OLD-FIELD SUCCESSION IN THE HIGH TROPICAL ANDES

Ecophysiology, local spatial interactions and plant community development

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Abstract

This thesis analyses vegetation regeneration in agricultural old-fields of the Venezuelan high Andes (páramos). Patterns of change in plant community structure in fallow fields in different stages of succession are quantified. Then, processes influencing changes in abundance of the dominant species are explored through the use of ecophysiological and demographic analyses and a plant-centred perspective on spatio-temporal processes. The results indicate that regeneration of vegetation physiognomy is relatively fast, with most dominant species colonising shortly after plot abandonment. However, the species richness of the mature ecosystem is not restored during the fallow times currently used by farmers. Comparative ecophysiological analysis supports the hypothesis that traits associated with fast growth (i.e. high photosynthesis and specific leaf area) are important for dominance during early succession, while traits associated with water stress resistance (e.g. high water use efficiency) are important during late seral stages. Successional changes in the spatial structure of the community as experienced by the dominant giant rosette species (*Espeletia schultzii*) are quantified using plant-centred spatial analysis techniques. A decrease in spatial aggregation between seedlings in early succession and adults in late succession suggests density-dependent regulation of population size. In addition, a successional increase in spatial segregation between *E. schultzii* and the dominant pioneer species (*Rumex acetosella*) suggests that competitive interactions could be involved in the decline of this introduced forb. However, the analysis of fine-scale spatio-temporal dynamics in permanent plots, indicates that late successional species (giant rosettes and shrubs) have a positive effect on the local drought-induced probability of mortality of *R. acetosella*. This emphasizes the potential contribution of late successional species on facilitating the long-term persistence of pioneer species, and the importance of analysing local neighbourhood interactions for understanding succession.

Contents

List of Figures

List of Tables

List of Plates

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Author's Declaration

Chapter 2 is based on collaborative research with Dr. Lina Sarmiento (ICAE, Universidad de los Andes) in the context the project coordinated by her: "*Effect of the fallow length, the successional vegetation and the grazing intensity on the soil fertility restoration in fallow agriculture of the high Venezuelan Andes*". The data on plant community structure used in this chapter was collected by L. Sarmiento (ICAE, Universidad de los Andes), technical staff from the ICAE (mainly N. Marquez) and myself in 1996. All data analysis for this chapter was done entirely by myself (based on previous work and discussions with L. Sarmiento). A paper based on an extended data set, including three further years of sampling has been accepted for publication in *Plant Ecology* (Appendix A): "*Sarmiento, L. Llambi, L.D. Escalona A. and N. Marquez. Vegetation patterns, regeneration rates and divergence in an old-field succession of the high Tropical Andes*". I made a substantial contribution to the data analysis and writing of this paper.

The soil physico-chemical data used in Chapter 2 was collected during my BA. Dissertation (Universidad Simón Bolívar) supervised by L. Sarmiento, and was subsequently published in: "*Llambí, L.D. and L. Sarmiento. 1998. Biomasa microbiana y otros parámetros edáficos en una sucesión secundaria en el páramo. Ecotrópicos 11: 1-14*".

Chapter 3 is based on collaborative research with Prof. Bernard Saugier, Magali Fontaine (Laboratoire d'Ecologie Végétale, University of Paris – Sud) and Dr. Fermin Rada (ICAE, Universidad de los Andes) as part of the TROPANDES (INCO-DC) project: "*Fertility Management in Tropical Andean Mountains: Agroecological Bases for a Sustainable Fallow Agriculture*". Data was collected by M. Fontaine (as part of her DEA dissertation), F. Rada and myself (except for the wet season data which was collected without my participation). The data analysis and writing up of this chapter was done entirely by myself. This chapter has been submitted for publication in *Arctic, Antarctic and Alpine Research*: "*Llambi, L.D. Fontaine, M. Saugier, B. Rada, F. and L. Sarmiento. Ecophysiology of dominant plant species during old-field succession in a high tropical Andean ecosystem*".

All other work described in this thesis was carried out entirely by myself.

Chapter 1. Introduction

In this chapter, a brief review of the conceptual development of the two areas of plant ecology that constitute the framework for this thesis is presented: succession theory and spatial ecology. In both cases, the emergence of a process-oriented, individualistic and plant-centred approach is emphasized. Then, the importance of old-fields research for the development of succession theory is summarized, drawing attention to the limited information available for the high tropical Andes. A synthetic view of these environments is presented, drawing attention to their unique ecological characteristics and the challenges for conservation posed by recent changes in their use for agricultural production. Finally, the general objectives and structure of the thesis are presented.

1.1 THEORETICAL BACKGROUND

1.1.1 Succession theory: from holism and reductioninsm to a mechanistic synthesis

The study of plant succession is a classic subject in ecology, and one of the most hotly debated areas in the discipline. There has been a long-standing divide across the literature between a holistic ecosystem approach and an individualistic population-community oriented approach (McIntosh 1981; Finegan 1984; McCook 1994). The ecosystem perspective has emphasised the study of emergent properties, such as the development of biological control over nutrient cycling in succession. Within this line of research, succession was traditionally perceived as an essentially autogenic and deterministic process that occurs as invasion waves in distinct stages (i.e. relay floristics) converging to a self-regulating climax. Moreover, colonization of late species was seen to be mainly facilitated by environmental change induced by early species (Clements 1916, 1936).

The ecosystem perspective on succession was consolidated by Odum (1969) in his classic work on the 'strategy of ecosystem development'. He proposed a set of tendencies to be expected during ecosystem regeneration, including a decrease in net primary productivity and an increase in soil organic matter, species diversity, and biotic immobilization of inorganic nutrients. This approach has subsequently integrated developments from community ecology, providing insights into problems such as the development of mechanisms of nutrient retention during forest succession (e.g. Jordan and Herrera 1980; Jordan 1985) and the functional importance of symbiotic interactions like nitrogen fixation (e.g. Ritchie and Tilman 1995) or mycorrhizal networks (e.g. Johnson *et al.* 1991).

By contrast, the 'individualistic' perspective regards succession as a process of continous changes in species abundances with no clearly defined stages (Gleason 1927; Pickett 1982), emphasizing the analysis of changes in the structure and dynamic responses of individual populations (Peet and Christensen 1980; Falinska 1991). Changes in species abundance during succession are perceived to be fundamentally the result of the processes of reproduction, dispersal, establishment, growth and mortality of individuals, and their intra- and inter-specific interactions (Peet and Christensen 1980; Pickett 1982; Falinska 1991; van der Valk 1992).

The population oriented approach has its roots in Gleason's (1926) individualistic view of community structure and Egler's (1954) 'initial floristic composition' hypothesis (see also Drury and Nisbet 1973). This hypothesis states that subsequent successional dynamics are strongly influenced by the initial structure of the plant community after disturbance, so that failure to colonize in early seral stages (when competition is assumed to be less intense) can reduce the chance of a species of becoming dominant in late seral stages. Hence, differences in initial conditions, as a result of spatial heterogeneity or stochastic events (e.g. stochastic colonization), can lead to divergence in community structure later in succession (see Horn 1976, 1981; Peet and Christensen 1980; Sousa 1984; Johnstone 1986; Glenn-Lewin and van der Maarel 1992). The recognition of this possibility has been central in the reevaluation of traditional notions of 'mature' or 'climax' communities as systems in a stable, deterministic equilibrium, emphasizing the role of historical contingency, local patch dynamics, non-linear dynamics and stochastic variation (Samuels and Drake 1997).

Another development stimulated by the individualistic perspective was the proposal by Connell and Slatyer (1977) of the facilitation, tolerance and inhibition mechanisms of succession. They indicated that the establishment of late successional (LS) species could be the result of their tolerance to the presence of early successional (ES) species without any positive facilitation effect. Moreover, they suggested that ruderal species could also have a negative or inhibitory effect on LS species. Further research has emphasized the possibility for the simultaneous operation of all three mechanisms (Pickett *et al.* 1989) and has shown that facilitation is common during primary succession in volcanic areas or recently deglaciated terrains (Matthews 1992; del Moral and Wood 1993; Chapin *et al.* 1994). Nevertheless, the role of both positive and negative intra-specific interactions in old-field successions in the highland tropics remains largely unexplored.

One of the central ideas of the individualistic perspective has been what McCook (1994) calls the 'strategic resource allocation concept': allocation of limited resources to different physiological functions generally involves trade-offs. As any organism cannot be simultaneously well adapted to all conditions, there should be adaptive strategies with contrasting life history and physiological traits in plants from different ends of the successional continuum. This idea has stimulated substantial research efforts in identifying the characteristic life-history strategies or 'vital attributes' (*sensu* Noble and Slatyer 1980) of species of different successional stages. Some of the traits found to be generally associated with ES species are: fast growth rates, high reproductive allocation and dispersal ability, short life cycles and small maximal heights (Drury and Nisbet 1973; Noble and Slatyer 1980). This concept has also stimulated research on the ecophysiology of successions, particularly in terms of the comparative analysis of characteristics associated with shade-intolerant early successional vs. shade-tolerant late successional species in lowland forest ecosystems (see Bazzaz,1979; Bazzaz and Pickett 1980; Bazzaz 1996). However, there is very limited information on the ecophysiology of successions in highland open ecosystems, where differences in light availability are unlikely to drive succession (see Chapter 3).

A central element for an synthesis of holistic and individualistic perspectives into a mechanistic theory has been the understanding of succession as a 'gradient in time' (Peet and Christensen 1980), specially in terms of resource availability. Three premises are at the basis of this integrated view (Huston and Smith 1987; Tilman 1993): (1) there are one or more factors that constrain growth and survival of plants; (2) plants face trade-offs in their abilities to compete and survive under these limiting factors; and (3) there are successional changes in the availability of these factors, partially as a result of their utilization by organisms themselves (e.g. light becomes more limiting in forests after the tree colonization). This can explain changes in community structure as different combinations of resource levels will differentially favour species of contrasting strategies. Furthermore, MacMahon (1981) emphasized that in different environments the resource gradients driving succession will not necessarily be the same (e.g. light and nutrients in forests, water and nutrients in deserts).

On the basis of the above considerations, Tilman (1990; 1993) proposed a set of hypotheses on the mechanisms driving successional change (see also Grime 1979; Smith and Huston 1989). These can be divided into two main groups (Rees *et al.* 2001):

(1) *The colonization-competition hypothesis*: early dominance is determined by the ability to rapidly colonize disturbed areas (because of high fecundity and long dispersal). However, these characteristics result in a poor competitive ability under limiting resource levels (e.g. light, nutrients or water), because higher allocation to reproductive structures (e.g. numerous seeds) results in lower allocation to resource capture and conservation. In the high tropical Andes, the presence of most dominant species from early seral stages suggests colonization ability is not likely to be a key factor for early dominance (see Chapter 2).

(2) *The maximum growth rate hypothesis*: in unproductive environments, where most species are present from early seral stages, early dominance is determined by the ability to grow fast. However, allocation to characteristics that allow fast growth such as high leaf area and photosynthetic capacity can result in limited competitive ability under low resource levels (e.g. low leaf longevity and limited nutrient conservation ability) or a higher susceptibility to herbivore or pest attack. The limited research in cold unproductive environments (e.g. tundra and alpine) offers an unclear picture on the ecophysiological characteristics associated with differences in growth rate between ES and LS species. Hence, the applicability of this hypothesis to tropical mountain environments is explored in Chapter 3.

1.1.2 Spatial ecology and successions: from patterns to processes

The analysis of the spatial structure of plant populations and communities has a long history in ecology. Much of this research was traditionally oriented towards the static description of the intensity and scale of spatial patterns, to then try to identify the factors responsible for their generation. Hence, a lot of emphasis was placed on the development of statistical techniques for the description of spatial structure and spatial associations (see Kershaw 1954; Greith-Smith 1964, 1983; Burrough 1999; Dale 1999). One of the main conclusions from this kind of analysis is that most plant species show spatial aggregation (i.e. a patchy or clumped distribution), with both random and regular patterns being relatively rare (Pacala 1997; Law *et al.* 2001). However, there has been a progressive decline in interest on this line of research, as it has produced limited insights into the process that determine vegetation dynamics (van der Maarel 1996a).

In recent years, there has been a paradigm shift placing spatial analysis right at the centre of plant ecology: spatial structure being taken not as a pattern to explain but as an essential element for understanding population and community dynamics. This conceptual shift has been based on the recognition that plant survival and growth are essentially determined by the interaction with other plants and environmental conditions within a small-scale neighbourhood around an individual (Mack and Harper 1977; Pacala and Silander 1990). Moreover, dispersal of propagules from a mother plant is usually limited to relatively short distances (Howe and Westley 1997). Hence, the usual non-random local spatial structure of natural populations and communities is likely to have an effect on vegetation dynamics. Spatial aggregation of conspecifics and heterospecifics results in a individual within a patch 'perceiving' higher densities than would be predicted by the calculation of the mean number of individuals across an area of interest, and hence, more opportunities for positive and negative interactions to take place (the 'plant's eye view' of Turkington and Harper 1977). In contrast, segregation should produce the opposite effect. Furthermore, these interactions can themselves change the spatial structure of the community. For example, intense inter-specific competition will tend to produce spatial segregation of heterospecifics, while local reproduction and dispersal will tend to increase conspecific aggregation. Hence, spatial structure and population-community structure should be dynamically linked, a fact that has often been assumed unimportant in the development of ecological theory.

Recent theoretical and experimental studies have demonstrated the link between spatial patterns and vegetation processes. Simulations by Law and Dieckmann (2000), based on a spatial version of the logistic equation, have shown that the interaction of local competition and dispersal can have large effects: a more limited dispersal range resulted in an increase in aggregation and a lower final density than predicted from the non-spatial model (all other things being equal); a more local scale for intra-specific competition resulted in more segregation and a higher final density. Another example is a recent experiment by Stoll and Prati (2001), which provides evidence on the potential effects of spatial structure for species coexistence. Four annual species in monocultures and mixtures were sown in a random pattern or with spatial aggregation of conspecifics. The results showed that the spatial structure strongly affected the outcome, with the weaker competitors greatly improving their performance when conspecifics were spatially aggregated.

In the context of successional research, the traditional static and descriptive approach to spatial structure has been dominant. It has concentrated on evaluating questions such as Greig-Smith's (1964) hypothesis that succession is accompanied by an increase in the scale of aggregations and a decrease in the intensity of aggregation (e.g. Anderson 1967; Brerenton, 1971; Yarranton and Morrison 1974; Dale and Blundon 1990; Schaefer 1993). The evaluation of this hypothesis has produced little more than a set of characterizations of vegetation spatial structure in successional environments. However, in recent years, a more process oriented perspective has started to develop , associated to an individualistic view of succession. This perspective has been based on the application of the new 'plant-centred' view to the analysis of the role of plant-plant interactions on successional dynamics in the field two main approaches have been used:

(1) Based on the link between local neighbourhood interactions and changes in spatial structure, some studies have used a comparative analysis of spatial patterns in different stages of succession to infer the operation of intra- and inter-specific interactions, specially competition (e.g. Frelich *et al.* 1993; Frelich and Reich 1995; Rejmanek and Leps 1996; Haase *et al.* 1997; Eshel *et al.* 2000; He and Duncan

2000). This is the strategy explored in Chapter 4. For example, the loss of spatial aggregation from seedlings in early stages of succession to adults in late seral stages has been seen to suggest density dependent regulation of population dynamics (e.g. Sterner *et al.* 1986; Gavin and Peart 1997).

(2) Recent studies have emphasized that a more direct link between spatial pattern and the underlying processes can be derived from an analysis of small-scale spatial dynamics in permanent plots. As the strength of plant-plant interactions is dependent on distance, the comparison of the local colonization and extinction probabilities of plants with different neighbourhood structure (in terms of conspecific and heterospecific abundances), can shed additional light into the processes of competition and species replacements (e.g. Thorhallsdottir 1990; Herben *et al.* 1993, 1995; Law *et al.* 1993; van der Maarel and Sykes 1993; Willems *et al.* 1993; Sykes *et al.* 1994; McLellan 1995; Rees *et al.* 1996). However, this approach has rarely been applied in the context of successional research (but see Partel and Zobel 1995; Ramsay and Oxley 1996) This is the strategy explored in Chapter 5.

1.1.3 Secondary succession in old-fields

The analysis of secondary succession in old-fields has been central to the development of succession theory (Pickett 1980; Finegan 1984). Agricultural disturbance and the subsequent regeneration of vegetation in abandoned areas, could be seen as one of the largest sets of 'field experiments' available to ecologists. The continuing fascination with the study of old-field succession seems to stem from: (1) the remarkable consistency across different ecosystems, in some patters of community structure change during succession (e.g. the characteristic sequence of change in the abundance of different life forms; the increase in evenness in the relative abundance of species). (2) the insights that the understanding of the mechanisms generating these patterns provide into the processes that determine the assembly, structuring and functioning of ecosystems; (3) the value of this knowledge for the design of strategies for natural resource conservation, restoration and management.

Substantial research efforts have been dedicated to analyse soil nutrient dynamics and vegetation regeneration in temperate ecosystems, and in the case of the tropics in lowland 'old-field to forest' systems (e.g. Aweto 1981; Uhl *et al.* 1982; Jordan *et al.* 1983; Mesquita *et al.* 2001; Ganade and Brown 2002). However, considerably less information is available for the high cold tropics, which have been largely ignored in the development of tropical ecology. Below, the unique ecological characteristics of the high mountain ecosystems of the tropical Andes are briefly discussed. The opportunities offered by the study of vegetation regeneration in old-fields under traditional agriculture are emphasized, summarizing the limited available information on this issue.

1.2 THE PÁRAMO ECOSYSTEM AND LONG FALLOW AGRICULTURE

1.2.1 The páramo: a unique tropical ecosystem

The páramo is a high-altitude open grassland situated above the montane forests and below the permanent snow line. It is found primarily in the equatorial Andes of northern South America. The ecosystem is discontinuously distributed as a set of high-altitude islands mainly in Venezuela, Colombia and Ecuador (Fig. 1.1). The landscape has been influenced by several glaciation events and it is extremely heterogeneous in terms of topography and geomorphology (Monasterio 1980; Luteyn 1992). Soils are generally of recent origin, well drained, acid, and with very high soil organic matter contents but very low available nutrient levels, making them relatively infertile (Malagon 1982). In contrast to the dry highland of the central Andes (locally known as *punas*), the climate is humid, with yearly rainfall varying from 500 to 3000 mm. In addition, the páramos are characterized by the unique climatic co-occurrence of low temperatures with large daily oscillations and no thermal seasons. However, they share other characteristics with high altitude temperate ecosystems such as low partial pressures of CO_2 and high levels of ultra-violet radiation (Sarmiento 1986; Rundel 1994).

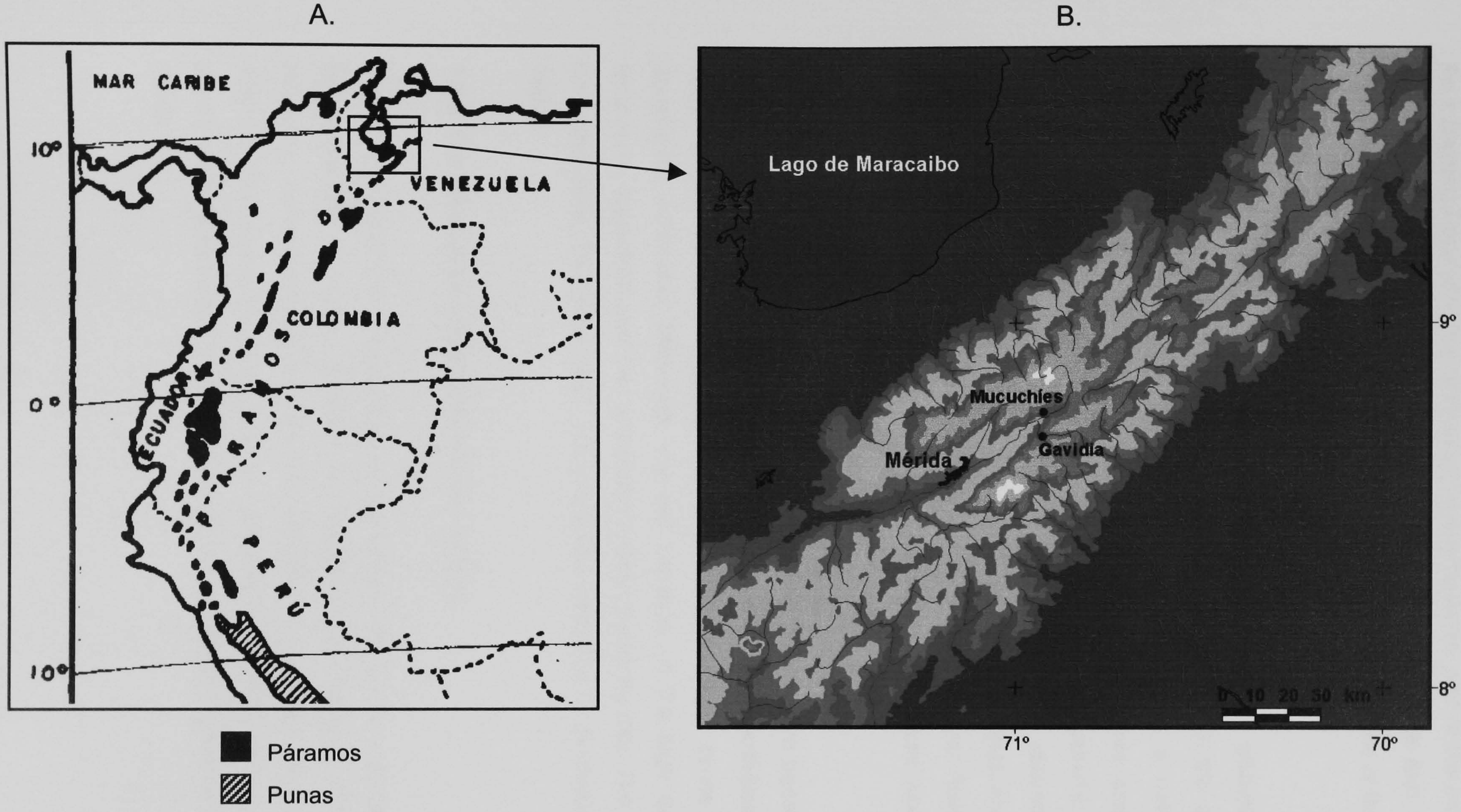

Fig. 1.1 Maps of the tropical Andes: A. Insular distribution of páramo areas in northern South America (adapted from: Luteyn 1999). B. Location of the Gavidia Valley (study area) in the Venezuelan Andes (Altitude bands: 510 m; min: 300 m; max: 4880 m).

As a consequence of these particular climatic features, and of the insular geographic distribution, a highly endemic and diverse flora has evolved. In fact, the páramo has the highest number of genera and species of the high mountains of the world (van der Hammen and Cleef 1986; Luteyn 1992).

Cuatrecasas (1958) divided the páramo belt into three altitudinal zones: the *subpáramo,* a shrubby transition zone between 3000-3500 m; the *grass páramo* or páramo proper, from 3000-4100 m; and the *superpáramo*, a more narrow zone between 4100-4800 m, with a higher proportion of bare soils and more extreme climatic conditions. The present study was undertaken in a páramo proper area. In this intermediate belt, the characteristic life forms are sclerophyllous shrubs (Hypericaceae, Asteraceae, Melastomataceae), giant caulescent rosettes like *Espeletia* (Asteraceae) and bunchgrassess (*Calamagrostis* and *Festuca*). These life forms show a high degree of convergent evolution with plants from other tropical alpine regions (Hedberg and Hedberg 1979; Hedberg 1992).

The páramo has been mainly compared with the arctic tundra because of its harsh climate, limited nutrient availability and absence of trees. Nevertheless, while tundras are mainly extensive flat areas, the páramo occupies steep zones of more limited geographic extension. Moreover, the soil ice layer in the high tropical Andes is temporary, superficial and thin, generally melting during the day. The growing season for plants lasts the whole year, with negligible variations in photoperiod (Diaz *et al.* 1997).

1.2.2 The páramo as a space for human activity

The páramo environment has been occupied and utilized for agro-pastoral activities for thousands of years, specially in Colombia and Ecuador (Ellemberg 1979). However, human occupation was characterized by low population density (Brush 1982). In the case of Venezuela, the pre-Hispanic populations seem to have used the páramo mainly as corridors, sites for rituals and as hunting grounds (Lopez del Pozo 1992).

After the Spanish conquest, fallow agriculture became the most commonly used practice in the Andes for the production of native crops, especially potatoes. This coexisted with newly introduced crops, such as wheat and oats. The fallow strategy allowed the restoration of fertility under a low input management regime and the restoration of the páramo vegetation in the old-fields, maintaining high levels of landscape diversity (Sarmiento *et al.* 1993; Luteyn 1999).

The sustainability of the traditional systems was based on the use of long periods of land abandonment under low population pressure. However, highland Andean populations are increasing at unprecedented rates of over 2.5 % a year and degrading forms of high input agriculture and cattle grazing have increased in importance (Little 1981; Luteyn 1999). This and other socio-economic transformations have resulted in intensification of the traditional systems, with a consequent reduction of fallow times and, in some cases, the introduction of organic fertilization. There has been a simultaneous extensification of land use, with an expansion of the agricultural frontier into areas not previously cultivated (Hess 1990; Sarmiento *et al.* 1993; Smith *et al.* 2001). This strategy seems to be related with the partial inability of the shortened fallow strategy to restore soil fertility levels after repeated cycles of cultivation, so that new areas of higher production potential are increasingly being used (Llambi 1997; Llambi and Sarmiento 1998; Smith *et al.* 2001). Hence, it is now essential to assess the sustainability of the current reduced fallow agroecosystems and their conservation role in terms of páramo regeneration, especially since a large number lie within established national parks.

1.2.3 The study area and the management system

The study was carried out in 'Las Piñuelas Valley' (Plate 1.1.A) in the Páramo de Gavidia, situated between 3300 and 3800 m asl, in the Sierra Nevada national park, in the Venezuelan Andes (8^0 35'-45' N, 70^0 52'-58' W). The relative location of the valley is shown in Fig. 1.1. Gavidia is in an area of glacial origin with well-drained and stony inceptisols (*Ustic Humitropept*) of a sandy-loam texture, low pH (4.3 to 5.5), high organic matter levels (up to 20%) but low mineral nutrient contents, as low temperatures limit the decomposition process (Llambí and Sarmiento 1998). The natural vegetation of the area is a rosette-shrubland páramo community dominated by *Espeletia schultzii* and *Hypericum laricifolium* (Monasterio, 1980).

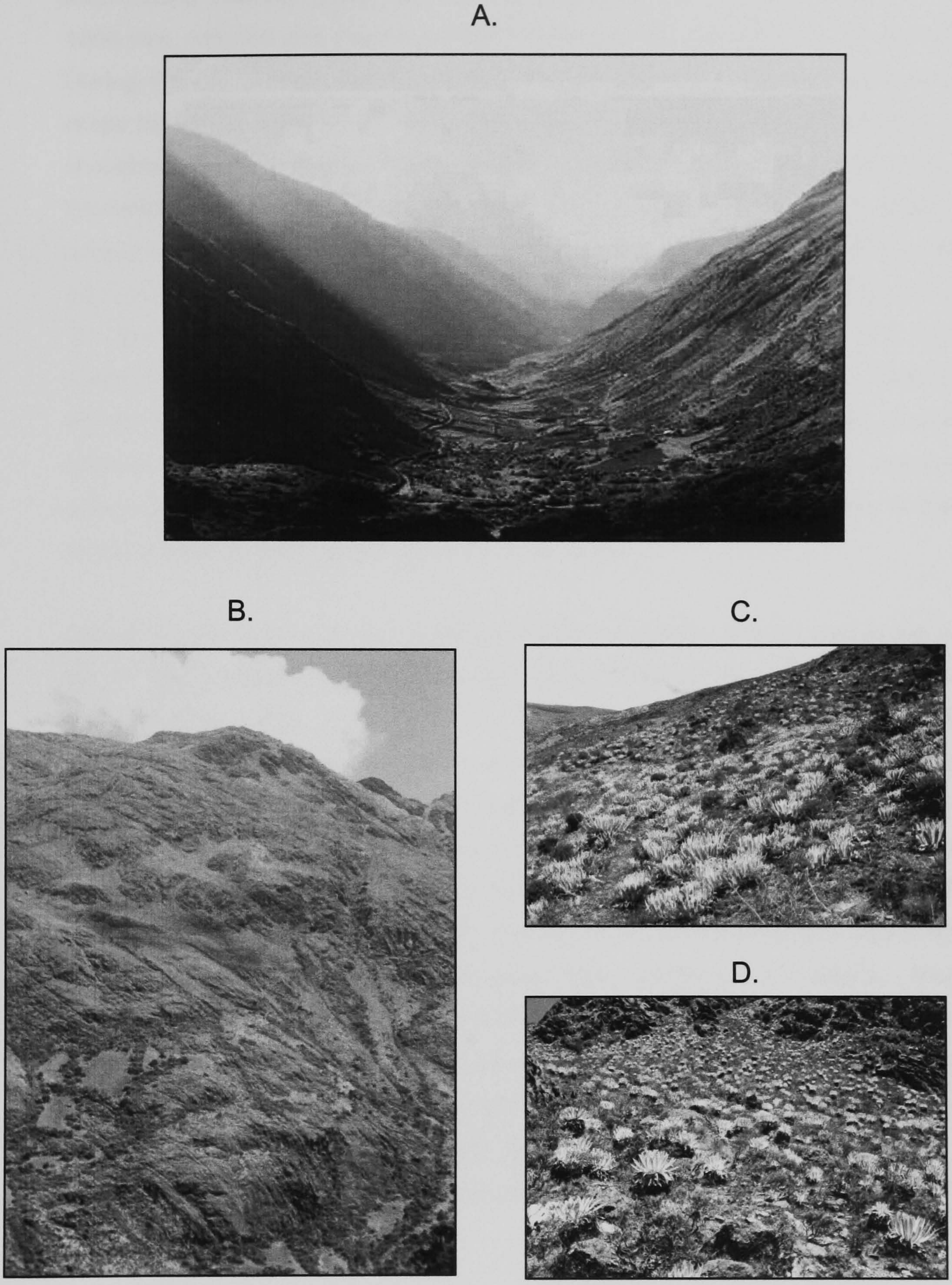

Plate 1.1 Views of Gavidia in the Venezuelan Andes: A. 'Las Piñuelas' Valley; B. Valley slope showing a mosaic of fallow plots and non-cultivated areas; C. Plot with eight years of fallow; D. Non-cultivated páramo (rosette-shrubland area dominated by *Espeletia schultzii* and *Hypericum laricifolium*).

The precipitation regime is unimodal, with a peak of rainfall between June and July and minima between December and January (Fig. 1.2). Mean annual rainfall is c. 1300 mm, with the wet season representing an average of 93% of total precipitation. During the dry season, soil moisture in the first 20 cm of the soil profile frequently drops below the wilting point (-1.5 MPa, Sarmiento, 2000). The temperature regime characteristic of these high tropical environments shows wide daily rather than yearly fluctuations: “a summer every day and a winter every night” (Hedberg 1964). Mean annual temperature in the valley goes from around 10^0C at 3200 to 6^0C at 3800 m a.s.l. Mean temperature is relatively constant during the year, with a range of only 2.5 ^{0}C between the coldest (January) and the warmest month (May, see Fig. 1.3). However, the amplitude between monthly maxima and minima is large, particularly in the dry season (with a range of c. 20 ^{0}C between the absolute monthly maxima and minima). During the driest months (December to April), night temperatures occasionally go below freezing (with absolute minima c. –1.8 ^{0}C). This is the main factor limiting agricultural activity to the rainy season.

Global incident solar radiation shows an unimodal pattern, with an annual mean of 15 MJ m^{-2} day^{-1}, maximum mean monthly levels c. 21 MJ m^{-2} day^{-1} during the dry season and minimum levels of c. 12 MJ $m\text{-}^2$ day^{-1} during the rainy season (Sarmiento, unpublished results). The annual mean radiation is very similar to that measured in other mesic paramo areas in the Venezuelan Andes (15-16 MJ m^{-2} day^{-1}) and lower than that in dryer ‘puna’ ecosystems in the high central Andes (c. 21 MJ m^{-2} day^{-1}), mainly because of a higher cloud cover in the wet season in the páramos. As for the dry season maximum, it is similar to that found in both lowland and alpine systems both in New Zealand and the European Alps (20-23 MJ m^{-2} day^{-1}). Maximum photosynthetically active radiation (PAR) levels are very high (c. 2300-2500 µmol photons m^{-2} s^{-1}, measured both in the wet and the dry season in clear days, see Chapter 3) going beyond those normally found in lowland sites, at least in temperate regions (c. 2000-2200 µmol photons m^{-2} s^{-1}) and reaching similar levels to those measured in the Ecuadorian páramos at 4000 m a.s.l (see Körner 1999, pgs. 27-29).

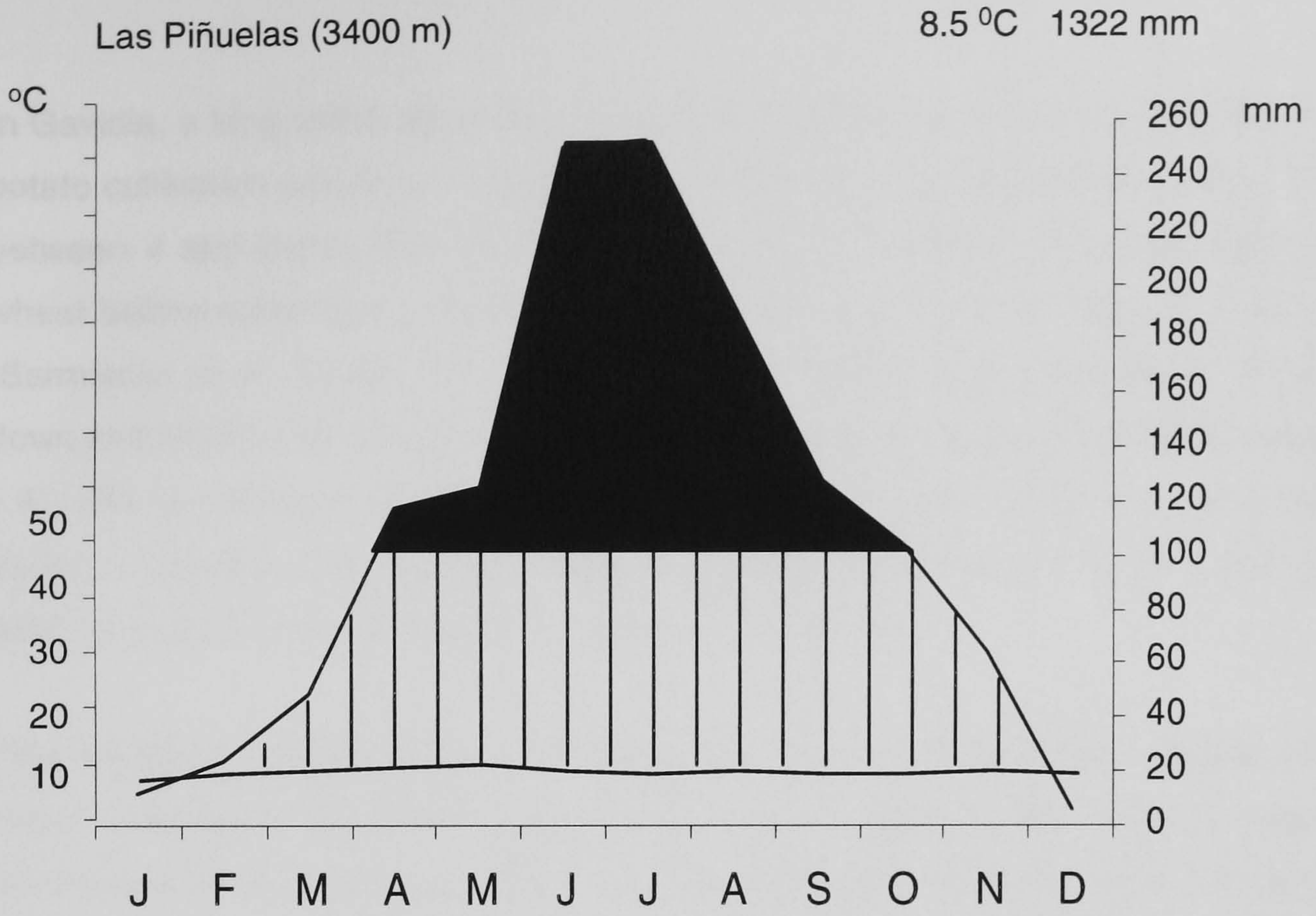

Fig. 1.2 Walter climate diagram for "Las Piñuelas" climatic station (Gavidia, Venezuela). Monthly average values of temperature (⁰C) and precipitation (mm) between the years 1992 and 2000. Humid period indicated with vertical stripes. Months with more than 100 mm rainfall indicated in black. Source: Universidad de los Andes, ICAE climatic data station.

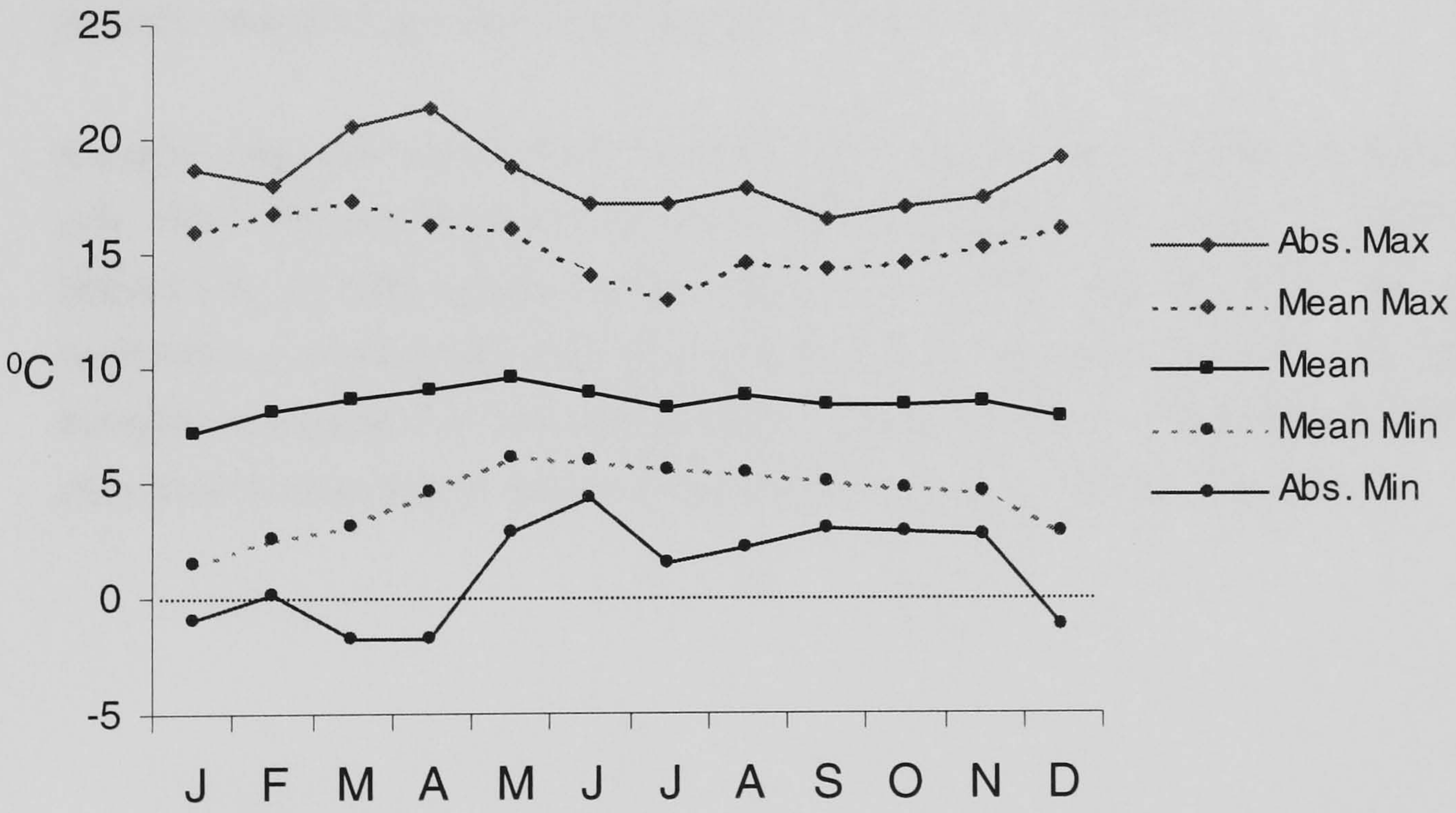

Fig. 1.3 Yearly pattern of air temperature (⁰C) at "Las Piñuelas" climatic station (Gavidia, Venezuela) between the years 1992 and 2000 (3400 m. asl). From top to bottom: absolute maxima, mean maxima, mean, mean minima and absolute minima. The absolute maxima and minima correspond to the period of 1996-1997. Source: Universidad de los Andes, ICAE climatic data station.

In Gavidia, a long fallow agricultural system for potato production is practised. A short potato cultivation period (1 to 3 years) is followed by a long fallow phase that can last between 4 and more than 10 years. Occasionally, fields are cultivated with oats or wheat before entering the fallow phase. The current average fallow time is 4-5 years (Sarmiento *et al.* 2000b). The phytomass accumulated during the fallow is then cut down and incorporated as green manure before starting the next cultivation cycle (Fig. 1.4). Mineral fertilization with high levels of different forms of NPK is also common during cultivation. The average fertilizer dosage applied in 50 fields under potato cultivation studied by Sarmiento (1995) was 1.8 tons/ha.

This traditional agricultural system generates a complex landscape mosaic of plots under cultivation, in different seral stages and patches with natural vegetation (Sarmiento *et al.* 1993; see Plate 1.1.B-D). Old fields are also used for extensive cattle, horse and sheep grazing, which can be become more intense in fallow fields adjacent to farmer houses. The non-cultivated mature páramo areas are also subjected to extensive cattle grazing. The highest pressures occur during the wet season, as cattle is concentrated in Las Piñuelas valley to graze both in fallow plots and non-cultivated areas. During the dry season, the animals are taken to communal grounds outside of the valley to graze over much larger extensions.

A spatial database is available for the páramo de Gavidia (Smith 1995, updated to the year 2000). This database contains information about the fallow lengths of 1200 fields, obtained by directly monitoring the valley since 1991 (see Fig. 1.5). The spatial database is managed with a GIS and also contains information on slope, area, aspect, elevation and distance to the valley bottom for all the fields. The selection of the fallow plots used in this study was carried out with the support of this GIS system.

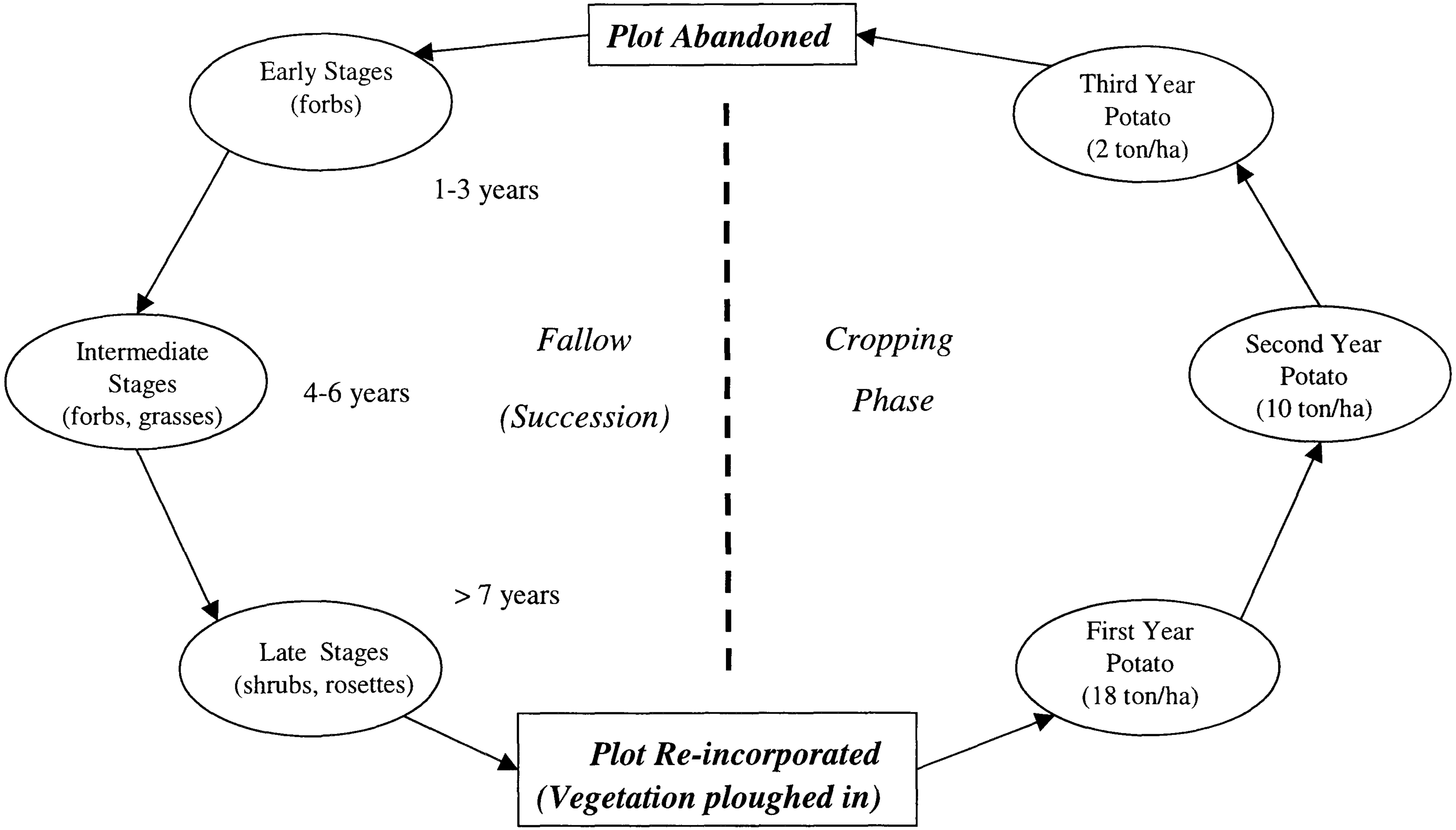

Fig 1.4 Management system used in traditional potato agriculture in the Gavidia valley of the Venezuelan Andes. The values for the cropping phase are average potato yields (source: Sarmiento 1995). The numbers for the fallow phase correspond to years of succession.

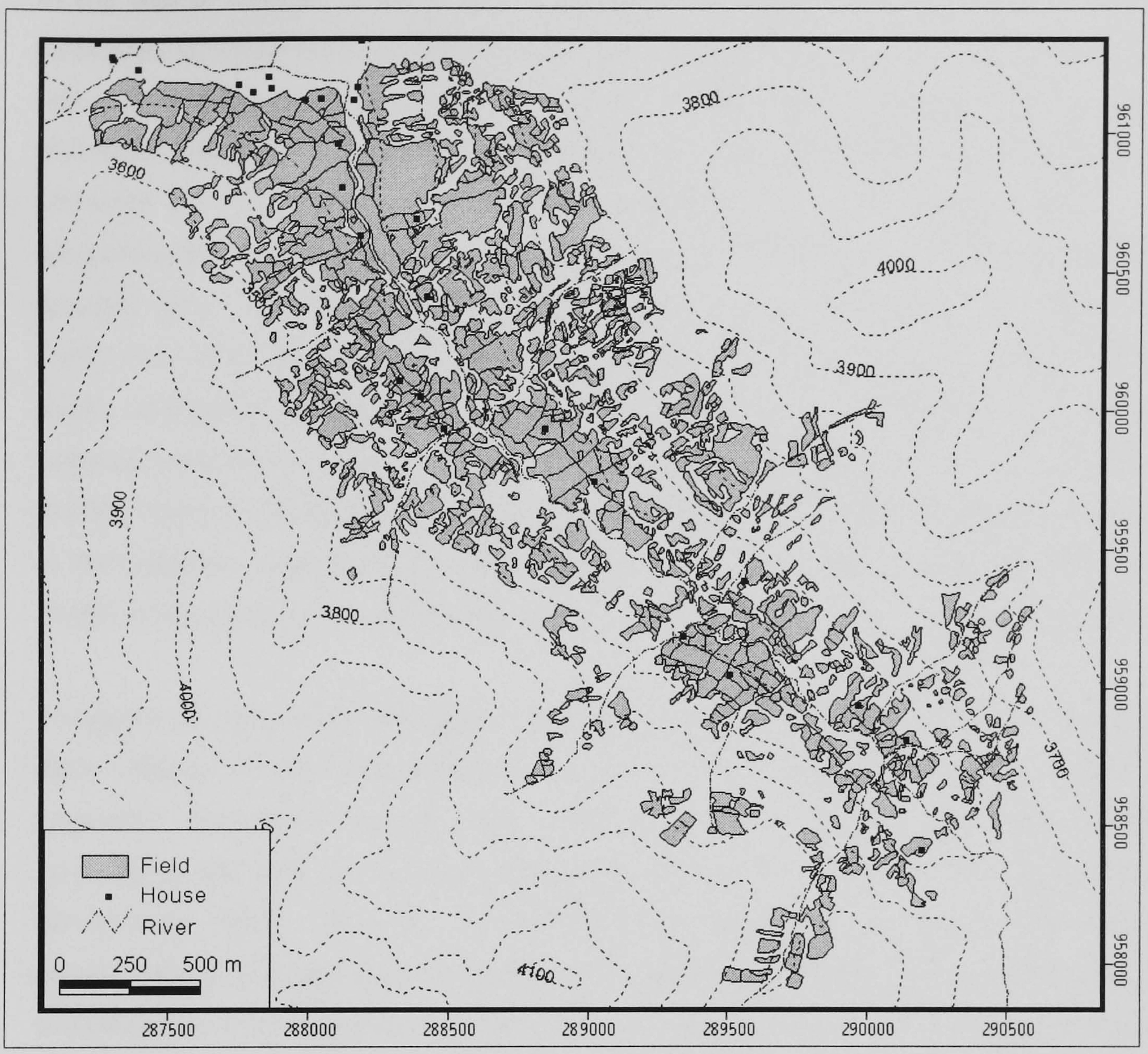

Fig. 1.5 Map of the agricultural fields in ‘Las Piñuelas’ Valley (Gavidia) in the Venezuelan Andes. Source: Smith’s (1995) GIS system. Updated to the year 2002.

1.2.4 Background on old-field succession research in the high tropical Andes

In the alpine context, authors like Urbanska (1997) have emphasized that multiple pathways of vegetation development should be expected, mainly as a result of the high environmental heterogeneity that characterizes mountain environments. Moreover, research on páramo regeneration after grazing and fire has suggested that because of the harsh environmental conditions (i.e. low nutrient levels, low temperatures, seasonal water limitations) vegetation regeneration is a relatively slow process (e.g. Janzen 1973, Horn 1989, Luteyn 1992, Hofstede *et al.* 1995). The common use of fallow agriculture in the páramos provides a unique opportunity to study vegetation succession in the context of the high topographic and edaphic heterogeneity that characterizes these high mountain valleys (Llambi and Sarmiento 1998). However, there have been very few studies on vegetation old-field succession in the páramo (see Ferweda 1987; Moreno and Mora-Osejo 1994; Montilla *et al.* 1992), and no study has measured successional divergence and regeneration rates.

Analyses of community structure changes in old-fields have shown that there is a clear change in the relative abundance of the dominant life-forms, with herbs and grassess dominating during early seral stages and shrubs and giant rosettes dominating the late seral stages (Ferwerda 1987; Montilla *et al.* 1992; Moreno and Mora-Osejo 1994). However, the results of numerous studies in the northern and central Andes suggest that these directional changes in vegetation structure are not paralleled by clear successional trends in soil organic matter, any of the important soil nutrients like total N or P, or microbial biomass nitrogen (Ferweda1987; Sarmiento and Monasterio 1993; Sarmiento *et al.* 1993; Hervé 1994; Llambí and Sarmiento 1998; Pestalozzi 2000). Only mycorrhizal colonization shows a marked increase during the fallow, linked with decline in dominance of non-mycorrhizal species (Montilla *et al.* 1992). Moreover, Sarmiento and Bottner (2002) found an increase in microbial biomass and C and N mineralization comparing a depleted field (cultivated for 3 consecutive years) and a field with 15 years of fallow. However, this fallow time is well above the average used by farmers in the area.

The lack of detailed understanding of both vegetation regeneration and fertility restoration during succession in old-fields has lead to the development of two complementary lines of research:

(1) The analysis of the ecological mechanisms of soil fertility restoration during the fallow, emphasizing the dynamics of N mineralization and immobilization in the soil organic matter, the role of the soil microbial community in modulating these processes, and the fluxes of N in the plant-soil interface.

(2) The detailed analysis of the changes in plant community structure during succession, the processes that determine these changes and the effectiveness of the reduced fallow strategy in terms of the regeneration of the natural páramo vegetation.

