); /*Carduus nutans*/
      strcpy(speciesname[25],"Cn"); /*Centaurea nigra*/
      strcpy(speciesname[26],"Ce"); /*Cerastium fontanum*/
      strcpy(speciesname[27],"Cm"); /*Conopodium majus*/
      strcpy(speciesname[28],"Cr"); /*Cratageous monogyna*/
      strcpy(speciesname[29],"Eo"); /*Euphrasia
 officinalis*/
      strcpy(speciesname[30],"Gv"); /*Galium verum*/
      strcpy(speciesname[31],"Ga"); /*Gentianella amarella*/
      strcpy(speciesname[32],"Hs"); /*Heracleum sphodylium*/
      strcpy(speciesname[33],"Hp"); /*Hieracium pilosella*/
      strcpy(speciesname[34],"Hr"); /*Hypochoeris radicata*/
      strcpy(speciesname[35],"Lm"); /*Lathyrus montanus*/
      strcpy(speciesname[36],"La"); /*Leontondon
 autumnalis*/
      strcpy(speciesname[37],"Lh");      /*Leontodon
 hispidus*/
      strcpy(speciesname[38],"Li"); /*Linum catharticum*/
      strcpy(speciesname[39],"Lo"); /*Lotus corniculatus*/
      strcpy(speciesname[40],"Pl"); /*Plantago lanceolata*/
      strcpy(speciesname[41],"Po"); /*Polygala vulgaris*/
      strcpy(speciesname[42],"Pe"); /*Potentilla erecta*/
      strcpy(speciesname[43],"Pr"); /*Primula veris*/
      strcpy(speciesname[44],"Pv"); /*Prunella vulgaris*/
      strcpy(speciesname[45],"Ra"); /*Ranunculus acris*/
      strcpy(speciesname[46],"Rb"); /*Ranunculus bulbosus*/
      strcpy(speciesname[47],"Rm"); /*Rhinanthus minor*/
      strcpy(speciesname[48],"Ru"); /*Rumex acetosa*/
      strcpy(speciesname[49],"Sm"); /*Sanguisorba minor*/
      strcpy(speciesname[50],"Sj"); /*Senecio jacobea*/
      strcpy(speciesname[51],"To"); /*Taraxacum officinale
 agg.*/
      strcpy(speciesname[52],"Th"); /*Thymus praecox*/
      strcpy(speciesname[53],"Tp"); /*Trifolium pratense*/
      strcpy(speciesname[54],"Tr"); /*Trifolium repens*/
      strcpy(speciesname[55],"Vc"); /*Veronica chaedrys*/
      strcpy(speciesname[56],"Vl"); /*Viola lutea*/
      strcpy(speciesname[57],"Vr"); /*Viola riviniana*/

}
```

```
/*  Begin main program loop  */

void main()

{

     set_species_names();
     menu();

}
```

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