Both of these research lines are currently being developed in the Gavidia Valley of the Venezuela Andes within the framework of two projects: (1) The TROPANDES project, on the regulation of soil fertility in traditional agroecosystems (EC, INCO-DC); (2) An IFS (International Foundation for Science) funded project, on successional vegetation and soil fertility dynamics and the impacts of grazing. This thesis was undertaken within the framework of these projects, focusing on the quantitative analysis of the successional changes in plant community structure during the fallow and the understanding of some of the processes that determine them. The exploration of some possible underlying mechanisms of vegetation change is done from an essentially individualistic perspective, combining ecophysiological and demographic analysis and a plant-centred perspective on spatio-temporal processes.

1.3 OBJECTIVES AND STRUCTURE OF THE THESIS

The objectives and structure of the thesis are as follows.

Chapter 2. *To provide a quantitative analysis of the patterns of plant community structure change during succession in old-fields of the high tropical Andes, and evaluate the effectiveness of páramo regeneration during the fallow times currently used by farmers.*

In Chapter 2 the successional changes in species richness and diversity and the abundance of the dominant species and life-forms are described using a chronosequence approach. Then, the divergence or convergence of vegetation structure is assesssed, evaluating the effect of environmental heterogeneity. Changes in the rate of succession are analysed, as well as the extent to which the structure of the plant community in the non-disturbed ecosystem is restored during the fallow times currently used by farmers in the study area. The results challenge generally expected patterns during secondary succession, particularly regarding changes in succession rates. In addition, the results question the conservationist value of the reduced fallow strategy. Finally, the applicability in the context of the highland tropics of the conceptual models on succession summarized above is discussed, emphasizing the potential contributions of an individualistic perspective. The chapter provides the descriptive basis necessary to develop a more process oriented understanding of community dynamics. This is the task to which subsequent chapters of the thesis are dedicated.

Chapter 3. *To compare the ecophysiological characteristics associated with differences in photosynthetic potential and stress resistance of species that dominate during different stages of succession.*

Tilman (1990; 1993) and Grime (1979) proposed that in unproductive environments, dominance in the different stages of succession is mainly determined by a trade-off between characteristics associated with high photosynthetic capacity (resulting in early dominance because of fast growth) and characteristics associated with stress resistance (Tilman's growth rate trade-off hypothesis). In Chapter 3, the potential contribution of these ideas for understanding páramo regeneration is evaluated. I analyse whether the slow growing dominant species of late successional fields (giant rosettes and shrubs) show lower photosynthesis at light saturation and specific leaf area than the species that dominate the early stages (fast growing forbs). Furthermore, since drought is the most important seasonal factor in these environments, I investigate whether the dominant late succession species have characteristics associated with a higher water stress resistance than species that dominate during early succession. (i.e. less changes in assimilation, stomatal conductance and leaf water potential between the dry and wet season and a higher intrinsic water use efficiency).

Chapter 4. *To explore how, integrating demographic analysis with the quantification in different stages of succession of changes in small-scale spatial structure contributes to understanding the effect of local plant-plant interactions on vegetation dynamics.*

In Chapter 4 the population density, size distribution and intra- and inter-specific spatial relations of the dominant giant rosette in the páramo (*Espeletia schultzii*) are compared in old-fields in different seral stages. In particular, changes in spatial aggregation between seedlings in early succession and adults in the late stages are evaluated to explore the potential role of density-dependent regulation on population dynamics. The analysis of the spatial association between *E. schultzii* and the dominant species during early succession (the introduced forb *Rumex acetosella*) is used to: (1) infer the effect of competitive interactions on the decline of ruderal species; (2) to evaluate if spatial segregation could be a contributing factor in the ability of mature páramo species to tolerate (*sensu* Connell and Slatyer 1977) the dominance of *R. acetosella* in early seral stages.

Chapter 5. *To explore how the analysis of small-scale spatial dynamics in permanent plots can contribute to the understanding of the role that intra- and inter-specific interactions play in successional vegetation dynamics.*

The static spatial analysis presented in Chapter 4 is based on inferring the operation of local plant-plant interactions from the observed changes in spatial structure. In Chapter 5, I demonstrate how extending the static approach, by analysing the dynamics of spatial relations in permanent plots, allows establishing a more direct link between changes in spatial patterns and the nature of local intra- and inter-specific interactions. More specifically, I analyse the wet-to-dry season transitions in the local abundance of the dominant ruderal species (*R. acetosella*). I evaluate the effects on its local survival to the seasonal drought of: (1) the abundance of conspecifics at different neighbourhood scales; (2) the spatial association with late successional heterospecific neighbours. The results indicate that the survival probability of *R. acetosella* can be modified by differences in the abundance of conspecifics in the local neighbourhood, with both negative and positive effects being possible depending on the spatial scale considered. Moreover, they emphasize the potential contribution of positive effects of LS species on facilitating the long-term permanence of this introduced forb in old-fields, and the importance that the development of size asymmetries can have in modulating positive plant-plant interactions. Both of these issues have received remarkably little attention in the context of successional and spatial research. In this chapter, I discuss the implication of these results for understanding the factors that contribute to the successional decline in the abundance of *R. acetosella*.

Finally, Chapter 6 is devoted to a general discussion of the results and conclusions of the thesis. Specifically, the implications for the development of an integrated, process oriented perspective on vegetation regeneration in the highland tropics are discussed. In addition, the potential contribution of a synthesis of functional, spatial and demographic perspectives to the development of succession theory is emphasized, exploring some general implications of the results of this thesis. Finally, I indicate some limitations of the research strategy used here and suggest what I perceive to be the key areas for further research.

Chapter 2. Community Structure Patterns, Regeneration Rates and Successional Divergence

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2.1. INTRODUCTION

The analysis of the patterns of plant community structure change during secondary succession has fascinated ecologists from the beginnings of the discipline. This is partly because of the remarkable consistency and predictability of these patterns for aspects such as the sequence of relative abundance of different life forms (Bazzaz 1996). Consequently, there are a number of generalizations in the literature on what to expect during secondary succession. They include an expected decline in importance of alien species (Pickett 1982; Vitousek 1986; Meiners *et al.* 2002), an increase in evenness in the relative abundance of species (Bazazz 1996) and a continous decrease of the rate of succession (Myster and Pickett 1994).

Other aspects of community structure change, like the successional trend for species diversity have generated substantial debate. Some authors such as Odum (1969) support the idea of a monotonic increase (see also Armesto *et al.* 1991; Collins *et al.* 1995; Willson *et al.* 1996) while others like Horn (1974, 1981) suggest that there should be a 'nearly universal decline' in late stages (e.g. Peet 1978; Brown and Southwood 1987). Another important area of disagreement has been whether to expect convergence in community structure towards a single climax (as suggested by the classical ideas of Clements) or divergence along multiple alternative states of vegetation development (see review by Leps 1991).

Most of these generalizations and discussions have been based on the analysis of forest succession in temperate ecosystems, and in the case of the tropics, on studies in lowland 'old-field to forest' systems (e.g. Aweto 1981; Mesquita *et al.* 2001; Ganade and Brown 2002). However, considerably less information is available on the highland tropics. Their unique climatic conditions (see Chapter 1) and treeless nature, makes them interesting systems for evaluating the generality of the expected trends specified above.

The páramo is a tropical alpine ecosystem that occupies the upper belt of the Northern Andes (3000 to 4800 m). Giant caulescent rosettes, shrubs and bunch grassess dominate the vegetation. Recently, the páramo has been subjected to an accelerated process of degradation and transformation, characterised by agricultural intensification and a continuous expansion of the agricultural frontier (Ferwerda 1987; Luteyn 1992; Hofstede 1995; Hess 1990; Drost *et al.* 1999). The increasing human intervention, frequently involving long fallow agriculture, provides the opportunity to analyse large numbers of old-fields in different regeneration stages. Moreover, it makes the study of secondary succession a priority for the preservation and management of this unique environment.

An important insight from recent theory, which can help in furthering the understanding of páramo succession, is to interpret vegetation development as a 'vector', analysing both its rate and its directionality (Bakker *et al.* 1996). On the one hand, several authors agree that these high altitude ecosystems are fragile, showing slow rates of plant growth and regeneration after fire and grazing (Janzen 1973; Horn 1989; Luteyn 1992; Hofstede *et al.* 1995). On the other hand, the predominance of multiple pathways of vegetation development has been emphasised in the mountain restoration context (Urbanska 1997). Apart from processes like random colonisation and non-linear species interactions, divergence in these systems could be due to the high spatial heterogeneity of mountain environments, which could differentially favour the persistence of the arriving species. The high topographic and edaphic heterogeneity that characterises páramo old-fields (Llambí and Sarmiento 1998) offers a unique opportunity to analyse this issue. Nevertheless, very few studies on vegetation dynamics in páramo old-field succession are available in the literature (but see Montilla and Monasterio 1987; Ferweda 1987; Moreno and Mora-Osejo 1994) and none has measured divergence and regeneration rates.

The general aim of this chapter is to provide a quantitative analysis of the patterns of vegetation structure change during secondary succession in old-fields of the Venezuelan high Andes. The specific objectives are: 1) to determine the patterns of successional change in species diversity, the relative abundance of the different life forms and the abundance of the dominant species; 2) to assesss whether vegetation regeneration is convergent or divergent and determine the relative importance of the fallow time and heterogeneity in edaphic characteristics in influencing differences in vegetation structure; 3) to compare vegetation structure of the fallow areas with that of the non-cultivated páramo to assess the degree of recovery achieved under the current regeneration times used by the farmers in the area; 4) to determine the changes in the rates of vegetation regeneration during the fallow and estimate the time required to reach a community structure similar to that of the non disturbed ecosystem.

2.2 METHODS

2.2.1 Fallow fields selection

A spatial database was utilised (Smith 1995, which has now been updated to the year 2002), which contains information on the fallow lengths of 1200 fields. Four old-fields were selected for each year of fallow between 1 and 9 years. Four areas with natural, never cultivated páramo (NCP) vegetation were also included. To reduce the heterogeneity between areas of the same fallow time, the following sectors of the valley were excluded: areas near to farm houses with a more intensive management regime; areas with water logged conditions in the valley bottom; plots that showed evidence of severe overgrazing.

2.2.2 Data collection

In each selected plot, the point-quadrat method was used to sample the vascular vegetation at the end of the wet season of 1996 (September-October), when most plants are flowering. A pin divided into 10 cm long sections was vertically placed 100 times at random and the species touched by the pin were recorded. Each species abundance (biovolume) was calculated as its total number of contacts in all 10 cm sections (Greig-Smith 1983). This information was used to construct a matrix of species vs. relevées.

An associated environmental matrix was constructed based on soil analysis performed by Llambi and Sarmiento (1998) in the peak of the rain season of 1996 in the same plots studied here (for details, see Llambi 1997; Llambi and Sarmiento 1998). This matrix included the following variables: texture (sand, silt and clay fractions, Bouyoucos gravimetric method), pH (measured in a 1/1 soil water mixture using a pH meter), total C (Walkley and Black method, Soil Conservation Service, 1967), total N (digestion and distillation using the Kjeldahl method), soluble N (extracted in a 1 N K_2SO_4 solution using a 1:5 soil:solution ratio), ammonium (NH_4, distillation with MgO), nitrates (NO_3, distillation using Dearda's alloy and MgO), microbial biomass N (N-MB, chloroform fumigation extraction method, Brookes *et al.* 1985), P (Bray I method, Black 1965), Cation Exchange Capacity (CEC), base saturation (Base sat), Ca, Mg, Na, and K (extraction with 1 M NH_4OAc, pH 7.0, IGAC 1973). Smith's (1995) spatial data base was also used to derive information on field management (inclusion of wheat in the last year of cultivation before abandonment), plot absolute altitude above sea level and distance to the valley bottom, and slope. This information was also included in the environmental matrix.

On the other hand, for the eight dominant species, the biovolume estimations were transformed into above-ground phytomass. For each the intermediate and late dominant species (*Lupinus meridanus*, *Espeletia schultzii*, *Baccharis prunifolia*, *Acaena elongata* and *Hypericum laricifolium*) at least 6 individuals belonging to 3 size classess were randomly selected (in a field with 12 years of fallow) and a 0.25 m^2 area was defined around them. The species abundance was estimated by placing a pin in 50 random points in this area. Then the total above-ground biomass in the area was extracted, dried for 2 days at 70^0 C and weighted. A linear regression was then used to estimate phytomass from the pin abundance measures (R^2 values ranged from 0.78 to 0.95 and all regressions were statistically significant at $p<0.01$). For the early dominant species (*Rumex acetosella*, *Vulpia myurus* and *Lachemilla* sp.) at minimum of 10 quadrats of 0.25 m^2 were located at random in a year 3 plot and the same procedure was applied (although in this case many individuals were present in the sampling area).

2.2.3 Data analysis

From the data on the relative abundance distribution of the species in each plot Buya's (1994) evenness index was calculated. By multiplying this evenness value by the species richness a diversity index was obtained as suggested by Buya (1994). This method has the advantage of having diversity respond linearly to both changes in evenness and the number of species (which can be seen as its two underlying components). As species richness, diversity and evenness showed a tendency to stabilize in the long-term after a fast initial increase, a rectangular hyperbola model was fitted to the data (using non-linear least square regression):

$$y = y_{\max} \frac{t}{a+t} \qquad \text{Eq. 2.1}$$

Here, y corresponds to the dependent variable of interest (number of species, evenness and diversity) and t corresponds to the number of years of fallow in each replicate plot. The two estimated parameters are: $y_{max,}$ which corresponds to the maximum asymptotic value of the dependent variable at infinite fallow time; and a, which measures the initial rate of increase of y. Using this procedure it was possible to estimate the time necessary to go back to the levels of species richness, evenness and diversity found in the NCP.

To analyse in more detail changes in the structure of dominance in the community rank abundance diagrams (RADs) were constructed as originally suggested by Whittaker (1972). These were obtained for the average of species abundances in replicate fields for each fallow year and the NCP.

To determine changes in life form abundance, all species were classified into 6 groups: herbs, grassess, shrubs, caulescent rosettes, acaulescent rosettes and cushions. For a more detailed evaluation of the changes in community structure a Detrended Correspondence Analysis (DCA) was carried out on the untransformed matrix of species abundances for the 103 species identified in all the plots studied. The analysis was done using the CANOCO 4.02 software (ter Braak and Smilauer 1999). The *detrending* (arc effect removal) was done by segments as suggested by Hill and Gauch (1980). The analysis was repeated excluding the NCP plots and using only the 20 most abundant species (to eliminate noise introduced by rare species missing in some census because of sampling error). To analyse the relationship between the vegetation structure and the topographical and soil characteristics of each plot, the correlation (Spearman's rank) between plot scores for the first three axes of the DCA and these environmental variables was also obtained.

The rate of succession has been understood in two ways in ecology: as the time it takes community structure to reach its climax stage, and as the year to year rate of change in the vegetation structure (Prach 1993). The first interpretation faces the difficulty of clearly defining what is considered to be the terminal stage. For the second interpretation, two main approaches have been proposed (Pickett 1982; Prach 1993; Myster & Pickett 1994; Donegan & Rebertus 1999): (1) calculating an index of species turn-over (e.g. Sorensen's) between consecutive years, ignoring changes in species abundance; and (2) calculating an index of community dissimilarity (e.g. Euclidean distance). The second approach was deemed the most promising in the case of the páramo, since the results indicate that succession is characterized by changes in species abundance more than species turnover.

Two methods were used, both based on calculating dissimilarity between all the plots of each fallow time and 1st year plots (called by Bakker *et al.* 1996 the *net rate of succession*). In one method chord distance was used as our dissimilarity index (i.e. Euclidean distance on the normalized matrix, Orloci 1978). For the other method, I used the distance in the DCA 1st axis scores, as this axis is strongly correlated to successional time (see results). If the rate of succession is constant, these distances should be linearly related with time, and the slope will correspond to the overall rate. This estimated rate can then be used (assuming it continues to be constant) to obtain an estimate of the time required to get a community structure similar to that of the NCP (using the average dissimilarity distance from the 1st year plots to the NCP). Finally, successional divergence in species composition was analyzed by comparing dissimilarity between all plots of a particular age (Christensen & Peet 1984). Chord distance was used as the dissimilarity measure.

2.3 RESULTS

2.3.1 Species richness, diversity and evenness

A total of 103 vascular plant species were recorded in all the plots studied. The changes in the average number of species, diversity and evenness per plot for the different stages of succession and in the non-cultivated páramo (NCP) are presented in Table 2.1.

Table 2.1 Average number of species (R), Evenness (E) and Diversity (D) in the different years of succession and for the NCP (standard error in brackets). The total number of species in all plots for each fallow year is also indicated. Estimates for the two parameters, *a* and y_{max}, of a rectangular hyperbola model fitted to the data are presented (95% confidence intervals for the estimates in brackets).

FALLOW STAGE (years)	Species Richness (R)	Total No. Species	Evenness (E)	Diversity (D)
1	6.3 (1.7)	19	0.20 (0.12)	1.73 (0.88)
2	14.3 (3.1)	29	0.39 (0.04)	5.39 (1.41)
3	13.8 (5.3)	28	0.39 (0.11)	5.42 (2.53)
4	15.3 (2.5)	40	0.49 (0.08)	8.18 (2.93)
5	15.5 (4.6)	31	0.51 (0.08)	7.71 (1.63)
6	15.0 (1.4)	31	0.51 (0.07)	7.73 (1.22)
7	15.8 (5.0)	35	0.54 (0.07)	8.53 (2.41)
8	21.0 (7.1)	45	0.51 (0.11)	10.31 (3.07)
9	18.5 (3.2)	42	0.53 (0.05)	10.08 (2.59)
NCP	27.3 (8.8)	58	0.47 (0.07)	12.61 (4.30)
a ($p<0.05$)	1.92 (1.47)	1.44 (1.30)	1.68 (0.93)	5.75 (4.93)
y_{max} ($p<0.001$)	22.2 (4.9)	45.93 (10.4)	0.65 (0.09)	16.41 (7.02)

The patterns of change during succession for all the variables analysed show a monotonic tendency to increase, progressively approaching an asymptote as the fallow time increases. The fit to a rectangular hyperbola model (non-linear least square regression) was significant in all cases ($p<0.01$), with R^2 values ranging from 0.45 to 0.69 (see Fig. 2.1). As can be seen in Fig. 2.1, species richness (both in terms of the average number of species per plot and the total number of species in each year) showed higher average values in the NCP than the asymptotic value predicted from the rectangular hyperbola equation (y_{max}), the average lying outside the 95% confidence interval for y_{max} (see Table 2.1). However, the high variability in species richness between plots suggests we should take this result with caution, as there is a high standard error associated with the estimations of the observed values for the NCP. Moreover, given that 100 sampling points were used in each plot, there could be an underestimation of the total number of species in each area. The stabilization of species richness (as predicted by y_{max}) below the level observed in the NCP, does not allow an estimate of the time that would be necessary to attain the average number of species in the mature ecosystem. In the case of evenness and diversity the observed average value in the NCP is lower than the estimated y_{max} , although the difference is not significant in the case of diversity (so that the mean observed value lies in the 95% confidence interval for y_{max}). Using the rectangular hyperbola model, 19 years where estimated to be necessary for reaching the average levels of diversity found in the NCP. In the case of evenness, the model indicated the NCP had similar values as those attained after 4 years of succession. It is interesting to note, that even though the average for species richness and diversity in the NCP is higher than that after 9 years of succession, because of the high variability between plots these differences are not statistically significant (Kruskal-Wallis, α=0.05). The same is true for evenness.

The rank abundance diagrams show a tendency to flatten out as succession proceeds. This reflects both an increase in the number of recorded species and a decrease in the difference in abundance between dominant species and the rest (Fig. 2.2).

2.3.2 Changes in life-forms and dominant species abundance

The analysis of the successional dynamics of the different life forms shows herbs as the dominant group throughout the first 7 years, when shrubs become more abundant. The caulescent rosettes show a general tendency to increase in importance during the fallow. Grassess have a more erratic behaviour with a dip in abundance in the 6th year of succession (probably as a result of sampling error). Together with shrubs and the caulescent rosettes they are the dominant life forms in the NCP ecosystem. The acaulescent rosettes and the cushions have very low abundances in all cases (Fig. 2.3).

As can be seen in Fig. 2.4, in terms of phytomass, *R. acetosella* is the dominant species for the first three years, being then replaced by *E. schultzii*, which continues to dominate also over the shrubs from there on (except for the 9th year, where *B. prunifolia* shows a higher abundance). The dominant species show very clear successional patterns with: a group of early species (mainly herbs) like *R. acetosella* and *Lachemilla* sp. continuously decreasing in abundance after an early peak; a group of species like *V. myuros* and *L. meridanus* with a peak abundance in intermediate stages; a group with maximum abundance in late stages like *A. elongata and B. prunifolia*; and a group of species like *E. schultzii* and *H. laricifolium* continuously increasing in abundance during the fallow and showing their peak in the non-cultivated páramo (Fig 2.4). As can be seen from the error bars, there are large variations in the abundance of the dominant species for plots with the same fallow age. Interestingly, most of the dominant species are present throughout succession, with successional changes reflecting changes in their relative abundance but no real replacements of one species by another.

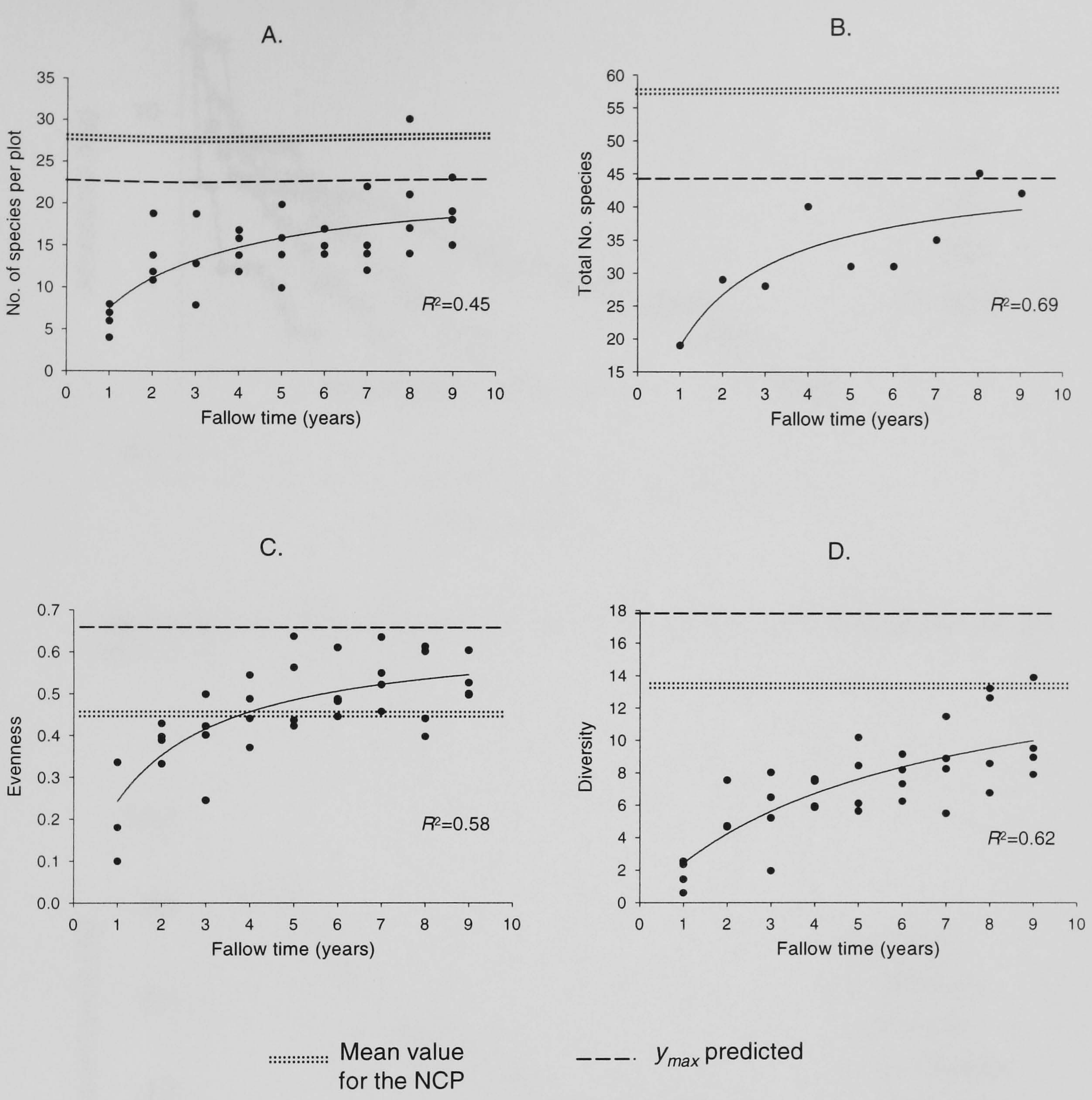


Fig. 2.1 Patterns of species richness, evenness and diversity in the different years of fallow. A rectangular hyperbola model is fitted to the data in all cases (see R^2 values). A single dashed line indicates the asymptotic maximum value at infinite time for each variable predicted by the model (y_{max}). A double dashed line indicates the mean value for each variable in the NCP plots. (A) Number of species in each plot; (B) Total number of species for each fallow time; (C) Evenness; (D) Diversity.

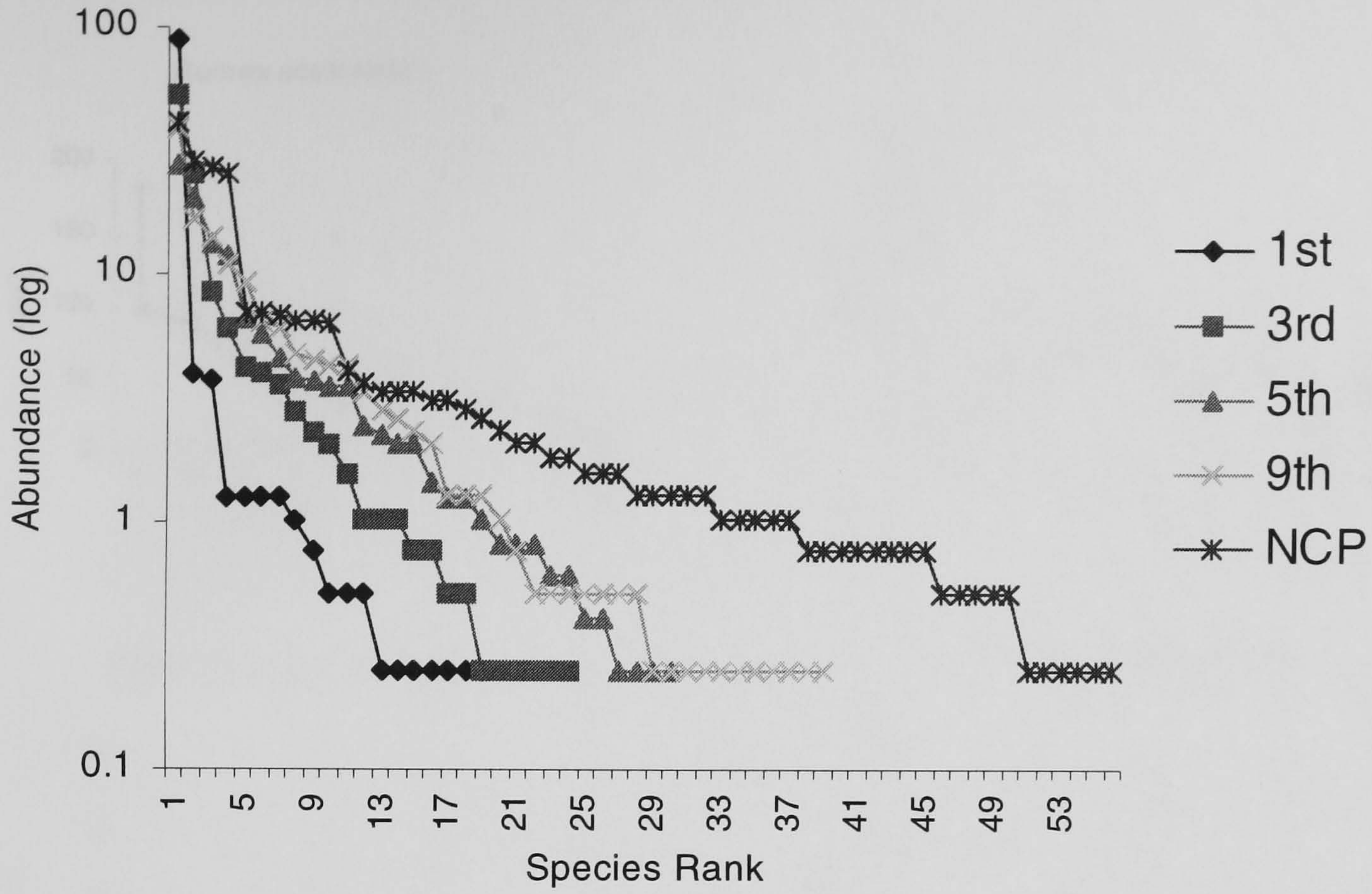


Fig 2.2 Rank abundance diagrams for the 1st, 3rd, 5th, 9th years of succession and the NCP.

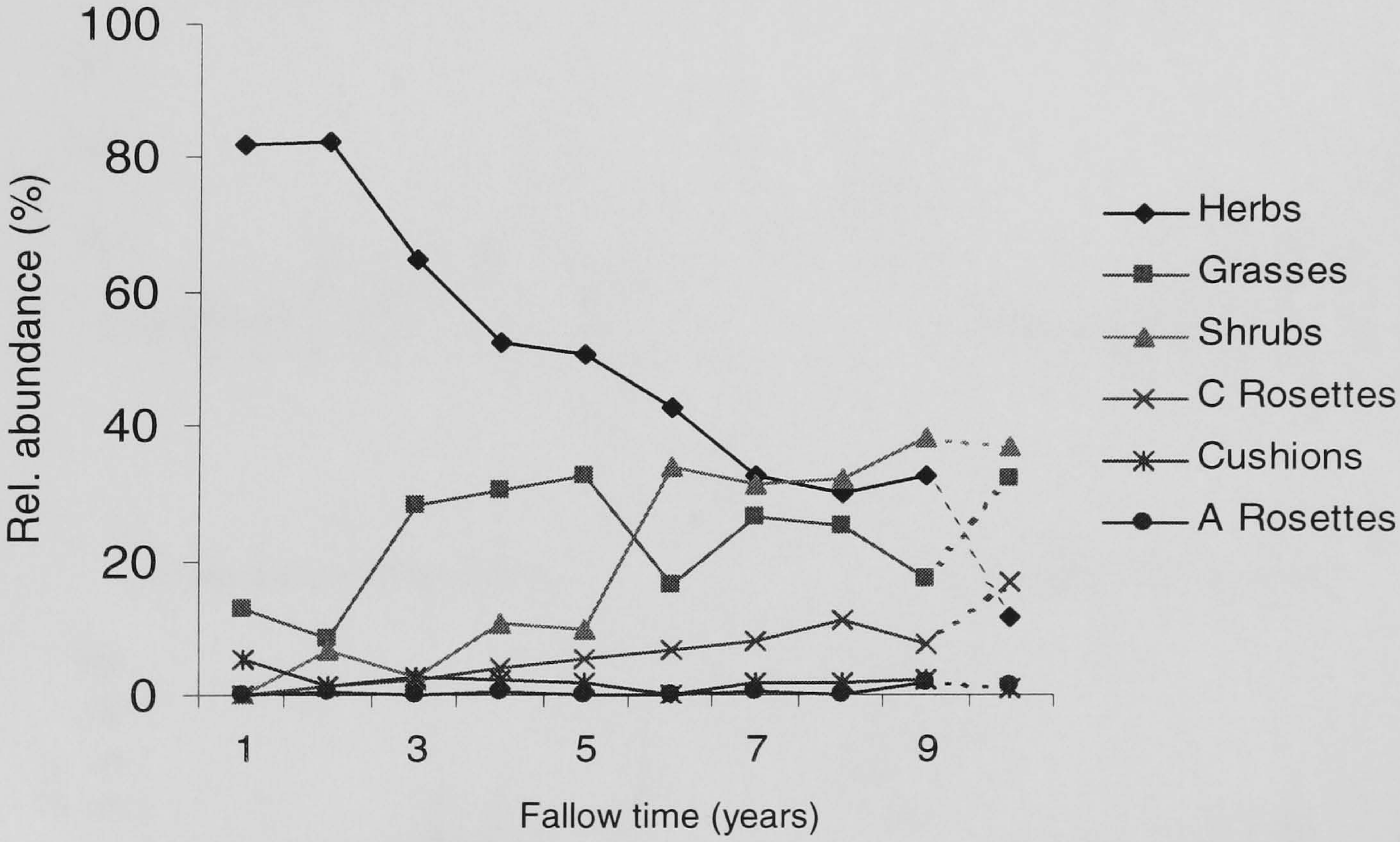


Fig 2.3 Changes in the percent of the total abundance represented by each life form in the different stages of succession and in the NCP.

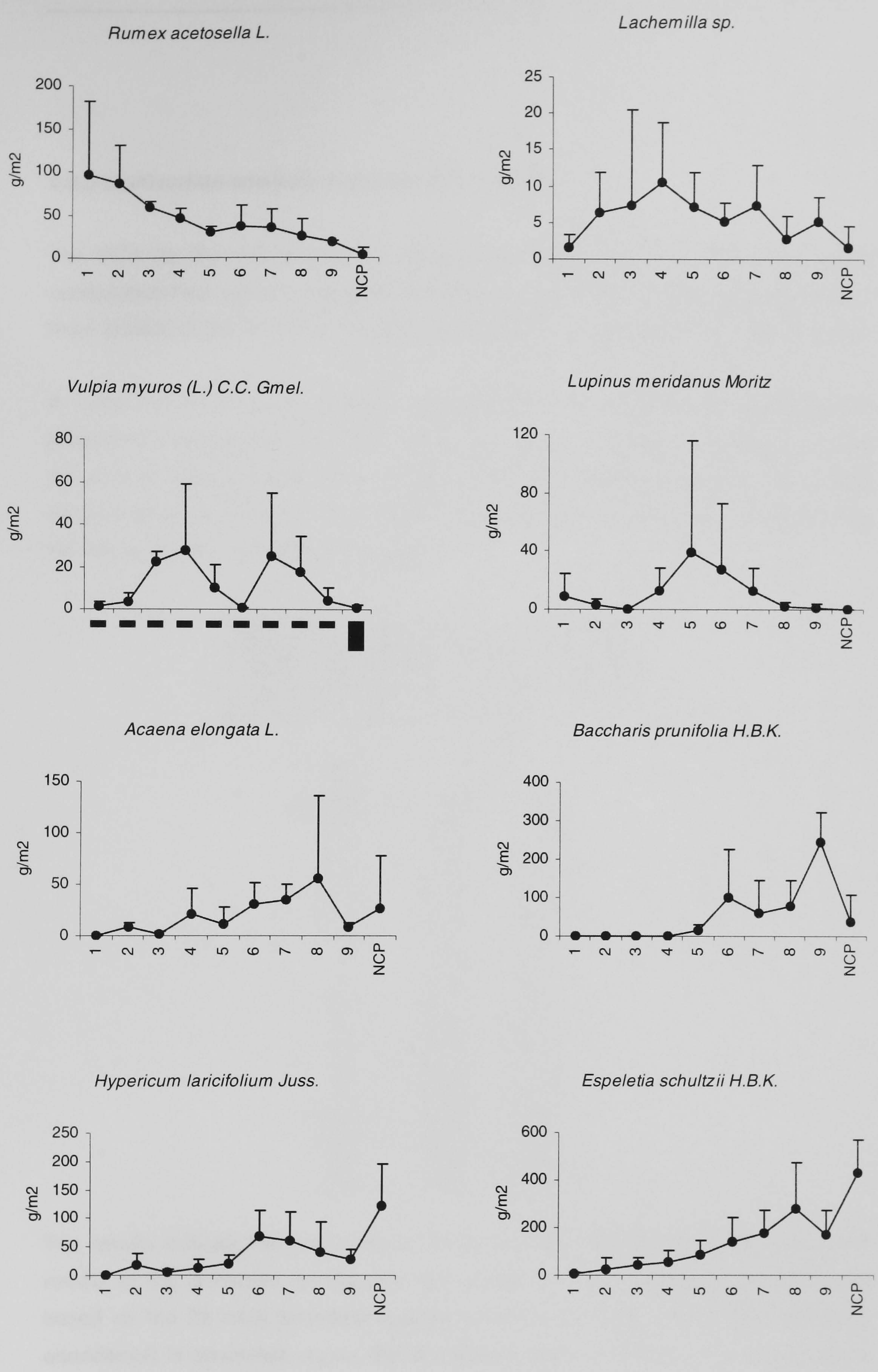


Fig. 2.4 Average aboveground biomass of the 8 dominant species for each fallow year and the NCP. Error bars: 95% confidence.

2.3.3 Multivariate analysis of community structure

The DCA for the 103 species identified clearly shows the changes in community composition from early to late succession along the 1st axis, so that earlier plots tend to be located to the left of the diagram The NCP plots are located in the right (Fig 2.5).

In Table 2.2 the correlation between the ordination axes and the soil parameters is presented. The fact that N-MB, total N and pH show a significant correlation with the 1st axis is mainly related to the NCP having the highest values for these three parameters, even though they don't show any significant tendency to increase during the fallow (Llambi and Sarmiento, 1998).

Table 2.2 Spearman's rank correlation between soil characteristics and the DCA ordination axes for the abundance of the 103 plant species in the 39 plots studied. Significant correlations, $\alpha=0.05$ (*).

Soil Parameter	1st Axis	2nd Axis
N-MB	*0.351	-0.288
C total	0.189	-0.186
N sol	0.248	*-0.323
N total	*0.328	-0.185
NH_4	0.201	0.152
NO_3	-0.279	0.274
pH	*0.355	*0.421
P	-0.286	0.073
CEC	0.227	-0.137
Ca	0.273	0.285
Mg	0.252	0.304
Na	0.223	-0.044
K	-0.102	0.011
Base-sat	0.048	*0.351
Sand	-0.273	-0.224
Silt	*0.349	0.125
Clay	0.080	0.184

The results indicate that the inclusion of the NCP is exerting major influence in the results of the ordination. In Fig. 2.6. the results of a DCA excluding the NCP and based on the 20 most abundant species (which accumulate 90% of the total plant abundance) is presented. Again, the distribution of the plots along the 1st axis goes from early to intermediate to late successional from the left to the right side of the diagram. The corresponding species loadings diagram (Fig. 2.7) clearly reflects the abundance replacement sequence presented in Fig. 2.4 with the dominant species going from early to late along the 1st axis.

The correlations between the first two ordination axes and the external environmental variables (Table 2.3) indicate that fallow time is the variable most strongly correlated with the 1st axis. All other correlations are relatively low. The positive correlation between the proportion of sand and the 1st axis seems to be the result of a very high percent of sand and low percent of silt in first year plots, which resulted from farmers having to select relatively marginal plots at that moment in time because of a potato plague attack. The rest of significant correlations with environmental variables are with the 2nd axis and show that high pH, Ca and Mg, base saturation and clay are positively associated with it. In contrast, total C and N, microbial biomass N and soluble N are all negatively associated with this axis. The fact that both soluble and total N and the abundance of *L. meridanus* are both associated to low values on the 2nd axis suggests a positive effect of this nitrogen fixer on soil N. Nevertheless, a closer examination reveals no significant correlation between the biomass of *L. meridanus* and the values of any of these variables (r=0.112 and 0.208 for Ntot and Nsol).

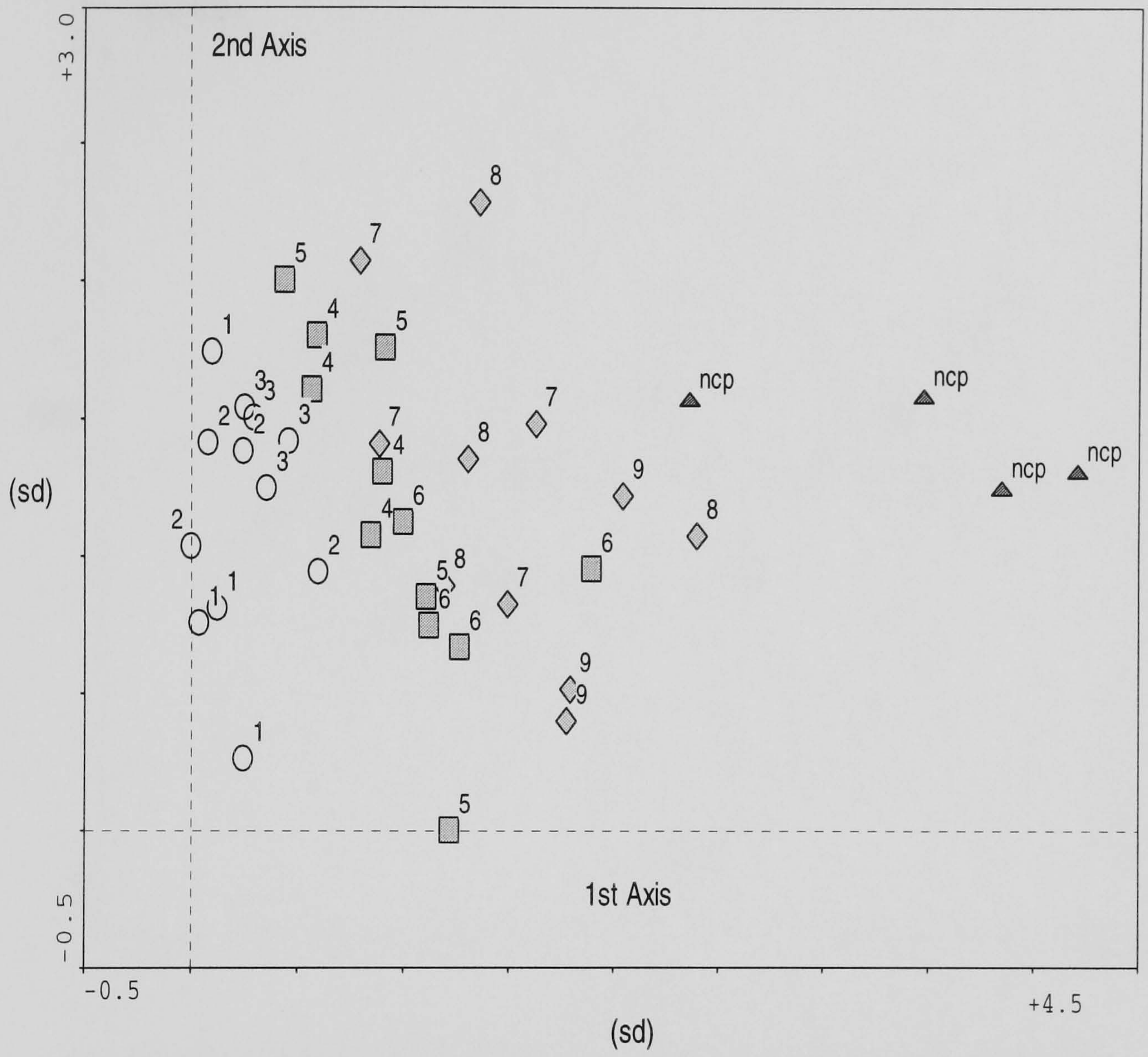


Fig. 2.5 DCA of the abundance for the 103 species in the 39 plots studied. First and second axis presented (16.9 and 22.7 % of cumulative variance). 1st to 3rd year: open circles; 4th to 6th year: squares; 7th to 9th year: diamonds; non-cultivated paramo (ncp): triangles. Numbers in the figure correspond to fallow time in each plot.

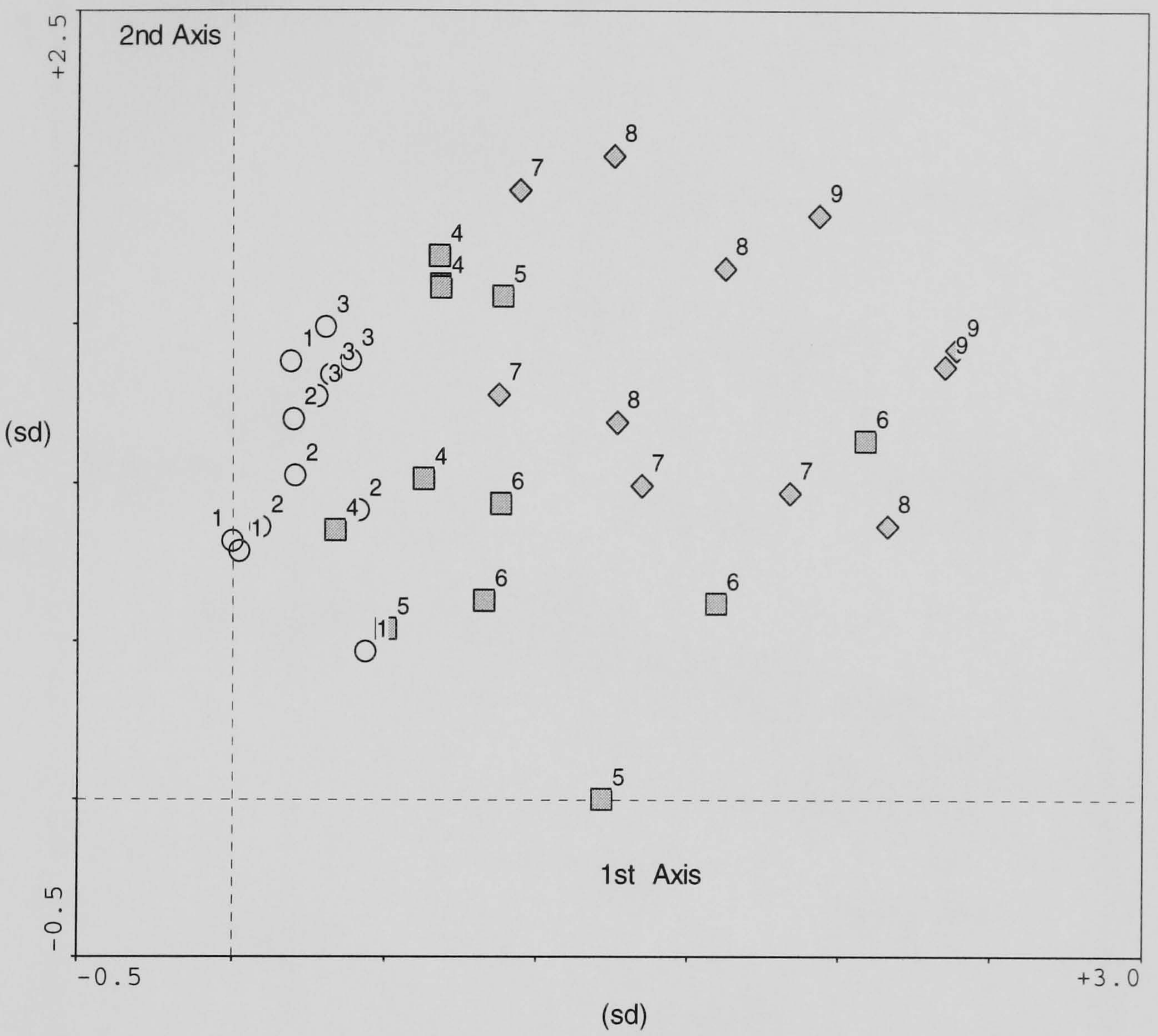


Fig. 2.6 DCA ordination diagram of the 35 fallow plots studied based on the abundance of the 20 dominant species. First and second axis presented (23.1 and 34.7 % of cumulative variance). 1st to 3rd year: open circles; 4th to 6th year: squares; 7th to 9th year: diamonds. Numbers in the figure correspond to fallow time of each plot.

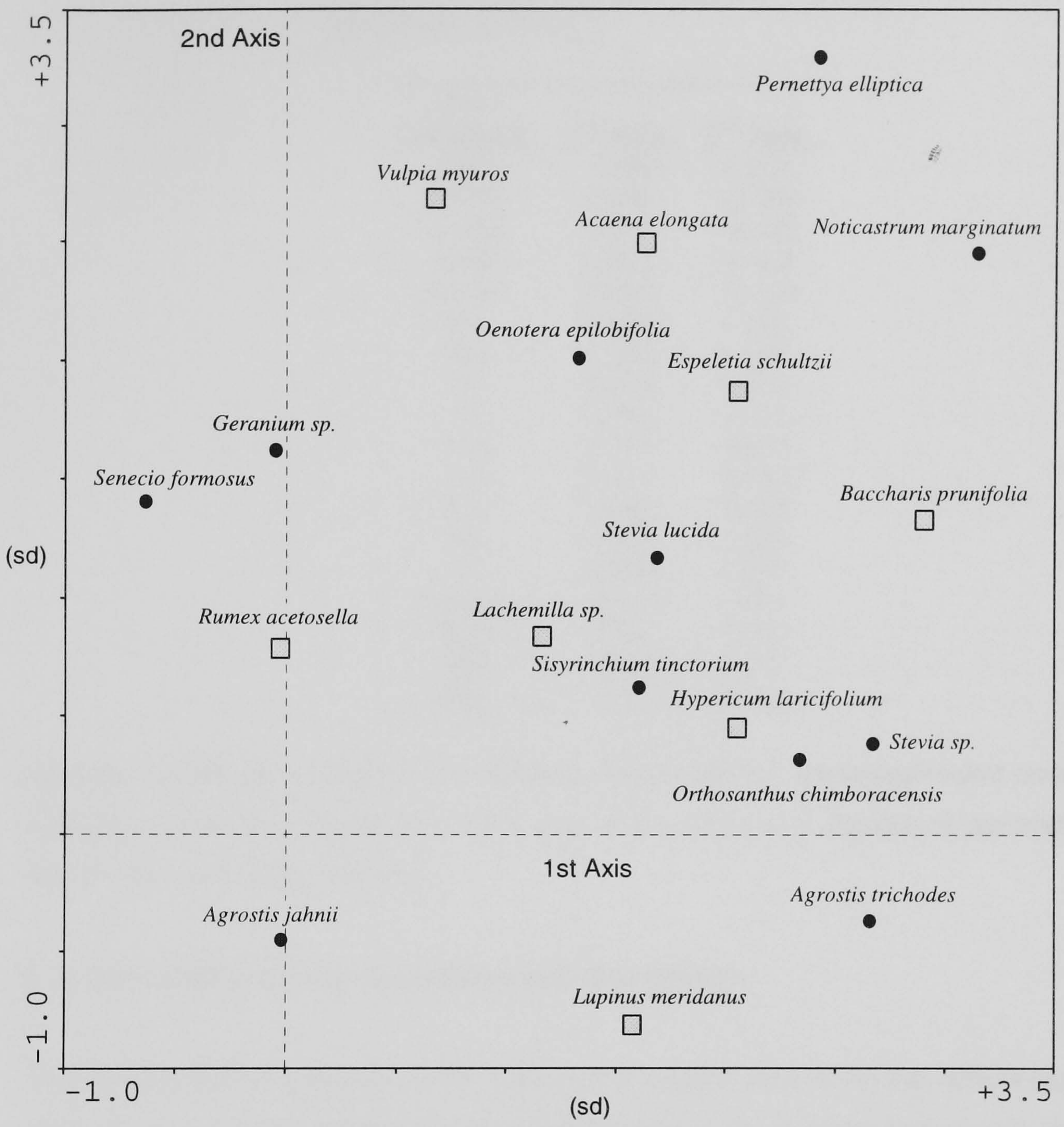


Fig. 2.7 DCA ordination diagram of the 20 dominant species loadings in the 35 fallow plots studied. First and second axis presented (23.1 and 34.7 % of cumulative variance). The most abundant species included in Fig. 2.5 are indicated with squares.

Table 2.3. Spearman's rank correlation between soil characteristics and the DCA ordenation axes for the biovolume of the 20 dominant plant species in the 35 fallow plots studied. Significant correlations, α=0.05 (*).

Soil Parameter	1st Axis	2nd Axis
Year	*0.923	0.324
N-MB	0.068	*-0.369
C total	-0.008	*-0.522
N sol	0.215	*-0.455
N total	0.097	*-0.503
NH_4	0.274	0.314
NO_3	-0.260	0.190
pH	0.244	*0.630
P	-0.089	-0.001
CEC	0.154	-0.263
Ca	0.151	*0.365
Mg	0.056	*0.506
Na	-0.014	-0.239
K	-0.265	0.039
Base-sat	-0.046	*0.450
Sand	*-0.391	-0.265
Silt	*0.516	0.136
Clay	0.178	*0.373

Altitude, aspect and distance to the valley bottom did not show significant correlations with any of the three axes. However, plot slope showed a significant correlation with the 2nd axis (r=0.53, p=0.001).

2.3.4 Succession rates and patterns of divergence

The results for the analysis of the rate of succession, based on the differences in the DCA 1st axis scores, suggest its is constant during the 9 years included in the study (Fig. 2.8). Although there is some variability around the trend, a linear relationship is evident. An almost identical result is obtained if chord distance instead of the DCA scores is used as a community dissimilarity index. Using the regression slope as an index of succession rate I obtained an estimate of 17 years of succession to reach a community composition similar to that of the NCP.

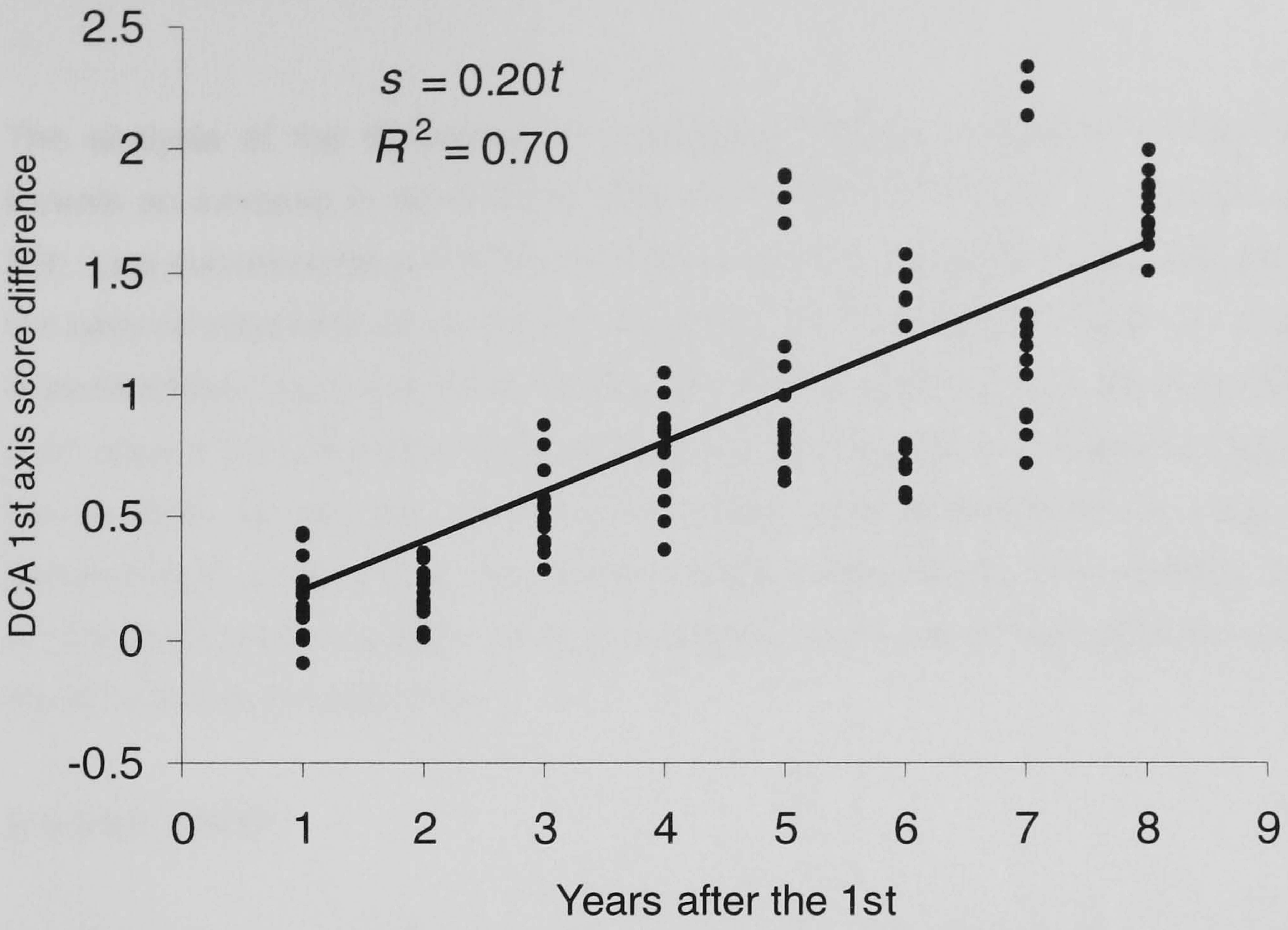


Fig. 2.8 Difference in the first axis ordination scores between plots with different fallow times and first year plot scores (*s*). The x axis values represent the numbers of years after the 1st year of succession *(t)*. A linear regression between *s* and *t* is presented (the slope in this model represents the constant succession rate). The ordination scores are from the DCA analysis of plots between 1 and 9 years, considering the 20 dominant species.

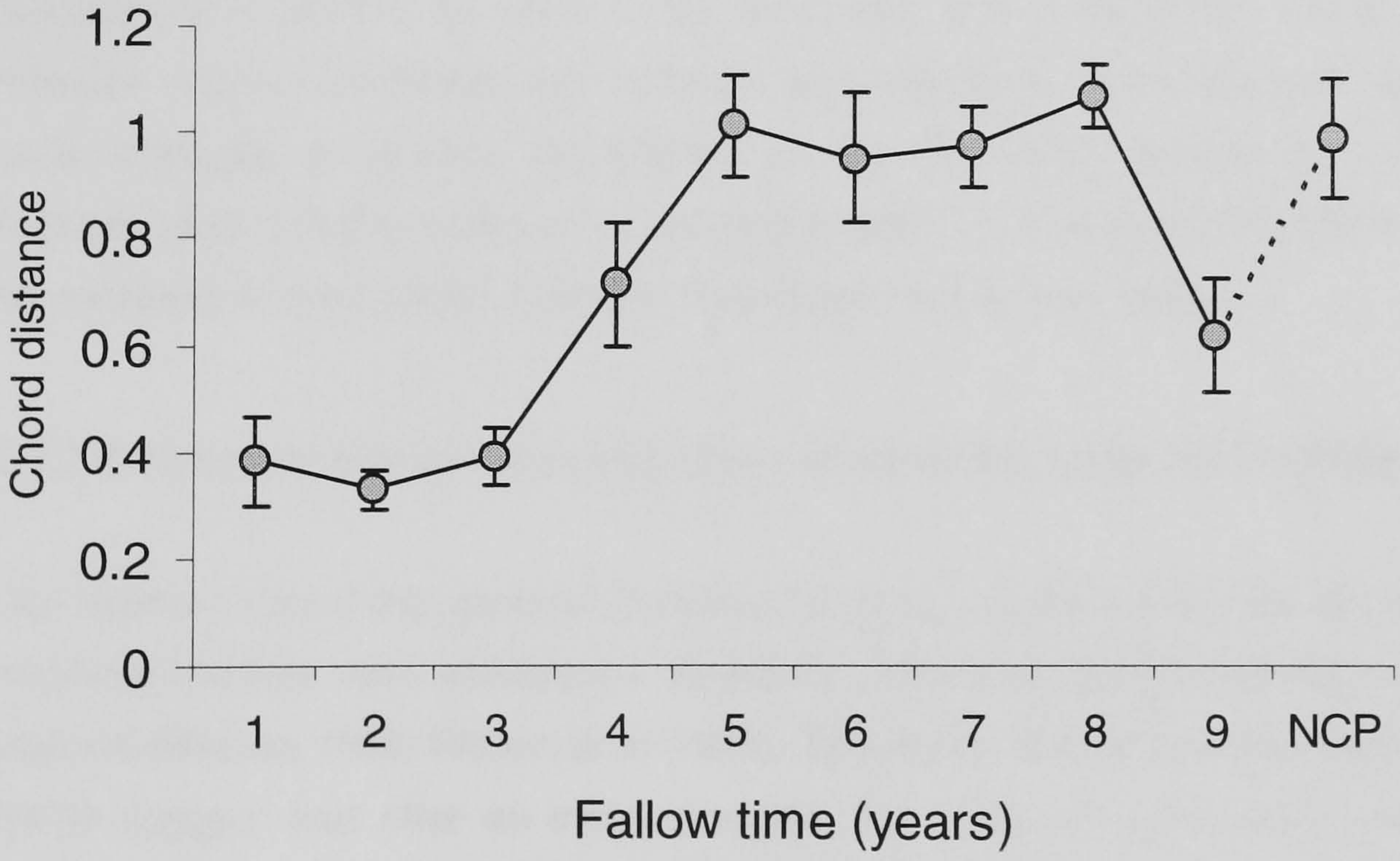


Fig. 2.9 Average chord distance (dissimilarity index) in species composition for all pairs of plots of a particular fallow time. Error bars: Standard error.

The analysis of the divergence of community structure based on chord distance reveals an increase in dissimilarity between the 3rd and 5th year of succession (Fig. 2.9). Late successional and NCP areas show a more heterogeneous composition than the early successional plots, with the exception of 9th year plots, that show a decrease in dissimilarity. This could be associated with the fact that 9 year plots were all located in an area of the valley dominated by *B. prunifolia*. In general, the results suggest that the structure of the plots in the early stages after abandonment is very similar, converging to species poor community strongly dominated by *R. acetosella.* After the 4th year community structure starts to diverge to the levels of heterogeneity shown by the non-disturbed ecosystem.

2.4 DISCUSION

Based on the results of this and other studies on long fallow agriculture in the páramo (Montilla and Monasterio 1987; Ferweda 1987; Moreno and Mora-Osejo 1994; Jaimes 2000) we can identify a set of common patterns for vegetation change during old-field succession: (1) an monotonic successional increase of richness, evenness and diversity; (2) a consistent sequence of life forms and dominant species change. Perennial herbs (e.g. *R. acetosella*) dominate the early stages and are progressively replaced as dominants by the more characteristic life forms of the páramo: sclerophyllous shrubs (of genera like *Baccharis* and *Hypericum*), caulescent giant rosettes (mainly *Espeletia*) and tussock grassess (e.g. *Calamagrostis effusa*); (3) clear changes in relative abundance of the dominant species but no species replacements; (4) the existence of divergent patterns of vegetation regeneration, with an increase in community structure dissimilarity during succession.

2.4.1 Patterns of species diversity: the conservation value of the fallow strategy

Our results support the general tendency for early successional vegetation to exhibit relatively vertical rank abundance diagrams, reflecting strong dominance by a few species (Bazzaz 1996; Wilson *et al.* 1996). The results for the evenness index and the RADs suggest that after an initial increase, the distribution of relative abundances rapidly attains values similar to those in the NCP. The low evenness during the early stages of succession seems to be related with the ability of the invader *R. acetosella* to increase in abundance rapidly after plot abandonment: it strongly dominates the early seral stages, with a peak of about 80 % of the total abundance during the 1st year of fallow.

The general tendency for species richness, diversity and evenness is to monotonically increase, progressively approaching an asymptote as the fallow time increases. The total number of species for each fallow year stabilizes at values below those found in the NCP (see Fig. 2.1.B). To some extent, this questions the value of the traditional fallow strategy in the conservation páramo species richness, at least under the current management system (see Sarmiento *et al.* 2002b). This is emphasized by the fact that most dominant species during early succession are introduced (Sarmiento *et al.* 2002a).

However, there is a large variability in the average number of species between different fallow areas and there are no significant differences between the average number of species in the 9 year fallow plots and the mature páramo areas. In the case of species diversity, the estimated time to attain similar average values to those found in the NCP is 19 years, which is very close to the estimate of the time necessary for a restoration of vegetation physiognomy based on the analysis of the rate of succession. The values for both evenness and diversity become more similar during the first 9 years of succession to those found in the NCP than those for species richness. This suggests that while community structure in terms of the species relative abundances shows a relatively fast restoration, the complete restoration of the total number of species occurs on a longer time scale.

In the alpine belt context, generalizations about the patterns of change in diversity during succession seem difficult to derive. For example, Barni and Siniscalco (2000) found a similar monotonic increase in richness and diversity in the early stages of potato old field succession in the Alps; Rikhari *et al.* (1993) analyzing a secondary sere in the Himalaya found an increase in species richness but diversity peaked in intermediate stages of succession; and Tsuyuzaki (1995) reports no changes in any of the three parameters during primary succession in Mt Usu, Japan.

The hypothesis of a decline in richness and diversity in late succession has been related to Connell and Sousa's intermediate disturbance hypothesis (Collins *et al.*

1995). This approach assumes that an increase in the intensity of competition and the displacement of early ruderal species in more stable late successional environments, would lead to a decline in species diversity. However, in páramo old-fields, even though early dominants decline in abundance during succession, they are not completely excluded from the late stages or the mature ecosystem. Hence, the predicted decline in species richness does not occur. The increase in species richness and diversity seems to be the results of the differential arrival and 'packing up' of the páramo regional pool of rare species. This suggest that most of these rare species are relatively poor colonizers and survive because of safe-sites within the heterogeneous matrix of the rosette páramo, where particular combinations of soil or micro-climatic conditions provide refuges from competitive exclusion. However, understanding the mechanisms allowing for coexistence in the diverse páramo community (i.e. spatial heterogeneity, competitive ability/migration tradeoffs, niche separation and resource partitioning, small scale disturbance and patch dynamics) is an exciting area open for further research.

2.4.2 Life forms and dominant species dynamics

As indicated above, the results of this and other studies in páramo old fields show a very consistent sequence in the relative importance of the different life forms and dominant species. This is clearly reflected in the ordination of the plots along the 1st axis of the multivariate analysis (see Fig. 2.7). Interestingly, the directional changes in vegetation composition do not seem to be paralleled by any clear successional trends in soil organic matter, microbial biomass, nutrients or pH (Ferwerda 1987; Moreno and Mora-Osejo 1994; Llambi and Sarmiento 1998; Jaimes 2000; Morales 2000). Going from a mean field approximation (i.e. an analysis based on mean properties across whole fields), to the analysis of internal plot heterogeneity, should be a critical step for shedding additional light into the relationships between species distributions and soil characteristics.

The giant rosettes, tussock grassess and sclerophyllous shrubs that dominate vegetation physiognomy, show a remarkable degree of convergence between the Andes and other high mountain regions of the tropics (Hedberg and Hedberg 1979; Hedberg 1992). These life forms present morphological and ecophysiological adaptations to the typical conditions of the high tropics, such as low temperatures, extreme daily temperature fluctuations, water stress and nutrient deficits (Goldstein *et al.* 1984; Monasterio & Sarmiento 1991; Squeo *et al.* 1991; Rada 1993; Meinzer *et al.* 1994). However, probably as a result of trade-offs with their adaptations to the extreme conditions of the páramo, they show relatively low growth rates.

All of the introduced species (e.g. *R. acetosella*, *Poa annua* and *Erodium cicutarium*) are fast growing perennial herbs and grasses and continuously decline in abundance during the fallow (see Sarmiento *et al.* 2002a). Both *R. acetosella* and *P. annua* have been found to be common páramo invaders after disturbances like agriculture and fire (e.g. Grubb, 1970; Ferweda 1987; Moreno and Mora-Osejo 1994; Ramsay and Oxley 1996). The decrease in importance of exotic species during succession is a common trend in other ecosystems (Vitousek 1986; Meiners *et al.* 2002). Late successional and high diversity sites have been suggested to be more difficult to invade by alien species because of higher 'species packing' (Bazzaz 1996; Tilman 1997).

The clear successional decline of the introduced species could be related to the strong environmental filters of the páramo environment. In the climatically more extreme case of the Venezuelan super-páramo (above 4100 m) permanent plot studies have not found re-colonization by *R. acetosella* after disturbance (Smith & Young 1987). Interestingly, endemic fast growing forbs that are able to show explosive colonization, like *L. meridanus,* only have their abundance peaks after 4 or 5 years. Given this consideration, a comparative analysis of ecophysiological strategies of the dominant species in relation to differences in growth rate and stress tolerance should substantially contribute to our understanding of successional dynamics in this ecosystem. This is the strategy explored in the next chapter.

2.4.3 Páramo regeneration as an autosuccession

The pattern of successional dynamics in which there are changes in relative abundance more than species replacements was called *autosuccessions* by Muller (1952). This kind of successional dynamics, in which most dominant species are present from the initial stages of regeneration, has been proposed as a characteristic of chronically unproductive environments like tundras and deserts (MacMahon 1981; Svoboda and Henry 1987; Urbanska 1997). As emphasized by Sarmiento *et al.* (2002a) and illustrated by the results in Fig. 2.4, the patters of changes in abundance of the dominant species suggests that páramo environments show autosuccessional dynamics. However, it is important to note that Sarmiento *et al.* (2002a) demonstrate that some less abundant introduced species are excluded during succession. Moreover, only some rare mature páramo species are late colonizers or are completely absent in the fallow times analysed (up to the 12 year of succession).

Autosuccessional dynamics are clearly compatible with Egler's (1954) initial floristic composition model (IFC). Egler proposed that the failure to colonize early could reduce the chance of a species of becoming dominant later in succession (see Chapter 1). Hence, tolerance by the seedlings of the late successional (LS) species of the dominance of early successional (ES) species such as *R. acetosella* could be essential for long-term survival (i.e. the tolerance mechanism of Connell and Slatyer 1977; see Chapter 4). Although Egler suggested the IFC as a general model for secondary successions, Finegan (1984) indicates that in most temperate and tropical forest, late successional tree species are late colonizers of old-fields (see also Richards 1970; Whitmore 1975). Tilman (1993) saw this as evidence that recruitment-limitation can be one of the critical forces of succession. However, if recruitment limitations are not important for dominant páramo species (as suggested by their ability to colonize early in succession), the colonization-competition trade-off hypothesis (see Chapter 1) could have limited applicability in understanding their reestablishment during succession.

2.4.4 Divergence in community structure and environmental heterogeneity

The results from the DCA indicate that while variation in community structure between plots is strongly influenced by their fallow time, differences in soil conditions are also important. Furthermore, the results on the changes in dissimilarity (chord distance) during succession provide evidence to suggest that community structure becomes more divergent during late stages, while early successional plots have relatively similar species composition (see also Sarmiento *et al.* 2002a). The lower heterogeneity in community structure in the early succession stages is linked to the strong dominance of *R. acetosella*. Its ruderal habit ensures a universal presence at this stage, probably making its colonisation less dependent on local abundance.

Plot scores in the DCA were significantly correlated with plot differences in soil biology and chemistry only for the 2nd axis, which is independent of successional time: soil pH, Ca, Mg, base saturation and clay were positively correlated with it while parameters that we would expect to be associated with high soil organic matter (e.g. total N and MB-N) were negatively correlated. This suggest that there are plots were soil nutrient dynamics is controlled by the cation exchange complex in clays, while in others organic matter plays a more critical role. The alternating high abundance of intermediate species as *L. meridanus* and *V. myuros* seems to be associated with these differences in soil characteristics, so that they occupy opposite extremes on the 2nd axis (Fig. 2.7). So, the pattern of successional divergence found in this study could be linked to the soil heterogeneity that is characteristic of these mountain environments. I did not find plot altitude and distance to the valley bottom to be associated with any of the first 3 ordination axes. However, Sarmiento *et al.* (2002a), on the basis of the analysis of a larger number of plots, indicated that divergence could be partially explained by the distance of the plots to the valley bottom, a variable that could be related to grazing pressure. Moreover, they found absolute altitude as an explanatory factor for divergence, probably linked to the identity of the natural vegetation surrounding the plots.

In the mountain context, Rikhari *et al.* (1993) have associated divergent pathways of succession with differences in slope and soil depth between plots. In the Colombian páramo, Moreno and Mora-Osejo (1993) were able to link different pathways to fire and grazing intensity, while Ferweda (1987) associated them with differences in slope and altitude.

Sarmiento and collaborators recorded changes in community structure during the 4 following years (1997-2000) in the same plots used in this chapter. The analysis of this information using a diachronic approach (which we intend to complete in the near future), should be an important step in elucidating the effect of spatial heterogeneity on successional divergence (Bakker *et al.* 1992). Moreover, as emphasized by Samuels and Drake (1997), it is possible that while at the species level community structure appears to diverge, the relative importance of the main life forms or functional groups could converge during succession. The evaluation of this hypothesis could contribute to explore the relevance of the 'sequence of arrival' and 'guild proportionality' models of community assembly (see Samuels and Drake 1997) to the process of vegetation regeneration in the high Andes.

Interestingly, the results presented here do not suggest the existence of clearly defined alternative pathways of succession. Frelich and Reich (1995) called this kind of multiple pathway response 'individualistic' and suggested that it is likely to result from the interaction of stochastic factors such as climatic fluctuations, random colonization events and local disturbances. Herben *et al.* (1993) suggested that this kind of individualistic response could also be the result of non-linearities linked with processes such as small scale spatial interactions between species. Horn (1981), based on the analysis of the dynamics of convergence in community structure using a markovian approach, theoretically demonstrated that processes like neighbourhood dependent self-replacement can lead to the development of multiple alternative states. This emphasizes the importance of spatial structure for understanding community dynamics during succession.

2.4.5 Succession rates: slow and slowing down?

The result presented in Fig. 2.8 of a constant rate of succession contradicts the generally accepted hypothesis of a *continuous* and *monotonic* slow down from initial stages to the 'climax' (Shugart and Hett 1973; Armesto *et al.* 1991; Myster and Pickett 1994). While Brown and Southwood (1987) found a constant rate of species turnover, other authors have found a non-monotonic decrease in the rate of succession (Prach 1993) or a cyclic behavior (Donnegan and Rebertus 1999). Myster and Pickett (1994) argued that longer life-spans of LS species should slow down species turn-over rates and that the number of invasion windows should also decline as the community becomes more resistant to further invasions. However, this explanation does not seem to be applicable to systems with autosuccessional dynamics since long-lived species are present from the early stages and there is limited species turn-over. On the other hand, the argument of Myster and Pickett (1994) is to some extent tautological, as necessarily, if the mature or climax state is defined as the point in which there is no further change in species composition, the rate of succession will have to approach zero as this climax state is approached.

The early rate of succession in this tropical mountain system seems to be basically determined by the constant decline of introduced species and the increase in abundance of the dominant páramo species as individuals slowly gain biomass. However, we could expect that later in succession, when the dominant shrubs and rosettes start the process of self-replacement, further community structure change could be mainly determined by the slow colonization of rare páramo species. Consequently, the figure of 17 to 18 years for the regeneration of the páramo structure, assuming a constant rate, could be an underestimate. Based on the analysis of a higher number of plots, Sarmiento *et al.* (2002a) estimated about 30 years for the restoration of vegetation physiognomy. Their data also showed that after 12 years of succession, the relative abundance of the dominant life-forms is very similar to that in the NCP.

If the estimations presented here are compared with regeneration times calculated for forest ecosystems, which range from hundreds to thousands of years (MacMahon 1981), páramo succession seems relatively fast (partially as a result of the longer mean generation time for most trees compared to páramo species). In other cold ecosystems like the tundra, vegetation restoration can take from c. 50 years to several hundred years (Peterson and Billings 1980; Cargill and Chapin 1987). Hence, the results presented here suggest we should be cautious about the accepted wisdom that vegetation regeneration in alpine environments is a very slow process (e.g. Billings 1973), which has also found its echo in the páramo literature (e.g. Janzen 1973; Smith and Young 1987; Horn 1989; Luteyn 1992; Vargas-Rios 1997). Nevertheless, it is important to consider that the fast regeneration of páramo physiognomy is not linked with a complete restoration of other ecosystem properties like soil organic matter and microbial biomass (Llambi and Sarmiento 1998; Llambi and Sarmiento 1999). This emphasizes the fact that different components of the structure and function of an ecosystem can show different regeneration rates (Samuels and Drake 1997). Hence, the perception of the conservation value of the fallow strategy depends on the priority given to the maintenance of these different properties of the ecosystem, and their roles in sustaining the environmental services that the páramo is expected to provide.

2.4.6 Conclusions

The results presented in this chapter confirm some generally expected trends during secondary succession. There is a clear sequence of relative abundance of the different life forms, with introduced forbs dominating in early seral stages while native shrubs and giant rosettes dominate late in succession. This changes are accompanied by an increase in evenness of species abundance. As in other relatively unproductive environments, there are no complete species replacements. Furthermore, the analyses show that most dominant species are present from the early stages of regeneration (i.e. autosuccession). In addition, as in other alpine successions, there is some evidence for divergence in community structure, probably due to the high edaphic and topographic heterogeneity in these high mountain valleys.

The results also question some generally accepted ideas about the rate of succession. First, the idea of a continous decline in the rate of vegetation change is not supported here: succession rates stay constant during the first 9 years of regeneration. In addition, the relatively fast regeneration of vegetation physiognomy found in this chapter questions the supposedly slow restoration of alpine ecosystems in general, and páramo ecosystems in particular.

Interestingly the fast restoration of vegetation physiognomy, contrasts with the stabilization of species richness below the levels observed in the undisturbed ecosystem. This challenges the idea of a high conservation value of long fallow agriculture in this areas, generally located in nature reserves and national parks. The current trend of a reduction in the fallow times used by the farmers, could contribute to the loss of a number of rare native species that are slow in recolonizing disturbed areas. Sarmiento *et al.* (2002b) propose the intensification of agriculture (i.e. elimination of the fallow and introduction of more effective soil fertility management techniques) as a possible alternative. This would reduce the total area under cultivation while maintaining production levels and improving biodiversity, given that representative natural areas are set aside for protection.

This chapter provides a general view of the patterns of vegetation change during old-field succession in the páramo. This provides the necessary basis from which a more process oriented understanding of vegetation dynamics can be developed. In the following chapters, I explore how the analysis of some aspects of the ecophysiology of the dominant species and of changes in population and spatial structure and local spatial interactions can provide further insights the processes and mechanisms that drive successional change.

Chapter 3. Ecophysiology of the Dominant Species

3.1 INTRODUCTION

In cold and chronically unproductive environments, such as those found in arctic, temperate alpine and tropical mountain regions, changes in plant community structure during succession tend to be characterized by shifts in relative abundance more than by species replacement, with most dominant species being present from the very early stages (see Chapter 2; MacMahon 1981; Svoboda and Henry 1987; Urbanska 1997; Sarmiento *et al.* 2002a). This pattern of vegetation regeneration is known as *autosuccession* (Muller 1952).

Tilman (1990; 1993) suggested that in unproductive habitats with autosuccessional dynamics, the difference between being dominant during early or late succession is likely to be due to differences in potential growth rate more than with differences in colonization ability. Grime (1979) and Tilman (1993) hypothesized that differences in growth rate should be the result of trade-offs between maximum leaf area and photosynthetic capacity, and other characteristics that confer competitive advantages under limiting conditions (i.e. low temperatures, water or nutrient deficits).

Common among the adaptations of dominant species in unproductive habitats are leaf properties such as xeromorphy (e.g. a thick cuticle which reduces potential transpiration and water loss) and a high longevity, which allows the conservation and accumulation of nutrients (Grime 1979). These characteristics have also been found to be associated with a low leaf area per unit leaf mass (specific leaf area, SLA) and with low herbivore palatability (Brown and Southwood 1987; Chapin *et al.* 1996; Grime *et al.* 1997; Reich *et al.* 1997; Diemer 1998; Schippers *et al.* 1999). All of these properties, which involve higher allocation to traits such as structural carbohydrates, must result in a trade-off with the allocation of resources to photosynthetic capacity and light capturing area per unit leaf mass.

Although there is abundant evidence on the comparative ecophysiology of succession in tropical and temperate lowland forests (see reviews in Bazzaz 1979; Bazzaz and

Pickett 1980; Huston and Smith 1987; Bazzaz 1996), there is much less information available for the open and cold environments characteristic of arctic and high mountain regions (see Bliss and Peterson 1992 for a review of the evidence for the Arctic). Moreover, the few available studies in these environments offer conflicting evidence on the ecophysiological differences between early and late successional species. The expected trend of a successional decline in growth rates and photosynthetic capacity can be inferred comparing the results of studies in early (Stoner and Miller 1975; Oberbauer and Oechel 1989) and late successional species (Chapin and Shaver 1985) in arctic riparian communities including forbs and shrubs. However, in arctic mire graminoids no differences in photosynthetic potential were evident between fast-growing pioneer and slow-growing climax species (Miller *et al.* 1978; Oberbauer and Oechel 1989). In a study of photosynthetic responses to light of high altitude forbs in the Alps no clear differences were found between pioneer and climax species neither in photosynthetic potential nor in SLA (Körner and Diemer 1987).

In the context of mountain environments, a decrease in SLA and an increase in xeromorphy are some of the most consistent trends in leaves along altitudinal gradients (Gale 1973; Woodward 1983; Körner and Diemer 1987; Körner *et al.* 1989). Laboratory and field studies have suggested that the characteristic slow growth rate of alpine species could be associated with their low SLA (Körner and Diemer 1987; Körner and Pelaez Menendez-Riedl 1989; Atkin *et al.* 1996). However, Loveys *et al.* (2002) showed in plants of different life-forms and ecosystems, grown at three temperatures, that inter-specific differences in SLA were not important in determining differences in relative growth rates in the low temperature treatment (18^0 C). Hence, for arctic and alpine environments, the evidence available offers an unclear view of whether differences in growth rates between early and late successional species are associated with differences in their photosynthetic potential and SLA. This is even less clear for high tropical mountain environments, where, to our knowledge, there have been no studies on the comparative ecophysiology of succession.

Tropical high mountain ecosystems are the only tropical systems subjected to freezing temperatures. Due to their tropical situation, they differ from temperate alpine systems in that they show low variability in the yearly cycles of temperature (but high variability in their daily cycles), so that drought becomes the most important seasonal factor

(Meinzer *et al.* 1994). However, they have other characteristics generally found in high mountains such as generally low nutrient availability, low partial pressures of CO_2 and intense ultra-violet radiation (Sarmiento 1986; Rundel 1994). This combination of environmental determinants has resulted in the evolution of a unique set of adaptations and the dominance of life forms such as giant caulescent rosettes and sclerophyllous shrubs across the highland tropics (Hedberg and Hedberg 1979; Hedberg 1992). Their unique environmental conditions and autosuccessional vegetation regeneration (see Chapter 2 and Sarmiento *et al.* 2002a), make tropical high mountain ecosystems an interesting, but largely unexplored environment, for evaluating the generality of Grime's (1979) and Tilman's (1993) hypothesis on the ecophysiology of succession in unproductive ecosystems.

Ecophysiological studies in the páramo have found an altitudinal increase in xeromorphic characteristics and SLA for the dominant species of the mature ecosystem (Baruch 1979; Mora-Osejo *et al.* 1994; Carlquist 1994; Castrillo and Simoes 1997; Briceño *et al.* 2000). In particular, giant rosette species of the genus *Espeletia* have large thick pubescent leaves and a medullar parenchyma that functions as a water reservoir (Goldstein *et al.* 1984; Meinzer *et al.* 1994). These, and other attributes of *Espeletia* have been shown to be important in water stress avoidance, the maintenance of a favourable thermal balance and the protection against UV-B radiation (Baruch, 1979; Meinzer and Goldstein 1984; Monasterio and Sarmiento 1991; Beck 1994; Meinzer *et al.* 1994; Rada *et al.* 1998; Cross 2001). However, other growth forms have received comparatively little attention and their adaptive value is poorly understood (Smith and Young 1987; Meinzer *et al.* 1994; Ramsay 2001).

In this chapter I compare some ecophysiological characteristics of the plant species that dominate different successional stages in old-fields of the Venezuelan high Andes. Based on Tilman's (1993) and Grime's (1979) ideas I evaluate the following hypotheses: 1) The slow growing dominant species of late successional and mature páramo areas (giant rosettes and sclerophyllous shrubs) should show a lower photosynthesis at light saturation (A_{max}) and SLA than the species that dominate the early stages (fast growing forbs); 2) As drought is the most important seasonal factor, dominant late succession species should have a higher water stress resistance than species that dominate during early succession. Hence, they are expected to show less change in A_{max}, stomatal conductance at light saturation (g_{max}) and midday leaf water potential between the dry and wet season and to have a higher intrinsic water use efficiency (WUE_i) during the dry season (CO_2 assimilation per unit of stomatal conductance).

3.2 METHODS

3.2.1 Páramo old-field succession and species selection

Based on the results presented in Chapter 2 and in Sarmiento *et al.* (2002a), I selected the six most abundant species of the three life forms that dominate the different seral stages in old-fields in the Gavidia Valley (see Plate 3.1). *Rumex acetosella* is a perennial forb and is the dominant species in the initial stages of succession. It shows a clear tendency to decrease in abundance throughout the fallow; *Lupinus meridanus* is a nitrogen-fixing forb, present throughout the fallow, and shows its peak in the intermediate stages; *Acaena elongata, Baccharis prunifolia* and *Hypericum laricifolium* are sclerophyllous shrubs; *Espeletia schultzii* is a giant caulescent rosette. These last four species are present from the early stages of succession and continuously increase in abundance. In Table 3.1 I summarize some of the relevant information available for each of these species, including their relative abundance at the moment of their peak biomass.

A. *Rumex acetosella* L. (2nd year) B. *Lupinus meridanus* Moritz (5th year)

C. *Acaena elongata* L (8th year) D. *Baccharis prunifolia* H.B.K. (12th year)

E. *Hypericum laricifolium* Juss. (páramo) F. *Espeletia schultzii* H.B.K. (páramo)

Plate 3.1 Dominant species during old- field succession in the Venezuelan páramo. The fallow year in which they show their peak abundance is indicated in brackets (from: Sarmiento *et al.* 2002a).

3.2.2 Ecophysiological measurements

Measurements were taken during the year 2000 in three adjacent fallow fields of different ages: 3, 6 and 12 years. Fields of longer fallow times are not available in the area. However, Sarmiento *et al.* (2002a) found that the relative abundance of the different life forms attained very similar values after 12 years of succession as those found in the mature ecosystem.

All plots were located at c. 3450 m a.s.l. Each species was analysed in the field where it showed its highest abundance. Measurements for gas exchange and leaf water potential were taken separately during the wet and dry season, as in this environments there are marked seasonal changes in water availability. Rainfall during the wet season represents an average of 93.3% of the total precipitation and during the dry season, soil moisture in the first 20 cm of the soil profile frequently drops below the wilting point (Sarmiento 2000).

Below, I indicate the methods used for measurements of gas exchange, specific leaf area and leaf water potential and for calculating intrinsic water use efficiency.

(1) *Gas exchange*:

A portable infrared gas analyser unit was used in the field (LCA-4 System, The Analytical Development Co. Ltd. Hoddesdon, Herts, England) to determine the net rate of CO_2 uptake per unit leaf area, stomatal conductance to water vapour (g), and photon flux density (measured as photosynthetically active radiation, PAR). Leaves were artificially shaded during measurement in order to change light intensities to construct photosynthesis-light response curves. The photosynthetic response at different radiation levels was measured on different leaves. Three randomly selected fully expanded healthy leaves were measured per plant (a minimum of 15 plants were used in each case) until I obtained a minimum of 45 measurements for the light response curve per species. Measurements were taken on March 10 and 17 for the dry season and on May 26 and June 12 for the wet season on sunny days between 10:30 and 16:30 h. The light response curves were described using a standard rectangular hyperbola equation (Ceulemans and Saugier, 1991):

$$A = \frac{qI\ A_{\max}}{qI\ + A_{\max}} - R_d \qquad \text{Eq. 3.1}$$

In which, A is the net CO_2 assimilation rate, I is incident PAR, q is the apparent quantum yield, A_{max} is the assimilation at light saturation and R_d the dark respiration rate.

I present only the light response curves for the wet season, as these curves are intended to show the response of assimilation to variations in PAR levels with the minimum possible interference from water limitations (which is more likely to result in the dry season). I calculated A_{max} (per unit leaf weight) as the average net assimilation observed at high PAR (above 1200 μmol m^{-2} s^{-1}) for both the dry and the wet season (the number of replicate measurements for calculating average A_{max} varied between 10 and 32) to evaluate the effect of water limitations on photosynthesis. Maximum stomatal conductance (g_{max}) was calculated in the same way. A_{max} values from the rectangular hyperbola model were not used in this analysis, as they were unrealistically high because they are asymptotic values at infinite PAR.

(2) *Specific leaf area*:

During the wet season, the area of 10 replicate groups of randomly selected healthy looking green leaves was determined using a LICOR LI 3100 area meter. These same leaves were then oven dried for 72 h at 70^0C and weighed. The specific leaf area (SLA) was calculated as the ratio of area per unit leaf mass.

(3) *Leaf water potential*:

Midday xylem water potential (ψ) was determined in the field with a portable pressure chamber. Five randomly selected leaves from five adult plants per species were measured. Measurements were carried out between 12:00 and 14:00 h on March 10 (dry season) and May 26 (wet season).

(4) *Intrinsic water use efficiency*:

The intrinsic water use efficiency (WUE_i) was calculated as the ratio of A_{max} per unit of g_{max}. This is a more appropriate expression to compare water use efficiency in CO_2 assimilation between different species than the commonly used quotient of assimilation per unit of transpiration, as the effect of external factors on transpiration is excluded (Osmond *et al.* 1980).

3.2.3 Statistical analysis

The SPSS v. 10.0 was used for all statistical analysis. For the comparison of means between species and seasons for A_{max}, g_{max}, ψ, and SLA, a non-parametric Kruskal-Wallis test was used: the one-way ANOVA assumptions of homoscedasticity (Levene's test) and normality (Kolmorogov-Smirnov test) were not satisfied. Multiple treatment comparisons were done using Dunnett's C test, which does not assume homoscedasticity.

3.3 RESULTS

3.3.1 Carbon assimilation and specific leaf area.

The light response curves showed high light saturation points well above 1000 μmol m^{-2} s^{-1} for all species (Fig. 3.1). *Baccharis prunifolia* and *E. schultzii* showed a lower quantum yield (lower initial slopes) than the rest of the species (statistically significant differences in the estimation of the parameters by least square regression, α=0.05). The high R^2 values obtained on the fit to a rectangular hyperbola (from 0.87 to 0.98) indicate that possible differences in stomatal conductance in the measuring interval did not play a significant role in our analysis of the response of assimilation to light.

A_{max} rates were higher in the wet season for all species (Kruskal-Wallis, $p<0.001$) except for *B. prunifolia* (K-W, $H_{(1,N=53)}=2.43$, $p=0.121$) and *E. schultzii* (K-W, $H_{(1,N=52)}=0.63$, $p=0.426$), which did not show significant differences in photosynthesis between seasons (Fig. 3.2). Differences in A_{max} *among species* were significant for both seasons: dry (K-W, $H_{(5,N=145)}=103.96$, $p<0.001$) and wet (K-W, $H_{(5,N=99)}=74.93$, $p<0.001$). In the dry season, *L. meridanus* and *R. acetosella* presented significantly higher A_{max} compared to the rest of the species. In the wet season *R. acetosella* showed the highest average rate, followed closely by *L. meridanus* and then by *A. elongata*, while the late species showed the lowest rates (Fig. 3.2). There were significant differences between the SLA of the different species (K-W, $H_{(5,N=60)}=55.20$, $p<0.001$): *Rumex acetosella* showed the highest SLA followed by *L. meridanus*. Then, *A. elongata* - *B. prunifolia* and *H. laricifolium* - *E. schultzii* formed two groups with successively lower values (Fig. 3.3).

3.3.2 Water relations

Leaf water potential was higher for all species in the wet season (K-W, $p<0.05$) except for *E. schultzii,* which showed no significant differences between seasons (K-W, $H_{(1,N=10)}=3.35$, $p=0.067$). There were significant differences between species in ψ both in the dry (K-W, $H_{(5,N=35)}=18.88$, $p=0.002$) and the wet season (K-W, $H_{(5,N=35)}=25.84$, $p<0.001$). In the dry season, *Baccharis prunifolia* showed the lowest average ψ whereas *E. schultzii* maintained the highest, with the rest of the species having intermediate values. *Espeletia schultzii* also exhibited the highest potential in the wet season followed by *R. acetosella* and then the rest of the species (Table 3.2). Average g_{max} was considerably higher in the wet season than in the dry season for all species (K-W, $p<0.05$). In both seasons g_{max} was much higher in *L. meridanus* than in the rest. *Rumex acetosella* showed intermediate values while the late species had lower averages (Table 3.2). The percent reduction in stomatal conductance was lowest in *E. schultzii* (41.2%) and highest in *R. acetosella* (79.3%). WUE_i in the dry season showed a very clear trend to increase from the early successional forbs to the late successional shrubs with the highest value in *E. schultzii* (Table 3.2).

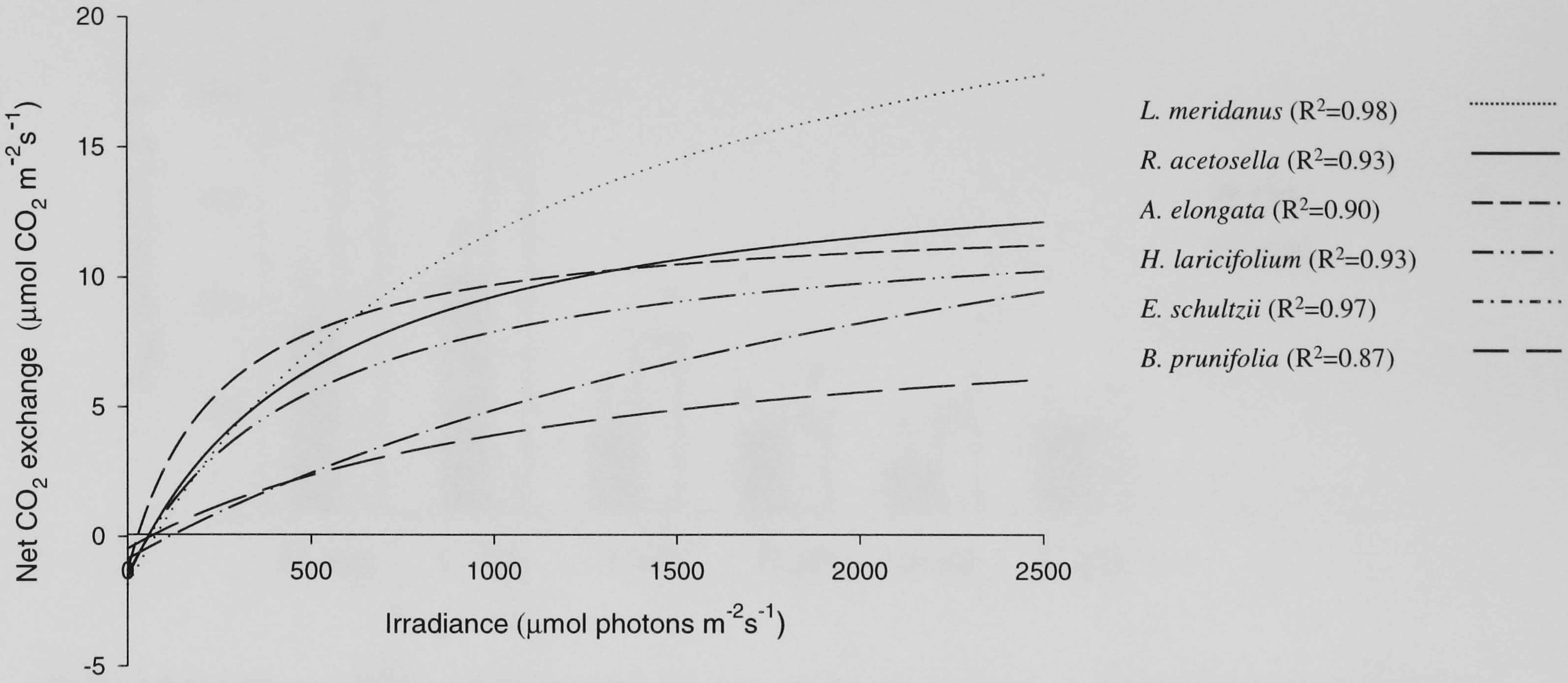


Figure 3.1 Net CO_2 exchange for the wet season as a function of the photosynthetically active radiation (irradiance) as predicted by a rectangular hyperbola model fitted through least squares regression (see R^2 values). The species in the legend appear in the same order as their corresponding light response curve.

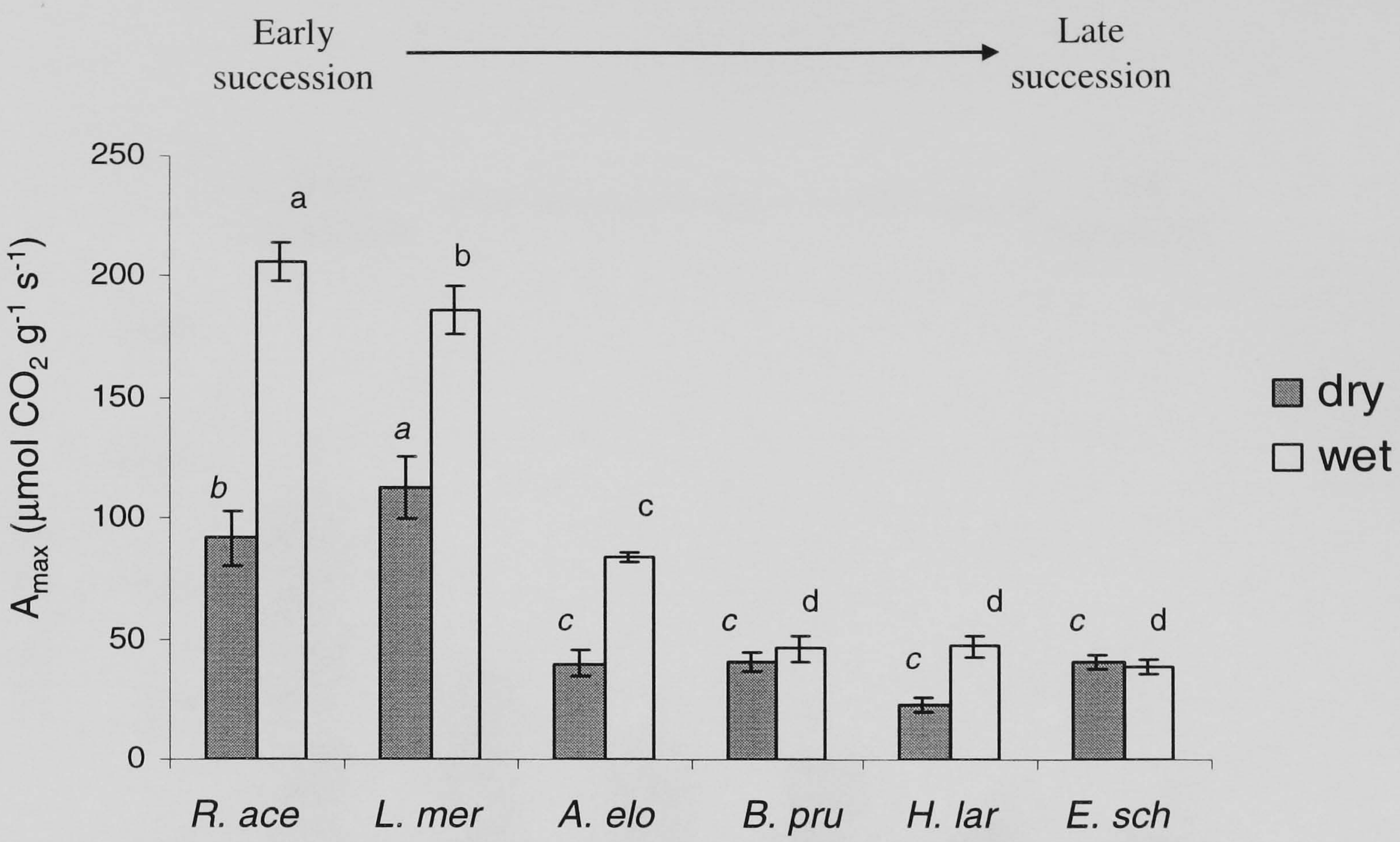


Figure 3.2 Net CO_2 assimilation at light saturation (A_{max}) on a leaf mass basis for the different species shown in the order of peak dominance in succession from left to right: *R. acetosella* (R. ace), *L. meridanus* (L. mer), *A. elongata* (A. elo), *B. prunifolia* (B. pru), *H. laricifolium* (H. lar) and *E. schultzii* (E. sch). The letters correspond to comparisons between species in the same season. Values with the same letter are not significantly different (Dunnett's multiple comparison test). Error bars: standard error.

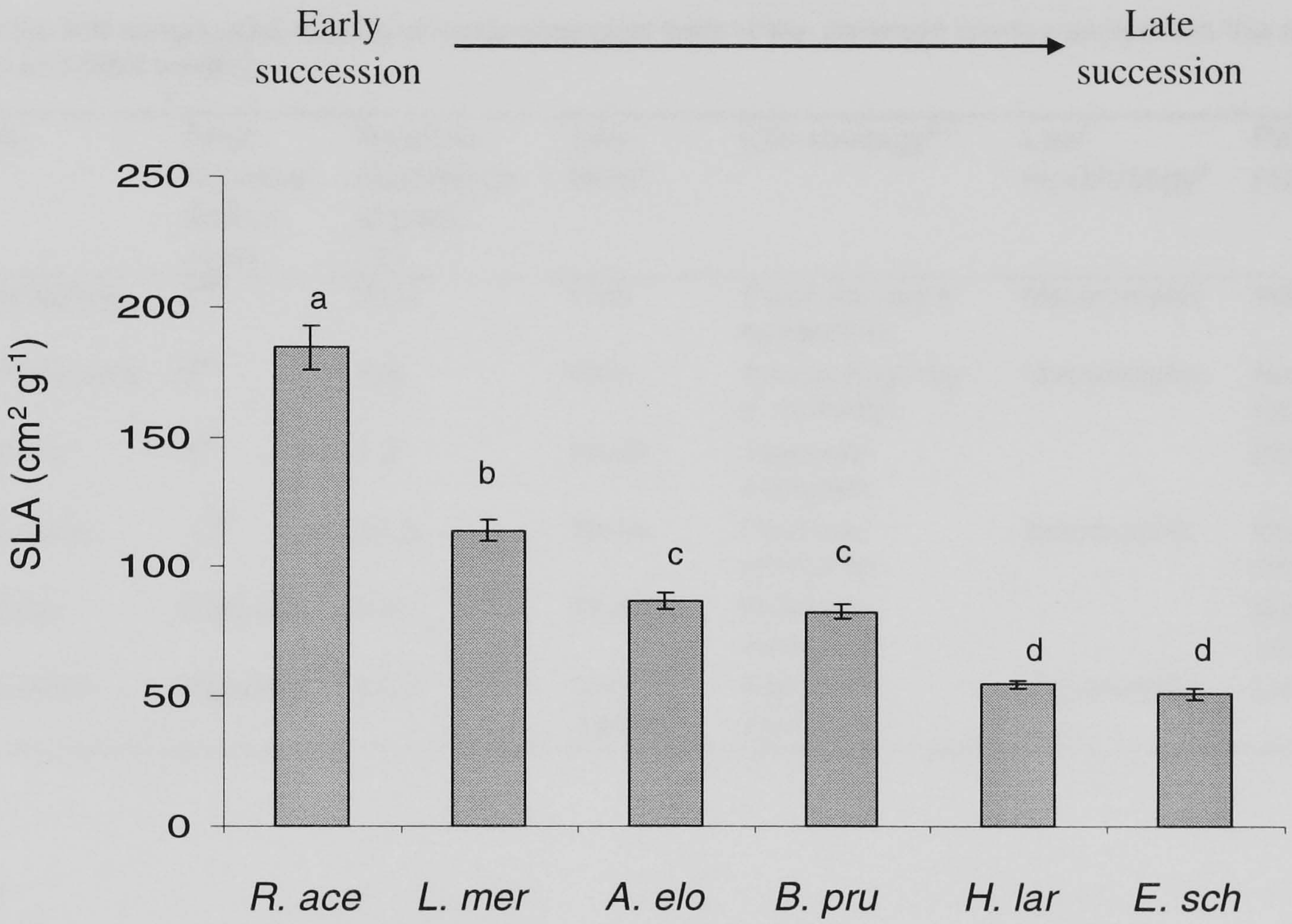


Figure 3.3 Specific leaf area (SLA) of the different species (in the wet season) shown in the order of peak dominance in succession from left to right: *R. acetosella* (R. ace), *L. meridanus* (L. mer), *A. elongata* (A. elo), *B. prunifolia* (B. pru), *H. laricifolium* (H. lar) and *E. schultzii* (E. sch). Values with the same letter are not significantly different (Dunett's multiple comparison test). Error bars: standard error.

Table 3.1 Relative abundance and comparative ranking of some ecological traits of the dominant species analyzed in this chapter. LWR=Leaf weight ratio (leaf weight per unit plant weight).

Species	Family	Peak biomass[1] (fallow year)	Relative abundance at peak[1] (%)	Life-form[2]	Life-strategy[2,3]	Leaf morphology[3]	Palatability[4] (cattle)	LWR[2]	Total leaf N[2,5]
Rumex acetosella	Polygonaceae	2nd	54.4	Forb	Perennial (dry s. as rosette)	Mesomorphic	Intermediate	Low	High
Lupinus meridanus	Papilioneaceae	5th	8.8	Forb	Annual (high dry s. mortality)	Mesomorphic	Not consumed	-	High
Acaena elongata	Rosaceae	8th	7.7	Shrub	Perennial evergreen	-	Intermediate	Interm.	Interm.
Baccharis prunifollia	Compositae	12th	23.5	Shrub	Perennial evergreen	Xeromorphic	Not consumed	High	Interm.
Hypericum laricifolium	Guttiferae	Páramo	9.9	Shrub	Perennial evergreen	-	Not consumed	High	Interm.
Espeletia schultzii	Compositae	Páramo	11.7	Giant rosette	Perennial evergreen	Xeromorphic	Low	Very high	Low.

[1] Sarmiento *et al.* (2002)
[2] Berbesi (1990)
[3] Roth (1973), Mora-Osejo *et al.* (1994) and Briceno *et al.* (2000)
[4] Molinillo and Monasterio (1997) and Perez (2000)
[5] Sarmiento, unpublished results

Table 3.2 Means (and standard errors) for water potential (ψ) and maximum stomatal conductance (g_{max}) for the dry and wet seasons. The percent reduction in average stomatal conductance between seasons and the intrinsic water use efficiency (WUE_i) for the dry season are also presented. Species appear in the order of peak dominance in succession from top to bottom. Values with the same letter are not significantly different (Dunnett's multiple comparison test, α=0.05).

Species	Water potential (MPa) dry	Water potential (MPa) wet	g_{max} (mol m^{-2} s^{-1}) dry	g_{max} (mol m^{-2} s^{-1}) wet	Reduction in g_{max} (%)	WUE_i (A_{max}/g_{max}) dry
R. acetosella	-1.45 (0.08)^a	-0.64 (0.04)^a	0.12 (0.01)^a	0.37 (0.07)^a	79.3	41.4
L. meridanus	-1.58 (0.04)^a	-0.95 (0.02)^b	0.27 (0.04)^b	0.96 (0.14)^b	71.8	36.4
A. elongata	-1.46 (0.03)^a	-1.10 (0.02)^b	0.05 (0.01)^c	0.11 (0.01)^c	56.2	90.8
B. prunifolia	-2.32 (0.13)^b	-1.07 (0.02)^b	0.05 (0.01)^c	0.10 (0.01)^c	46.5	94.0
H. laricifolium	-1.61 (0.07)^a	-1.08 (0.04)^b	0.03 (0.01)^c	0.13 (0.01)^c	76.2	136.3
E. schultzii	-0.58 (0.04)^c	-0.35 (0.07)^c	0.04 (0.01)^c	0.07 (0.01)^c	41.2	192.4

3.4 DISCUSSION

The results presented in this chapter show that there is a consistent trend for a decline in photosynthesis at light saturation and specific leaf area from species that have their peak of abundance during early seral stages to species that dominate during late succession. This suggests that in tropical mountain environments, the fast growth of early successional (ES) species could be associated with a maximization of light capturing area and photosynthetic potential per unit leaf mass. Moreover, the results suggest that presence of thick xeromorphic leaves, a higher water use efficiency and the ability to maintain stable leaf water potentials and CO_2 assimilation rates during the dry season (in the case of *E. schultzii*) could be important for dominance during late seral stages.

Below, I discuss the relationships between the different ecophysiological and life history strategies of species that dominate the different stages of succession in this tropical highland ecosystem. I then briefly indicate some possible directions for further research and discuss the implications of the available information for understanding vegetation regeneration dynamics in these highland tropical ecosystems.

3.4.1 Relationships between ecophysiological characteristics

All the studied species present light response curves with high light saturation points. This heliophytic behaviour has been recognized as characteristic of alpine plants, probably related with the avoidance of photoinhibition in this high radiation environment (Körner and Diemer 1987). Our values for A_{max} are within the ranges reported by Körner (1999) from an extensive review of the literature for alpine forbs, shrubs and rosettes, which showed their mean photosynthetic capacity to decrease in the same order reported in this chapter. This suggests that to some extent, the lack of consistent successional trends for A_{max} (and also for SLA) in the arctic and alpine literature between pioneer and climax species, could be due to whether or not the species compared belong to the same life-form.

It is also important to consider that other components apart from SLA and A_{max} can influence differences in relative growth rates, such as whole plant biomass allocation patterns. Data from Berbesi (1990) in the Venezuelan páramo suggests that the proportion of plant mass allocated to leaves (leaf mass ratio, LMR) increases from early successional to late successional species (Table 3.1). Hence, the lower assimilation rates per unit leaf mass in the late successional (LS) species could be partially compensated by a higher plant biomass allocation to photosynthetic tissues. However, a comparative analysis of the relationship between relative growth rate and biomass allocation patterns of the dominant species is necessary before it is possible to derive more definitive conclusions.

The successional decrease of A_{max} shown in this chapter is probably associated to the higher leaf nitrogen concentration (per unit leaf mass) in the dominant ES species reported by Berbesi (1990) in the Gavidia Valley (Table 3.1). Several authors have found the same positive relation between A_{max} and leaf N concentration (Davies 1998). Interestingly, Reich *et al.* (1997) report in a comparative analysis of a set of extremely contrasting biomes (from tropical rainforest to tundra ecosystems) that A_{max} increases with increasing leaf N, increasing SLA and decreasing leaf longevity (see also Field and Mooney 1986; Ceulemans and Saugier 1991).

The clear decrease in SLA from ES to LS species appears to be associated to an increase in xeromorphy (Roth 1973; Mora-Osejo *et al.* 1994; see Table 3.1). For example, in *B. prunifolia,* xeromorphic characters include thickened epidermal cell walls covered by cuticle and water storage in epidermal cells. Some of the suggested roles of xeromorphic traits in páramo shrub leaves are the avoidance of excessive transpiration and protection against high UV-B levels (Hedberg 1964; Smith and Young 1987; Mora-Osejo *et al.* 1994). Furthermore, Molinillo and Monasterio (1997) and Perez (2000) found that *R. acetosella* and *A. elongata* were relatively more palatable for cattle than *E. schultzii*. *Hypericum laricifolium*, *L. meridanus* and *B. prunifolia* were not consumed at all (Table 3.1). These observations support the idea that xeromorphy and a low SLA could be associated to the resistance of páramo species to grazing by cattle. The low palatability of *L. meridanus* is likely to be related to the presence of chemical defence mechanisms more than to leaf xeromorphy.

In drought adapted species photosynthesis should decline less during dry periods (Lambers *et al.* 1998). This behaviour is found here in *E. schultzii* and *B. prunifolia*. These two species showed no significant differences in assimilation between both seasons. The maintenance of a stable A_{max} between seasons and of a high ψ by *E. schultzii* has been reported by other authors (e.g. Goldstein *et al.* 1984; Rada *et al.* 1998). While in *E. schultzii*, drought *avoidance* mechanisms like the presence of a water storage pith in the stem are of primary importance (Goldstein *et al.* 1984), in tropical alpine shrubs lacking sufficient water storage capacity, drought *tolerance* mechanisms should be expected (Meinzer *et al.* 1994). This idea is supported by the fact that the shrubs showed a more pronounced reduction in g_{max} between both seasons and lower midday water potentials in the dry season than *E. schultzii*. The capacity of shrubs like *B. prunifolia* to tolerate low leaf water potentials during the dry season (see Table 3.2), could be related to their small and thick leaves. These characteristics could be associated with a higher osmotic potential (at turgor loss point) and cell wall elasticity (Smith and Young 1987).

Finally, the clear successional increase in WUE_i suggests that in LS species their lower stomatal conductance could allow them to drastically reduce water loss while reducing assimilation proportionally less than the ES species (Körner 1999).

3.4.2 Caveats

In general, it would be important to evaluate the extent to which the ecophysiological differences identified here between ES and LS species are also applicable to the large number of sub-dominant and rare species in these systems. A more extensive species sample should allow evaluating if differences in photosynthetic potential and SLA are also evident in species that have their peak of abundance in different seral stages but that belong to the same life-form. Further, it is necessary to include tussock grassess, which are the only important life-form in the páramo not considered in this chapter. This is the only life-form that does not show clear trends in abundance during the fallow (see Chapter 2 and Sarmiento *et al.* 2002a). There is also a need to include other life-history and ecophysiological factors in the analysis to get a more clear view of whether species that dominate during the different stages of succession constitute consistent functional groups. In particular, it would be important to confirm the inferred differences between ruderal and climax species in relative growth rate, leaf and whole plant longevities, susceptibility to grazing, nitrogen use efficiency, reproductive allocation and dispersal ability.

Finally, it would be important to extend the ecophysiological measurements on the dominant species to replicate plots in different seral stages, to assess the changes in performance of the same species in different successional environments. An evaluation of the variability for parameters such as photosynthesis through daily courses, would also contribute to determine the extent to which factors such as a midday depression in assimilation could have affected the comparative analysis of species responses.

3.4.3 Conclusions: Ecophysiology and community structure changes in succession

The results presented here suggest that fast growing species that dominate during early succession in tropical highland ecosystems have a high SLA and A_{max}, while traits associated with drought resistance appear to be associated with dominance during late succession. This supports Grime's (1979) and Tilman's (1990, 1993) ideas about the expected ecophysiological differences between ES and LS species in unproductive environments with autosuccessional dynamics. The differences found in this chapter between ES and LS species could be the results of two kinds of trade-offs: 1) between the decrease of water losses through stomatal control and the increase of photosynthesis rates; 2) between having a high leaf area per unit leaf mass (and hence photosynthetic leaf area) and allocating a high proportion of leaf mass to xeromorphic characteristics such as a thick cuticle.

The high WUE_i and thick xeromorphic leaves of late successional species are likely to be related to the ability of shrubs and giant rosettes to retain their leaves during the dry season (allowing them to be more effective in nutrient conservation and to maintain a positive carbon balance throughout the year, Berbesi 1990). In contrast, the annual *L. meridanus* suffers high mortalities during the dry season and individuals of the perennial *R. acetosella* either die or survive as smaller rosettes or underground rhizomes (Briceño *et al.* 2000; see Chapter 5). The evergreen strategy is also common in dominant mature species in tundra ecosystems, where old leaves have been shown to act as storage organs from which nutrients, lipids and proteins are mobilized to new leaves (Billings 1987).

Fast growing forbs are probably able to dominate during early succession by rapidly exploiting the available resources. A more efficient use of water and a progressive nutrient sequestration in perennial standing phytomass in the dominant mature páramo species could be one of the factors explaining their ability to displace as dominants the ES species. The initial exploration of the ecophysiology of páramo succession presented in this chapter suggests that a functional perspective holds much promise for furthering our understanding on the factors that determine vegetation regeneration in tropical mountain environments.

Chapter 4. Successional Changes in Small-Scale Spatial Structure: the reestablishment of a giant rosette species

4.1. INTRODUCTION

Increasingly, the ecological theory of succession is emphasizing the understanding of the structure and dynamics of populations (Peet and Christensen 1980; Falinska 1991; McCook 1994). This 'population based' approach has focused on processes like dispersal, establishment and growth of individuals, their intra- and inter-specific interactions and the modifying effect that environmental heterogeneity has on them (Pickett 1982; Falinska 1991; van der Valk 1992). It has also encouraged the analysis of the role that life history and ecophysiological trade-offs between species of different seral stages play in their successional dynamics (see Chapter 3; Drury and Nisbet 1973; Grime 1979; Noble and Slatyer 1980; Bazzaz 1996; Rees *et al.* 2001).

The analysis of development of age and size structure in natural populations can offer insights into the process that determine their dynamics as they reflect both the past and present opportunities for establishment (dispersal and germination), survival and reproduction (Hutchins 1997). Most studies on population structure changes during succession have come from temperate forest and have shown continous recruitment to generate complex size and age hierarchies. In particular, authors like Knowles and Grant (1983), Parker and Peet (1984) and Woods (2000) have shown there are distinctive patterns for the size distribution of populations of trees in different stages of forest succession: a smaller proportion of individuals in the small size classess seems characteristic of late succession and mature forest species. This is generally the combined result of self-thinning and a decrease in the potential for seedling establishment in late seral stages because of increased competition. The detailed demographic analysis of age and size structures of forb species in meadow to forests successions by Falinska (1991), has also demonstrated a close relationship between the successional phase of the community, and the population structure of its dominant species.

There is also a growing recognition within plant ecology of the importance of the analysis of small-scale spatial structure. This is because plant performance is more likely to be affected by the density of conspecifics, individuals from other species and the environmental conditions within a small scale neighbourhood around a plant (the 'plant's eye view' of Turkington and Harper 1977) than by the mean values of this factors across large areas (Tilman *et al.* 1997;Pacala 1997; Law *et al.* 2000; Stoll and Weiner, 2000). The 'mean-field' values are likely to differ from local values because of the non-randomness in spatial structure that is characteristic of most plant populations (Mahdi and Law 1987; Silvertown and Lovett-Doust 1993; Hutchings 1997; Dale 1999) and communities (e.g. the 'regeneration complex' of Watt 1947; Gibson and Greig-Smith 1986; Podani *et al.* 1998; Prudden 2002). Both theoretical (e.g. Bolker and Pacala 1997; Law and Dieckmann 2000; Law *et al.* 2002) and empirical evidence (e.g. Pacala and Silander 1990; Stoll and Prati 2001) suggests that processes which typically operate at local scales (e.g. competition and dispersal), combined with non-random spatial structure, can have important consequences in the dynamics of populations and communities.

Given that both an analysis of demographic and spatial structure can offer useful insights, the combination of these two approaches should be an important tool for understanding vegetation regeneration (Kenkel *et al.* 1997). On of the main applications of this line of research has been the analysis of the increase in regularity or loss of aggregation in the spatial pattern of shrub populations in extreme environments like tundra and deserts. This loss of aggregation has been seen to suggest local density dependent mortality as a key process determining the population structure (Phillips and MacMahon, 1981; Fowler, 1986; Chapin *et al.* 1989; Haase *et al.* 1997). This is interesting to evaluate in the case of the tropical high mountain environments, because of their extreme characteristics in terms of low nutrient availability and seasonal water stress (Sarmiento, 1986). The low resource availability suggests that this kind of competitive effect could be strong enough to override factors favouring aggregation like limited dispersal.

In successional research, two different approaches for the analysis of spatial structure have been dominant. The traditional approach has been to focus on the characterization of changes in the *intensity* and *scale* of spatial patterns (see Dale, 1999), to then attempt to identify factors determining these changes (e.g. successional changes in environmental heterogeneity). Accordingly, the techniques used for spatial analysis (e.g. block-quadrat variance and local quadrat variance) have tended *not* to be 'plant-centred' (*sensu* Purves and Law, 2002), emphasizing multiple scale patterns across whole fields. These kind of studies have mainly been concerned with issues such as evaluating Greig-Smith's (1964) hypothesis that succession is accompanied by an increase in the scale of aggregations and a decrease in the intensity of aggregation. (e.g. Anderson 1967; Brerenton; 1971; Yarranton and Morrison; 1974; Dale and Blundon 1990; Schaefer 1993). The evaluation of this hypothesis has produced little more than a set of descriptions of vegetation spatial structure in successional environments, and very little insights into the processes that determine vegetation dynamics. Perhaps a more relevant contribution of this line of research has been the analysis of the relation between changes in local soil conditions and micro-topography on vegetation structure (e.g. Zedler and Zedler 1969; Sterling *et al.* 1984; Jumpponen *et al.* 1999). For example, Sterling *et al.* (1984) showed the spatial structure in early successional Spanish grasslands changed during vegetation development from being associated with 'fine-grained' microtopographical factors to 'coarse-grained' differences in geomorphology at larger spatial scales. In the mountain restoration context, Urbanska (1997) has emphasized the usefulness of small-scale spatial analysis for exploring aspects such as the identification of the environmental characteristics of safe-sites.

The second, and less frequently used approach, has been considering spatial analysis as a means to understand the *processes* influencing population and community structure changes in succession, rather than an end in itself. These more 'process oriented' studies have tended to use neighbourhood or plant-centred techniques (e.g. spatial autocorrelation, nearest neighbour and the spatial covariance functions used in this chapter). They have looked at questions such as the spatial association of one or more species at small spatial scales, as a means of deriving hypothesis on the effects of intra-specific competition and the mechanisms of species replacement in time (e.g. Frelich *et al.* 1993; Frelich and Reich 1995; Rejmanek and Leps 1996; Haase *et al.* 1997; Eshel *et al.* 2000; He and Duncan 2000). For example, studies on the spatial inter-specific relationships in temperate forest succession have shown that late successional (LS) species can only recruit successfully in the openings formed by the deaths of pioneer trees. Hence, the LS species are often clumped in the canopy gaps and negatively spatially associated with overstorey pioneer species (e.g. Peterson and Squiers 1995; He and Duncan 2000).

Plant-centred studies of spatial structure changes in succession have mostly been done in lowland forest ecosystems. Moreover, they have rarely combined the analysis of population size (or age) structure with the analysis of intra- and inter-specific spatial associations at small scales. To analyse changes in local spatial interactions of a given species in the different stages of its life cycle is important: properties like competitive ability are known to be strongly dependent on plant age and size (Grace 1985, 1988; Bazzaz 1990). Hence, the general objective of this chapter is to explore how integrating demographic analysis with the analysis of intra- and inter-specific small-scale spatial structure (using 'plant-centred' techniques) can contribute to understanding some of the processes that control plant successional dynamics. Here, I use this approach to the analysis of successional changes in demographic and spatial structure of *Espeletia schultzii*, the dominant species in late seral stages and the mature páramo in the study area.

The large size (up to 1.2 m in height) and discrete nature of individuals of the *Espeletia* genus, distributed in a herbaceous/grassland matrix, make them ideal for spatial analysis: individuals are very easy to count and locate. Moreover, the existence of a detailed database on large numbers of fallow fields available for the Gavidia páramo (Smith 1995), provides an excellent opportunity. It allows to study long-term changes in spatial structure during succession using a chronosequence approach with extensive replication (a common problem in many spatial structure analysis of succession has been the lack of replication, see He and Duncan 2000).

Even though the giant rosettes of the *Espeletia* genus are emblematic of the tropical Andes, there have been no studies of its changes in population and spatial structure during succession. More generally, there have been very few studies in the area of vegetation structure and dynamics at a plant neighbourhood scale. Two notable exceptions based on the Venezuelan páramo are: the work of Perez (1992) on differences in soil properties (e.g. soil organic matter) around giant rosette plants; and the analysis by Smith (1980,1981), based on neighbourhood techniques, of the effects of seedling and adult conspecifics in the performance of *E. schultzii* individuals in mature areas.

The results from páramo old-fields presented in Chapter 2 indicated the importance of early colonization for subsequent dominance, as most dominant species are present from the very early stages of succession. This suggests that changes in vegetation structure can be mainly the result of subsequent population dynamics (see Drury and Nisbet 1973; Pickett 1982). Moreover, the ecophysiological analysis presented in Chapter 3 indicated that dominant late species like *E. schultzii* grow slowly possibly as a result of a trade-off between photosynthetic capacity and stress tolerance. Hence, *E. schultzii* can become dominant only during late succession because of its slow gain in biomass.

To shed additional light into the demographic processes associated with the increase in biomass of this late successional dominant, I analyse here the changes in the density and size distribution of populations of *E. schultzii* in different stages of succession and the mature ecosystem. Moreover, I evaluate the changes in the spatial structure separately for seedling and adults. This allows to determine whether, as found in other extreme environments, there is a decrease in spatial aggregation from seedlings in early seral stages to adults in the late stages of succession, which could result from strong local intra-specific competition. I also analyse the spatial associations between seedlings and adults in the late stages of succession. This permits exploring the relative contributions of limited dispersal and intra-specific competition in the regeneration of the population.

Finally, I analyse the spatial interactions between the distribution of *E. schultzii* and other early (*R. acetosella*) and late (*H. laricifolium*) dominant species and with microtopographic heterogeneity. The early colonization of LS species, implies that to dominate during the late stages, species like *E. schultzii* must be able to tolerate as seedlings the dominance of *R. acetosella* early in succession (the tolerance mechanism of Connell and Slatyer 1977). Hence, small-scale spatial analysis should allow determining the extent to which *E. schultzii* seedlings are able to colonize early by establishing preferentially in areas of low *R. acetosella* abundance. Moreover, it should contribute to determine if the increase in dominance of *E. schultzii* is related to the successional decline of *R. acetosella* through competition.

4.2 METHODS

4.2.1 Selected species: *Espeletia schultzii.*

The genus *Espeletia* (Asteraceae) contains c.130 species and is endemic to the northern tropical Andes (Monasterio and Sarmiento 1991). Most of the species in the genus form large unbranched caulescent rosettes with a crown of long pubescent leaves. A thick cover of marescent leaves encases the trunks. The fact that the same life form has evolved independently in the high mountain belts of East Africa, the central Andes, Hawaii, New Guinea, and the Canary Islands, suggests that it is an adaptive response to the particular characteristics of tropical highland ecosystems (Hedberg and Hedberg 1979). Some aspects of the population biology of giant rosette species have been studied in *afroalpine* environments (Young 1994; Smith and Young 1994). In the high tropical Andes, the genus *Espeletia* is probably the best known in terms of population biology: several authors have studied aspects like pollination, seed germination and survival (see Smith and Young 1987). In addition, Silva *et al.* 2000 analysed the population dynamics of a super-páramo species using matrix population models. In the context of succession, Suarez and Medina (2001) and Kovar (2001) looked at responses in population structure to burning and grazing in Ecuador.

In the Venezuelan Andes, *E. schultzii* is one of the most widespread species throughout the elevational range of the páramos, becoming particularly abundant within rosette-shrubland associations of *E. schultzii-H. laricifolium* (Baruch 1979; Farinas and Monasterio 1980). Its population biology has been studied in some detail in mature páramo areas by Smith (1980, 1981,1984). The species occurs in a wide range of conditions from dry ridges and exposed slopes to edges of bogs and wet valley floors. It has a semi-woody unbranched stem up to 1.2 m tall supporting a single evergreen rosette and it is polycarpic and relatively long lived (50 to 100 years, see Smith 1984). Annual height growth has been found to be around 1.2 cm at 3600 m in the mature ecosystem (Smith 1981). The slow growth of *E. schultzii* is consistent with its low photosynthetic capacity and stress tolerant strategy (see Chapter 3).

4.2.2 Data collection

I selected plots in areas high on the valley slopes, in which the mature vegetation tends to be co-dominated by *E. schultzii* and *H. laricifolium*. Areas closer to the bottom of the valley tend to be more intensively disturbed and dominated by *Bacharis prunifolia* and other large shrubs. In the high valley areas, I randomly selected five year 3 fallow plots (also called below early successional), five year 8 plots (also called late successional) and five areas of never cultivated páramo (NCP). Plots in the third year of fallow were used, as they permit to analyse the establishment phase of the population (in earlier plots there are too few seedlings to allow spatial analysis). The adult populations present in year 8 plots (when adults start to be common) are very likely to be the survivors of seedlings established in year 3 plots, as it takes a minimum of 4 to 5 years for individuals to reach that size and colonization before the third year of succession is limited. The selection of the fallow plots for the study was based on Smith's (1995) spatial database (updated to the year 2002).

In each plot, I set up a lattice of 20 x 20 square cells, with cell dimensions of 0.5 x 0.5 m. The lattice was oriented so that one axis was perpendicular to the main slope direction, and its left-bottom coordinate was randomly positioned in the plot. In each cell the density of *E. schultzii* individuals was determined. An individual was considered to lie within the cell if the cell contained the central point of the rosette (the apical meristem). Individuals were classified into 3 size classess: small (< 5 cm in rosette diameter), intermediate (5-25 cm diameter) and large (> 25 cm diameter).

To analyse the spatial association between *E. schultzii* and other dominant species, I also determined the abundance of *R. acetosella* and *H. laricifolium*. *Rumex acetosella* abundance was determined by visually classifying each cell into 10 categories, going from 0 (absent) to 9 (high cover in the cell). For *H. laricifolium*, the co-dominant species in late successional and NCP areas, I determined the density of individuals in each cell, classifying them into two size classess: small (< 10 cm in height) and large (> 10 cm in height).

To analyse the spatial association between *E. schultzii* and the microtopography in each plot, I also determined the presence-absence of superficial stones and estimated the slope in each cell. Stones were considered to be present if they showed more than a visually estimated 50% cover in the cell, and were recorded as absent otherwise. Slopes, were visually classified into 3 classess using a protractor and a weight: steep (>60^0), intermediate (60^0-30^0) and low (<30^0). I then assigned values from 2 to 0 to each of these categories. All the sampling was carried out at the end of the wet season of 2001 (November).

4.2.3 Quantification of spatial structure

The small-scale spatial structure in each grid was analysed using non-centralized spatial covariance functions, which essentially quantify the density of pairs of observations at a given displacement. These are very close to the centralized spatial covariance, spatial autocorrelation and semi-variogram techniques commonly used in the spatial statistics ecological literature (see Burrough 1995). The techniques used here are based on those described by Purves and Law (2001, see also Condit *et al.* 2000), which by virtue of being non-centralized are mathematically simpler and have a direct biological interpretation (see below). However, one problem with most of these techniques is that they assume a spatial stationary process (for a detailed discussion on the importance of non stationarity see Rossi *et al.* 1992; Burrough 1999). Based on a visual inspection of our data, it was obvious that the patch sizes were in a few cases large relative to the grid size so that large differences in density across the grid were apparent (i.e. *non stationarity*). Hence, I suggest a modified version of the non-centralized covariance functions that deals more appropriately with differences in density across the grid, based on the non-stationary (or so called 'non-ergodic') spatial covariance and autocorrelation functions described by Rossi *et al.* (1992).

Consider a finite lattice of K cells, using $p_i(x)$ to denote the presence or absence of species i in cell x, with Cartesian coordinates (x_1,x_2); $p_i(x) = 1$ if species i is present in the cell and 0 if it is absent. Alternatively, for density data, $p_i(x)$ denotes the value of species i within cell x. The same arguments apply for other abundance measures or for the values of environmental variables like slope.

The spatial covariance of species j with a vector displacement of ξ (with perpendicular components ξ_1,ξ_2) from species i, is (Purves and Law 2001)

$$C_{ij}(\xi) = \frac{1}{|S_\xi|}\sum_{x\in S_\xi} p_i(x)\cdot p_j(x+\xi) \qquad \text{Eq. 4.1}$$

where $S_\xi = \{(x, x+\xi)\}$ is the set of all pairs of cells where the second cell is displaced by ξ, and $|S_\xi|$ is the number of such pairs. If $i = j$, Eq. 4.1 defines the spatial autocovariance within species i, and when $i \neq j$ Eq. 4.1 is the spatial crosscovariance between species i and j.

A normalized measure of the departure from randomness, which considers large-scale variations in cell values across the lattice (i.e. non-stationarity) can be obtained. This is done by dividing Eq. 4.1 by the expected value, $E[C_{ij}(\xi)]$ under randomisation of the cell values over the region of the finite lattice comprised respectively by the tail and the head of the vector displacement ξ (see Fig. 4.1). Hence, $E[C_{ij}(\xi)]$ keeps in place the observed values in cells of species i and species j respectively at the tails and heads of the vector displacement ξ

$$E[C_{ij}(\xi)] = \frac{\sum_{x\in S_t} p_i(x)}{|S_t|}\cdot\frac{\sum_{x\in S_h} p_j(x)}{|S_h|} \qquad \text{Eq. 4.2}$$

Here S_t is the set of all x cells at the tail of vector displacement ξ while S_h corresponds to the set at the heads of ξ. $|S_t|$ and $|S_h|$ are the number of such cells. So, Eq. (4.2) represents the product of the average densities in the areas of the lattice occupied by the heads and tails of a given ξ. It is obvious that for $i = j$, this will be very different at large displacement distances under marked non stationarity (e.g. a strong trend in the number of occupied cells or density across the grid, see Fig. 4.1). Since $|S_t| = |S_h| = |S_\xi|$, Eq. (4.2) can be rewritten as

$$E[C_{ij}(\xi)] = \frac{1}{(|S_\xi|)^2}\sum_{x\in S_t} p_i(x)\cdot\sum_{x\in S_h} p_j(x) \qquad \text{Eq. 4.3}$$

In the absence of spatial structure, i.e. if species i and j are distributed independently and at random, $C_{ij}(\xi)/E[C_{ij}(\xi)] = 1$ for all displacements ξ. The exception to this is $\xi =$

(0,0) and $i = j$, which is not considered further as it does not provide any useful information (see Purves and Law 2001 for details).

Aggregation (i.e. underdispersion) between i and j at displacement ξ gives values higher than 1. Correspondingly, segregation (i.e. overdispersion) gives values lower than 1. If the variable measured is density, a value of 1.5 can be interpreted as a 50 % increase in the number of pairs of individuals at that displacement above the value expected under randomness, giving the function a direct biological interpretation.

Since ξ is a vector, it can be thought of as having a magnitude of r and a direction ϕ. Hence, I calculated the average of all $C_{ij}(\xi)/E[C_{ij}(\xi)]$ (the full covariance function) for each of a series of radial Euclidean distance classess irrespective of direction (in this case, eight classess of 1 cell width each). This is referred to as the radial covariance. I also calculated the average of the full covariance function for each of a series of angular bins classess irrespective of distance (but up to the maximum displacement distance used of 4 m), referred to as the angular covariance (see Purves and Law 2002 for details). In this case I used 8 angular bins of 45^0 each, the first bin being always aligned parallel to the main direction of the slope in the plot. This allowed exploring the existence of directionality in the spatial pattern: whether there was a higher number of pairs of individuals in a particular direction than expected by chance. Given the extreme slopes in most of the plots studied (in some cases of more than 45^0), I wanted to assess the extent to which this could have a consistent effect on the spatial patterns studied (because of the possible effects of steep slopes on drainage patterns, etc). The existence of directionality in spatial patterns is referred to as anisotropy, and is generally not measured in ecological studies (Burrough 1999).

Monte Carlo procedures were used to test the statistical significance of the departures from randomness quantified by the spatial covariance functions. In the autocovariance case, the position of the cell values was randomised without restrictions 1000 times and the radial and angular autocovariances calculated for each resulting randomised grid. The actual value within each cell was not modified or randomised, only its position in the grid.

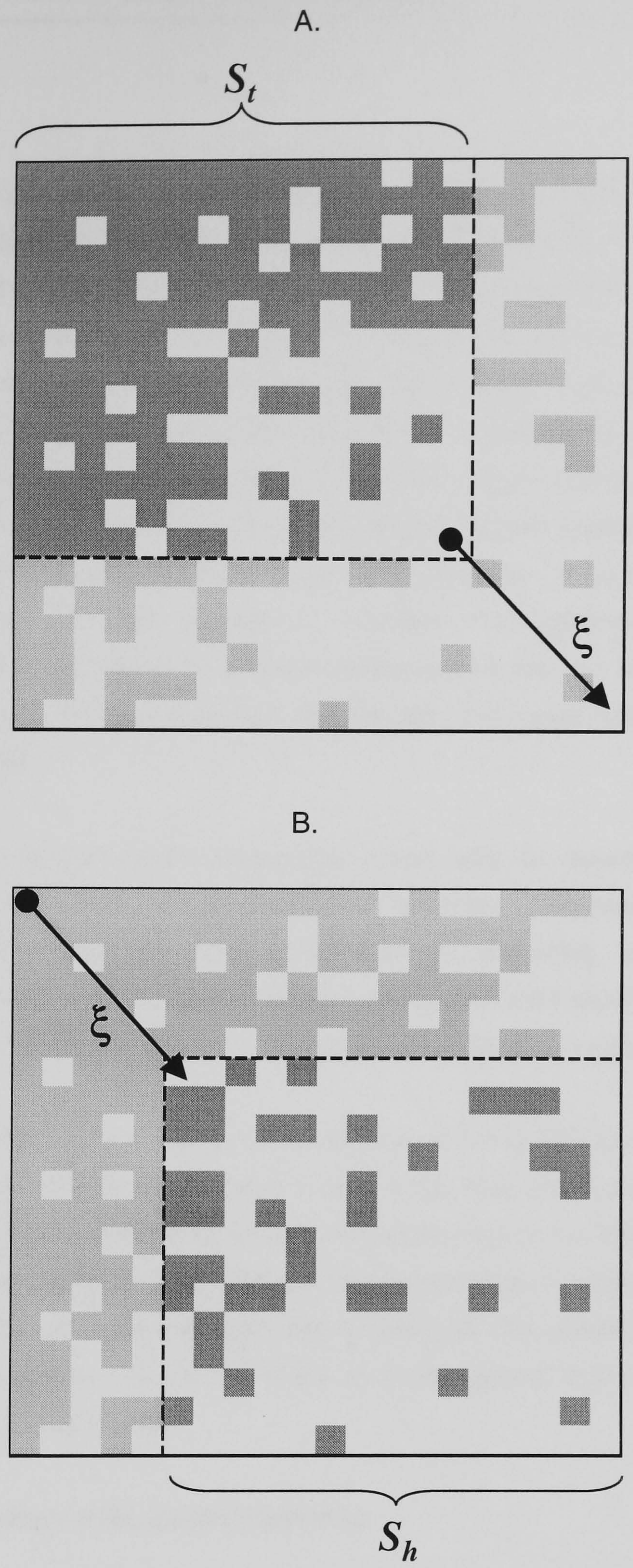


Figure 4.1 An hypothetical lattice showing strong non-stationarity as a trend in the proportion of occupied cells from the upper left corner to the lower right corner. The sets of all possible tail and head cells for a given displacement ξ are indicated as ***St*** (A.) and ***Sh*** (B.) respectively (enclosed areas with darker occupied cells). It is obvious from the figure that the proportion of occupied cells is much higher in ***St*** than in ***Sh***. The non-stationary correction for the covariance functions takes this into consideration.

In the crosscovariance case a random-shift null model (Palmer and van der Maarel 1995) was deemed the most appropriate (see Roxburgh and Matsuki 1999 for a discussion of this an other null models to test for spatial association). This means that the positions of all the cells in the grid of the two species were shifted by a random amount (using a so-called 'toroidal shift') 1000 times. This preserves the internal spatial structure of each species to a large extent (when strong aggregation is present patches might be split when shifted if they happen to coincide with the 'wrapped' boundary). The null hypothesis of interest is that the two species co-occur in the grid independently of one another at any given displacement given the spatial structure of each species. The test statistic to evaluate this hypothesis is obviously the crosscovariance functions at different displacement. So, for each pair of randomly shifted patterns corresponding to a species pair, the radial crosscovariance function was calculated.

Through the randomisation procedures I was able to derive the 95% and 99% significance envelopes for the covariance functions. Covariance values above the Monte Carlo boundaries were interpreted as indicating statistically significant aggregation, while values below the boundaries indicated significant segregation. All calculations were done using a *C++* program developed by myself.

It is important to point out that because there are only 400 possible positions in the grid, to repeat 1000 times the random-shift procedure will necessarily result in some of them being used more than once in the generation of the Monte Carlo boundaries (for the crosscovariance case). Hence, strictly speaking, it could be more appropriate in this case to use a permutation test in which all 400 possible displacements are evaluated. However, this is not likely to have caused any important bias in the interpretation of the results.

4.2.4 Application of the spatial statistics

The radial autocovariance functions were used to analyse the changes in the spatial structure of the different size classess of *E. schultzii* during succession. We were particularly interested in the small and large size classess as they were chosen to represent correspondingly the establishment phase of the individuals as seedlings and their adult reproductive stage. Smith (1981) indicates that 25 cm of diameter is close to the critical size separating reproductive from non-reproductive individuals; Exclusion of the intermediate size class was intended to guarantee that the two size classess represented two different life stages, avoiding as much as possible growth suppression effects to interfere with this interpretation. The crosscovariance functions were used to evaluate the spatial association between small and large individuals of *E. schultzii,* with the other dominant species (*R. acetosella*, *H. laricifolium*) and with the microtopographic factors.

4.2.5 Evaluation of the random mortality hypothesis

The use of a chronosequence approach allowed to determine changes in spatial structure from the establishment of *E. schultzii* populations in year 3 plots to their adult stage, which they reach at around the seventh to eight year of succession. Hence, I assumed large individuals in the year 8 plots developed from populations of seedlings in early succession with a similar spatial structure to that observed in year 3 plots. This allowed to evaluate whether or not populations of *E. schultzii* show the loss of aggregation from seedlings to adults that has been found in other dominant species in extreme environments. Furthermore, this assumption allows testing if the change in spatial structure from seedlings to adults is compatible with a spatially random mortality process (i.e. the random mortality hypothesis of Kenkel, 1988) or whether there is evidence in favour of a higher mortality in high density areas.

I started from the year 3 lattices for the small *E. schultzii* plants, and randomly thinned them down to the densities observed for the large individuals in each of the year 8 plots. A restriction to the maximum number of individuals allowed in the cells had to be introduced, as it is not physically possible to fit more than 3 or 4 adult individuals in each cell. Hence, the maximum for the final density was set to 3, which was the maximum observed number of large individuals per cell. For each of the 25 combinations (five year 3 initial patterns vs. five year 8 resulting patterns for the adults) I did 1000 simulations of the random thinning process and calculated the resulting autocovariance function after thinning in each case. From this, I calculated the 95 and 99 % Monte Carlo boundaries for the covariance function under random mortality. I then compared the observed covariance function in the adults with the Monte Carlo boundaries. If density dependent mortality produced more segregation than expected by chance, the covariance function should lie below the lower boundary, specially at small spatial scales. This procedure is based on the tests for the random mortality hypothesis suggested by Sterner *et al.* (1986).

4.3 RESULTS

4.3.1 Changes in density and population structure in succession

The average total density of *E. schultzii* was lower in the NCP plots than in the fallow plots, but did not differ between year 3 and year 8 plots. (Table 4.1). However, there was a very sharp drop in the density of the seedlings from early to late stages and still lower density values in the mature páramo. The drop was partially balanced in late successional plots by an increase in the density of the intermediate individuals, thus resulting in no significant overall change in total density in the successional plots.

It is clear from Table 4.1 that the size distribution becomes more even during succession. Furthermore, comparing the initial density of small plants in the early plots with the density of adults in the year 8 plots suggests that mortality is large during the growth of the early cohorts in succession.

Table 4.1 Successional changes in average density (m^{-2}) and standard deviation (in brackets) of *E. schultzii* separated into 3 size classess. Differences between successional stages for each size class and for total density are compared using a non-parametric Kruskal-Wallis (K-W) test. Values with different letters denote significant differences (Dunnet's C multiple comparisons test).

Stage	Seedlings (<5 cm)	Intermediate (5-25 cm)	Adults (>25 cm)	Total
Year 3	9.5 (2.6) ^{a}	0.5 (0.6)^{a}	0	10.1 (2.5) ^{a}
Year 8	4.5 (3.3) ^{b}	1.9 (1.6)^{b}	0.5 (0.2)	6.9 (4.8) ^{a}
NCP	0.9 (0.8) ^{c}	0.5 (0.1)^{a}	0.5 (0.2)	1.9 (0.8) ^{b}
K-W	p=0.004	p=0.024	p=0.530	p=0.007

4.3.2 Changes in spatial structure of the *E. schultzii* populations

Changes in the spatial structure were analysed through the use of radial covariance functions. To illustrate the general trends found in the data in Figs. 4.2 and 4.3 I present representative examples of the spatial maps and their corresponding radial covariance functions for seedlings and adults in the different seral stages. Fig. 4.2 illustrates how while there was a large decrease in the density of the seedlings along succession, their spatial structure remained significantly aggregated in the three plots. This was in fact the case for all plots but one (a NCP plot where it was random). Aggregation is shown by a peak above 1 in the values of C_{ii} for short displacement distances. The scale of significant aggregation can be interpreted as the distance at which the function crosses the Monte Carlo boundary. Aggregation in the seedlings during succession occurred to a scale of up to >4 m (the most common scale was 1.5 m). However, in the NCP the scale of aggregation went down to 0.5 m as densities and patch sizes decreased (see examples in Fig. 4.2).

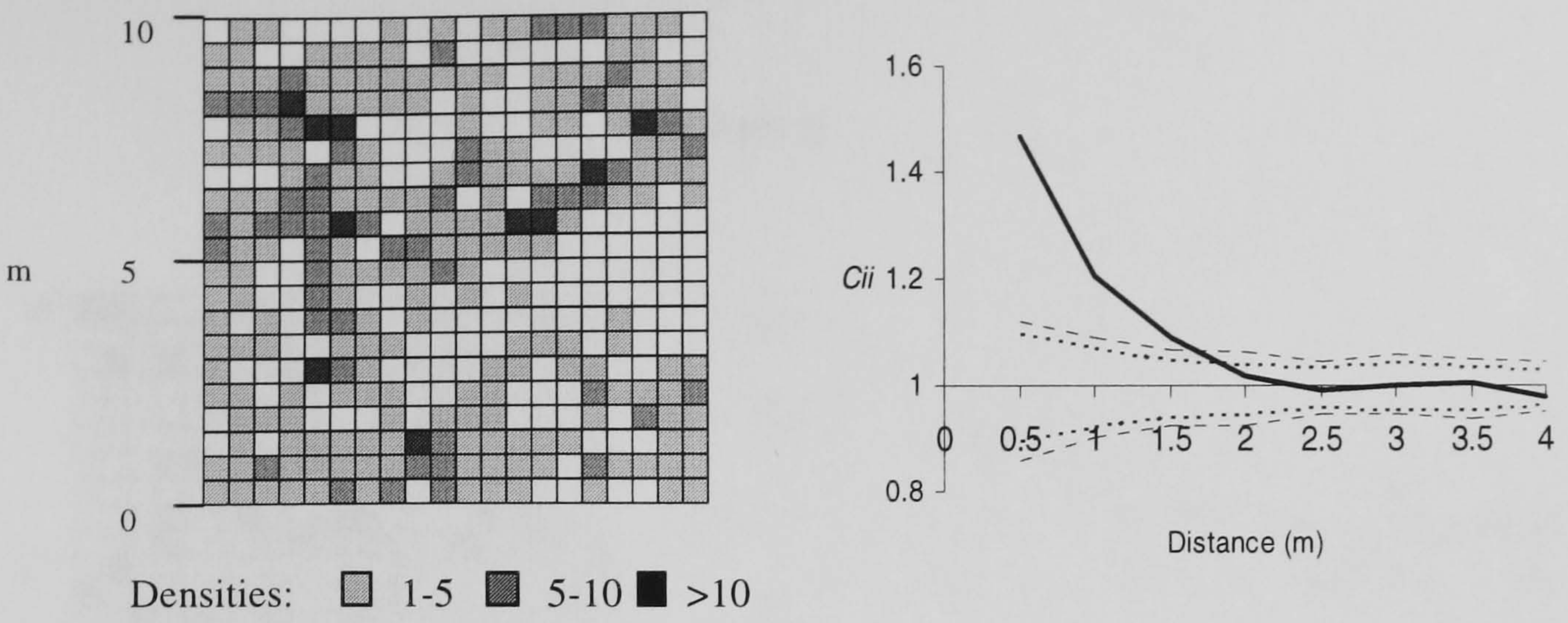
Interestingly, while seedlings showed an aggregated spatial pattern, the adults had a random pattern in all the year 8 and NCP plots studied (except for one year 8 plot in which it showed significant aggregation but at the 1.0-1.5 m scale). This is illustrated by the examples in Fig. 4.3 where it can be seen that the covariance function oscillates around 1, without crossing the Monte Carlo boundaries at any distance.

The averages of the intensity of aggregation in all replicate plots for all seral stages and size classess are summarized and compared in Table 4.2. Since most functions showed a peak at the shortest displacement distance of 0.5 m the results are presented only for that distance. To facilitate comparison between grids of different densities, the value of the $C_{ii}(0.5)$ was divided by the upper Monte Carlo boundary to provide an index of aggregation intensity for each replicate. Hence, in table 4.2, values higher than 1 indicate that the covariance function was above the upper Monte Carlo boundary (in average) and values lower than1 indicate that it was below.

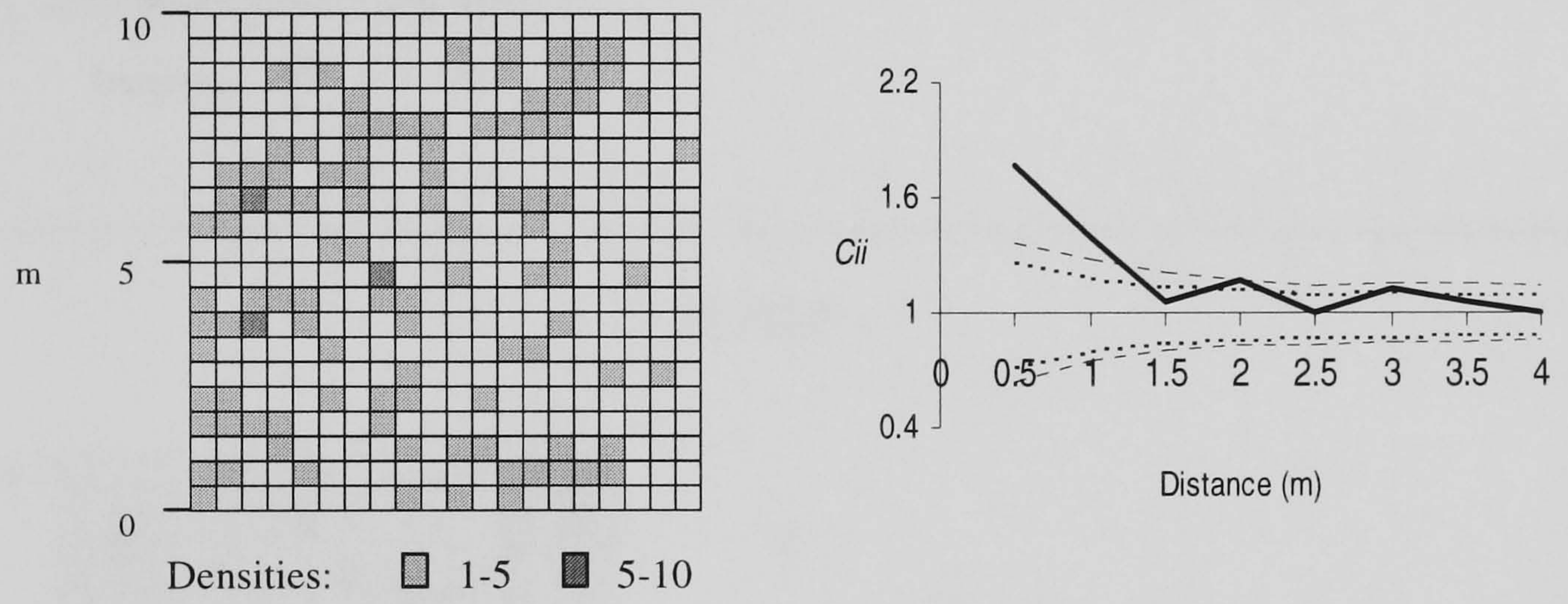
For each size class, no significant differences where found between the different stages of succession in the intensity of aggregation (Table 4.2). The densities and spatial patterns for the intermediate size class were very variable (changing from aggregated to random) and will not be considered further.

Adults in the late stages showed in all 5 replicate plots a lower intensity of aggregation than the small individuals in the early plots, with the average intensity of aggregation being significantly different (Kruskal-Wallis: $H_{(1,10)}=6.818$; $p=0.009$).

A. Year 3



B. Year 8



C. NCP

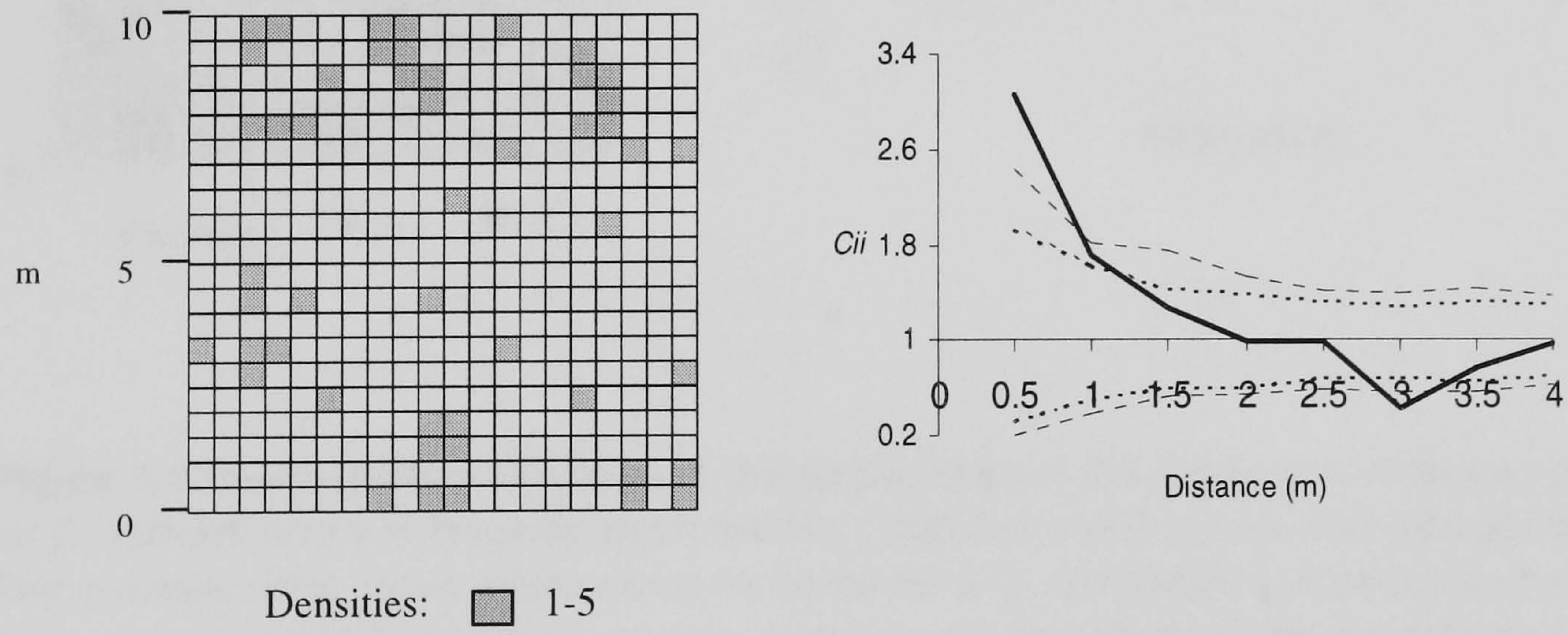
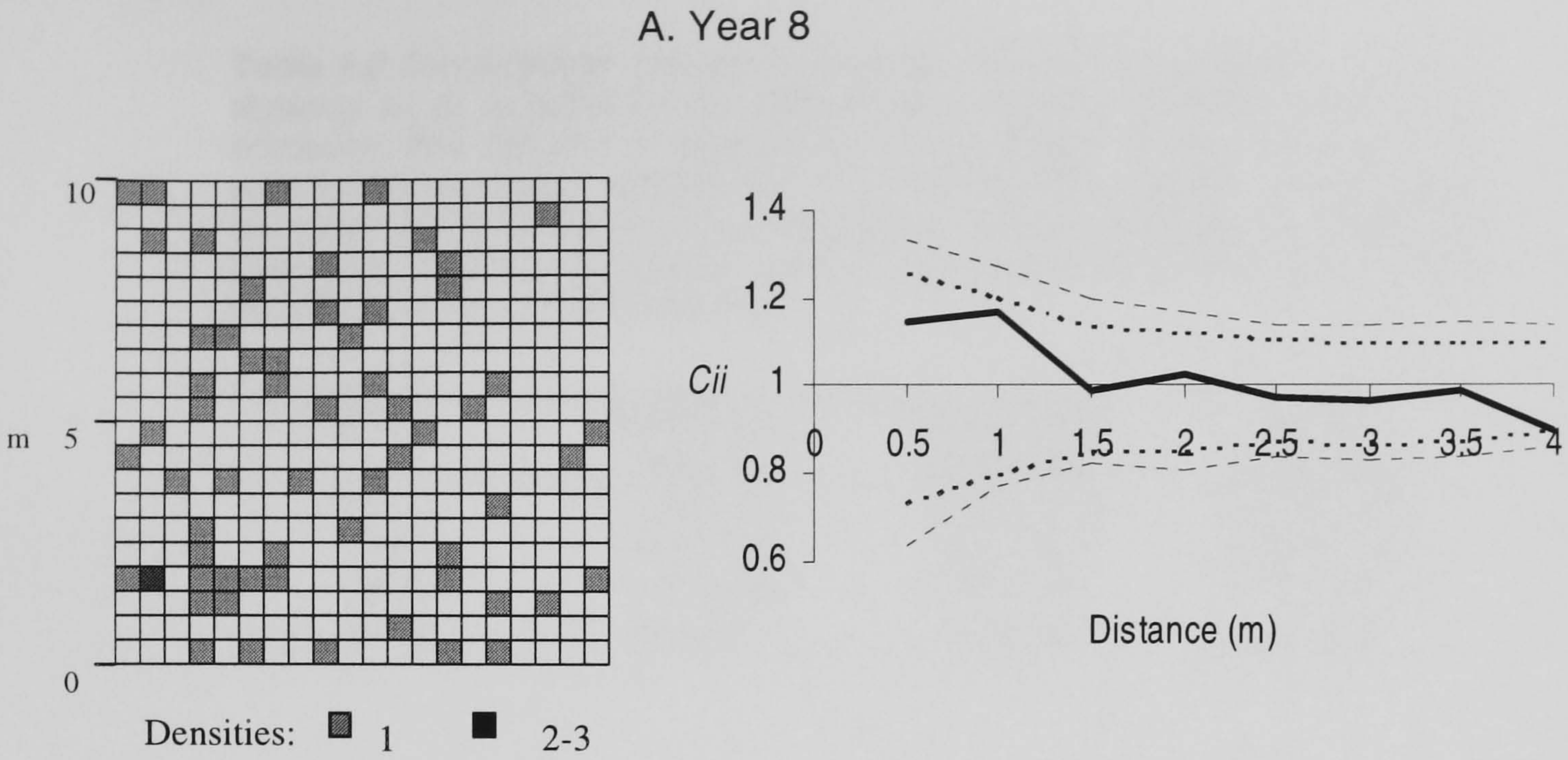


Figure 4.2 Representative examples of the spatial maps of density (m^{-2}) for *E. schultzii* seedlings in the grids (each cell has 0.5x0.5 m and there are 400 cells per grid). The corresponding radial autocovariance functions (C_{ii}) in each grid are presented (continous line), together with the Monte Carlo boundaries for a 95% and 99% confidence (dashed lines): A. Year 3 plot; B. Year 8 plot; C. Never cultivated paramo (NCP).



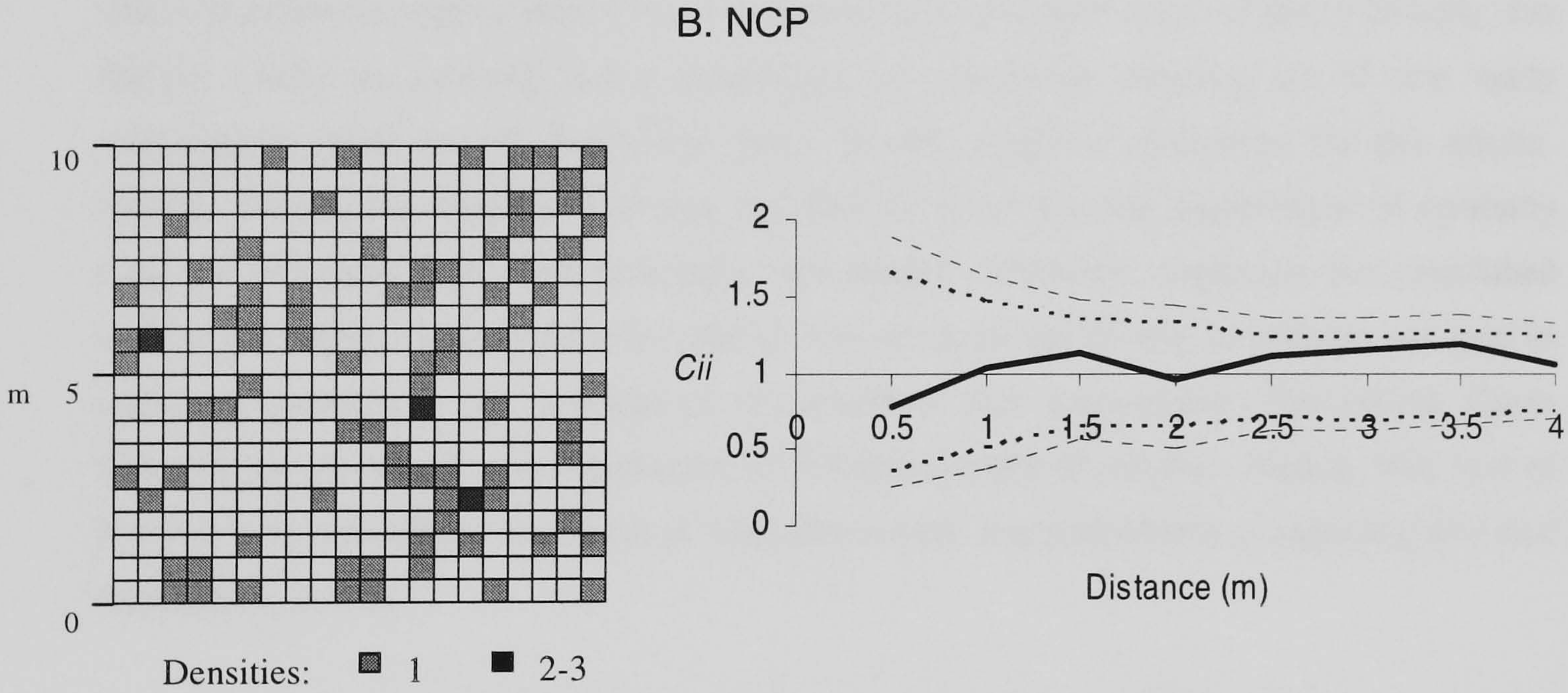


Figure 4.3 Representative examples of the spatial maps of the distribution of density (m^{-2}) for *E. schultzii* adults in the grids (each cell has 0.5x0.5 m and there are 400 cells per grid). The corresponding radial autocovariance functions (C_{ii}) summarizing spatial structure in each grid are presented (continous line), together with the Monte Carlo boundaries for a 95% and 99% confidence (dashed lines). A. Year 8 plot; B. Never cultivated páramo (NCP).

Table 4.2 Successional changes in average intensity of aggregation at 0.5 m distance for *E. schultzii* for the different size classess (standard deviation in brackets). The intensity of aggregation was calculated as the quotient of the autocovariance value divided by the corresponding upper Monte Carlo boundary (99%) at that distance. Differences between successional stages for each size class are compared using a non-parametric Kruskal-Wallis (K-W) test (the data is not homocedastic).

Stage	Seedlings (>5cm)	Intermediate (5-25 cm)	Adults (>25 cm)
Year 3	1.29 (0.24)	0.75 (0.25)	no individuals
Year 8	1.47 (0.33)	1.59 (0.84)	0.59 (0.23)
NCP	1.03 (0.30)	0.93 (0.34)	0.65 (0.20)
K-W	p=0.185	p=0.210	p=0.602

With regard to the evaluation of the random mortality hypothesis, the results showed the observed autocovariance function for the adults to be contained within the Monte Carlo boundaries (95% and 99%). As indicated in section 4.2.5 of the methods, the Monte Carlo boundaries were generated by randomly thinning all of the early succession grids for the seedlings down to the observed densities for the adults. Hence, the results indicate it is not possible to reject the null hypothesis of spatially random mortality using this simulation procedure. However, because the simulated mortality process was so severe, going from an average of 954 seedlings per grid in early succession to an average of 53 adults in late succession, the Monte Carlo boundaries were very wide (because of the low density of adults). Hence, this test of the random mortality hypothesis is relatively weak: the probability of rejecting the null hypothesis is low.

However, it is unlikely that the five spatial patterns of the adults in late succession were less aggregated than the patterns of seedlings in early succession just by chance (i.e. under an underlying process that is spatially random). Assuming an equal probability of 0.5 for the intensity of aggregation in the adults to be above or below that found in the early seedlings, the probability of it being below in all five cases is 0.5^5=0.031. This suggests there is some degree of non-random density dependent mortality operating. It could be argued that there is nothing surprising in expecting a loss of aggregation through density dependent mortality: the density of seedlings within each cell is far above the maximum possible density of adults (which is probably around 3 individuals per cell), suggesting that density dependent mortality is caused by competition for space. However, the intensity of aggregation of the seedlings once their density is taken down to a maximum of 3 individuals per cell (by deterministically removing all extra individuals), was also higher than that found for the adults in the year 8 plots (Kruskal-Wallis: $H_{(1,10)}=6.818$, $p=0.009$). In fact, even transforming the year 3 data for seedlings from density into presence-absence, there still was a higher intensity of aggregation in all of them than that observed in all the year 8 grids for the adults. Thus, it is likely that there is a density-dependent effect beyond the obvious within cell competition for space that causes a loss of aggregation.

4.3.3 Interactions between small and large individuals

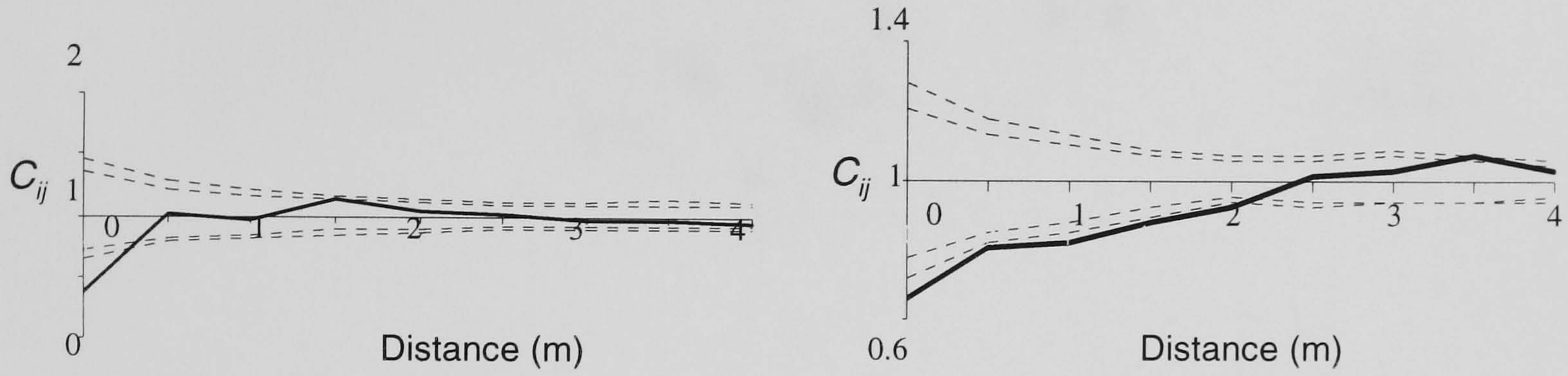
Both in the late successional plots and in the NCP, all crosscovariance values at distance zero for large vs. small individuals were smaller than 1, indicating spatial segregation between them (see examples in Fig. 4.4). Of the ten plots analysed, four showed this segregation to be significant (Table 4.3). In all significant cases the scale of segregation was below the 0.5 m scale, except for one plot in which it went up to 1 m. Given there should be an equal probability of 0.5 for the $C_{ij}(0)$ to be above or below 1 under the null hypothesis of independence in the spatial distribution of the two size classess, the probability of observing in all ten plots a $C_{ij}(0)$ value below 1 would be $0.5^{10}=0.0009$. Hence, it is very unlikely that such consistent segregation would have resulted under an independent spatial distribution of seedlings and adults.

4.3.4 Interactions with other dominant species

Seedlings of *E. schultzii* showed no consistent spatial interactions with *R. acetosella:* the crosscovariance values (distance 0) were both above and below 1 in early and late succession plots. The seedlings of *E. schultzii* showed no consistent spatial interactions with *H. laricifolium,* except in the NCP plots, where they showed spatial segregation from both large and small *H. laricifolium* individuals in all plots evaluated. However, segregation was only significant in one case.

A. *E. schultzii* seedlings (Year 8)

B. *R. acetosella* (Year 8)



C. *H.laricifolium* small (NCP)

D. Slopes (NCP)

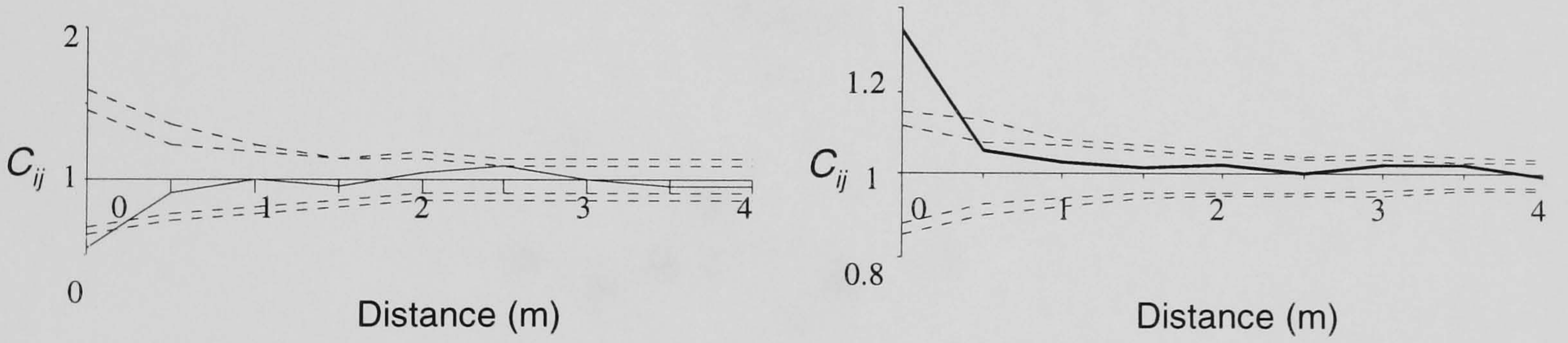
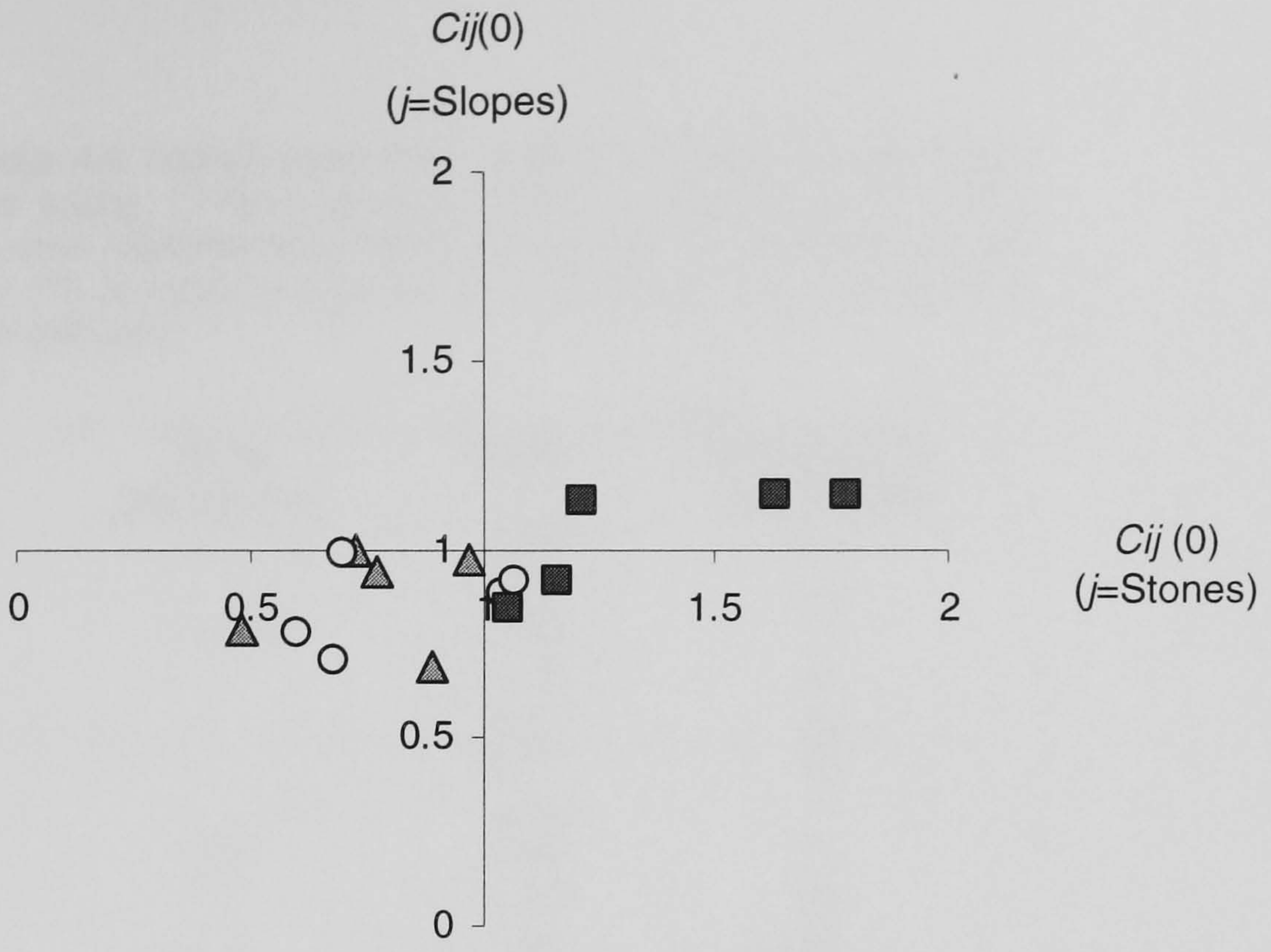


Figure 4.4 Representative examples of the radial crosscovariance functions (C_{ij}) and their corresponding Monte Carlo boundaries (95% and 99%) evaluating the spatial relations between adult *E. schultzii* plants and: *A. E. schultzii* seedlings in an year 8 plot; *B. R. acetosella* in an year 8 plot; *C.* Small *H. laricifolium* plants in the NCP; *D.* Slopes in the NCP.

A. *E. schultzii* seedlings



B. *E. schultzii* adults

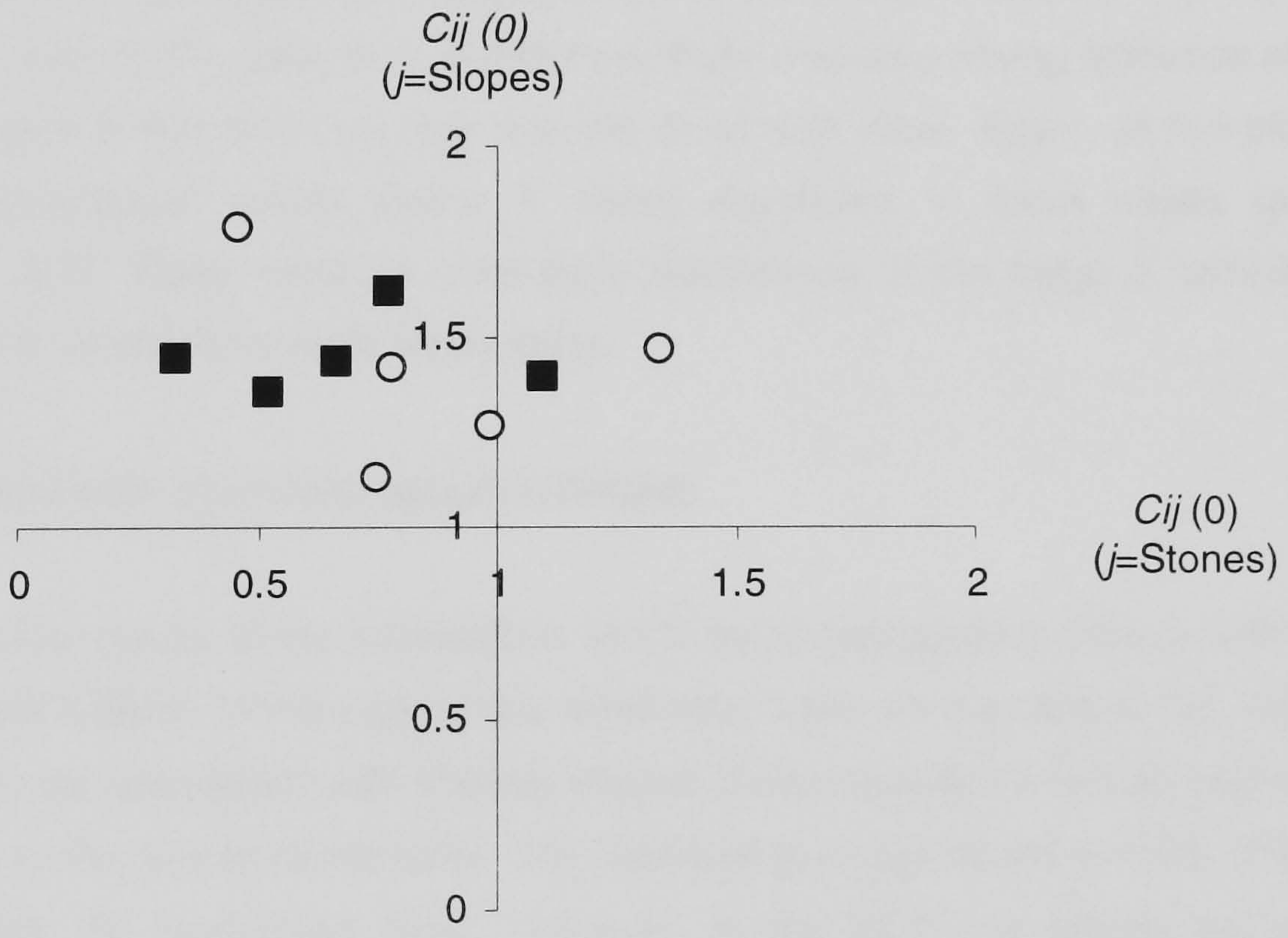


Figure 4.5 Values of the radial crosscovariance functions at distance zero ($C_{ij}(0)$) for the spatial association between *E. schultzii* and superficial stones (x axis) and local slopes (y axis), with each point representing the values for the functions in one plot: year 3 plots (grey triangles) , year 8 plots (open circles) and NCP areas (dark squares). *A.* Relations between the microtopography and seedlings; *B.* Relations between microtopography and adults.

Table 4.3 Spatial association between *E. schultzii* seedlings and adults. Crosscovariance values at distance zero ($C_{ij}(0)$) for each replicate plot. Values going below the lower 5%(*) and 1% (**) confidence intervals for the Monte Carlo simulations are indicated.

Plots (replicates)	$C_{ij}(0)$	Monte Carlo boundaries
Year 8	0.38	**
	0.57	ns
	0.52	*
	0.36	ns
	0.70	ns
NCP	0.71	ns
	0.00	**
	0.00	**
	0.90	ns
	0.85	ns

For the *E. schultzii* adults, there was more clear evidence for spatial segregation with *R. acetosella* in the year 8 plots. All five showed crosscovariance values below 1 (distance 0), and the interaction was significant at the 99% level in three of them (see example in Fig. 4.4). In the case of *H. laricifolium*, there was also strong evidence of a negative interaction in the NCP, but only with the small size class. Again, all five plots showed crosscovariance values below 1, being significant in three cases (see example in fig. 4.4). There were no consistent interactions of the large *E. schultzii* individuals with *H. laricifolium* in the fallow plots.

4.3.5 Interactions with micro-topographic factors

We summarize the results of the interactions of the micro-topographic factors with *E. schultzii* in figures 4.5A-B. In the case of the small size class, we can see in Fig. 4.5.A that they tend to be associated with shallow slopes (crosscovariance values below 1 in all 10 cases) in the successional plots. The relationship is significant in three of the ten cases at the 1% confidence level. However, in the NCP the results are not consistent and there are no significant values. As for the relationship of the seedlings with superficial stones in early plots, seedlings and stones tend to be spatially segregated, while in the NCP they tend to be positively associated. However, there are no significant interactions at the 99% confidence level.

As we can see in figure 4.5.B all plots show a positive spatial association between steep slopes (crosscovariance values above 1) and the location of *E. schultzii* adults. This association is significant (95 %) in 8 of the 10 plots. (see example in Fig. 4.4). In all cases this spatial association was significant at the within cell scale (it did not extend beyond the 0.5 m). There was no consistent spatial association of adults with stones.

4.3.6. Directionality in spatial structure

The results of the angular covariance functions were mixed. For both the intra-specific (i.e. autocovariance) and the inter-specific (i.e. crosscovariance) functions there was a varying proportion of replicates showing both anisotropy (i.e. directionality in the spatial pattern) and isotropy (i.e. no directionality). The only clear pattern was for the intra-specific data for *E. schultzii*, where the angular autocovariance functions showed a higher proportion of plots with anisotropic patterns in the seedlings (80% of replicates) than in the adults (20% of replicates). However, the directions in which there was significant spatial structure were not consistent with respect to slope direction. This is illustrated in Fig. 4.6, in which I present the angular covariance for the seedlings in all the year 3 plots. For example, in the replicate shown in Fig. 4.6.A there was significant aggregation perpendicular to the slope (90^0-270^0), but in the replicate in Fig. 4.6.C there was evidence of segregation on one of the diagonal axes (135^0-315^0). Fig. 4.6.D illustrates a case with no significant directionality, while Fig. 4.6.E. shows a replicate plot in which the scale of aggregation was beyond the maximum displacement distance (4 m), so that the angular covariance function showed significant aggregation in all directions.

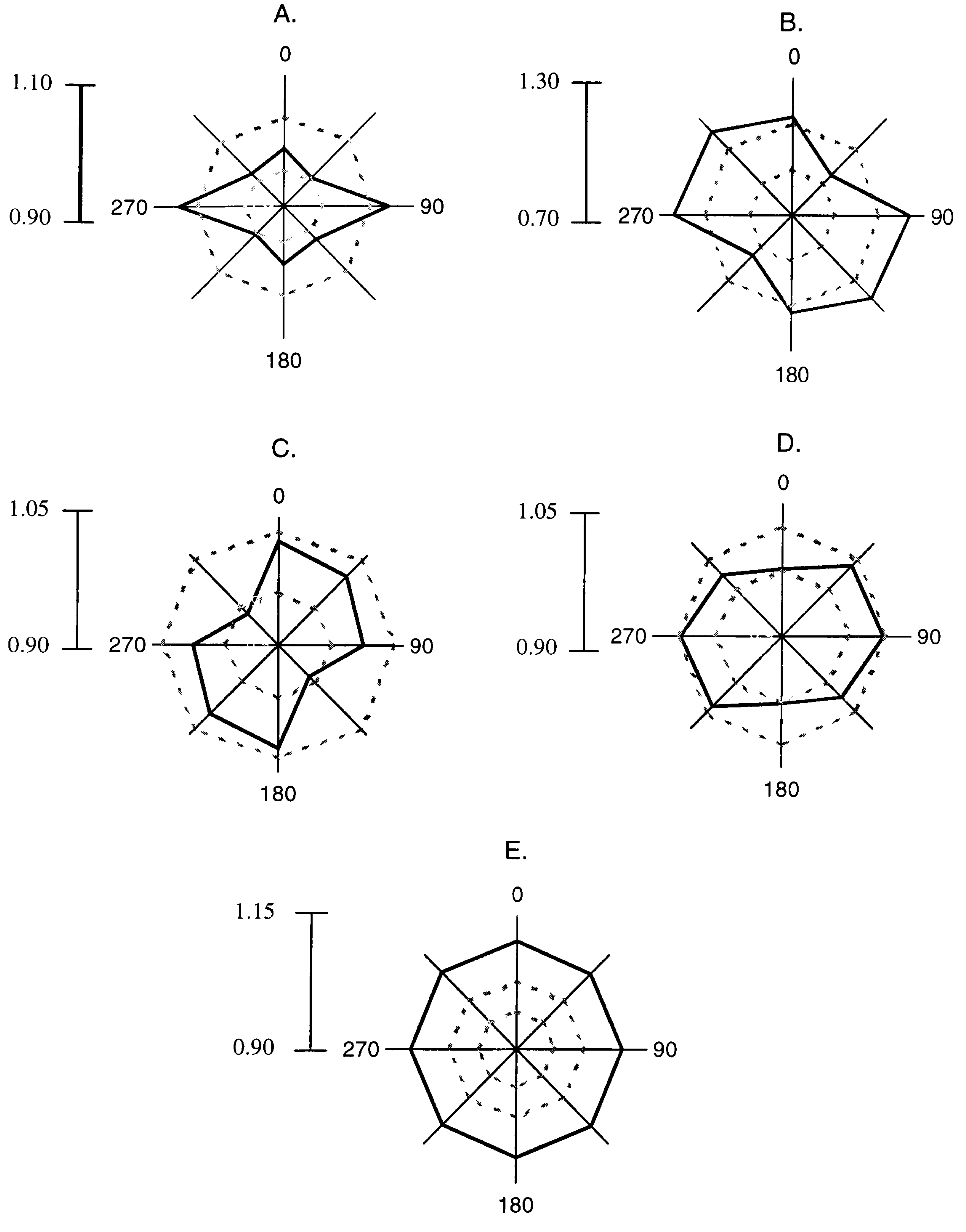


Figure 4.6 Angular autocovariance for *E. schultzii* seedlings in all the year 3 replicates. The 0^0-180^0 axis is aligned to be parallel to the main direction of the slope within each plot. The continuous line corresponds to the observed values. The dashed lines represent the 99% Monte Carlo boundaries. The bar next to each figure is the scale for the covariance values.

4.4. DISCUSION

4.4.1 Changes in population density and size structure in succession

As demonstrated in Chapter 2, there is a clear successional trend for an increase in the above ground biomass of *E. schultzii* in succession, with a maximum in the NCP (see also Sarmiento *et al.* 2002a). The density data presented here indicates this increase is the result of a large increase in average individual plant weight as the few individuals that survive to the adult stage slowly gain biomass during the fallow. This is consistent with the findings of Smith (1981) of large mortalities in individuals below 25 cm diameters at similar elevations in the Venezuelan Andes. Smith found this mortality to be more severe during the dry season, particularly for individuals below 5 cm in diameter.

Interestingly, the colonization potential for new seedlings seemed to drastically decrease during succession. A change in size and age distributions towards a higher proportion of older and larger individuals has been considered as a general trend during succession (Silvertown and Lovett-Doust 1993; Woods 2000) although there can be exceptions (e.g. facultative biennials in Falinska 1991).

The densities of large sized individuals reported here are within the range reported by Smith (1984) of 0.5 to 1.0 adults m^{-2}. However, the densities of small plus intermediate individuals (which Smith classified as juveniles) in the NCP areas were much lower. This is likely to be the result of unfavourable germination conditions some time before sampling. Smith (1984) showed that year to year variations in climate can have dramatic effects on seedling mortality. The extensive cattle grazing that is common in the fallow and mature páramo areas in the Gavidia valley could also be a contributing factor for the lower densities of seedlings (probably as a result of trampling of small individuals).

Comparison of densities in the small size class between early, late and NCP situations suggests that during succession, conditions become less conducive for colonization, germination and/or establishment of *E. schultzii*. This is unlikely to be the result of a lower availability of viable propagules in the seed bank accumulated in the previous fallow cycle: the maximum dormancy time reported by Pannier (1969, cited in Smith 1981) for *E. schultzii* was of 2-3 years, which coincides with the normal time span of cultivation. The majority of new seeds must come from outside the plot during early succession (there are no adults within the plot producing seeds at this stage) and there is no reason to expect this 'external' seed rain to decrease during succession. Hence, the decrease in the number of seedlings in succession is more likely to be the result of a decrease in seedling establishment. This could be driven by competition with already established large con-specifics (see below). It could also be the result of an increase in inter-specific competition with other species. In fact, Smith (1984) reported data from removal experiments in a mature páramo showing a significant effect of the bulk of biomass of other páramo species on *E. schultzii* seedling survival.

4.4.2 Changes in spatial structure

The fact that the distribution of adults in late succession is random while it is aggregated for seedlings in early succession suggests there is some local density dependent mortality operating, which favours mortality in dense patches. The results indicated this effect is likely to go beyond the more obvious competition for space (self-thinning through overcrowding) among tightly packed seedlings. Smith (1984) reported that seedling mortality was indeed correlated with seedling density in a mature páramo, but only in exposed relatively xeric areas.

Losses of aggregation strength in the development of a population as a result of strongly local competitive interactions have been predicted by theoretical studies (e.g. Bolker and Pacala 1997; Law and Dieckmann 2000; Law *et al.* 2002) and demonstrated experimentally (Mithen *et al.* 1984). In the context of successional population development a loss of aggregation strength beyond what would be expected under random mortality has commonly been observed in temperate forest ecosystems (e.g. Christensen 1977; Sterner *et al.* 1986; Gavin and Peart 1997), although there are exceptions (e.g. Peterson and Squiers 1995). In the case of deserts and tundras the majority of the observed changes have been from aggregated seedlings to *less* aggregated or random distributions of adults. The final pattern in the adults has only rarely been found to be regular (Fowler 1986; Chapin *et al.* 1989).

If as argued above, most of the *E. schultzii* seedlings that become established during early succession are derived from the external seed rain, their initial spatial pattern could be expected to be random. The fact that it is aggregated suggests that spatially non-random factors such as patchy safe sites for germination and establishment are important for early success. Interestingly, only Brisson and Reynolds (1997) have explored the consequences of local competitive interactions on changes in population spatial structure *starting* from an aggregated pattern (see also Silvertown and Bastow Wilson 2000, for community scale effects of non-random initial patterns 2000). They showed in an even-aged monoculture lattice model the expected shift from clumped towards more regular spatial pattern during self-thinning. Murrell *et al.* (2001) have recently emphasized the lack of detailed understanding of the consequences of initial non-random spatial patterns for subsequent population and community dynamics.

Another potentially important aspect that has been commonly ignored in spatial ecology research has been the existence of directionality in spatial patterns (but see Kershaw 1957; Upton and Fingleton 1985; Purves and Law 2002). In fact, most spatial analysis in the literature has as a hidden assumption the absence of anisotropy (i.e. they assume non-directionality). However, ignoring anisotropy when present can induce errors, especially in the estimation of the scale of pattern, as average patch size will vary with direction (see Rossi *et al.* 1992; Burrough 1995). Moreover, important underlying explanatory factors may consequently be ignored (e.g. differences in geomorphology and soil characteristics, see Burrough 1995).

The results from the angular covariance functions showed directional spatial patterns to be common in our data. To a certain extent this could be the result of large patch sizes relative to the size of the grids sampled. However, the higher proportion of anisotropic patterns in *E. schultzii* seedlings than adults, suggest seedling could be more sensitive to directional environmental factors, such as light incidence angles and local topographic variations in slope and soil characteristics. Since no consistent directionality was found with respect to the main direction of the slope within the plots, it does not seem possible to suggest a unique explanatory variable that could account for the anisotropy. However, it is important to acknowledge its presence, as it suggests some caution in the interpretation of the values obtained from the radial covariances (they correspond to an average across all directions), in particular regarding the estimation of the scale of pattern.

4.4.3 Spatial segregation between seedlings and adults.

The spatial relation between seedlings and adults is the result of the balance between processes that act to produce opposite effects. On the one hand, processes such as limited dispersal (or similarity in environmental preferences) should tend to produce aggregations of seedlings around adults. On the other hand, processes like intra-specific competition or other forms of negative effects for seedlings of being near their parents (such as species specific pests, see Janzen 1970) should produce segregation between them. Simulations by Law *et al.* (2002), using a spatial version of the logistic equation, show that localized dispersal can result in an increase in aggregation, while stronger local intra-specific competition can promote spatial segregation.

In the case of *E. schultzii*, Smith (1984) found that on a level site at 3600 m, 91% of all fruits from an adult fell within 2 m of the plant. So, the clear segregation of seedlings and adults found here could be the result of a strong negative effect of adults on seedlings, which is able to override the tendency towards aggregation. This is especially true for the NCP, where seedlings are more likely to have developed from seeds coming from adults within the plot. In fact, Smith (1984) found in mature páramo areas that in a dry year the removal of adults produced a significant reduction on seedling mortality. Moreover, he reported less survival for individuals with close nearest adult neighbours in sites with relatively open vegetation cover. The adults showed a competitive effect on adjacent vegetation cover, which indirectly favoured seedling survival only in strongly mesic areas in valley bottoms. Thus, there is a need to explore what is the modulatory effect of cover of other species and environmental heterogeneity on the interaction between seedlings and adults.

4.4.4 Spatial association with other dominant species and microtopography

The negative spatial relation between *E. schutlzii* adults and small individuals of *H. laricifolium*, suggests that proximity to *E. schultzii* adults has some negative effect on the re-establishment of this late co-dominant shrub. Interestingly, we do not find evidence of spatial segregation between the seedlings of *E. schultzii* and *R. acetosella* in the early successional plots. This indicates, that at least at this scale, the mechanism for *E. schultzii* tolerance as seedlings of the high dominance of *R. acetosella* in the early stages of regeneration does not involve spatial segregation.

The spatial segregation between *E. schultzii* adults and *R. acetosella* in the year 8 plots suggests that a negative competitive effect of *E. schultzii* could contribute to explain the successional decline of this invader. However, it is interesting to note that *R. acetosella* is not spatially segregated from the seedlings neither in early nor late successional stages. This emphasizes the need of analysing separately the inter-specific spatial interactions for different size classess. As individuals grow, and especially when the change is size is of several orders of magnitude (as is the case in *Espeletia*), their competitive effects on neighbours is likely to change. This is clearly illustrated in a study by Rejmanek and Leps (1996). They noted changes in the spatial association between two early successional weeds of conifer plantations (a biennial and a shrub species) as a result of a reversal in their competitive hierarchy, as the average size of shrub individuals increased during succession. Some studies in forest ecosystems have also looked at the influence of the spatial relations between distributions of canopy adults and understory seedlings on species transitions and successional dynamics (e.g. Frelich *et al.* 1993; Frelich and Reich, 1995; He and Duncan, 2000). However, most studies of spatial structure changes in communities have ignored this dynamic nature of neighbourhood interactions with changes in individual size (Stoll and Weiner 2000).

In terms of the relation between micro-topography and the distribution of *E. schultzii*, the clearest result is that of a positive association of the adults with steep slopes. As mentioned before the giant rosette life forms presents a series of adaptations to water stress (Monasterio and Sarmiento 1991). Some of them are likely be more effective in individuals of large size (e.g. water storage in the stem). All of this suggests as a hypothesis that *E. schultzii* adults could be facing less competition from other less drought tolerant species by growing in more xeric, steeper sections of the plot. The finding of this kind of spatial relationships is encouraging, as it suggests that spatial techniques could be further used to analyse the response of the different species to soil and topographic heterogeneity *within* fallow fields.

4.4.5 Conclusions

The results presented in this chapter indicate that the clear tendency of *E. schultzii* to increase in biomass during succession is due to an increase in size of the few individuals that survive to the adult stage. In addition, there seems to be a reduction in the potential for seedling recruitment during succession, suggesting that early colonization could be critical for the establishment of *E. schultzii* populations.

The neighbourhoods of *E. schultzii* clearly differ from those expected in a perfectly mixed spatially homogeneous system in terms of the density of con-specifics, the abundance of other dominant species and the microtopographic conditions. The strong aggregation of seedlings suggests they experience higher intra-specific competition than expected from their average density, and that this results in a less aggregated pattern in the adults. The segregation at small spatial scales of *Espeletia schultzii* adults from conspecific and from *R. acetosella* could be the result of competitive interactions, although niche differences cannot be rejected as an alternative explanation. This could contribute to explain the decline of this introduced species throughout the fallow.

Authors such as Rejmanek and Leps (1996) and He and Duncan (2000) have advocated the use of spatial association analysis as a tool for hypothesis generation on competitive interactions in succession, emphasizing the difficulties of interpretation for alternative strategies like removal experiments (see also Aarssen and Epp 1990; McLellan *et al.* 1995). In this chapter I demonstrate the usefulness of combining population and spatial structure analysis using a chronosequence approach for understanding long-term successional plant dynamics on the basis of short-term information. However, the snap-shot character of the observations and the possibility of alternative explanations for segregation between species (such as differences their habitat and regeneration niches, Grubb 1977), indicate these results should be taken mainly as a source of hypotheses for further research. The recent tendency towards the use of permanent plot analysis of small-scale species transitions appears a sound, but rarely pursued alternative, which should allow reaching more definitive conclusions on the role of small-scale competitive interactions in determining vegetation dynamics. This is the strategy explored in the next chapter.

Chapter 5. Spatio-Temporal Dynamics of a Pioneer Forb: successional and seasonal changes in neighbourhood interactions

5.1. INTRODUCTION

One of the central themes of plant ecology has been to understand the importance that plant-plant interactions have in determining the structure and dynamics of populations and communities (McIntosh 1995). On the one hand, density dependence through intra-specific competition has been one of the central concepts of population biology (see review by Antonovics and Levin 1980). Experiments in monocultures have greatly contributed to understanding density dependent regulation and the establishment of powerful generalizations like the self-thinning law (Silvertown and Lovett Doust 1993). However, there has been longstanding controversy on the measurement and importance of density dependence for the regulation of population dynamics in the field (Slade 1977; Strong 1986; Law and Watkinson 1989). On the other hand, the analysis of the importance of inter-specific interactions for community organization has resulted in three main kinds of research programs (Law *et al.* 1997): (1) to measure life-history and ecophysiological properties of the species that can help to predict their effects on each other; (2) to explore the mechanisms of plant-plant interactions using neighbour manipulation experiments in the field; (3) to measure the intensity of interactions in sub-sets of species from communities grown in artificial conditions.

All of the approaches mentioned above have provided important insights. For example, experiments on neighbour introductions and removals have indicated that positive plant-plant interactions (such as nurse plant effects) could play a more important role on community organization than previously envisaged (see Aarsen and Epp 1990; Goldberg and Barton 1992). However, manipulative experiments in the field have problems of interpretation of the results and with the design of appropriate controls (see Law and Watkinson 1989; Aarsen and Epp 1990; McLellan *et al.* 1995), while in glasshouse experiments it is difficult to assess how relevant the results are to more complex field conditions (Law *et al.* 1997). In addition, a problem with most experimental studies of competition has been their tendency to ignore the effects of spatial structure on plant-plant interactions (Stoll and Weiner 2000).

As discussed in Chapter 4, plant performance is more likely to be affected by conspecific and heterospecific neighbours at a local scale than by mean densities across large areas. While up to the mid-eighties the study of density dependence was focused on mean plant behaviour in populations, more recently the emphasis has shifted towards the analysis of local effects from an individual centred perspective (Stoll and Weiner, 2000). Experimental studies of local neighbourhood interactions in monocultures have shown that local crowding tends to reduce growth, reproductive output and survival and that the effects of neighbours attenuate with distance (e.g. Pacala and Silander 1990; Condit *et al.* 1994; Hubbell *et al.* 2001). At the community scale, there have been surprisingly few experiments analysing the effects of spatial structure on the outcome of inter-specific competition (Murrell *et al.* 2001). One notable exception is the experiment by Stoll and Prati (2001) summarized in Chapter 1: as mentioned before, the results showed that the spatial structure strongly affected the outcome, with the weaker competitors greatly improving their performance when spatially aggregated.

In natural communities, static analyses of spatial structure have been used in a large number of studies to infer intra- and inter-specific interactions. As discussed in Chapter 4, although important insights can be gained from these studies, the analysis of the temporal dynamics of local spatial structure in permanent plots can provide a more direct understanding of the relationship between patterns and processes. Even though the importance of considering the spatio-temporal nature of community dynamics was recognized at least since Watt's (1947) classic analysis of patch dynamics and cyclic regeneration, there are few available studies on the temporal dynamics of spatial patterns (see Thorhallsdottir 1990; Herben *et al.* 1993, 1995; Law *et al.* 1993; van der Maarel and Sykes 1993; Willems *et al.* 1993; Sykes *et al.* 1994; McLellan 1995; Rees *et al.* 1996).

The studies on spatio-temporal community dynamics have mainly been conducted in temperate grasslands and have been based in dividing an area into discrete cells arranged in a regular grid, in which the presence or abundance of different species are then recorded at different moments in time. Using this approach, Law *et al.* (1993)

showed in a limestone grassland that for many species the colonization of a target cell was strongly dependent on the presence of conspecifics in neighbouring cells. However, both colonization and extinction probabilities were for the most part independent of their heterospecific neighbourhood composition. Hence, these authors suggested that inter-specific interactions in this grassland communities were weak (see also Rees *et al.* 1996).

The study of small-scale spatial dynamics has also opened up new perspectives on community organization (Partel and Zobel 1995). For example, Thorhallsdottir (1990), van der Maarel and Sykes (1993) and Herben *et al.* (1993) found that in stable grassland communities, local species mobility was surprisingly high (i.e. high local species turn-over, see also McLellan 1995; Sykes *et al.* 1994) but there was no directionality in small-scale species replacements (no definite order in which species replace each other in one particular location). van der Maarel and Sykes (1993) synthesized these results in the carousel model (see van der Maarel 1996b and Herben *et al.* 2000 reviews on this, and other conceptual models of local spatial dynamics).

Interestingly, Herben *et al.* (1993) showed that species replacements became directional when an 'external' driving factor (in their case the addition of manure) moved the system away from a stable community structure. This lead Partel and Zobel (1995) to hypothesize that small-scale species turn-over would be faster in successional communities, where there is an obvious large-scale directional replacement of species. However, comparing successional and mature alvar grasslands, they found all sites to have equally fast local turn-over. Ramsay and Oxley (1996) analysing post-fire regeneration in the páramos of Ecuador did find higher local species replacement rates in the disturbed than in the non-disturbed sites and showed that there were many more *directional* species replacements during post-fire regeneration (see also Ramsay 2001). However, there are very few other studies to my knowledge of spatio-temporal dynamics in permanent plots in succession (but see Lippe *et al.* 1985).

In the context of succession theory, competition has been recognized as one of the important causal mechanisms of community development from as early as the work of Clements (1916). Competition plays a central role in some of the most influential conceptual models on succession such as the triangular model of plant strategies of Grime (1979) and the resource-ratio hypothesis of Tilman (1988, 1990). Moreover, the possibility of both positive and negative effects of early on late successional species is central to Connell and Slatyer (1977) influential framework on the facilitation, inhibition and tolerance mechanisms of succession. The most detailed evidence for the mechanistic understanding of the role of plant-plant interactions in succession has come from resource and neighbor manipulation experiments. In particular, the detailed research programs of Bazzaz and collaborators and Tilman and collaborators in old-fields of the United States, have shown the importance of factors like size asymmetry and changes in resource levels in altering the balance of competition during succession (see reviews by Bazzaz 1990 and Tilman 1990). However, as indicated above, most successional studies of competition have ignored the effects of spatial structure. Hence, its importance in modulating plant-plant interactions during succession is still unclear.

In the high tropical Andes, the role of plant-plant interactions in community organization in general, and in successional dynamics in particular, remains largely unexplored. The only two exceptions to my knowledge are: the experimental analyses by Smith (1981,1984) on the effects of competitive interactions on the population dynamics of *E. schultzii* in the páramo of Venezuela (see Chapter 4); and the work on small-scale species replacements during post-fire succession in the Ecuadorian páramos by Ramsay and Oxley (1996) and Ramsay (2001).

In this chapter, I explore how the analysis of small-scale spatial dynamics in permanent plots can contribute to the understanding of the role that intra- and inter-specific interactions (both positive and negative) play in successional vegetation dynamics. More specifically, I evaluate how the abundance of conspecifics at different neighbourhood scales and the distance to late successional heterospecific neighbours can affect local survival for an early successional (ES) species. In turn, I look at the effect of these interactions on changes in its small-scale spatial structure. This approach is applied to the analysis of the effect of successional changes in local interactions on the abundance and spatial structure of *Rumex acetosella*, an introduced forb that strongly dominates the early stages of regeneration in old-fields of the high Tropical Andes.

The results presented in Chapter 2 showed that *R. acetosella* progressively declines in abundance during the fallow, while the dominant shrub and giant rosette species of the mature ecosystem (*Hypericum laricifolium* and *Espeletia schultzii*) show the opposite trend. Moreover, the spatial segregation in late successional plots between *E. schultzii* and *R. acetosella* found in Chapter 4, suggested as a hypothesis that the dominant late successional (LS) species have a negative effect on *R. acetosella* colonization and/or survival. This could contribute to the decline of this invader species. Furthermore, in the páramo, there are very marked seasonal changes in rainfall and soil water availability, so that in the dry season, soil moisture frequently drops below wilting point (Sarmiento 2000). This results in a large mortality of *R. acetosella* shoots, while the individuals of *E. schultzii* and *H. laricifolium* (specially when large, Smith 1981) tend to be able to retain green leaves and to survive the drought (Berbesi 1990 and personal observations).

The objective of this chapter is to evaluate the effects that the abundance of conspecifics and the presence of *E. schultzii* and *H. laricifolium* in the small-scale neighbourhood of *R. acetosella*, have on its probability of mortality from the wet to the dry season. I analyse how these local interactions are related to seasonal changes in spatial structure, and how these effects change from early to late successional stages. In turn, this should shed light into some of the processes responsible for the successional decline of this invader forb. The analysis was done separately in early and late successional fields to look at how the decline in the density of *R. acetosella* affects the strength of local density dependence and how the large changes in individual sizes of the LS species modify inter-specific effects (i.e. the effect of the development of size asymmetries).

5.2 METHODS

5.2.1 Selected species: *Rumex acetosella*

Rumex acetosella (Polygonaceae) is a perennial forb (hemicryptophyte) with erect shoots that reach a maximum height of about 40 cm. Its seeds are relatively large (mean weight of 0.4 mg), lack specific adaptations for long-range dispersal, and are unspecialised in terms of dispersal agent (Grime *et al.* 1988; Salisbury 1964). *R. acetosella* has been noted to have relatively limited dispersal ability in old fields studied by Tilman (1987) at the Cedar Creek experimental station. However, livestock can disperse the seeds, and they survive ingestion by domestic mammals (horses and cattle). It has a long-lived seed bank (5 to more than 20 years) and a dual vegetative and sexual reproductive strategy. During vegetative reproduction it forms extensive patches by producing adventitious buds on horizontal roots. The clones are superimposed so that their origin is not recognizable (Steinbauer and Grigsby 1958; Salisbury 1964; Putwain *et al.* 1968; Grime *et al.* 1988; Berbesi 1990).

In Europe, *R. acetosella* is commonly found in fallow and wasteland sites and it is typical of dry, well drained sandy and peat soils of low pH and nutrient levels (characteristics that correspond closely with the conditions in typical páramo soils). Its highest abundances are usually recorded in low diversity sites. Among species exploiting acid soils, *R. acetosella* is known for having high potential relative growth rate (consistent with the high photosynthesis rates for *R. acetosella* found in early successional fields of the Gavidia valley, see Chapter 2). In Grime's (1979) triangular classification scheme this species is considered to have an intermediate strategy between C-R-S and stress-tolerant ruderal (Grime *et al.* 1988). In old-fields in France, Houssard and Escarré (1995) have shown it is characteristic of early seral stages and progressively declines during succession. In addition, they reported that its aerial biomass and reproductive allocation decreased during succession, and that it tended to be overgrown in late succession by other larger forbs species of higher competitive ability.

Rumex acetosella was introduced from Europe into the Venezuelan Andes as a weed of wheat during the 18th century (Salgado-Labouriau and Schubert 1977). It is probably the most common invader of early successional areas disturbed by agriculture and fire across the northern Andes (Grubb 1970; Ferweda 1987; Moreno and Mora-Osejo 1994; Ramsay and Oxley 1996; Jaimes 2000; Sarmiento *et al.* 2002a). In the páramo, it shows high dry season mortality of above-ground structures and individuals can survive the dry season as a small rosette near the ground or as below-ground root buds. In the wet season it produces non-lignified shoots that extend from the roots and which bear the seeds during the peak of the wet season (Berbesi 1990). A study in the Colombian páramo on its root morphology (Sierra and Mora-Osejo 1994) showed that the roots are superficial, running parallel to the soil surface (the maximum root depth recorded was 7 cm) in some cases forming large networks up to 1 m long. In a study of the dominant species in fallow fields of the Gavidia valley, Montilla *et al.* (1992) showed *R. acetosella* to be a non-mycorrhizal species. An analysis of the seed bank in old-fields after potato cultivation in the Colombian páramo found *R. acetosella* to form a persistent seed bank (Jaimes 2000). The highest seed densities were recorded in early successional fields (3 years fallow), but the species continued to be present at lower densities in the seed bank of fields with more than 20 year of fallow.

5.2.2 Data collection

The selection of the fallow plots for the study was based on the spatial database of Smith (1995, updated to the year 2002). Twelve year 3 plots and twelve year 8 plots were selected. In each case, six were located in high areas of the valley were *E. schultzii* and *H. laricifolium* are the dominant mature páramo vegetation and six in areas near the bottom of the valley where large shrubs dominate the undisturbed vegetation. Both in high and low altitude areas, two groups of three plots each were selected for each successional stage. Each group was located in a different sector of the valley. This allowed considering the effect of local conditions on *R. acetosella* abundance and spatial structure. However, both for early and late succession no significant differences were identified between each of the 4 sectors of the valley nor between the high and low valley areas in the total abundance of *R. acetosella* or small scale spatial structure (intensity of aggregation). Hence, I took each of the twelve year 3 and year 8 plots to represent an independent replicate for all subsequent analysis in this chapter.

Within each fallow field, a sampling plot of 4 x 1 m was randomly established with the following restrictions: (a) a 1 m boundary around the edge of the field was excluded from the potential sampling area, to avoid edge effects (Fig 5.1); (b) the random origin of the sampling plot was placed in a band between 1 and 10 m from the boundary. This implied that in large fallow fields the whole of the central area was not sampled. This was done to control for the possibility of limited successional colonization in the central area of fields when their size is very large. The sampling plot was always oriented so that the longest side was perpendicular to the main slope direction within the field. The plot was rectangular to allow sampling without disturbing the vegetation within. Disturbance to vegetation outside the sampling plot was minimized as much as possible.

Each rectangular plot was divided into four sections of 1x1 m marked by plastic tubes inserted into the ground, which established ten permanent corners in the grid. For data collection, a 1x1 m metal-framed quadrat divided into 100 cells of 10x10 cm was used. This quadrat had legs that could be inserted into the plastic tubes buried in the soil. This allowed repositioning the quadrate accurately in repeated sampling occasions. In this way I established permanent sampling plots of 400 cells (each 10x10 cm) in each of the 24 fallow areas (see Fig 5.1). These plots were sampled in two occasions: at the end of the wet season 2001 (25 October - 10 November) and the end of the dry season 2002 (05 - 19 April). In the dry season, the permanent marks for one of the year 8 plots could not be relocated. Consequently, one replicate was lost for subsequent analyses.

In every plot, I recorded the presence-absence of *R. acetosella* in each of 9 internal *sub-cells* into which the cells were divided (with the help of a small portable frame, see Fig 5.1). *R. acetosella* was recorded as present when above-ground living phytomass (stems, leaves, and reproductive structures) was observed inside the sub-cell. This provided a measure between 0 (total absence in the cell) and 9 (all sub-cells occupied) of the *within-cell frequency* $f(x)$. Here, x specifies the coordinates of each cell (x_1,x_2). The two sampling occasions were represented by $f(x)$ for the wet season and and $f\,'(x)$ for the dry season. Examples of the data structure are provided in Figs. 5.2 and 5.3. Because of the small relative size of *R. acetosella* individuals, a single sub-cell could some times contain several shoots (especially in year 3 plots).

I also recorded the presence-absence within each cell, $p_i(x)$ (where i corresponds to the species identity) of the above-ground living tissues of *E. schultzii* and *H. laricifolium* (steams and leaves). I concentrated on the interaction of *R. acetosella* with these two mature páramo species because of their clear dominance during late succession and their large maximum size compared with most other species in the system. Because of their large adult sizes, a single individual of both *E. schultzii* and *H. laricifolium* could occupy more than one contiguous cell, especially in the year 8 plots (see examples of the data structure in Fig. 5.4). However, several small sized individuals could also occupy a single cell (especially in year 3 plots). A cell could also

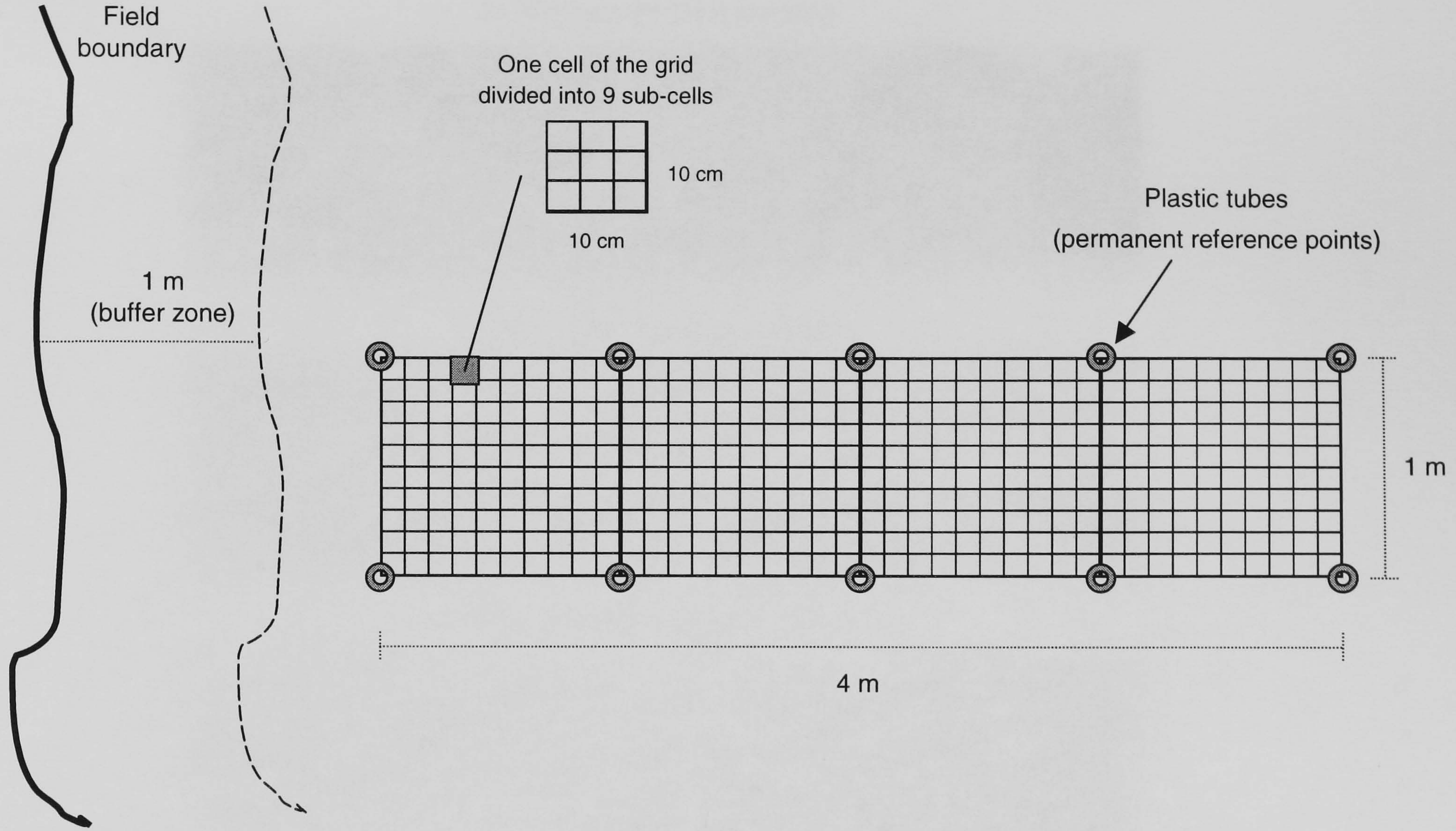
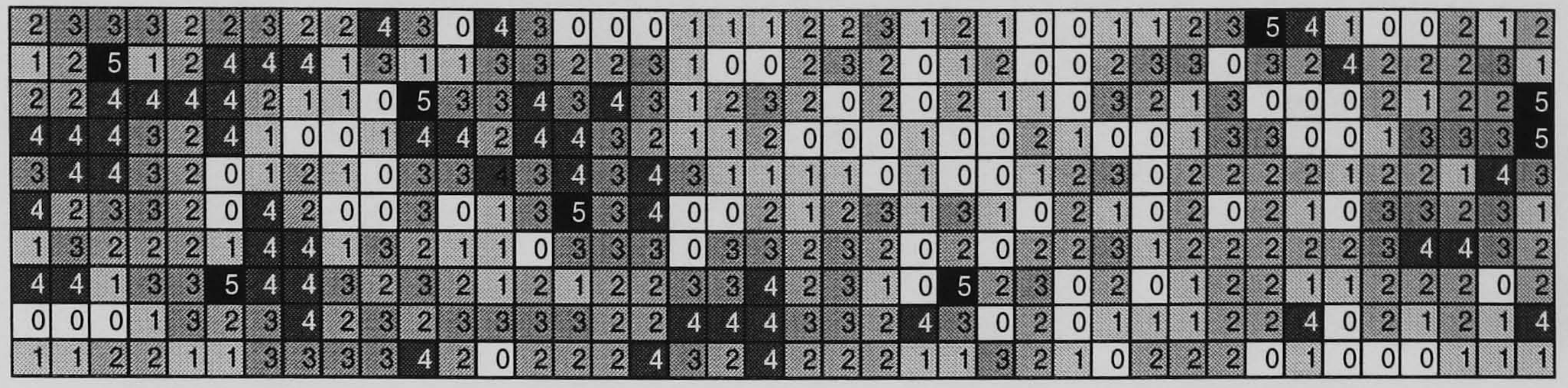


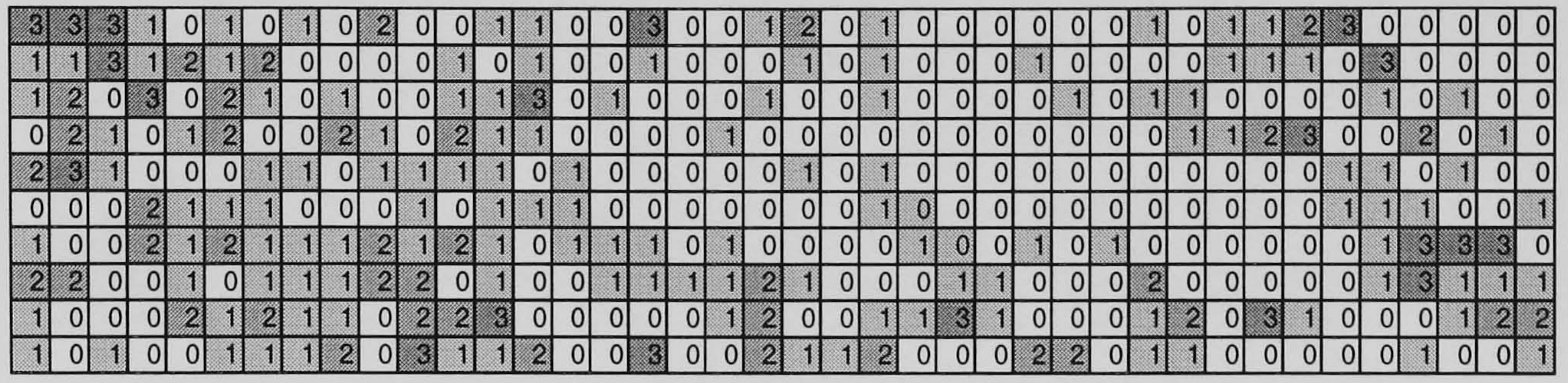
Figure 5.1 Schematic representation of a sampling plot (4x1 m). The lower-left corner of the plot was randomly located outside a 1 m buffer zone defined from the field boundary. Each plot was divided into 4 areas of 1x1 m each and plastic tubes inserted into the ground to mark the corners. Then a quadrat of 1x1 m^2 divided into 100 cells each of 10x10 cm was placed sequentially in each of the four 1 m^2 areas to sample all 400 cells in the plot. Each 10x10 cm cell was divided into 9 square sub-cells. The abundance of *R. acetosella* was recorded as the number of sub-cells within each cell where the species was present.

A. Wet season (first census)



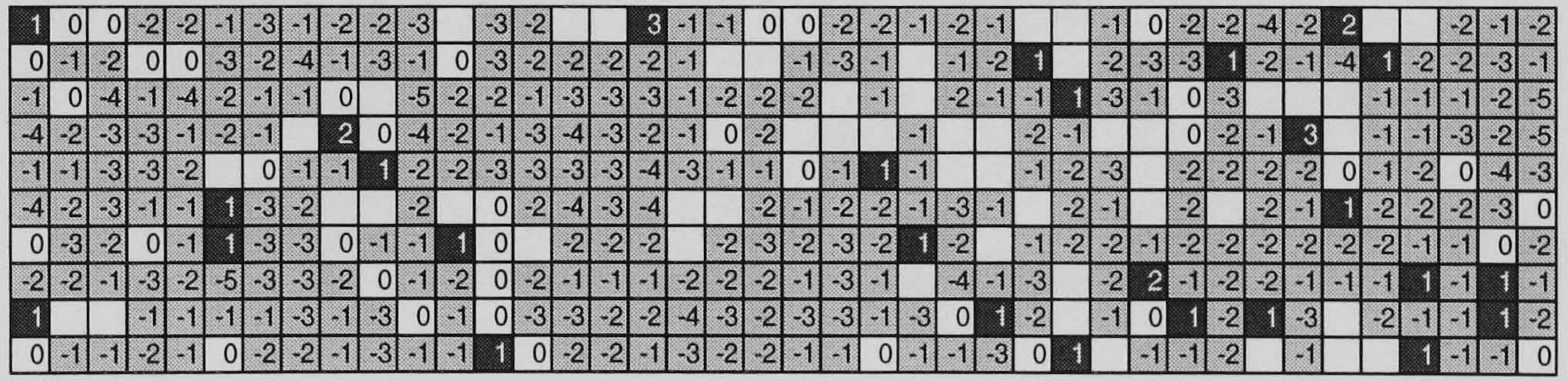
2	3	3	3	2	2	3	2	2	4	3	0	4	3	0	0	0	1	1	1	2	2	3	1	2	1	0	0	1	1	2	3	5	4	1	0	0	2	1	2
1	2	5	1	2	4	4	4	1	3	1	1	3	3	2	2	3	1	0	0	2	3	2	0	1	2	0	0	2	3	3	0	3	2	4	2	2	2	3	1
2	2	4	4	4	4	2	1	1	0	5	3	3	4	3	4	3	1	2	3	2	0	2	0	2	1	1	0	3	2	1	3	0	0	0	2	1	2	2	5
4	4	4	3	2	4	1	0	0	1	4	4	2	4	4	3	2	1	1	2	0	0	0	1	0	0	2	1	0	0	1	3	3	0	0	1	3	3	3	5
3	4	4	3	2	0	1	2	1	0	3	3	4	3	4	3	4	3	1	1	1	1	0	1	0	0	1	2	3	0	2	2	2	2	1	2	2	1	4	3
4	2	3	3	2	0	4	2	0	0	3	0	1	3	5	3	4	0	0	2	1	2	3	1	3	1	0	2	1	0	2	0	2	1	0	3	3	2	3	1
1	3	2	2	2	1	4	4	1	3	2	1	1	0	3	3	3	0	3	3	2	3	2	0	2	0	2	2	3	1	2	2	2	2	2	3	4	4	3	2
4	4	1	3	3	5	4	4	3	2	3	2	1	2	1	2	2	3	3	4	2	3	1	0	5	2	3	0	2	0	1	2	2	1	1	2	2	2	0	2
0	0	0	1	3	2	3	4	2	3	2	3	3	3	3	2	2	4	4	4	3	3	2	4	3	0	2	0	1	1	1	2	2	4	0	2	1	2	1	4
1	1	2	2	1	1	3	3	3	3	4	2	0	2	2	2	4	3	2	4	2	2	2	1	1	3	2	1	0	2	2	2	0	1	0	0	0	1	1	1

B. Dry season (second census)



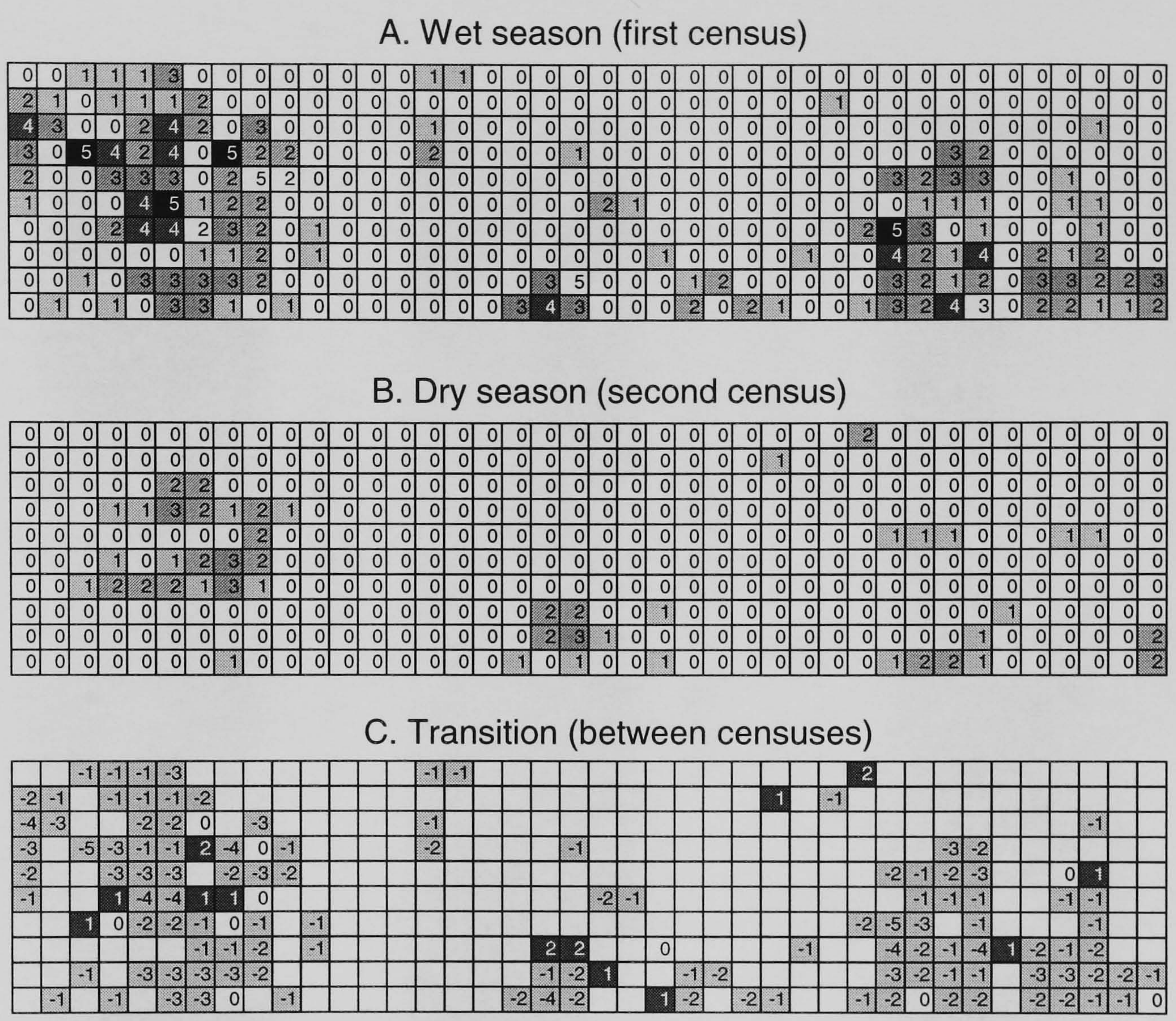
3	3	3	1	0	1	0	1	0	2	0	0	1	1	0	0	3	0	0	1	2	0	1	0	0	0	0	0	0	1	0	1	1	2	3	0	0	0	0	0
1	1	3	1	2	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	3	0	0	0	0
1	2	0	3	0	2	1	0	1	0	0	1	1	3	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0
0	2	1	0	1	2	0	0	2	1	0	2	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	2	3	0	0	2	0	1	0
2	3	1	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
0	0	0	2	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
1	0	0	2	1	2	1	1	1	2	1	2	1	0	1	1	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	3	3	3	0
2	2	0	0	1	0	1	1	1	2	2	0	1	0	0	1	1	1	1	2	1	0	0	0	1	1	0	0	0	2	0	0	0	0	0	1	3	1	1	1
1	0	0	0	2	1	2	1	1	0	2	2	3	0	0	0	0	0	1	2	0	0	1	1	3	1	0	0	0	1	2	0	3	1	0	0	0	1	2	2
1	0	1	0	0	1	1	1	2	0	3	1	1	2	0	0	3	0	0	2	1	1	2	0	0	0	2	2	0	1	1	0	0	0	0	0	1	0	0	1

C. Transition grid (between censuses)



1	0	0	-2	-2	-1	-3	-1	-2	-2	-3		-3	-2			3	-1	-1	0	0	-2	-2	-1	-2	-1			-1	0	-2	-2	-4	-2	2			-2	-1	-2
0	-1	-2	0	0	-3	-2	-4	-1	-3	-1	0	-3	-2	-2	-2	-2	-1			-1	-3	-1		-1	-2	1		-2	-3	-3	1	-2	-1	-4	1	-2	-2	-3	-1
-1	0	-4	-1	-4	-2	-1	-1	0		-5	-2	-2	-1	-3	-3	-3	-1	-2	-2	-2		-1		-2	-1	-1	1	-3	-1	0	-3				-1	-1	-1	-2	-5
-4	-2	-3	-3	-1	-2	-1		2	0	-4	-2	-1	-3	-4	-3	-2	-1	0	-2				-1			-2	-1			0	-2	-1	3		-1	-1	-3	-2	-5
-1	-1	-3	-3	-2		0	-1	-1	1	-2	-2	-3	-3	-3	-3	-4	-3	-1	-1	0	-1	1	-1			-1	-2	-3		-2	-2	-2	-2	0	-1	-2	0	-4	-3
-4	-2	-3	-1	-1	1	-3	-2			-2		0	-2	-4	-3	-4			-2	-1	-2	-2	-1	-3	-1		-2	-1		-2		-2	-1	1	-2	-2	-2	-3	0
0	-3	-2	0	-1	1	-3	-3	0	-1	-1	1	0		-2	-2	-2		-2	-3	-2	-3	-2	1	-2		-1	-2	-2	-1	-2	-2	-2	-2	-2	-2	-1	-1	0	-2
-2	-2	-1	-3	-2	-5	-3	-3	-2	0	-1	-2	0	-2	-1	-1	-1	-2	-2	-2	-1	-3	-1		-4	-1	-3		-2	2	-1	-2	-2	-1	-1	-1	1	-1	1	-1
1			-1	-1	-1	-1	-3	-1	-3	0	-1	0	-3	-3	-2	-2	-4	-3	-2	-3	-3	-1	-3	0	1	-2		-1	0	1	-2	1	-3		-2	-1	-1	1	-2
0	-1	-1	-2	-1	0	-2	-2	-1	-3	-1	-1	1	0	-2	-2	-1	-3	-2	-2	-1	-1	0	-1	-1	-3	0	1		-1	-1	-2		-1			1	-1	-1	0

Figure 5.2 An example of the spatial maps of within-cell frequency for *R. acetosella* in a Year 3 permanent plot (each cell has 10x10 cm and there are 10x40 cells per grid). A. Wet season, *f*(*x*); B. Dry season, *f'*(*x*) ; C. Transition: the value within each cell corresponds to the difference between dry and wet season frequencies ($\Delta f(x)$). In this last grid, cells where frequency declined are indicated in light grey while cells where frequency increased are indicated in black. Cells where frequency did not change are marked with a 0 and cells that did not contain *R. acetosella* in any of the two occasions are empty.



A. Wet season (first census)

0	0	1	1	1	3	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
4	3	0	0	2	4	2	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
3	0	5	4	2	4	0	5	2	2	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0
2	0	0	3	3	3	0	2	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	3	3	0	0	1	0	0	0
1	0	0	0	4	5	1	2	2	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0
0	0	0	2	4	4	2	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	3	0	1	0	0	0	1	0	0
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0	0	1	0	3	3	3	3	2	0	0	0	0	0	0	0	0	0	3	5	0	0	0	1	2	0	0	0	0	0	3	2	1	2	0	3	3	2	2	3
0	1	0	1	0	3	3	1	0	1	0	0	0	0	0	0	0	3	4	3	0	0	0	2	0	2	1	0	0	1	3	2	4	3	0	2	2	1	1	2

B. Dry season (second census)

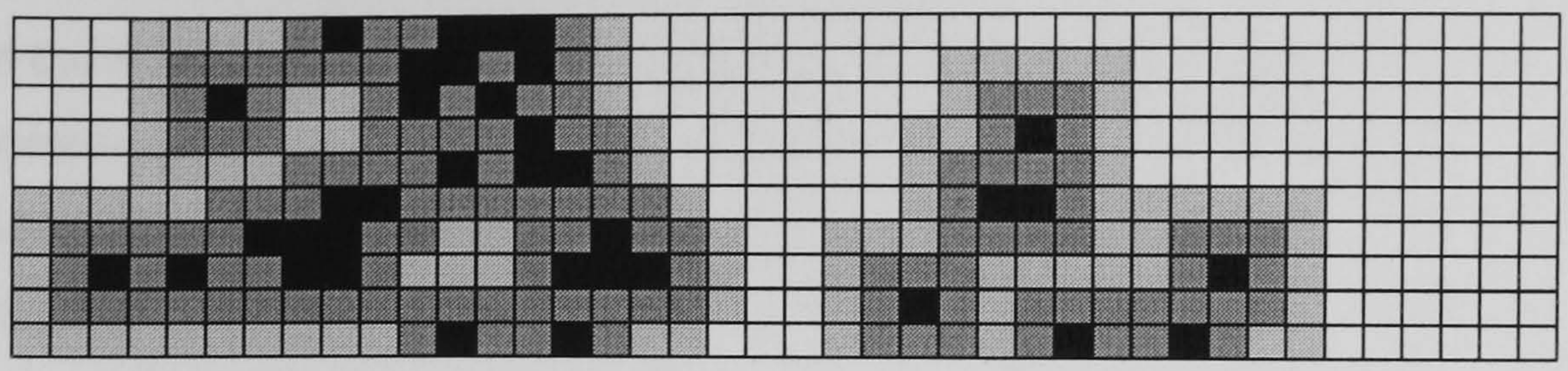
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	1	3	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0
0	0	0	1	0	1	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	2	2	2	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	2	2	1	0	0	0	0	0	2

C. Transition (between censuses)

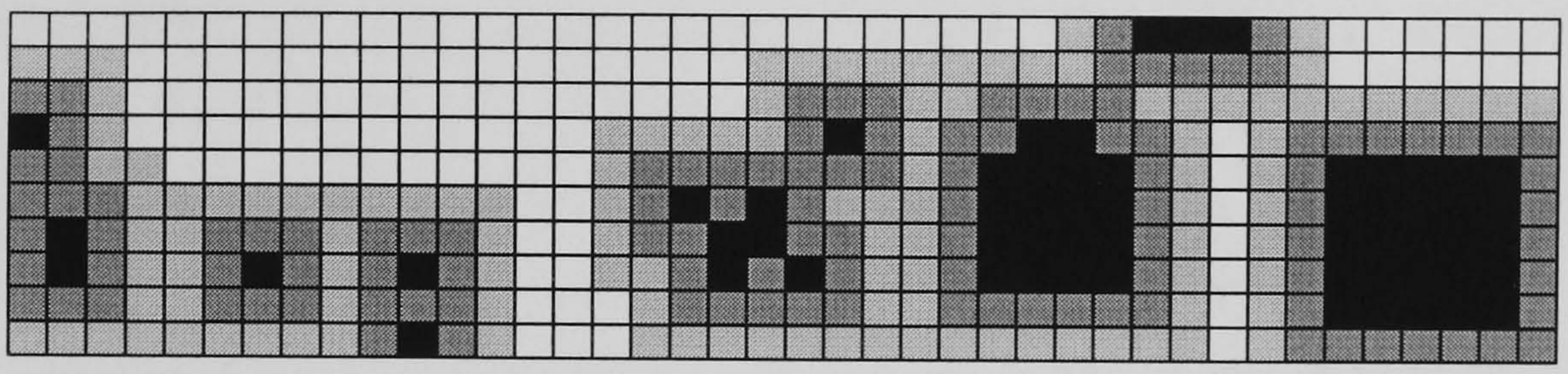
		-1	-1	-1	-3									-1	-1														2										
-2	-1		-1	-1	-1	-2																				1		-1											
-4	-3			-2	-2	0		-3						-1																						-1		
-3		-5	-3	-1	-1	2	-4	0	-1					-2					-1													-3	-2						
-2			-3	-3	-3		-2	-3	-2																					-2	-1	-2	-3			0	1		
-1			1	-4	-4	1	1	0												-2	-1										-1	-1	-1			-1	-1		
		1	0	-2	-2	-1	0	-1		-1																			-2	-5	-3		-1				-1		
						-1	-1	-2		-1								2	2			0					-1			-4	-2	-1	-4	1	-2	-1	-2		
		-1		-3	-3	-3	-3	-2										-1	-2	1			-1	-2						-3	-2	-1	-1		-3	-3	-2	-2	-1
	-1		-1		-3	-3	0		-1								-2	-4	-2			1	-2		-2	-1			-1	-2	0	-2	-2		-2	-2	-1	-1	0

Figure 5.3 An example of the spatial maps of within-cell frequency for *R. acetosella* in a Year 8 permanent plot (each cell has 10x10 cm and there are 10x40 cells per grid). A. Wet season, *f*(*x*); B. Dry season, *f'*(*x*) ; C. Transition: the value within each cell corresponds to the difference between dry and wet season frequencies ($\Delta f(x)$). In this last grid, cells where frequency declined are indicated in light grey while cells where frequency increased are indicated in black. Cells where frequency did not change are marked with a 0 and cells that did not contain *R. acetosella* in any of the two occasions are empty.

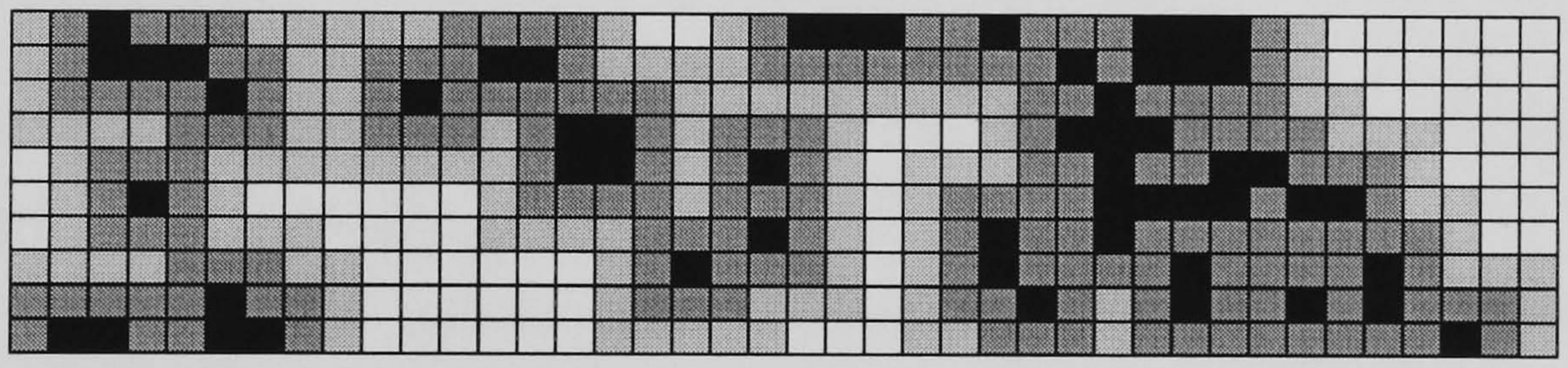
A. *E. schultzii* (Year 3)



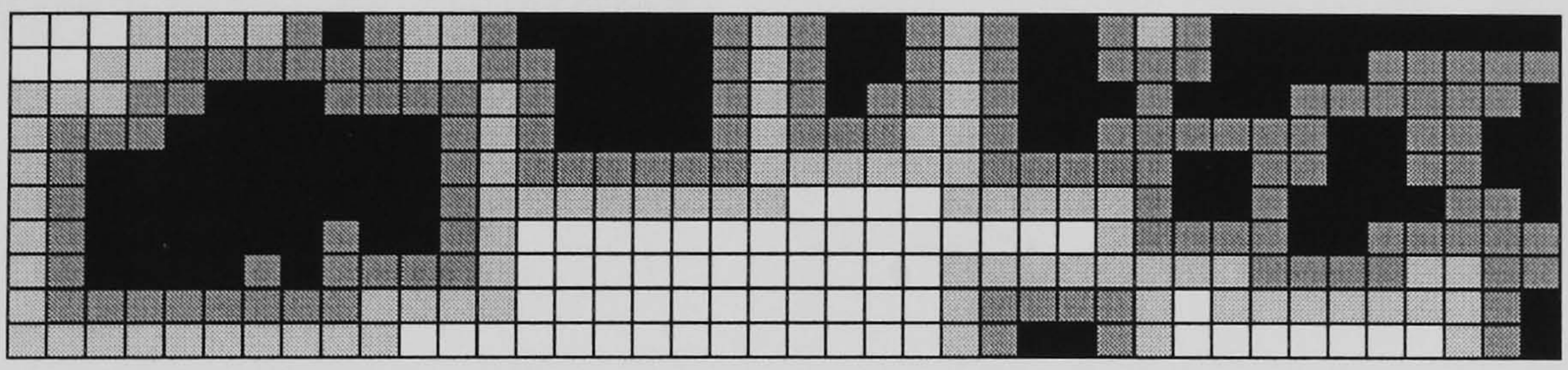
B. *E. schultzii* (Year 8)



C. *H. laricifolium* (Year 3)



D. *H. laricifolium* (Year 8)



■ 0 cm ▨ 10-20 cm □ 20- 30 cm

Figure 5.4 Examples of the spatial maps for the distribution of the two late dominant species during the wet season in the permanent plots (each cell has 10x10 cm and there are 400 cells per grid). Black: species present within target cell (0 cm); Dark grey: 10-20 cm to the nearest occupied target cell; Light grey: 20-30 cm to the nearest occupied target cell. The first two maps correspond to the distribution of *E. schultzii* in a year 3 and year 8 plot (A,B). The bottom two maps correspond to *H. laricifolium* in a year 3 and year 8 plot (C,D).

be simultaneously occupied by all three species. The only exception to this were cells at the base of the stem of large rosette individuals of *E. schultzii* in year 8 plots, as the compact giant rosette structure prevented *R. acetosella* individuals to extend into the same cell. The presence of other dominant species in the sampling plots was also recorded, but their abundances were too variable between the different replicate areas to be included in the analysis.

While some previous studies on small-scale spatial dynamics have included a large number of the plant species present in the community, this has resulted in a low number of replicate areas being analysed because of time constraints (e.g. Law *et al.* 1993). In the present chapter, including a low number of species allowed the use of extensive replication, giving more confidence to the generalization of the results: this is particularly relevant in the highly heterogeneous conditions of these high mountain environments (see Chapter 2; Llambi and Sarmiento 1998).

5.2.3 Analysis of changes of *R. acetosella* abundance in the permanent grids

To characterize changes in the average abundance of *R. acetosella* in each sampling plot I calculated the average within-cell frequency in all cells ($\overline{f}$). This allowed comparison of the abundance of *R. acetosella* in early and late successional plots and within each plot between the wet and dry season. Comparisons were done using a Kruskal-Wallis non-parametric analysis of variance. To obtain $\overline{f}$, I calculated the total number of occupied sub-cells in each grid, *S:*

$$S = \sum_{x} f\,(x) \qquad \text{Eq. 5.1}$$

Then, $\overline{f}$ was calculated as:

$$\overline{f} = \frac{S}{T} \qquad \text{Eq. 5.2}$$

Where T is the total number of cells in the grid ($T = 400$).

To characterize changes in abundance between the two seasons, I also calculated the *net* change in within-cell frequency in each cell as:

$$\Delta f(x) = f'(x) - f(x) \qquad \text{Eq. 5.3}$$

Two examples of the resulting grid maps of $\Delta f(x)$ values are presented in Figs. 5.2 and 5.3. On the basis of this information, I counted the proportion of all cells in each plot that showed positive values for $\Delta f(x)$ (net gain of sub-cells, so that the loss of occupied sub-cells is outweighed by new sub-cell colonization). I also obtained the proportion of cells occupied in the wet season that showed negative values of $\Delta f(x)$ (net loss of occupied sub-cells between the two seasons) and the proportion with no change in frequency. The proportion of cells showing negative transitions was much larger than that with net sub-cell gains, suggesting that colonization events were very limited (see Table 5.1). Hence, the analysis concentrated on the process of sub-cell loss through *R. acetosella* mortality between the wet and dry seasons.

I assumed that the sum of all the negative $\Delta f(x)$ (net occupied sub-cells losses) in a grid corresponded to the *total* or absolute number of occupied sub-cells lost (i.e. any balance between gain and loss of sub-cells is not considered). Given this assumption, the number of sub-cells lost, D, was calculated as:

$$D = \sum_{\{x:\, \Delta f(x) < 0\}} \Delta f(x) \qquad \text{Eq. 5.4}$$

Where the set $\{x: \Delta f(x) < 0\}$ corresponds to all the cells with negative transitions in the grid. Then, the global probability of sub-cell mortality in each grid, m_g was calculated as:

$$m_g = \frac{D}{S} \qquad \text{Eq. 5.5}$$

Where S is the sum of all occupied sub-cells in the wet season. The global sub-cell mortality probabilities, m_g, in year 3 and year 8 plots were compared using a Kruskal-Wallis non-parametric analysis of variance. For simplicity, in the reminder of this chapter I will refer to the loss of occupied sub-cells between the wet and dry season simply as mortality and to m_g simply as the mortality probability of *R. acetosella* (even though it is clear that the loss of a sub-cell can involve the balance of births and death processes of more than one shoot).

5.2.4 Spatial structure analysis

To analyse changes in the small-scale spatial structure of *R. acetosella* and its spatial interactions with the late dominant species I used non-centralized spatial covariance functions (see Condit *et al.* 2000; Purves and Law 2001). I corrected the covariance function to account for non-stationarity across the whole grid, using the non-ergodic covariance function introduced in Chapter 4. The reason for making this correction was that *R. acetosella* patches were sometimes large, producing, in a few cases, large differences in $f(x)$ across the grid.

In this chapter, I use the radial average of the full covariance function for each of 8 distance classess (d), each of 10 cm (i.e. one cell width, see Chapter 4 for details). To compare the spatial structure of *R. acetosella* between seasons and between year 3 and year 8 plots, I calculated the radial autocovariance functions ($C_{ii}(d)$) using $f(x)$, as the abundance measure. This calculation was done separately for each replicate grid and for each season. This gave a measure of the intra-specific aggregation of *R. acetosella* for each plot at the two survey times.

To evaluate the spatial association between the spatial distributions of *R. acetosella within the same grid* in the two seasons, I calculated the radial crosscovariance, $C_{ij}(d)$ between the frequency in the wet ($f(x)$) and dry seasons ($f'(x)$), taking the i and j to represent in this case the two sampling times. This provided an idea of whether the centres of high *R. acetosella* abundance were maintained between the two seasons, or whether the pattern was more 'fluid' (with the centres of high abundance shifting from one survey time to the next).

Finally, I used crosscovariance functions, $C_{ij}(d)$, to evaluate how the spatial distribution of *R. acetosella* in both seasons was related to the presence/absence, $p_i(x)$, of *E. schultzii* and *H. laricifolium.* Presence-absence of both LS species refers here only to the wet season: I took this to represent the initial conditions before wet-to-dry season mortality took place. Only plots in which the number of cells where the LS species presence was above 25 were included for this analysis of the spatial association between *R. acetosella* and the LS species. This lower limit to the number of occupied cell was arbitrarily chosen to guarantee that there were enough occupied cells to provide information about the spatial relationship between the early and LS species.

For all covariance calculations, Monte Carlo procedures were used to test the statistical significance of the departures from randomness of the covariance functions (see Chapter 4 for details).

5.2.5 Local density dependence of wet-to-dry season mortality: effect of within-cell frequency

To evaluate the effect of local density on mortality of *R. acetosella* I examined how the probability of sub-cell loss from the wet to the dry season depended on: (a) the within-cell frequency $f(x)$ in the wet season; (b) the abundance of *R. acetosella* in neighbouring cells in the wet season (sub-section 5.2.6). The local abundance of *R. acetosella* in the wet season was used as the explanatory variable in this analysis: it was taken to represent the initial conditions before wet-to-dry season mortality took place.

For the analysis of the effect of within-cell frequency on mortality, I calculated for each grid, the vector of the probabilities of mortality for each possible initial value of $f(x)$. I called this vector m, and each of its elements m_z, with $z \in \{1,2,...,k\}$. Here, k is the maximum observed value of $f(x)$ in each particular grid (which in some grids was less than the highest possible value of 9). So, the vector m can be written as:

$$m = (m_1, m_2, ..., m_k) \qquad \text{Eq. 5.6}$$

To calculate the elements of m, I first obtained the vector n, of the total numbers of occupied sub-cells in the set of cells with each possible initial frequency value z. Each element of n was calculated as:

$$n_z = \sum_{\{x: f(x)=z\}} f(x) \qquad \text{Eq. 5.7}$$

I then calculated the vector *d* of the total number of occupied sub-cells lost between the wet and dry season, for each possible initial frequency value *z*. Each element of *d* was calculated as:

$$d_z = \sum_{\{x:\, f(x)=z \text{ and } \Delta f(x)<0\}} \Delta f(x) \qquad \text{Eq. 5.8}$$

Here, the sum is over all *x* cells where *f*(*x*)=*z* and where there was a loss of occupied sub-cells between the two seasons, so that $\Delta f(x)<0$.

Finally, each element of *m* was calculated as:

$$m_z = \frac{d_z}{n_z} \qquad \text{Eq. 5.9}$$

So, each element of *m* corresponds to the proportion of occupied sub-cells lost from the wet to the dry season for each initial frequency value *z*.

If the mortality probability m_z was independent of the within-cell frequency, all the elements of *m* should be equal to the global probability of mortality in the grid, m_g. Moreover, the Pearson's correlation coefficient (*r*) between m_z and *z* should equal 0: there should be no correlation between the probability of mortality and the initial frequency value of the cells. This was the null-hypothesis tested. This approach is based in one of the common methods to evaluate density dependence in terms of the relationship between mortality and initial density (see Enright 1976). The alternative hypothesis evaluated was that mortality was density dependent and hence a significant correlation between m_z and *z*. To test this hypothesis, it would be inappropriate to evaluate the significance of the observed correlation using the parametric tables for Pearson's coefficient. The spatial nature of the data violates the assumption that observations of *f*(*x*) are an independent random sample of the population, because of their spatial autocorrelation (see spatial structure analysis results) and because the sampling was systematic (grid based). This is a problem that has not been appropriately dealt with in most previous analysis of small-scale dynamics in permanent grids (parametric analysis like contingency tables have been used on spatially autocorrelated data, e.g. Herben *et al.* 1990 and Herben *et al.* 1993).

To avoid these problems, Law *et al.* (1993, see also McLellan 1995) suggested the use of Monte Carlo and permutation techniques to test hypothesis on the influence of neighbours on spatial transitions.

In this case Monte Carlo procedures were used to generate a simulated distribution of r values for the relationship between m_z and z and to derive confidence intervals for r against which to compare the observed correlation value. For each simulation, sub-cells were randomly removed one by one from a list of all occupied sub-cells in the wet season (initial conditions in each plot). The total amount of sub-cells removed was equal to D, the observed number of sub-cells lost between seasons. Then, for each of 1000 simulations, the m vector of sub-cell mortality probabilities was calculated, and the correlation between m_z and z obtained. Here I verified that the average of each of the elements of m_z from all the 1000 simulations was equal to m_g, and also that the average of all the simulated r values was equal to 0: therefore, the Monte Carlo simulations reproduced the null hypothesis correctly. From the distribution of r values obtained in the 1000 simulations, the 95 % and 99 % confidence intervals were derived for the correlation coefficient and the observed values were compared with them. If the observed r was higher (or lower) than the Monte Carlo boundaries, the null hypothesis of local density independent mortality was rejected (two tailed test). I considered this as evidence in support of the hypothesis of a negative (or positive) density dependent effect of within-cell initial frequency on the mortality probability. All calculations were done using a *C++* program designed by myself (the same applies to the two sections below).

5.2.6 Local density dependence of wet-to-dry season mortality: effect of neighborhood frequency

To evaluate the effect on the probability of sub-cell loss of the total frequency of occupied sub-cells in the neighbourhood of a target cell, the same approach of the previous section was used. The vector m of the probability of sub-cell loss between the two seasons was calculated in cells with different initial frequencies in their neighbourhood. The first step was to define the cells included in the neighbourhood, $N(x)$. In this analysis, three neighbourhood sizes were used: the 4 nearest cells to a target cell (also known as the 'von Neumann' neighbourhood); the 8 nearest cells (known as the 'Moore' neighbourhood); and the 24 nearest cells (see diagrams in

Figure 5.5). Then the total number of occupied sub-cells in the neighbourhood of each target cell, *g*(*x*) was calculated as:

$$g(x) = \sum_{y \in N(x)} f(y) \qquad \text{Eq. 5.10}$$

Where *y* corresponds to the coordinates of all the cells included in the neighbourhood of each target cell *x*. In the analysis based on 4 and 8 cells, all the cells on the border of the grid were not considered, as some of their neighbourhoods were located outside of the sampling plot. For the 24 cell case, all the cells located 'one or two cells away' from the border were excluded for the same reason. So, the analysis was performed on 304 and 216 cells from the total of 400 cells. Because of this loss of cells for analysis as the neighbourhood size was increased, larger neighbourhood scales were not considered.

The next step was to divide the cells in the grid into different groups depending on their total initial frequency of occupied sub-cells in their neighbourhood, *g(x)*. The range of possible values for *g*(*x*) was much larger than the range for *f*(*x*) in the within-cell scale analysis. In the case of 4 cells, *g(x)* could take values between 0 and 36 occupied sub-cells (9 in each neighbourhood cell). In the case of 24 cells, *g(x)* could range between 0 and 216. Hence, cells were classified by dividing *g*(*x*) into discrete classess; for the 4 cell neighbourhood each class had a range of 3 sub-cells; for the 8 cells case the range was of 6 sub-cells; for the 24 cells case the range was of 12 sub-cells. Cells with 0 sub-cells occupied in their neighbourhood were considered as a separate class. This procedure assigned a *g(x)* class to each target cell, based on the neighbourhood frequency of *R. acetosella*, but *not* including the frequency in the target cell itself.

Then, as in the previous sub-section, the vector *n* of the total number of occupied sub-cells *in the target cells* for each *g(x)* class was calculated. For example, for the 4 cells neighbourhood case, the element of *n* corresponding to all cells with 1 to 3 sub-cells in their neighbourhood, $n_{1\text{-}3}$, was calculated as:

$$n_{1-3} = \sum_{\{x:\, 1 \le g(x) \le 3\}} f(x) \qquad \text{Eq. 5.11}$$

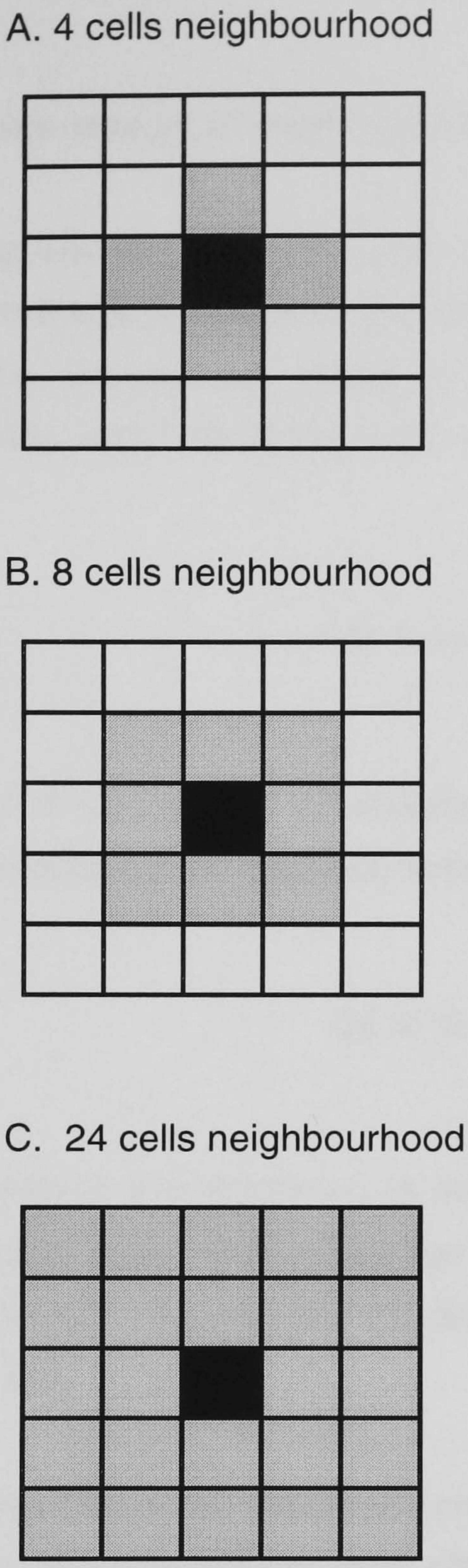


Figure 5.5 Diagrams of the three neighbourhood scales used in the analysis of local density dependence on the probability of sub-cell loss. The grey cells represent the set of cells included in the neighbourhood *N*(*x*) of a target cell *x* (the black central square).

The same formulation was used for all neighbourhood sizes and all $g(x)$ classess.

As before, the next step was to obtain the vector d of the number of occupied sub-cells that were lost from the target cell from the wet to the dry season for each $g(x)$ class. Using the same example as above (4 cells case), the element of d corresponding to all cells with 1 to 3 sub-cells in their neighbourhood, $d_{1\text{-}3}$, was calculated as:

$$d_{1-3} = \sum_{\{x:\, 1 \le g(x) \le 3 \text{ and } \Delta f(x) < 0\}} \Delta f(x) \qquad \text{Eq. 5.12}$$

Finally, the $m_{1\text{-}3}$ element of the vector m of the probability of sub-cell mortality of cells with 1 to 3 occupied sub-cells in their neighbourhood was calculated as:

$$m_{1-3} = \frac{d_{1-3}}{n_{1-3}} \qquad \text{Eq. 5.13}$$

Eq. 5.13 just corresponds to the proportion of sub-cells lost from those originally occupied in the wet season (given in this case that $1 \le g(x) \le 3$). All the elements of vector m for the different $g(x)$ classess and the different neighbourhood sizes were calculated in the same way.

For example, in the case of the 4 cell neighbourhood, the vector corresponded to, $m = (m_0, m_{1\text{-}3}, m_{4\text{-}6}, \ldots, m_{34\text{-}36})$. For convenience, each element of m was denoted as before as m_z. Here, z corresponds to the rank of each of the classess in which the values of $g(x)$ could fall. For example, for the 4 cell neighbouhood case: z=1 corresponds to the cells where $1 \le g(x) \le 3$; and z=12 corresponds to the cells where $34 \le g(x) \le 36$.

As in the previous section, if the mortality probability was independent of the abundance of conspecifics in the neighbouring cells, all the elements of m should be equal to the global mortality probability in the grid, m_g. Moreover, the correlation between each m_z element and z should equal 0 (i.e. the probability of mortality should be independent of how 'crowded' the neighbourhood is). As before, this constituted the null hypothesis against which I contrasted the hypothesis of mortality being correlated with neighbourhood abundance. The same randomisation procedure described in the previous section was used to generate the Monte Carlo boundaries for each of the elements of m and for their correlation with z.

5.2.7 Effects of inter-specific interactions on wet-to-dry season mortality

Finally, I evaluated the effect that the presence of the two LS species, *E. schultzii* and *H. laricifolium,* had on the local probability of sub-cell loss for *R. acetosella*. The effect of the two LS species was analysed separately. Their interaction with *R. acetosella* was evaluated in terms of the effect that the distance *from* a target cell occupied by *R. acetosella* (in the wet season) *to* the nearest cell occupied by *E. schutlzii* or *H. laricifolium* had on the probability of sub-cell loss between the two seasons. The expectation was that *R. acetosella* would have higher drought induced mortality when occupying the same cell or cells adjacent to individuals of the LS species because of negative competitive effects.

A different approach was used (considering presence-absence of the LS species at a given distance rather than within cell *abundance* as in the intra-specific interactions case), because of the large differences in individual size between *R. acetosella* and the two LS species, and because the abundance of these two late species was recorded in terms of presence-absence, $p_l(x)$.

To calculate the vector m of the probabilities of sub-cell loss for each distance to the nearest cell where a LS species individual is present, cells in the grid were first classified in terms of this distance, $h(x)$. Three distance classess were analysed: $h(x)=0$, 0 cm (i.e. LS species present in the cell); $h(x)=1$, from 10 to 20 cm; $h(x)=2$, from 20 to 30 cm (see example in Fig. 5.4). No more distance classess were calculated as the numbers of cells that were beyond 30 cm from *E. schultzii* or *H. laricifolium* individuals was in some cases too low. The rest of the calculations were done in the same way as in the two previous sections. So each element of the vector n (total number of occupied sub-cells for cells of each distance class) was calculated as:

$$n_z = \sum_{\{x:\,h(x)=z\}} f(x) \qquad \text{Eq. 5.14}$$

Where z represents here each of the possible values for $h(x)$ (0,1 or 2). The vector d of the number of sub-cells lost in cells occupied by *R.acetosella* for each distance class was calculated as:

$$d_z = \sum_{\{x:\, h(x)=z \text{ and } \Delta f(x)<0\}} \Delta f(x) \qquad \text{Eq. 5.15}$$

Then, the elements of m were calculated dividing d_z by n_z (Eq. 5.9). As in the case of the effects of conspecifics, if there was no effect of the distance to *E. schultzii* or *H. laricifolium* individuals on the probability of *R. acetosella* mortality, all the elements of m should be equal to m_g and there should be no relationship between this distance and m_z. However, in this case I did not test the null hypothesis by looking at the correlation between distance and m_z, as there were too few distance classess to use in the correlation. Instead, I used exactly the same Monte Carlo simulation approach as before, and looked at the 95 and 99 % confidence intervals of the simulated values of $m_z$directly. With this statistical test it was possible to see how different the observed mortality of *R. acetosella* was from mortality that was random and independent of the presence of other species (at different distances).

5.3 RESULTS

5.3.1 Successional and seasonal changes in *R. acetosella* abundance in the permanent grids

The average abundance of *R. acetosella,* in the year 3 plots was higher than in the year 8 plots both for the wet and dry season. This is evident from Table 5.1, where both the average within cell frequency ($\bar{f}$) and the total number of occupied sub-cells in the grid (S) are shown to be significantly higher in the early successional plots. These results are in agreement with the data presented in Chapter 2 on the clear successional decline of *R. acetosella* abundance during the fallow. However, there was considerable variability in the abundance of *R. acetosella* in the grids (see the high standard deviation values in Table 5.1).

The transition from the wet to the dry season caused a strong decline in the abundance of *R. acetosella* in all replicate plots in early and late succession (except for one year 8 plot where average frequency in the cells showed a slight increase). The difference between average frequency in all plots between the wet and dry season was significant both in the 3rd year ($H_{(1,24)}$=12.00, p<0.001) and the 8th year ($H_{(1,22)}$=6.06, p=0.014). In Fig. 5.2 and Fig. 5.3 I present as an example the data for one year 3 and one year 8 permanent plot. It is clear from both figures that the decline in the frequency of *R. acetosella* is the result of a much larger proportion of cells showing a negative net change in frequency than a positive one (see Fig 5.2.C and Fig 5.3.C). In fact, the average across all replicate plots for the proportion of occupied cells in the wet season showing negative net declines was 81.3 % and 71.2 % for year 3 and year 8 plots respectively, while only 8.2 % (year 3) and 12.1 % (year 8) of all cells showed a positive net change (Table 5.1). The proportion of occupied cells that stayed constant in value was also low (an average of 9.2 % and 8.2 % respectively for the year 3 and year 8 plots). This evidence indicates that colonization of new cells was relatively unimportant in determining changes in abundance between both seasons. The global sub-cell mortality rate, m_g, was high both for the year 3 and year 8 plots, with no significant differences between the two successional stages (Table 5.1).

There was a weak negative relationship between the total number of occupied sub-cells in a plot in the wet season, S, and the global mortality rate, m_g. The Pearson's correlation coefficient between these two factors was –0.60 (p=0.039) for the year 3 plots and -0.36 (p=0.285) for the year 8 plots.

5.3.2 Successional and seasonal changes in small-scale spatial structure

The spatial structure of *R. acetosella* was significantly spatially aggregated at small spatial scales (10 cm displacements) in all the replicate plots studied, and in both the wet and dry seasons. The only exception was one year 8 plot where abundance decreased to very low levels in the dry season and the spatial structure changed from aggregated to random (this plot was subsequently removed from statistical comparisons of aggregation intensity as an outlier).

Table 5.1 Changes in *R. acetosella* abundance between the wet and dry season in the permanent plots. Averages and standard deviations (in brackets) from all the replicates are presented for: a) the average within cell frequency, $\bar{f}$; b) the number of occupied sub-cells in each grid, *S*; c) the total number of sub-cells lost between the two seasons, *D*; d) the global probability of sub-cell loss in the grid, m_g; e) the proportion of the cells occupied in the wet season where the cell frequency decreased in the dry season; f) the proportion of all cells where frequency increased between the two seasons. Differences in $\bar{f}$ (for each season) and m_g between early and late succession are evaluated using the non-parametric Kruskal-Wallis test (*K-W*).

Year	$\bar{f}$ **(wet)**	$\bar{f}$ **(dry)**	**S** ***(wet)***	**S (dry)**	**D (wet to dry)**	$\mathbf{m_g}$ **(wet to dry)**	**Cells where Freq. decrease d (%)**	**Cells where Freq. increased (%)**
3	2.7	1.0	1081.2	414.5	710.6	0.69	81.3	8.2
	(1.1)	(0.8)	(458.8)	(310.0)	(232.1)	(0.12)	(6.9)	(4.6)
8	1.1	0.5	441.5	213.2	306.0	0.73	71.2	12.1
	(0.6)	(0.5)	(231.4)	(217.5)	(152.7)	(0.18)	(19.1)	(10.6)
K-W	$H_{(1,23)}=11.45$	$H_{(1,23)}=4.90$				$H_{(1,23)}=0.99$		
	$p=0.0007$	$p=0.0267$	-	-	-	$p=0.3248$	-	-

There was a significant increase in the average aggregation intensity from early to late succession both for the plots in the wet and the dry season (Table 5.2). On the other hand, the transition between wet and dry season caused an increase in the intensity of spatial aggregation in all year 3 permanent plots and in eight of the eleven year 8 plots. The average intensity of aggregation was significantly higher in the dry season than in the wet season both for year 3 (Kruskal-Wallis: $H_{(1,24)}=10.08$, $p=0.0015$) and year 8 plots (Kruskal-Wallis: $H_{(1,21)}=5.73$, $p=0.0167$). This is illustrated both in Fig. 5.6 and Fig. 5.7, which present the autocovariance functions for the two permanent plots presented as examples in Fig. 5.2 and Fig. 5.3. It is clear that the covariance function peaks at higher values in the dry season than in the wet season. By comparing the frequency maps in parts A. and B. of Figures 5.2 and 5.3 it can be visually appreciated that the patchiness in the spatial distribution of *R. acetosella* becomes more 'distinctive' (sharper contrast between high and low frequency areas) in the dry season. The two permanent plots presented as examples also suggest that the scale up to which spatial aggregation is significant (which can be interpreted as the scale of aggregation, see Chapter 4) is higher in the wet season than in the dry season (see

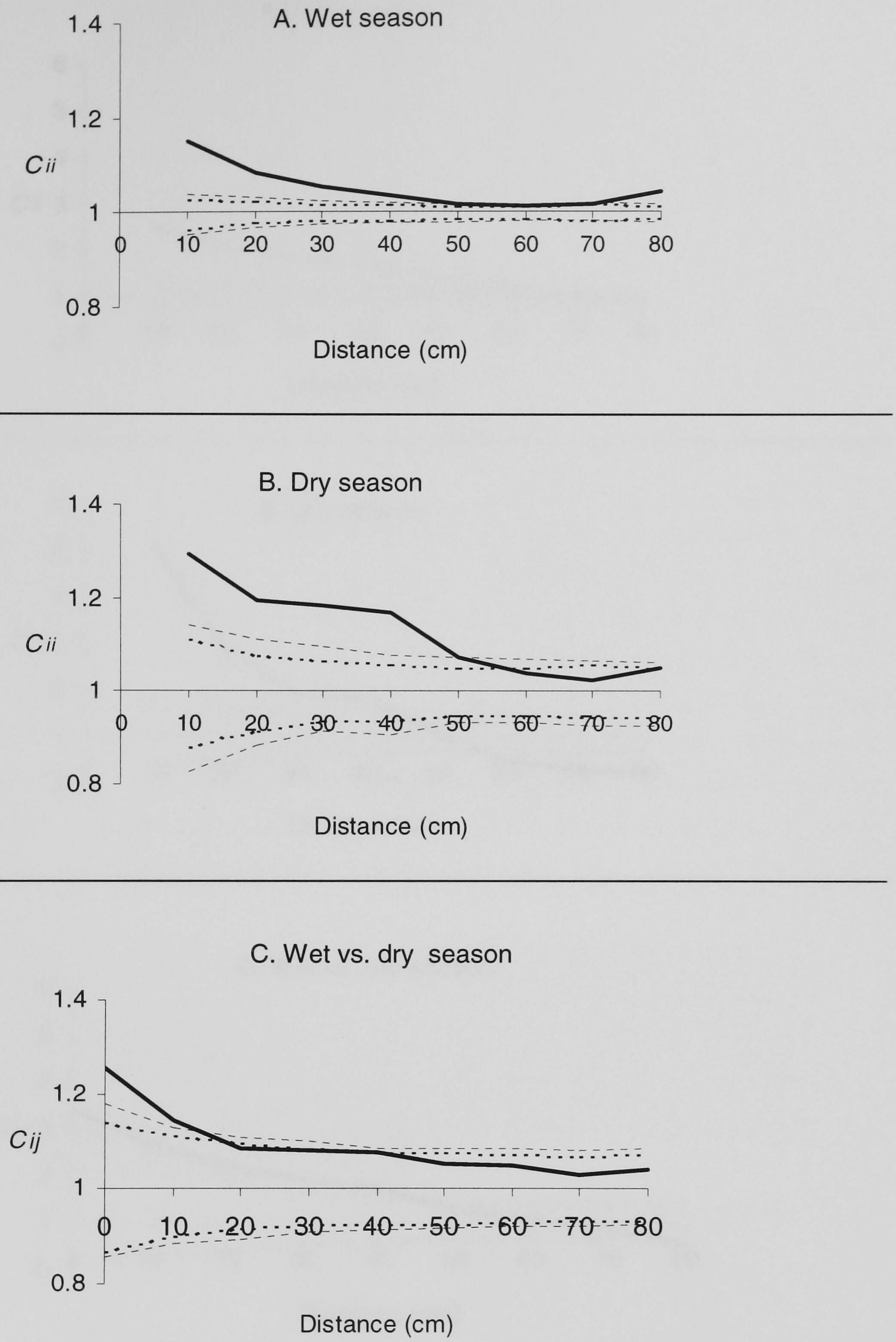


Figure 5.6 Radial covariance functions (continous line) for *R. acetosella* frequency in the Year 3 permanent plot presented in Fig. 5.2. A. Wet season (autocovariance, C_{ii}); B. Dry season (autocovariance, C_{ii}); C. Relation between the spatial distribution in the wet vs. dry season (cross-covariance, C_{ij}). Monte Carlo boundaries for a 95% and 99% confidence are indicated as dashed lines.

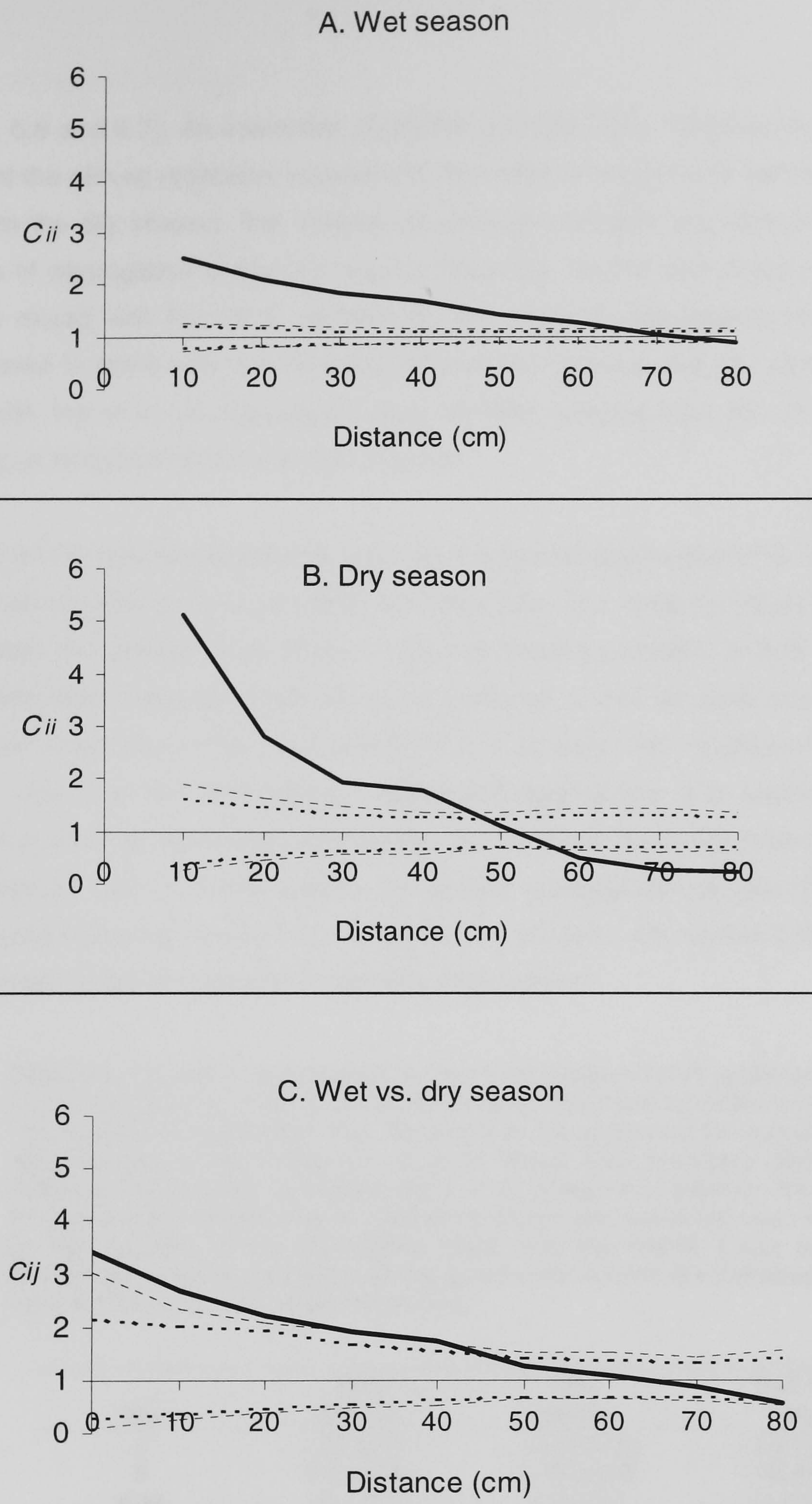


Figure 5.7 Radial covariance functions (continous line) for *R. acetosella* frequency in the Year 8 permanent plot presented in Fig. 5.3. A. Wet season (autocovariance, C_{ii}); B. Dry season (autocovariance, C_{jj}); C. Relation between the spatial distribution in the wet vs. dry season (cross-covariance, C_{ij}). Monte Carlo boundaries for a 95% and 99% confidence are indicated as dashed lines.

Figs. 5.6 and 5.7). An inspection of all the replicate plots indicated that in the year 8, five of the eleven replicates showed this decrease in the scale of aggregation from the wet to the dry season, five showed no change and only one replicate had a larger scale of aggregation in the dry season. However, for the year 3 plots the results are more mixed with five plots maintaining the scale of aggregation, three showing a decrease in scale and four showing an increase between the wet and dry season. In general, the scale of aggregation was variable, ranging from 80 cm (the maximum distance analysed) to a minimum of 20 cm.

I also evaluated the relationship between the spatial distribution of *R. acetosella* in the wet season and dry season within the same plot. The results for the crosscovariance between the spatial distributions in the two seasons showed a loss of aggregation intensity when compared with the autocovariance values for each season (see Table 5.2 and examples in Fig 5.6.C and 5.7.C). In general, the crosscovariance functions were very near the limit between significant aggregation and randomness. Hence, although the high mortality between the two seasons made the spatial distribution of abundance lose to some degree its spatial correspondence (as areas that were occupied in the wet season are not in the dry season), the spatial distributions in the two seasons did not become completely independent.

Table 5.2 Intensity of aggregation at the 10 cm distance for *R. acetosella* in Year 3 and Year 8 plots in the wet and dry season (standard deviation in brackets). The intensity of aggregation was calculated as the quotient of the autocovariance value divided by the corresponding upper Monte Carlo boundary (99%) at that distance. The average crosscovariance value (distance 0) between frequency in the wet and dry season in each permanent plot is also presented (also calculated as the quotient of the covariance value and the Monte Carlo boundary). Differences between successional stages for each season are compared using a non-parametric Kruskal-Wallis (*K-W*) test.

Year	Wet season	Dry season	Wet vs. dry
3	1.13 (0.08)	1.33 (0.18)	1.06 (0.11)
8	1.43 (0.26)	1.76 (0.55)	1.05 (0.08)
K-W	*p*=0.005	*p*=0.003	*p*=0.901

5.3.3 Successional and seasonal changes in inter-specific spatial associations

For the spatial analysis of changes in inter-specific spatial association, only plots where the abundances of the two LS species were high enough for spatial analysis were included (plots with more than 25 occupied cells). The number of cells occupied by the two species in the plots included is indicated in Tables 5.3 and 5.4.

Table 5.3 Change in the spatial crosscovariance ($C_{ij}(0)$, i.e. distance 0) between *R. acetosella* and *E. schultzii* from the wet to the dry season in year 3 and year 8 plots. Asterisks indicate a significant departure in spatial association from randomness at the 95 % (*) and 99 % (**) levels. The number of cells where *E. schultzii* was present (out of the 400 cells in each grid) is indicated.

Year	No. of occupied cells Wet season (*E. schultzii*)	$C_{ij}(0)$ Wet season	$C_{ij}(0)$ Dry season
3	65	0.63	1.03
3	32	0.90	0.67
3	48	1.06	1.55 **
3	36	1.13	1.07
3	34	0.79 *	1.04
3	93	0.72 **	0.92
3	29	0.90	1.14
8	54	0.95	1.42
8	81	1.06	2.03 *
8	117	0.54 **	1.76 **
8	56	0.35 **	1.16
8	94	0.65	1.12
8	59	0.60 *	1.78

In Fig. 5.4 examples of the spatial distribution of *E. schultzii* and *H. laricifolium* in the permanent grids are presented. In early succession, occupied cells contained one or more small sized individuals and only in few occasions the same individual occupied more than 1 cell. However, during late succession, the larger maximum size of individuals meant that the same individual could by recorded as present in a large number of contiguous cells, resulting in large patches of occupied cells (see Fig. 5.4).

During the wet season the most common situation was for *R. acetosella* and *E. schultzii* to be spatially segregated at the minimum displacement distance (the scale of significant segregation was variable, but did not extend beyond 30 cm). In the year

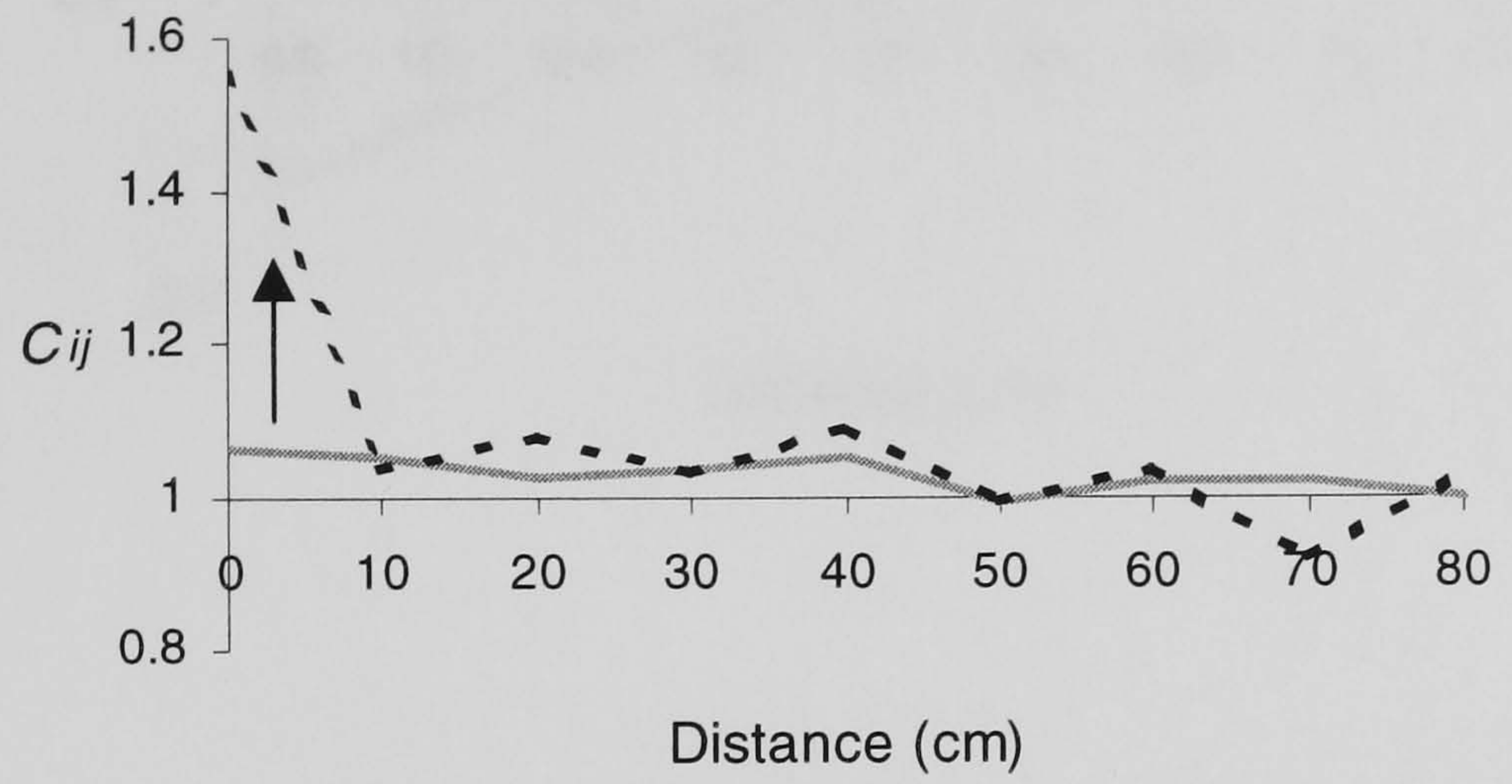
3 plots, five of the seven plots had crosscovariance values below 1 indicating segregation between the two species. However, in only two cases this segregation was significant. In year 8 plots five of the six plots had covariance values below 1, with three significant cases. More importantly, the spatial relation between the two species was altered by the drought towards a more aggregated spatial pattern (see examples in Fig. 5.8). In year 3 plots, the crosscovariance increased between the two seasons in five of the seven plots, while in year 8 plots, all the replicates showed an increase in crosscovariance values towards aggregation (Table 5.3).

The same general trend for an increase in the crosscovariance values between the two seasons was found in the case of the spatial relations between *R. acetosella* and *H. laricifolium*, (see examples in Fig. 5.9). All year 3 plots showed an increase in the crosscovariance function at distance 0 from the wet to the dry season, as did all but one of the year 8 plots included in the analysis. In early succession, the change was from covariance values below 1 (indicating segregation) to values above 1 (indicating aggregation) in all cases but one (although there were only three cases where the spatial patterns were significantly different from random). Curiously, during late succession, while in one plot the change was from significant segregation to significant aggregation in two others it was from significant aggregation to even stronger aggregation (see Table 5.4).

5.3.3 Local density dependence in drought induced mortality

To look at the effect of local density on the mortality probability, I looked first at the change in this probability as a function of the initial target cell frequency. In Fig. 5.10 the relationship between these two variables in one year 3 and one year 8 plot is presented. In the year 3 plot (Fig. 5.10.A) it is clear that the probability of mortality (m_z) was higher for sub-cells that were located in cells of high initial frequency. As indicated in the methods, if mortality was independent of initial cell frequency, it should equal m_g for all initial frequencies. The Pearson's correlation coefficient between the two variables is significantly higher than would be expected from random mortality across the grid. In the year 8 plot (Fig. 5.10.B) it can be seen that there is no clear relationship between initial within cell frequency and mortality probability, with the observed mortality oscillating around m_g.

A. Year 3



B. Year 8

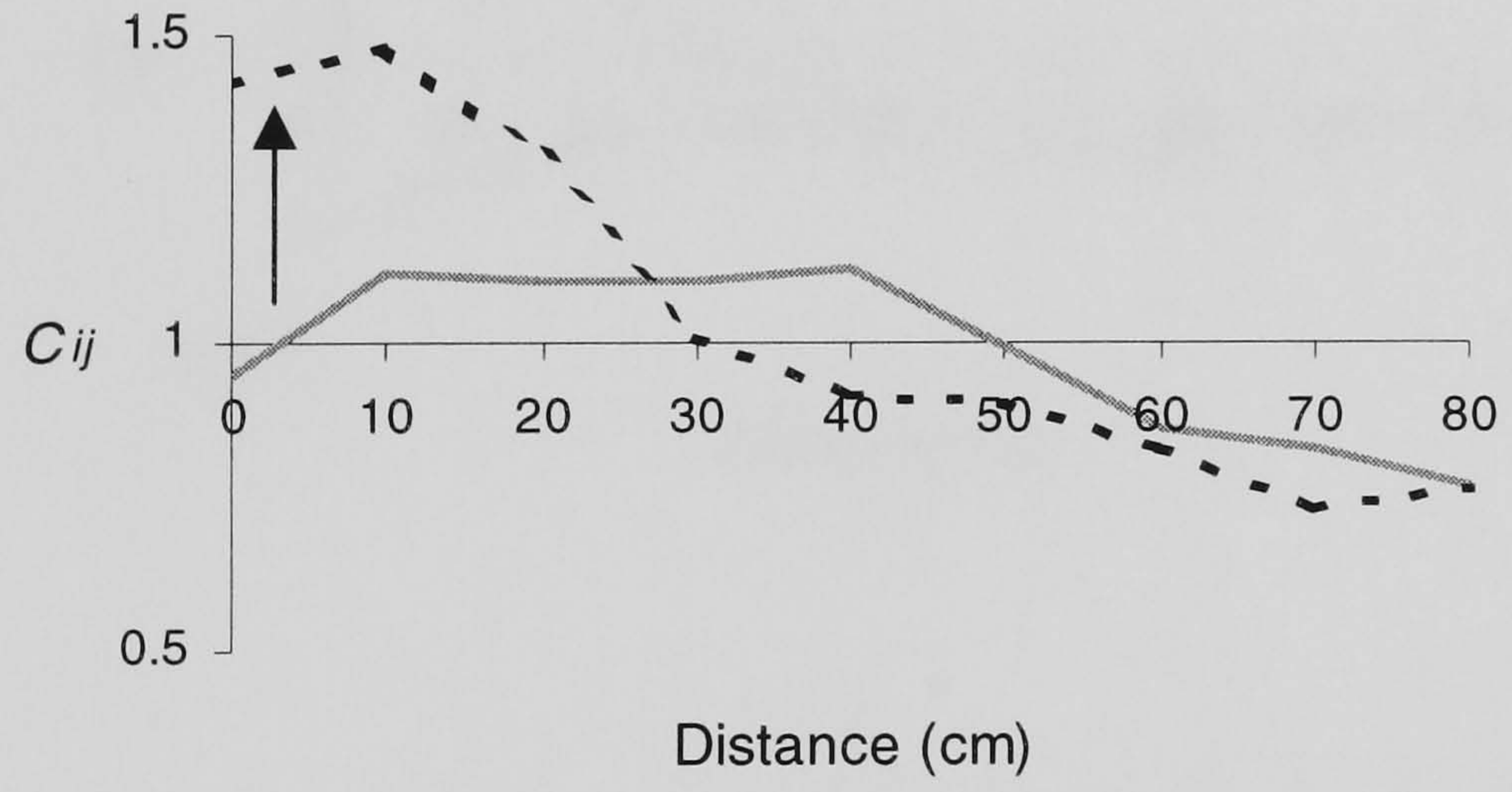


Figure 5.8 Radial crosscovariance functions (C_{ij}) for the spatial interaction between *R. acetosella* and *E. schultzii* in one year 3 (A.) and one year 8 (B.) plot. Wet season: continous line; Dry season: dashed line. The arrow indicates the clear shift of the covariance function at small spatial scale towards stronger spatial association (higher values) between the two species from the wet to the dry season.

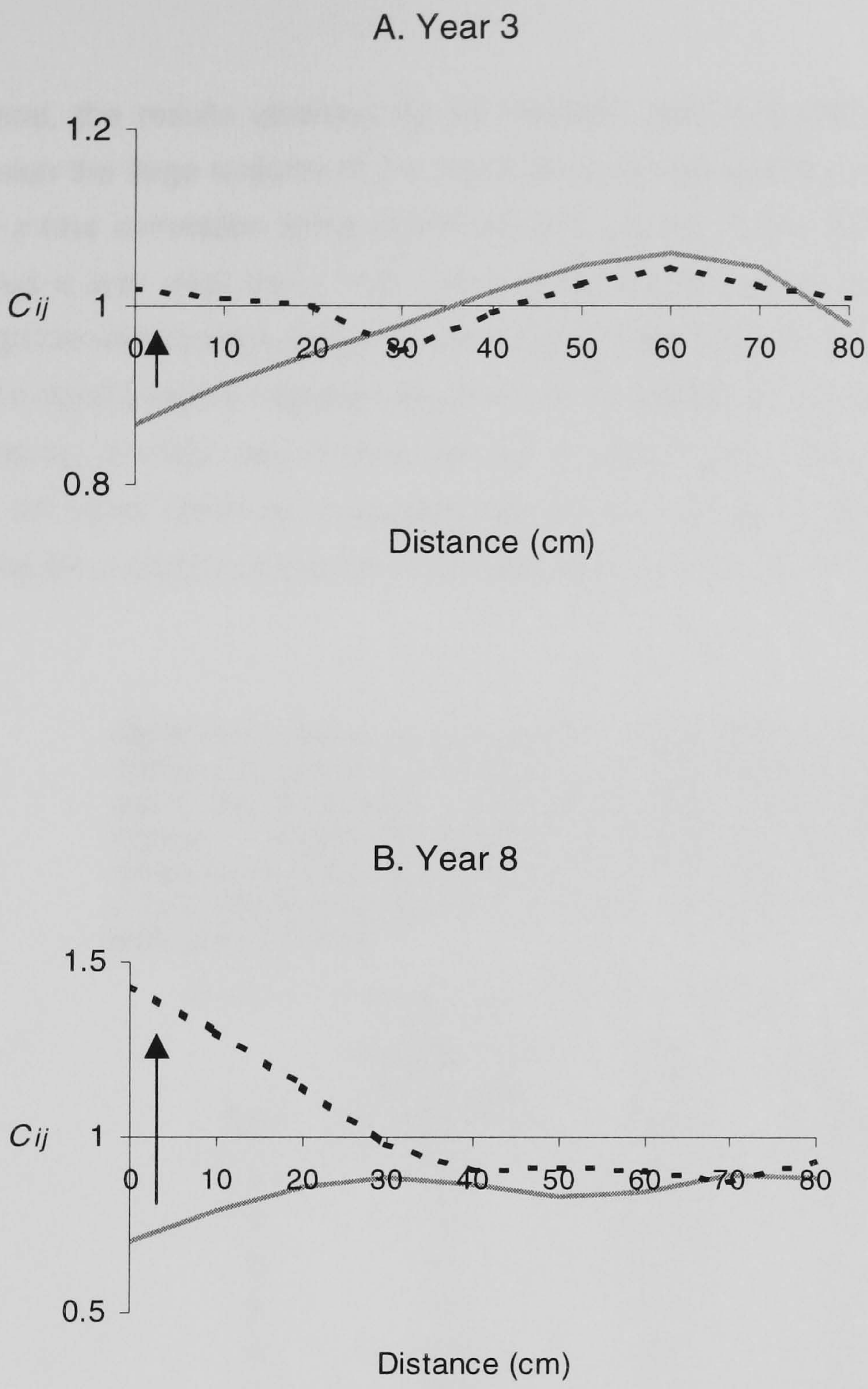


Figure 5.9 Radial crosscovariance functions (C_{ij}) for the spatial interaction between *R. acetosella* and *H. laricifolium* in two year 3 (A.) and year 8 (B.) plots. Wet season: continous line; Dry season: dashed line. The arrow indicates the clear shift of the covariance function at small spatial scales towards stronger spatial association (higher values) between the two species from the wet to the dry season.

In general, the results obtained for all replicate plots indicated that while in early succession the large majority of the replicates had high positive correlations between m_z and z (the correlation being significant in 6 cases), in the late successional plots there was a less clear trend, with only one significant correlation, and both positive and negative relationships being observed (see Table 5.5). Hence, the results suggest that local density had a negative effect on the probability of survival (negative density dependence) in most year 3 plots but not in year 8 plots. As is obvious from Fig. 5.10.A, the initial within-cell frequency had in some cases a large effect in terms of modifying the mortality probability from that observed at the whole plot scale.

Table 5.4 Change in the spatial crosscovariance ($C_{ij}(0)$,i.e. distance 0) between *R. acetosella* and *H. laricifolium* from the wet to the dry season in year 3 and year 8 plots. Asterisks indicate a significant departure in spatial association from randomness at the 95 % (*) and 99 % (**) levels. The number of cells where *H. laricifolium* was present (out of the 400 cells in each grid) is indicated.

Year	**No. of occupied cells Wet season (*H. laricifolium*)**	**$C_{ij}(0)$ Wet season**	**$C_{ij}(0)$ Dry season**
3	127	0.87 *	1.02
3	78	0.78 **	1.20
3	55	0.99	1.12
3	113	0.92	1.21
3	176	0.91	1.52 **
3	35	1.02	1.34
8	56	1.91 *	3.33 **
8	64	0.95	0.87
8	134	1.32 *	1.63 **
8	113	0.70 **	1.43
8	168	0.66 **	1.45 **

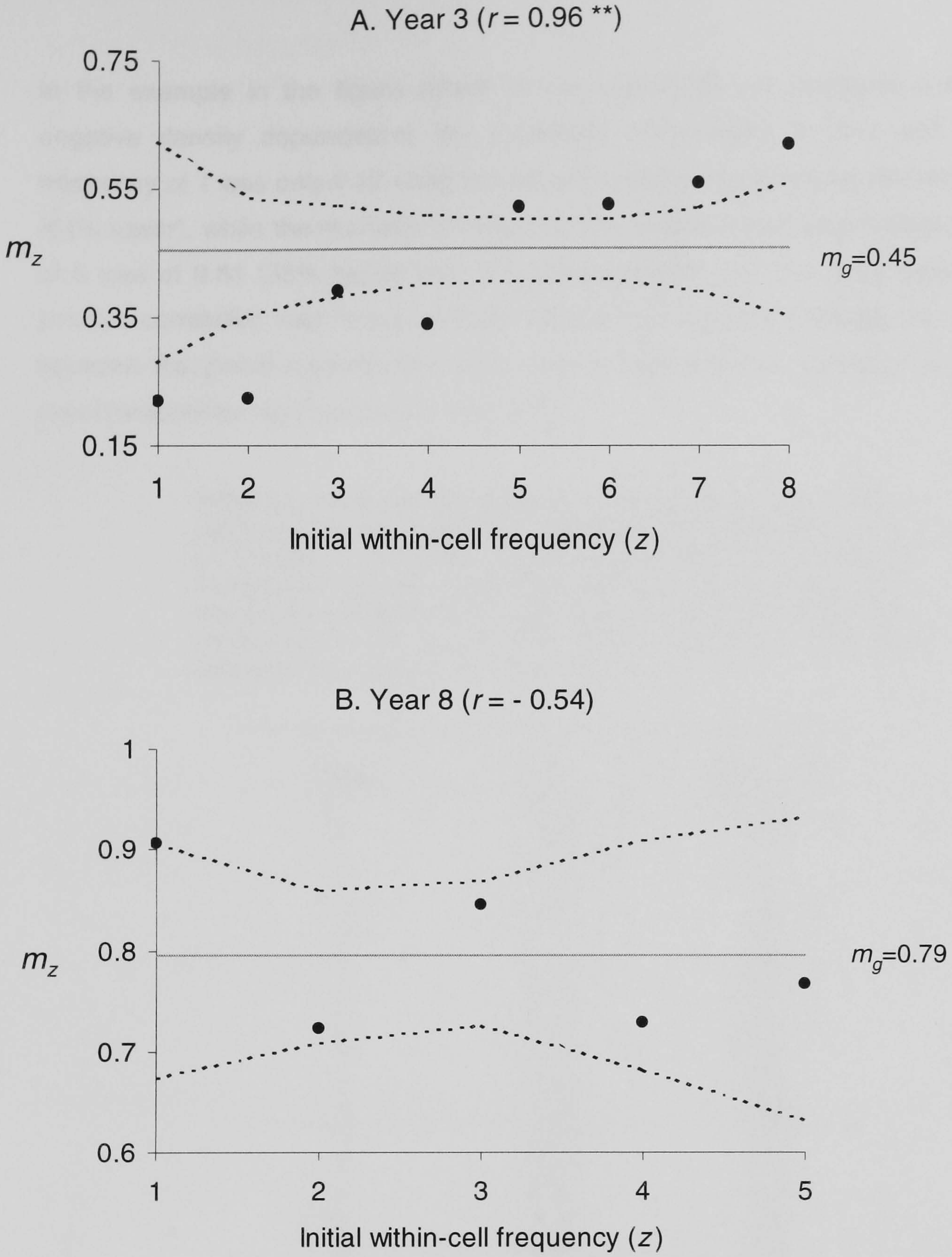


Figure 5.10 Two examples of the relationship between *R. acetosella* initial within cell frequency (*z*) and the observed probability of sub-cell loss, m_z (black circles). The Pearson's correlation coefficient (*r*) between these two variables is indicated (the two asterisks indicate a significant correlation at the 99% level. The continous horizontal line corresponds to the null hypothesis of density independent mortality (i.e. constant mortality equal to the global mortality probability, m_g). The dotted lines represent the 95% confidence intervals for the mortality probabilities for each initial within cell frequency (derived from Monte Carlo simulations). A. Year 3 plot; B. Year 8 plot.

In the example in the figure (which is the case with the strongest evidence for negative density dependence) the probability of mortality in cells with an initial frequency of 1 was only 0.22 while the global mortality across the whole plot was 0.45 (51% lower), while the mortality in cells with the maximum observed initial frequency of 8 was of 0.61 (35% higher than the global mortality). In the other plots where a positive correlation was found between initial frequency and mortality, the difference between the global mortality and that found in cells with the minimum or maximum initial frequencies was between 9 and 16 %.

Table 5.5 Pearson's correlation coefficient between initial within cell frequency and observed probability of sub-cell mortality (m_z) for all year 3 and year 8 plots. Asterisks indicate correlation coefficients that are significantly higher than expected from Monte Carlo simulations of random sub-cell removal at the 95 % (*) and 99 % (**) levels. The global probability of sub-cell mortality (m_g) in each plot is also indicated.

Year	m_g	Pearson's *r*
3	0.72	-0.43
3	0.68	-0.43
3	0.45	0.96 **
3	0.71	0.77
3	0.77	0.69
3	0.71	0.94 *
3	0.79	0.65
3	0.62	0.84 *
3	0.70	0.86 *
3	0.90	0.82 *
3	0.52	0.26
3	0.66	0.89 *
8	0.79	-0.51
8	0.89	0.52
8	0.79	-0.54
8	0.75	-0.41
8	0.91	0.02
8	0.92	0.89
8	0.39	0.88 *
8	0.61	0.53
8	0.45	-0.88
8	0.86	-0.24
8	0.63	0.51

When the analysis of the effects of local density on the probability of mortality is extended from the within cell scale to the local neighbourhood scale, the general trend is for a higher mortality probability in target cells occupying areas of low neighbour density. This is illustrated in Fig. 5.11, in which I present as an example the results from the same year 3 plot shown in Fig. 5.2. It is obvious from Fig. 5.11 that there is a negative (but not significant) correlation between the number of occupied sub-cells in the neighbourhood and the probability of mortality in the target cell, and that this effect is retained as the number of cells included in the neighbourhood is increased (from 4 to 8 and 24 cells).

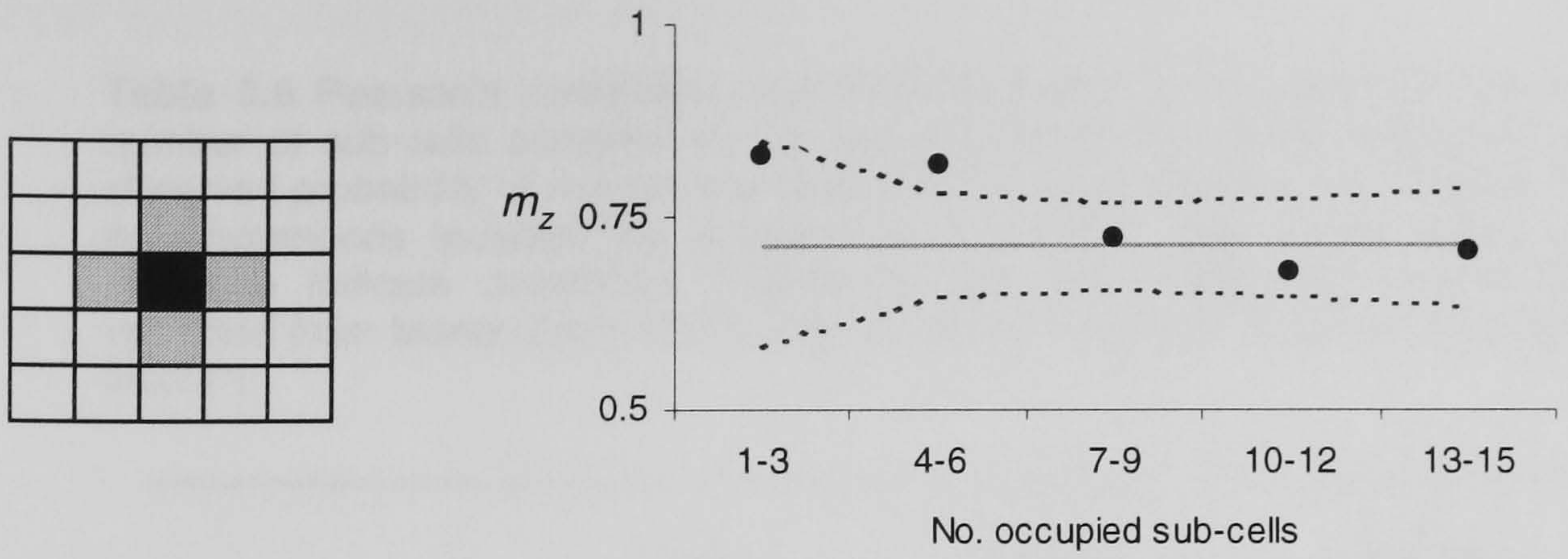
As can be seen in Table 5.6, in a large number of all replicate plots there is a negative correlation at all scales examined. When the correlation is significant it is always negative, with the significance being maintained across all scales. However, there is more variability in the correlation coefficients than in the case of the within cell effects and the number of significant results is much lower. Hence, the data suggests there is a reversal from negative density dependent mortality at the within target cells to a weaker positive density dependence at larger spatial scales, both in early and late successional plots.

The apparent positive relationship between the frequency of cells in the neighbourhood of a target cell and the probability of survival is not necessarily the direct result of neighbourhood crowding (as there are alternative explanations such as environmental heterogeneity being related with a higher probability of mortality in relatively isolated occupied cells). In the case of the neighbourhood effects, there appear to be no clear differences between year 3 and year 8 plots.

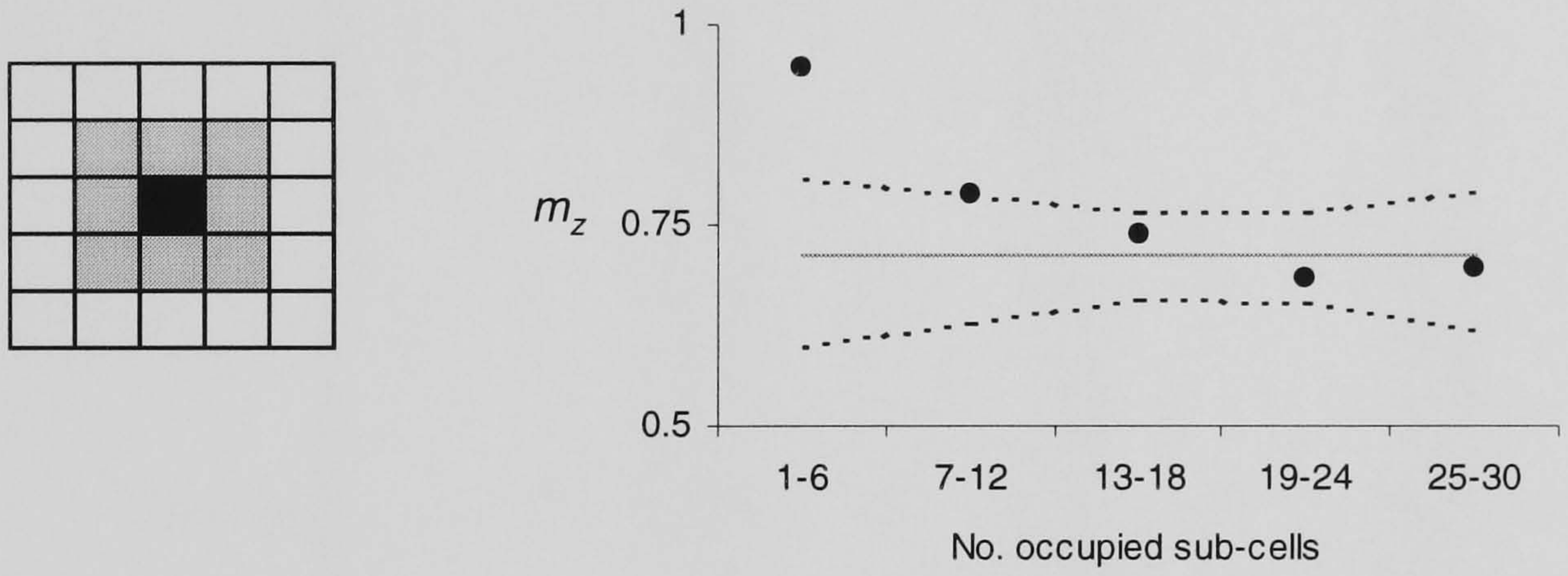
5.3.4 Effect of local inter-specific interactions on drought induced mortality

The probability of sub-cell loss between the wet and dry season generally increased from a minimum in cells in which *R. acetosella* coexisted both with *H. laricifolium* or *E. schultzii* to the cells that were in the 20-30 cm band away from the nearest individual (see Figs. 5.12 and 5.13). The evidence for this trend was more clear in year 8 plots than in year 3 plots, where the results were more mixed.

A. 4 cells neighbourhood (r = - 0.89)



B. 8 cells neighbourhood (r = - 0.90)



C. 24 cells neighbourhood (r = - 0.65)

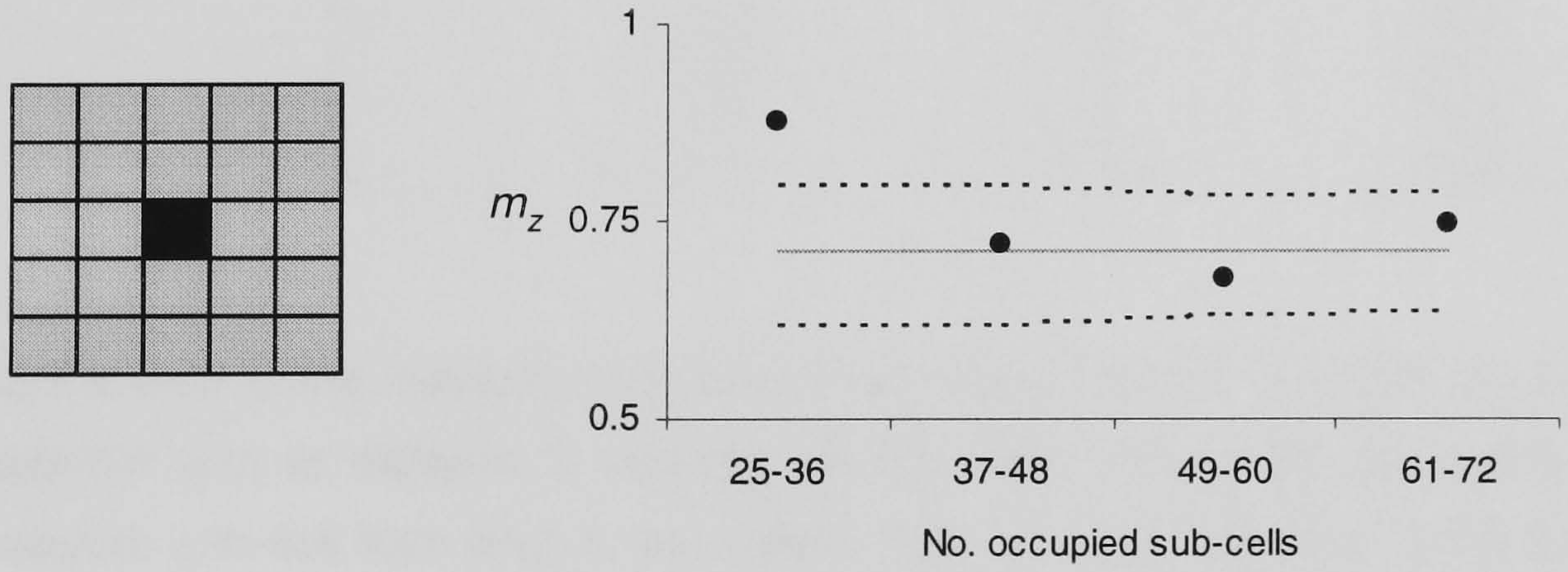


Figure 5.11 Relationship between the number of occupied sub-cells of *R. acetosella* in the neighbourhood of a target cell and the observed probability of sub-cell loss, m_z (black circles). Data corresponds to the year 3 plot shown in Fig. 5.2. The Pearson's correlation coefficient (r) between these two variables is indicated. The continous horizontal line corresponds to the null hypothesis of density independent mortality (i.e. constant mortality equal to the global mortality probability, m_g=0.71). The dotted lines represent the 95% confidence intervals for the mortality probabilities (Monte Carlo simulations). The diagram next to each figure indicates the neighbourhood cells (grey squares) around the target cell (black square) included in each case: A. 4 cells; B. 8 cells; C. 24 cells.

Table 5.6 Pearson's correlation coefficient between, *z*, the class for the total number of sub-cells occupied in the neighbourhood of a target cell (*g*(*x*)) and observed probability of sub-cell mortality (m_z) for all year 3 and year 8 plots. The neighbourhoods included the adjacent 4, 8 and 24 cells to the target cell. Asterisks indicate correlation coefficients that are significantly higher than expected from Monte Carlo simulations of random sub-cell removal at the 95 % level (*).

Year	4 cells neighbourhood (Pearson's *r*)	8 cells neighbourhood (Pearson's *r*)	24 cells neighbourhood (Pearson's *r*)
3	-0.31	-0.75	-0.76
3	-0.65	-0.67	0.64
3	0.55	0.70	0.61
3	-0.89	-0.90	-0.65
3	-0.82	-0.85	-0.71
3	-0.58	0.93	-0.01
3	0.11	-0.29	-0.04
3	-0.56	-0.82	-0.32
3	-0.18	-0.35	0.28
3	0.51	-0.30	0.40
3	-0.89 *	-0.97 *	-0.91 *
3	0.35	0.43	-0.75
8	-0.95 *	-0.98 *	-0.97 *
8	-0.78	-0.99 *	-0.97 *
8	-0.39	-0.69	-0.42
8	-0.93	-0.89	-0.12
8	0.78	0.00	0.26
8	-0.01	-0.15	0.11
8	0.09	-0.04	-0.19
8	-0.69	-0.23	-0.69
8	-0.95 *	-0.98 *	-0.91 *
8	0.42	0.85	0.95
8	0.13	-0.76	-0.63

In the case of the interaction between *R. acetosella* and *E. schultzii*, the probability of sub-cell loss at distance 0 was significantly lower than expected under completely random sub-cell loss only in two cases, both for early and late successional plots. However, while in year 3 plots three of the six replicates showed m_z to be clearly lower at distance 0 than in the two other distance bands, in the year 8 plots all 6 replicates showed the lowest m_z at distance 0. In all year 8 cases, m_z at distance 0 was lower than the global plot mortality. While in year 3 plots the results were more mixed for the other two distance classess, in year 8 plots there was a consistent trend for m_z to increase with distance and in all plots but one. In the 10-20 cm band m_z was lower than m_g (being significantly lower than expected by chance in 1 case) while in the 20-30 cm bands it was higher (being significantly higher in two cases).

In the case of the interaction between *R. acetosella* and *H. laricifolium*, the evidence for a significant decrease of sub-cell loss in cells where the two species coexisted was more clear, with three of the six replicates showing m_z to be significantly lower than expected for random mortality in year 3 plots and four of the five replicates showing significant effects (at the 99% confidence level) in year 8 plots. Again, the majority of plots presented a clear trend for m_z to increase with the distance to the nearest *H. laricifolium* neighbour. In all but one year 3 plot and all year 8 plots m_z was higher than m_g in the 20-30 cm band, while m_z in the 10-20 cm band varied between being slightly lower and slightly higher than the global mortality probability (see Fig. 5.13).

Interestingly, both in the case of the results for the interactions with *E. schultzii* and *H. laricifolium*, differences between m_z and m_g for all distance classess were higher in the late successional plots (see Figs. 5.12 and 5.13). This meant that in year 8 plots, sub-cells occupied by *R. acetosella* had as much as 19% less chance of being lost between the wet and dry season when in cells occupied by *E. schultzii* and 30 % less chance in cells occupied by *H. laricifolium*. In general, these results suggest that both *E. schultzii* and *H. laricifolium* have an local positive effect on the survival of *R. acetosella* between the wet and dry season in late successional plots and that this effect decays over relatively short distances.

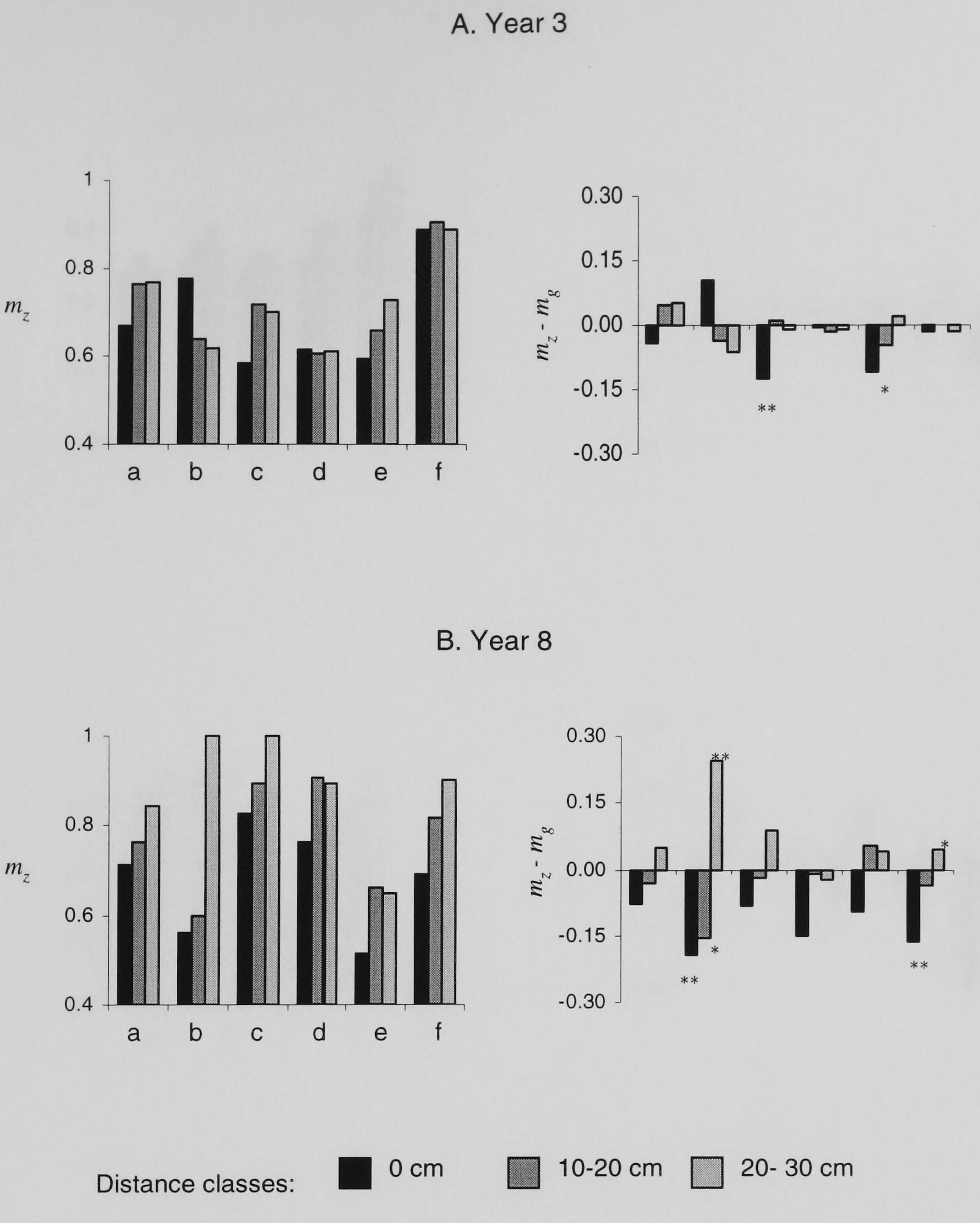


Figure 5.12 Observed probability of sub-cell loss between the wet and dry season (m_z) of *R. acetosella* in cells with different distances to the nearest cell where *E. schultzii* was present (left side charts). Each group of three columns corresponds to a different replicate plot (indicated by a different letter). The difference between the observed probability of sub-cell loss in each distance class and the global probability of sub-cell mortality (m_z- m_g) is also presented (right side charts). Asterisks indicate the cases in which the observed mortality for a given distance class was significantly lower (bars pointing downwards) or higher (bars pointing upwards) than expected from random sub-cell loss (Monte Carlo boundaries **: 99%, * 95%). A: year 3; B: year 8.

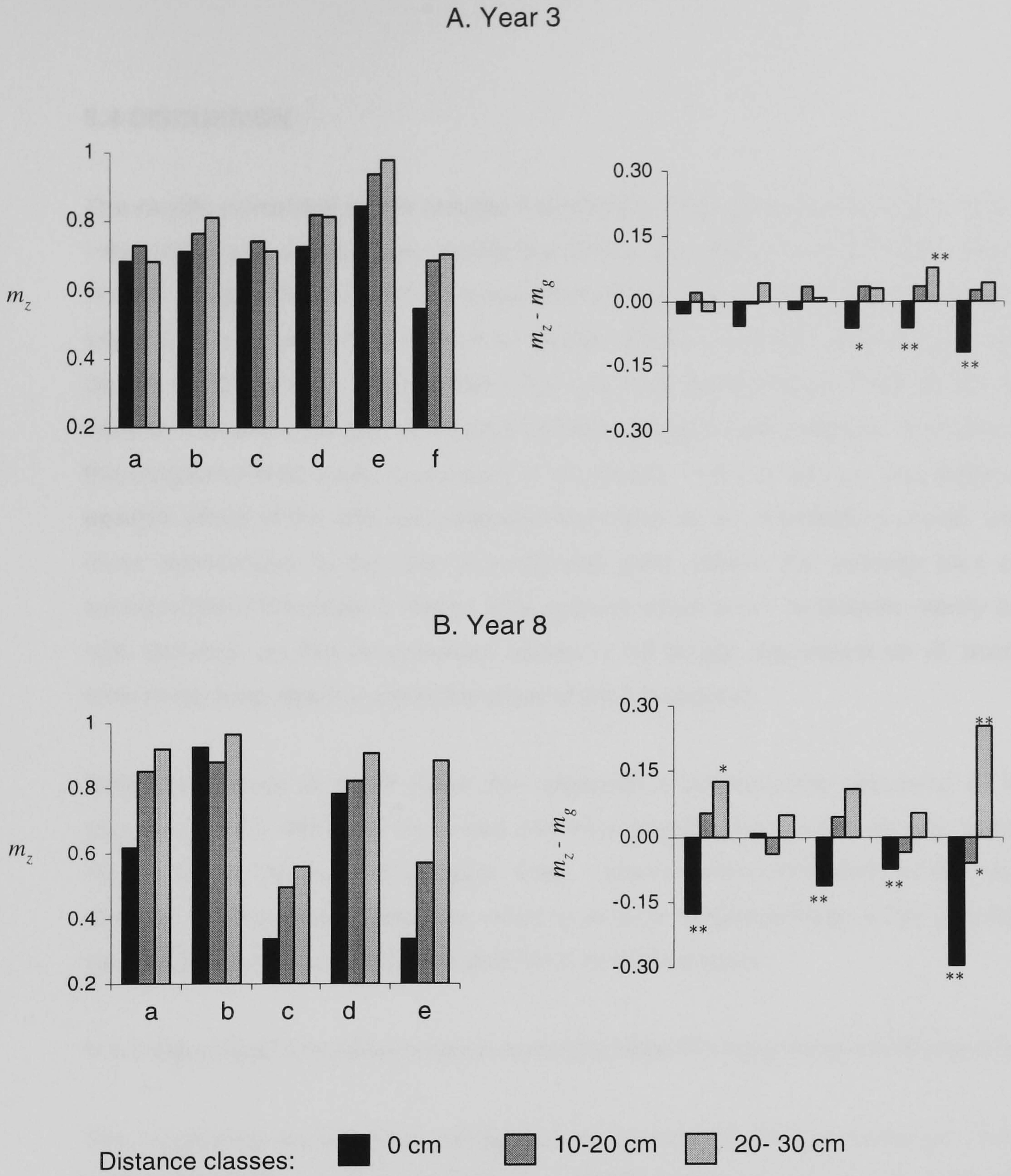


Figure 5.13 Observed probability of sub-cell loss between the wet and dry season (m_z) of *R. acetosella* in cells with different distance to the nearest cell where *H. laricifolium* was present (left side charts). Each group of three columns corresponds to a different replicate plot (indicated by a different letter). The difference between the observed probability of sub-cell loss in each distance class and the global probability of sub-cell mortality (m_z- m_g) is also presented (right side charts). Asterisks indicate the cases in which the observed mortality for a given distance class was significantly lower (bars pointing downwards) or higher (bars pointing upwards) than expected from random sub-cell loss (Monte Carlo boundaries **: 99%, * 95%). A: year 3; B: year 8.

5.4 DISCUSSION

The results presented in this chapter indicate that local intra-specific and inter-specific interactions can substantially modify the wet to dry season probability of mortality of *Rumex acetosella*. In addition, these interactions can produce clear changes in its intra-specific spatial structure and its spatial relations with the dominant LS species. Moreover, the results suggest that local negative density dependence is stronger in early successional stages, and that it surprisingly shifts from negative to positive when the neighbourhood scale considered is increased. There is also an unexpected local positive effect of the late successional dominants on *R. acetosella* survival, which is more pronounced in the late successional plots, where the average size of late successional individuals is larger. This positive effect on *R. acetosella* rapidly decays with distance, so that its operation seems to be largely dependent on *R. acetosella* individuals lying directly under the cover of the LS species.

Below, I discuss in more detail the relationship between the dynamics of spatial pattern and the effects of local intra and inter-specific interactions on the mortality of *R. acetosella*. used in this chapter. Then, I discuss some limitations of the research strategy, explore the implications of the results for understanding of the successional decline of this forb, and suggest directions for further work.

5.4.1 Dynamics of spatial pattern and intra-specific neighbourhood interactions

The vegetative reproductive strategy of *R. acetosella*, forming buds on horizontal roots extending up to 1 m (Grime *et al.* 1988), is likely to be an important factor in explaining its strong spatial aggregation in all the plots studied (with average aggregation scales that ranged from 20 to more than 80 cm). Putwain *et al.* (1968) showed that in early-successional grassland communities in Wales, *R. acetosella* relied almost exclusively on vegetative reproduction as very few seedlings became established under the closed sward (the importance of regeneration from seeds would have to be explored in the more open vegetation of fallow areas in the páramo). Clonally reproducing herbs generally form aggregated patterns, and so, in herbaceous communities, random or regular patterns are rare (Silvertown and Lovett Doust 1993; Herben *et al.* 2001)..

At a local scale, below the 10x10 cm occupied by a single cell, crowding seems to increase the probability of mortality, with this effect being stronger in early successional plots. In the year 3 plots, the number of cells with high initial within-cell frequencies was higher (see examples in Fig. 5.2 and 5.3), and so, there was more scope for local crowding to modify mortality. The negative density dependent mortality found at the within-cell scale would be expected to produce a decrease in the intensity of spatial aggregation between the wet and dry season (see discussion in Chapter 4). However, the opposite trend was observed with a more distinct patchiness in the distribution of *R. acetosella* in the dry season. This change in spatial pattern must be the result of a higher mortality probability in areas of low frequency. This is probably explained by the lower mortality found in cells with neighbourhoods of high *R. acetosella* abundance: in cells in low-density regions of the grid, individuals seem less likely to survive the drought. The fact that this effect was generally maintained across different neighbourhood distances, suggests that it is not the result of direct plant-plant interactions, but probably of heterogeneity in soil conditions, such as water availability across the plot.

Hutchings (1997) pointed out that when abiotic mortality factors are important, mortality can be higher in low density areas, because most plant deaths are expected to occur at the edge of the population distribution, where conditions are least favourable. For this same reason, Fowler (1988) suggested caution in inferring the operation of direct negative conspecific interactions from correlations between performance and abundance in heterogeneous environments (see also Rees *et al.* 1996). In fact, both the factors producing negative density dependence of *R. acetosella* mortality at the within-cell scale and apparent positive density dependence at larger spatial scales simultaneously affect the probability of mortality in any given cell. This can generate some problems of interpretation of the results. For example, given that *R. acetosella* was spatially aggregated and that higher within-cell frequencies were generally associated with higher mortalities, even if there had been no neighbourhood scale effects, cells in dense areas of the grid would have been expected to show a lower survival rate. This suggests that the weak positive density dependence at the neighbourhood scale identified in the data could be stronger than indicated by the analysis used. This is also suggested by the fact that the intensity of aggregation increased from the wet to the dry season, so that the neighbourhood scale effects had a more pronounced impact on the resulting dynamics of the spatial pattern than the within-cell effects.

A strategy to account for the interaction between within-cell and neighbourhood scale effects on mortality could be to use a logistic regression approach, with the probability of sub-cell mortality being a function of within-cell frequency in the wet season, the abundance of *R. acetosella* in neighbouring cells, and an equation term accounting for their interaction. Because spatial autocorrelation in the abundance of *R. acetosella* violates the assumption of independence of logistic regression, a more sophisticated auto-logistic model, incorporating autocorrelation effects should be used (see Augustin *et al.* 2001).

The observed change in the direction of density dependence from negative to positive as the spatial scale is increased emphasize the importance of examining different neighbourhood scales when studying intra-specific competition (see also Condit *et al.* 1994). For herbaceous species, the operation of local negative density dependent mortality is well documented (e.g. Watkinson *et al.* 1983; Mithen *et al.* 1984; Silander and Pacala 1985). However, positive effects of neighbourhood density on survival have also been reported, for example in Rees *et al.* (1996) permanent plot studies of sand-dune annuals. In this case, to explain these positive effects, they considered Allee effects as a possible alternative to environmental heterogeneity.

It is tempting to consider intra-specific competition for water as the most likely underlying mechanism for the negative density dependent mortality observed at the within-cell scale. However, alternative explanations such as density dependent pathogen or herbivory effects (Law *et al.* 2000) cannot be ruled out without further experimental and/or ecophysiological evidence. Interestingly, in a sheep grazed sward sown at different densities, Putwain *et al.* (1968) found evidence of negative density dependent mortality of *R. acetosella* shoots and of a plastic reduction in vegetative reproduction at high densities.

The examples presented in Fig. 5.2 and 5.3 of the changes in the spatial distribution of *R. acetosella* from the wet to the dry season suggest that the spatial dynamics can be characterized as a contraction of the area occupied, without a large shift in the location of the areas of high abundance. This interpretation is consistent with the fact that the intensity of spatial aggregation between the distribution of *R. acetosella* in the wet and dry seasons was significant in most cases (see Table 5.2 and Fig. 5.6 and 5.7). The fact that this pattern is maintained both for year 3 and year 8 plots suggests that during succession *R. acetosella* undergoes seasonal cycles of contraction (as a result of dry season mortality) and expansion (probably as a result of vegetative colonization and re-sprouting) of its spatial distribution, while it progressively declines in abundance.

The spatial aggregation between *R. acetosella* and the LS species only in the dry season, suggest that large individuals of *E. schultzii* and *H. laricifolium* could act as refuge nucleus to which *R. acetosella* 'retreats' during unfavourable periods. To test this, it would be necessary to have a longer-term record of the dynamics in permanent plots. In this way, it would be possible to evaluate if the spatial association of the distribution of *R. acetosella* between consecutive years is maintained, and if the spatial relations with the LS species are consistent over longer time scales.

The hypothesis of consistent refugial patches suggested here is the opposite of the 'drifting clouds of abundance' hypothesis proposed by Grubb (1986) on the basis of results from permanent transects in chalk grasslands (i.e. the idea that the refugial patches move around the community from year to year). If supported by further evidence, the idea of constant refugial patches would also shed some doubt on the applicability to páramo succession of the carrousel model of van der Maarel and Sykes (1993), which suggests that species move around the community in a 'random carousel'.

5.4.2 Dynamics of spatial pattern and inter-specific neighbourhood interactions

Perhaps the most interesting and unexpected result in this chapter is the increase in spatial aggregation between *R. acetosella* and the dominant LS species from the wet to the dry season. The increase in spatial aggregation is strongly consistent with the lower probability of mortality of this forb in the neighbourhood of individuals of both *E. schultzii* and *H. laricifolium*. This contradicts our original expectation of a competitive effect of the dominant late species increasing the wet-to-dry season mortality of *R. acetosella*, and hence, contributing to explain its decline in abundance during the fallow.

As can be seen in Fig. 5.12 and 5.13, the reduction in the probability of mortality was more pronounced in cells in which *R. acetosella* co-occurred with the late successional individuals (distance 0). In cells in the immediate neighbourhood (10-20 cm distance) the observed mortalities were closer to the global mortality across the plots, m_g, while in most cases it was higher than average in cells 20 to 30 cm away from the nearest late successional individual. This indicates that the positive effect of the LS species on *R. acetosella* mortality decayed at relatively short distances and was associated with the canopy of the shrub and the giant-rosette lying directly above the shoots of the forb.

The canopy of the late successional dominants could provide a refuge for *R. acetosella* from a series of potentially detrimental factors. Some of the possible mechanisms that could explain this positive effect are:

(1) Protection from the high radiation levels characteristic of the dry season in this mountain environments (see Chapter 2), which can increase leaf temperatures and evapotranspiration and produce UV-B induced damage to leaves. There is evidence that suggests that the presence of thick xeromorphic leaves and pubescence in shrubs and giant rosettes in the páramo can offer protection from both of these factors (Meinzer and Goldstein 1984; Beck 1994; Cross 2001; Ramsay 2001). This protection is less likely to be available in the case of the thin mesomorphic leaves of *R. acetosella* (see Chapter 2).

(2) A reduction in the frequency of frosts in the dry season, which could have less effect on *R. acetosella* individuals directly under the canopy of the LS species.

(3) A higher local soil water availability during the dry season, as the soil directly under the canopy of the LS species could retain more moisture as a result of lower evaporation. The fact that the roots of *R. acetosella* run parallel to the surface (with a maximum depth of about 7 cm, Sierra and Mora-Osejo 1994) while those of páramo shrubs and rosettes penetrate deeper into the soil (up to 30 cm in the case of *E. schultzii*, Smith 1981) suggest that *R. acetosella* could to some extent avoid water competition with the LS species. Perez (1992) showed that water content at field

capacity was significantly higher in soil samples adjacent to giant rosette plants in mature areas in the Venezuelan superpáramo.

(4) Protection from cattle and sheep grazing, which is common in the fallow plots. While in the páramo *R. acetosella* is commonly consumed by cattle, *H. laricifolium* is not and *E. schultzii* has very low palatability (Molinillo and Monasterio 1997).

(5) Competition with other species, which could be lower in the neighbourhood of the LS species (for a discussion of this kind of indirect effects, see Stone and Roberts 1991). Smith (1984) showed that the cover of other herbaceous mature páramo species, mainly tussock grasses, was significantly lower in quadrats placed directly at the base of *E. schultzii* adults than in quadrates 1 m away.

All of the factors suggested above could potentially contribute to a lower probability of mortality of *R. acetosella* under the canopy of the LS species. However, further ecophysiological and experimental evidence is required before it is possible to determine their relative importance. For example, Fonteyn and Mahall (1978) measured xylem water potentials in plants in which conspecific and heterospecifics neighbours were experimentally removed to evaluate if water was the resource for which plants were competing. This kind of removal experiment could provide more direct evidence of a causal link between the dynamics of *R. acetosella* and the presence of the LS species. The analysis of changes in mortality probability at different neighbourhood scales does not rule out the alternative that both the LS species and *R. acetosella* have high abundances in the dry season in favourable areas of the plot, without any direct interaction being responsible for their spatial association.

Facilitation of the colonization of LS by ES species has long been considered an important mechanism for successional change (Clements 1936; Connell and Slatyer 1977), particularly during primary succession (see del Moral and Wood 1993; Chapin *et al.* 1994). However, the possibility of positive effects of the late species on the long-term persistence of ES species has rarely been considered. In fact, positive plant-plant interactions have received relatively little attention in plant ecology (Aarsen and Epp 1990; Stone and Roberts 1991; Callaway 1995).

The classic example of a positive effect is that of 'nurse-plants' in arid environments. For example, Franco Pizana *et al.* (1996) showed how the seedlings of some desert plants could only establish under the shade of shrubs because of the protection provided from direct solar radiation. Another example usually cited is the effect of some shrub species in reducing herbivory on other species established under their canopies (e.g. Hjalten *et al.* 1993). In the case of high elevation communities in the high Andes of Argentina, Nunez *et al.* (1999) found that positive associations between several species in the community and flat cushion plants are the result of nurse plant effects, since the cushions strongly modify micro-environmental conditions.

The fact that the mortality reduction effect was much more clear in the late successional plots, in which the average size of the shrubs and rosettes is larger, suggests that the development of this size asymmetry could be an important modulating factor. A few studies have demonstrated that the direction and intensity of inter-specific competition can shift as a result of changes in the size relations between early and LS species (e.g. Peterson and Bazzaz 1979; Rejmanek and Leps 1996). However, there has been less emphasis in the increase in the strength of *positive* interactions as a result of the development of size asymmetries.

Another important aspect to consider is that *R. acetosella* and the LS species were in many cases spatially segregated during the wet season (particularly *E. schultzii* and *R. acetosella* in the late successional plots, see also Chapter 4). This suggests that there could be a shift from a positive to a negative interaction between the dry and wet season. The reasons for this shift are unclear, but it could be due to facilitation outweighing competitive effects only during the dry season: the net effect of one plant on another is the result of the balance between positive and negative interactions (see Berkowitz *et al.* 1995). Holmgren *et al.* (1997) cite several examples from relatively dry environments in which temporal and spatial variations in water availability can produce a shift from net facilitation to competition. However, the spatial segregation observed between *R. acetosella* and *E. schultzii,* could be related with the fact that the cells lying at the centre of a large *E. schultzii* individual could not be simultaneously occupied by *R. acetosella* (because of the compact structure of the rosettes).

5.4.3 Caveats

It is important to consider some of the limitations of the approach used in this chapter to examine plant-plant interactions. First, both conspecific and heterospecific effects are likely to simultaneously influence the probability of mortality of *R. acetosella* from the wet to the dry season. However, for the sake of simplicity, these effects were analysed separately. As mentioned above, the use of an auto-logistic model in which these interaction effects are explicitly analysed could help to explore this issue.

Another difficulty derives from the large differences in size between *R. acetosella* and the adults of the LS species. Hence, when dividing the sampling space into discrete cells, a compromise had to be considered between making the cells sufficiently small for intra-specific interactions between *R. acetosella* individuals to be detected, and making the total sampling area of the grid (1 x 4 m) sufficiently large to include several individuals of *E. schultzii* and *H. laricifolium*. Even so, the relatively small grid size used resulted in low numbers of individuals of the LS species being present in some cases. On the other hand, the relatively large cell size used meant that it was not feasible to base the analysis of population dynamics of *R. acetosella* on direct shoot counts (the cells contained too many individuals in some cases). An alternative method that could be explored is the use of sampling annuli of different radius established around the base of randomly chosen plants of the LS species. The abundance and performance of *R. acetosella* in these areas could then be compared with sampling units placed at random or at some specified distance away from the late successional individuals (e.g. see Smith 1981; Mahdi and Law 1987; Prudden 2002).

5.4.4 The successional decline of *R. acetosella*: what have we learned and where de we go from here?

As mentioned before, *R. acetosella* progressively declines in abundance thought the fallow, although it continous to be present in very low abundances in late successional fields and in the mature páramo (complete exclusion of ES species from old-fields is generally rare, Bazzaz 1990). Self-inhibition (negative conspecific effects) and inter-specific competition with LS species have been considered as the two most important mechanisms leading to the decrease in abundance of ruderal species (Connell and

Slatyer 1977; Grime 1979; Peet and Christensen 1980; Pickett 1982; Finegan 1984; Pickett *et al.* 1987; Tilman 1990).

In the context of forest succession, colonizing trees usually undergo self-thinning (He and Duncan 2000) and authors like Freilich and Reich (1995) have shown that in some cases ES species are unable to replace themselves as a result of self-shading. In the case of herbaceous species, intra-specific interactions have rarely been considered a direct mechanism for successional change (Bazzaz 1990). An exception is the cases in which autotoxicity (i.e. the liberation of self-inhibiting toxins) has been found to negatively affect re-colonization (e.g. Keever 1950; Abdul-Wahab 1967; Wilson and Rice 1968; McNaughton 1968). On the other hand, intra-specific resource competition with LS species has commonly been found to be important in the decline of early successional herbs and grassess in experimental studies in old-fields (see reviews by Bazzaz 1990 and Tilman 1990).

The results presented here indicate that negative density dependence at a local scale (within-cells), could be a contributing factor in the decline of *R. acetosella* abundance during the fallow. In general, there was a reduction from the wet to the dry season of the maximum within-cell frequencies observed, and this effect was stronger in the early successional stages (see Table 5.5 and examples in Fig 5.2 and 5.3). Furthermore, positive local interactions with the LS species seem to play an important role in modifying *R. acetosella* wet to dry season mortalities. This could contribute to explain the continuing presence of this introduced forb in the late successional stages and the mature ecosystem (more than its decline in abundance during the fallow, as I originally expected!). However, It is important to consider that *R. acetosella* showed similar abundances and average mortalities in replicate plots where the LS species were not present, and so, other factors must be important in explaining its presence during late seral stages.

In order to establish the importance of local intra- and inter-specific interactions in the long-term dynamics of *R. acetosella* during the fallow, it seems essential to extend the analysis in the permanent plots to (at least) a whole year cycle, including the transition dynamics *from the dry to the wet* season. This would allow us to establish how local spatial interactions influence the expansion of *R. acetosella* from its 'dry season refuges' as conditions become more favourable.

Moreover, as emphasized by Rees *et al.* (1996), to determine how local spatial interactions influence population dynamics, it is important to develop empirically parameterised spatial models. Several strategies have been used to model population and community dynamics from a spatially explicit perspective, including reaction-diffusion, discrete cellular automata and moment dynamics models (see reviews by Czaran and Bartha 1992; Tilman *et al.* 1997; Law and Dieckmann 2000). Because of the spatially discrete nature of permanent plot observations, the most directly applicable technique in this case could be the use of cellular automata models (CAMs).

CAMs are a class of discrete models in which the change in state in a particular cell depends on its current state and the state of cells in the immediate neighbourhood. These kinds of models have become increasingly popular in plant ecology to analyse problems such as the importance of spatial structure for species coexistence (e.g. Crawley and May 1987; Herben 1992). However, the neighbour dependent transition rules have rarely been based on direct empirical observations (but see Silvertown *et al.* 1992). The results presented here provide quantitative estimates of the effects of local intra-specific and inter-specific interactions on the wet to dry season probabilities of mortality of *R. acetosella*. Complementing this data, with observations on the dry to wet season dynamics, this information could be used to derive transition rules for a CAM, to explore how local spatial structure and neighbourhood interactions influence the long-term successional dynamics of this introduced forb.

5.4.5. Conclusions

As indicated in the introduction, there have been very few studies on the small-scale spatio-temporal dynamics of successional communities. The results presented in this chapter illustrate the potential of combining a chronosequence approach using extensive replication with the analysis of small-scale spatial dynamics in permanent plots. Using this approach I have shown that the probability of survival of an early successional herb can be substantially modified by differences in the abundance of conspecifics in its local neighbourhood, with both negative and positive effects being possible depending on the spatial scale considered. Besides, the results suggest that LS species can have a positive effect on the local probability of wet-to-dry season survival of the early successional dominant. The strength of this positive interaction appears to strongly depend both on the distance and the difference in relative sizes between individuals of the early and LS species. This results emphasize the importance of positive effects of LS species on facilitating the long-term permanence of early ruderals species in old-fields, and the importance that the development of size asymmetries can have in modulating positive plant-plant interactions. Both of these issues have received remarkably little attention in the context of successional research. Finally, the observed differences in the direction and intensity of plant-plant interactions at different spatial scales and in different moments in time (i.e. different seasons and seral stages), constitute a clear indication of the importance of explicitly considering both the spatial and temporal dimensions of plant successional dynamics.

Chapter 6. General Discussion

In this chapter, a general discussion of the results of the thesis is presented. First, a synthesis of the conclusions from the analysis of successional changes in plant community structure, ecophysiological characteristics of the dominant species and local spatial interactions is provided. The implications of the results for the development of an integrated view of the process of vegetation regeneration in the high tropical Andes are discussed. Then, the potential contributions to plant ecology of integrating functional, demographic and plant-centred perspectives on spatial dynamics are summarized, emphasizing some more general implications of the results of this thesis. Finally, the limitations of the research strategy used, and some possible directions for further research are discussed.

6.1 ELEMENTS FOR AN INTEGRATED VIEW OF OLD-FIELD SUCCESSION IN THE HIGH TROPICAL ANDES

In Chapter 2, some of the general patterns of vegetation structure change during old-field succession in the Venezuelan Andes are described. These patterns are consistent with results of similar studies in the páramos of Colombia (Ferweda 1987; Mora-Osejo *et al.* 1994; Jaimes 2000). The main trends identified were: (1) a monotonic successional increase of species richness and diversity; (2) a consistent sequence of life forms and dominant species change. More specifically, perennial forbs (e.g. *R. acetosella*) dominate the early stages and are progressively replaced as dominants by the more characteristic life forms of the páramo: sclerophyllous shrubs (of genus like *Baccharis* and *Hypericum*), caulescent giant rosettes (mainly of the *Espeletia* genus) and tussock grassess (e.g. *Calamagrostis effusa*); (3) clear changes in relative abundance of the dominant species but no clear species replacements (i.e. autosuccession); (4) the existence of divergent patterns of vegetation regeneration.

Below, I briefly discuss implications and hypothesis suggested by these patterns of vegetation change during succession. Then, I analyse the insights that the results of this thesis provide for understanding the processes that determine the clear sequence of change in the relative abundance of the dominant species.

6.1.1 Patterns of diversity, succession rates and divergence: páramo regeneration as an autosuccession

Successional dynamics have been considered to conform to one of two alternative conceptual models (see Egler 1954; Drury and Nisbet 1973): the Relay Floristics (RF) and the Initial Floristic Composition (IFC) models. The distinction between them is based on whether species turn-over dominates the dynamics (RF), or most species are present from the early stages of succession, showing subsequent changes in relative abundance, but no complete species replacement (IFC). The successional dynamics of the dominant species in the Venezuelan páramo conform to the predictions of the IFC model, so that vegetation regeneration can be interpreted as an autosuccession (see Chapter 2 and Sarmiento *et al.* 2002a). However, other less abundant species in this system show relay floristics: some mature páramo species are late colonizers of old-fields or are not able to colonize during the fallow times analysed (e.g. *Calamagrostis effusa*, see Sarmiento *et al.* 2002a for details). Moreover, some introduced species are completely excluded during succession. Thus, both the RF and the IFC models could be seen to adequately describe páramo regeneration, depending on whether the dynamics of all or only dominant species are emphasized. This has important implications for interpreting the apparent contradiction between the fast regeneration of vegetation physiognomy during succession and the incomplete restoration of the species richness observed in the mature ecosystem (see Chapter 2).

As indicated in Chapter 2, the relative abundances of the dominant life-forms reach similar levels to those found in the mature ecosystem relatively fast, as do the rank abundance diagrams and evenness. Moreover, it was estimated (based on an analysis of the *net rate of succession*, see Bakker *et al.* 1996) that less than 20 years could be necessary for a complete restoration of vegetation physiognomy (see also Sarmiento *et al.* 2002a) and species diversity. This contradicts the generally accepted view of vegetation regeneration as a slow process in alpine ecosystems in temperate and tropical regions (e.g. Billings 1973; Smith and Young 1987; Horn 1989; Luteyn 1992). However, this fast regeneration reflects to a large extent the dynamics of the dominant species and the fast increase in the evenness of the relative abundance of species. For the dominant species, recruitment limitation does not seem to be important in determining changes in abundance (dominant species are present from early seral stages). In contrast, a limited colonization ability of many rare páramo species or the existence of conditions during the first 9 years of succession which are not conducive to their germination and survival (e.g. low diversity and abundance of mycorrhizal fungi), could be important factors in explaining the incomplete recovery of the total number of species during the fallow times currently used by farmers in the area. In addition, other factors, such as demographic stochasticity, could also contribute to explain the drastic successional changes in abundance (and occasional local extinctions) of some rare species. A summary of these ideas is presented in Fig. 6.1.

Trends of vegetation change during the fallow are in general very clear, and this is reflected in a strong correlation between the 1st axis of a detrended correspondence analysis (DCA) of community structure and successional time. Nevertheless, there is large variability in species abundances for plots with the same fallow age. In addition, dissimilarity in community structure tends to increase during succession. The correlation between the 2nd and 3rd ordination axes and topographic and edaphic variables suggest that this could be partially explained by the high heterogeneity that characterizes these mountain environments (see Chapter 2; Sarmiento *et al.* 2002a). To shed additional light into the factors that determine successional divergence, there is a need to combine the synchronic approach used in this thesis (space for time substitution) with a diachronic approach based on following vegetation dynamics of the same plot through time. It would also be interesting to explore the extent to which internal spatial heterogeneity within each plot, stochastic effects on colonization, and local spatial interactions contribute to successional divergence.

6.1.2 Determinants of changes in abundance of the dominant species

One of the central questions in successional research is what determines the sequence of changes in abundance of the dominant species. In the context of the páramo regeneration this involves answering to complementary questions: (1) Why are dominant species in the mature ecosystem such as *H. laricifolium* and *E. schultzii* not able to dominate from the early stages of succession?; (2) Why do introduced forbs as *R. acetosella* continuously decline in abundance after dominating the early seral stages? Below, I discuss how integrating the results of the comparative analysis of the ecophysiology of the dominant species (Chapter 3) and the successional

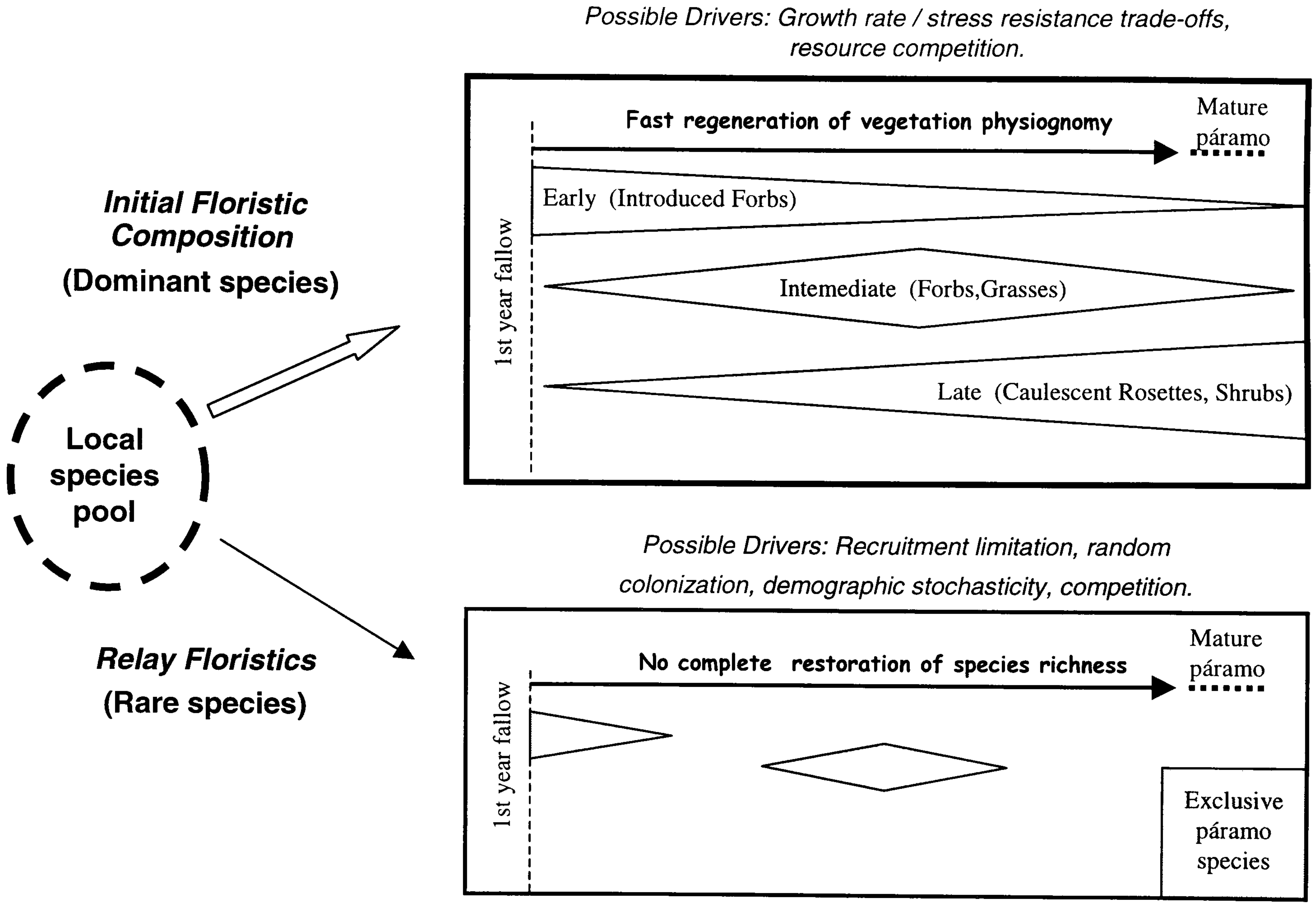


Figure 6.1 Diagrammatic representation integrating the main community structure changes during old-field succession in the Venezuelan páramo. Hypothesis on the driving processes are indicated in italics.

changes in spatial interactions (Chapters 4 and 5) can contribute to answering these questions.

The late dominance of shrubs and giant rosettes

The fact that all dominant species are able to colonize from early seral stages (see Chapter 2), suggests that the inability of late successional (LS) species to dominate during early succession could be the result of their slow relative growth rates. The results in Chapter 3 indicate that the slow growth rate of the LS dominants may be associated with low photosynthesis rates and light capturing area per unit leaf weight. It was suggested, on the basis of Grime's (1979) and Tilman's (1993) hypothesis, that differences in growth rate should be the result of trade-offs between leaf area and photosynthetic capacity, and other characteristics that could confer competitive advantages under limiting conditions.

The available literature indicates that the thick leaves (i.e. low specific leaf area) of mature páramo species present a series of xeromorphic characteristics such as a thick cuticle and water storage capacity in the medullar parenchyma (Roth 1973; Mora-Osejo *et al.* 1994; Meinzer *et al.* 1994). It is also well established that a low specific leaf area is generally associated with high leaf longevities low herbivore palatability (Brown and Southwood 1987; Chapin *et al.* 1996; Grime *et al.* 1997; Reich *et al.* 1997; Diemer 1998; Schippers *et al.* 1999). The results in Chapter 3 show that the LS species have a higher intrinsic water use efficiency (assimilation per unit of stomatal conductance) and that some of the species (e.g. *E. schultzii*) have the ability to maintain stable leaf water potentials and CO_2 assimilation rates during the dry season. This implies that the LS species could be more effective in water conservation and in the sequestration of nutrients in perennial standing phytomass. This characteristics could be important in explaining their ability to dominate during the late stages of succession in páramo ecosystems, which are characterized by low nutrient availability and seasonal water limitations.

The results in Chapter 4 provide a more detailed understanding of changes in abundance of *E. schultzii*, one of the most dominant late successional species. The results indicated that the population dynamics of *E. schultzii* are characterized by a large initial mortality of the seedlings established in early seral stages, so that few survive to become adults later in succession. The consistent decrease in the intensity of aggregation observed from seedlings to adults suggested that negative density dependence is likely to be important in regulating population size. Moreover, the results indicate there is a decrease during succession in the potential for further seedling establishment. Hence, the successional increase in abundance of *E. schultzii* seems to be mainly the result of an increase in biomass of few surviving individuals. This supports the idea that a slow relative growth rate could be one of the critical factors in explaining why the giant rosettes and shrubs are slow in becoming dominant.

The discussion presented so far still leaves unexplained the inability of species like *E. schultzii* to attain higher abundances than *R. acetosella* during early succession. This is unlikely to be the result of differences in the density of early successional (ES) and LS species in the seed bank. A study by Jaimes (2000) in old-fields of the Colombian páramo indicated that all species showed very low seed bank densities just after plot abandonment, even though the seeds of *R. acetosella* stayed viable longer than those of LS species. A more likely explanation for the early dominance of *R. acetosella* is its dual clonal and sexual reproductive strategy and high reproductive allocation (see Berbesi 1990), which could allow it to rapidly colonize plots after abandonment. Fast growth rates could also allow this pioneer forb to rapidly exploit the available resources and overgrow the seedlings of the LS species. Hence, the persistence in fallow areas of species like *E. schultzii* is likely to critically depend on their ability to tolerate the early dominance of *R. acetosella*. Results in Chapter 4 indicate that the mechanism for the seedlings of *E. schultzii* to tolerate the presence of *R. acetosella* does not involve spatial segregation from areas of high *Rumex* abundance. This is a problem that remains open for further research.

The successional decline of R. acetosella

Regarding the processes involved in the successional decline of *R. acetosella*, the results in Chapter 3 suggest that there could be a trade-off between its high photosynthetic potential and its water use efficiency, as a result of higher stomatal water losses. In addition, a high allocation to light-capturing area is linked to thin mesomorphic leaves, which could be more prone to damage from high radiation levels and desiccation (Mora-Osejo *et al.* 1994). This could be associated with the marked reductions found for *R. acetosella* in assimilation rates and water potential between the wet and dry season. Moreover, analysis in Chapter 5 show this species suffers high mortalities of above ground structures during the dry season. Hence, during each dry season, this species sharply decreases in abundance, freeing up space and resources for other species which are able to maintain their activity during this unfavourable period. In addition, the analysis of spatial dynamics suggested that negative density dependence in early seral stages could contribute to increase the mortality rates of *R. acetosella,* and could potentially contribute to its long-term decline in abundance.

One of the main mechanisms proposed in the literature for the decline in abundance of pioneer species is inter-specific competition with the LS species (Connell and Slatyer 1977; Picket 1982; Bazzaz 1990; Tilman 1990). The spatial segregation between *R. acetosella* and the adults of *E. schultzii* during late succession (Chapter 4) suggests the possibility of competitive effects. However, a more direct analysis of local inter-specific interactions and spatial dynamics (Chapter 5) indicates that the LS species may have a positive effect on *R. acetosella* survival during the dry season, resulting in an increase in spatial association between them.

An analysis of the underlying mechanisms involved in the interaction between the LS species and *R. acetosella* is necessary before it is possible to determine if direct competitive effects are involved in its decline. More information is needed to establish if water is a limiting factor for which *R. acetosella* has a lower competitive ability. The relatively open nature of the páramo suggests that changes in light availability are not likely to be important. In addition, the lack of clear successional trends for any of the most important nutrients analysed in old-fields of the high Andes (Ferweda 1987; Hervé 1994; Llambi and Sarmiento 1998; Pestalozzi 2000) complicates the determination of how changes in nutrient availability could be driving successional change. Since the low temperatures prevalent in the páramo limit the decomposition process (see Couteaux *et al.* 2002; Sarmiento and Bottner 2002), nutrients such as N are accumulated in the soil organic matter and the successional vegetation, with extremely low concentrations in the soil solution. The higher frequency of species with mycorrhizal associations among the LS species suggests they might be more effective in capturing nutrients (see Montilla *et al.* 1992). In addition, a slow growth rate and the presence of nutrient conservation mechanisms should allow the LS species to maintain lower rates of nutrient demand (synchronizing them with the rates at which resources become available). This could be related with the ability of the shrubs and rosettes to displace as dominants *R. acetosella* (see the R^* concept of competitive ability in Tilman 1988). The exploration of the mechanistic basis for the interactions between ES and LS species should be an important step in integrating individualistic and ecosystem perspectives in successional research in the high tropical Andes. It should also contribute to understand the role of vegetation dynamics on soil fertility restoration during the fallow. A model on competition for light, space and N which is currently being developed by Martineau (2001) and B. Saugier (University of Paris –Sud) in the context of the TROPANDES project.

6.1.3 Implications for conservation and management

As discussed in Chapter 2, the stabilisation of the total number of species and other ecosystem properties such as microbial biomass below the levels found in the non-disturbed ecosystem, questions the value of traditional agriculture to páramo conservation (see also Llambi and Sarmiento 1998; Llambi and Sarmiento 1999). This conservation value has been one of the justifications for the presence of traditional agricultural systems within national parks. The current trends for a reduction in the average fallow times and the continous expansion of the agricultural frontier into areas not previously cultivated, is likely to have serious consequences for the persistence of many mature páramo species which are slow in recolonizing fallow fields. As discussed by Sarmiento *et al.* (2002b) the elimination of the need for the fallow, through the intensification of agricultural production (by using more effective soil fertility management techniques) would reduce the area affected by cultivation while maintaining production levels. Given the high heterogeneity in plant community structure in these highland valleys, special care is needed to guarantee that representative areas in different topographic and geomorphologic situations are set aside for protection. Obviously, other criteria apart from the conservation of exclusive páramo species need to be considered as well. The benefits in terms of biodiversity conservation would have to be weighed against the environmental impacts of more capital intensive land use practices (e.g. inorganic and organic enrichment of river waters from fertilizer runoff).

In terms of the successional dynamics of mature páramo species such as *E. schultzii*, the results from Chapter 4 suggest that their establishment early in succession may be essential for their persistence in later stages. From this point of view, it would be interesting to evaluate the role of factors like grazing on the early dominance of introduced species such as *R. acetosella*, which could be slowing down the reestablishment of mature páramo species. Current experiments in the area, using cattle exclusion fences, suggest that grazing could actually be contributing to reduced abundance of introduced species such as *R. acetosella* (Sarmiento, unpublished results).

6.2 BROADER IMPLICATIONS: INTEGRATING FUNCTIONAL, DEMOGRAPHIC AND SPATIAL PERSPECTIVES

The results of this thesis emphasize the need for caution in applying to tropical highland ecosystems paradigms from research in lowland forest ecosystems. As pointed out by Urbanska (1997a), the traditional view of succession as a process of species turn-over is challenged by autosuccessional vegetation regeneration in mountain ecosystems (see above). In addition, the constant rate of succession found in Chapter 2 questions the generally accepted view of a continous slow down of vegetation regeneration rates after disturbance (Armesto *et al.* 1991; Myster and Pickett 1994).

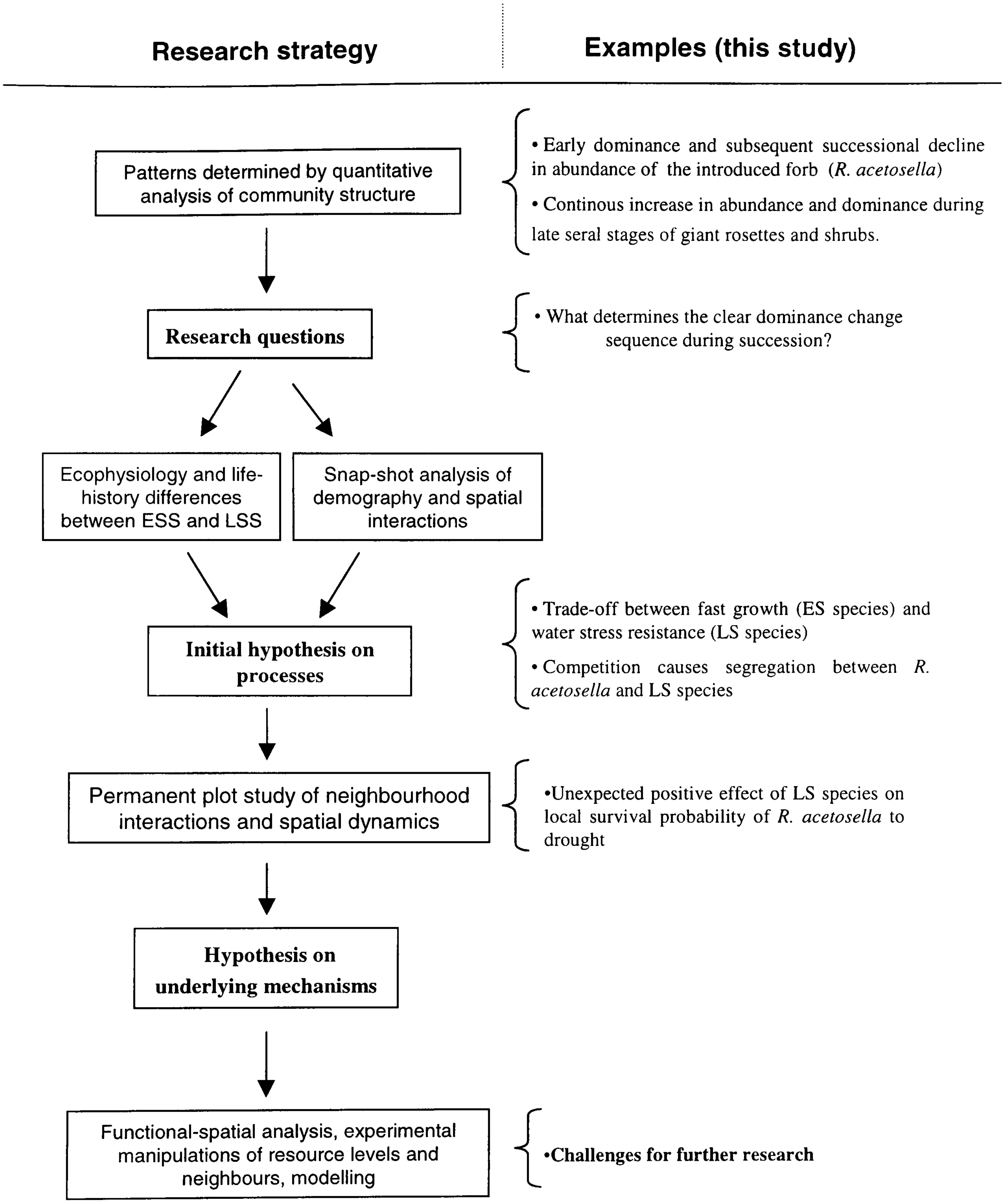
The discussion above (section 6.1), illustrates the value of the use of functional, demographic and plant-centred spatial analysis in the context of successional research (see diagram in Fig. 6.2). Their use allowed evaluating some of the possible roles of contrasting ecophysiological strategies and of positive and negative plant interactions in the clear dominance replacement sequence that characterizes succession in the high tropical Andes. In particular, the results presented in chapters 2, 3 and 4 support the applicability in the context of the highland tropics of the maximal growth rate hypothesis of succession (Tilman 1990;1993).

More generally, the results from Chapter 5 illustrate how analysing the dynamics of spatial relations in permanent plots allows establishing a link between changes in spatial patterns and the nature of local intra- and inter-specific interactions. The results show a pronounced decline with distance in the strength of facilitative effects of the LS species on the probability of survival of *R. acetosella*, emphasizing the local nature of plant-plant interactions. Moreover, this positive effects are more pronounced in late successional plots, where the size asymmetry between individuals of the LS species and *R. acetosella* is larger. Both of these results suggest it is important to consider how the distance and relative sizes between individuals modulates strength of their interactions, the so called 'interaction kernel' functions in neighbourhood models (see Stoll and Weiner 2000; Law *et al.* 2001; Purves and Law 2002). However, this kind of individual based spatial models have concentrated on analysing the effects of negative interactions on population and community dynamics and the development of spatial structure. The results in Chapter 5 emphasize the need to consider the consequences of positive facilitative effects as well.

Facilitation of the colonization of LS by pioneer species has long been seen as an important mechanism for successional change (Clements 1936; Connell and Slatyer 1977). However, the possibility of positive effects of the late species on the long-term persistence of ES species has rarely been considered. In addition, the observed differences in the direction and intensity of plant-plant interactions at different spatial scales and in different moments in time (i.e. different seasons and seral stages), are a clear indication of the importance of explicitly considering both the spatial and temporal dimensions of plant successional dynamics. However, there have been very few other studies on small-scale spatio-termporal dynamics in the context of successions (see Partel and Zobel 1995; Ramsay and Oxley 1996).

6.3 LIMITATIONS AND DIRECTIONS FOR FURTHER RESEARCH

Finally, it is important to point out some limitations of the functional and spatial research carried out in the context of this thesis, and the further research this should lead to. As indicated in Chapter 3, it is necessary to evaluate the extent to which the ecophysiological differences identified here between dominant ES and LS species, are also applicable to the large number of other sub-dominant and rare species in these high tropical ecosystems. With this information, it would be possible to see the extent to which differences in attributes such as photosynthetic potential are also evident in species that have their peak of abundance in different seral stages but that belong to the same life-form. Based on the results of this thesis, this issue is currently being investigated in the Gavidia valley. To be able to establish whether species that



- Early dominance and subsequent successional decline in abundance of the introduced forb (*R. acetosella*)
- Continous increase in abundance and dominance during late seral stages of giant rosettes and shrubs.

- What determines the clear dominance change sequence during succession?

- Trade-off between fast growth (ES species) and water stress resistance (LS species)
- Competition causes segregation between *R. acetosella* and LS species

- Unexpected positive effect of LS species on local survival probability of *R. acetosella* to drought

- **Challenges for further research**

Figure 6.2 Diagram of a framework to integrate different research strategies for the analysis of plant succession. Examples taken from this thesis of the application of these strategies are presented on the right hand side.

dominate during the different stages of succession can be classified into distinct functional groups, there is also a need to include other life-history and ecophysiological factors in the analysis (e.g. relative growth rate, leaf longevities, reproductive allocation and dispersal ability). The integration of life-history and functional information has proved remarkably successful in identifying trade-offs and plant 'adaptive syndromes' that determine the success of different species in contrasting successional environments and biomes of the earth (e.g. Grime et al. 1997; Reich *et al.* 1997). As recently pointed out by Rees *et al.* (2001) the success of this research strategy "has come from the recognition that many of the same environmental constraints and organismal trade-offs that shape the evolution of plants morphologies, life histories, and physiology also influence the dynamics of inter-specific interactions and the mechanisms of coexistence that control community and ecosystem functioning". The initial insights provided in this thesis suggest that this could be a productive approach for furthering our understanding of old-field succession in high mountain ecosystems.

Concerning the analysis of the effects of local spatial interactions on community organization, we need to extend the research carried out in Chapter 5, to consider other species in long-term permanent plot studies. This information is needed to determine the extent to which directional (i.e. non-random) local species replacements underlie the directional changes in relative dominance during succession (see Herben *et al.* 1993; Partel and Zobel 1995). By combining this analysis with more detailed information on the species life-histories and physiology, it should be possible to establish a link between local species replacements and the functional attributes of interacting species. This would shed additional light into questions such as whether competitive hierarchies are size based (as suggested by some studies in grassland communities, see Silvertown and Bastow Wilson 2000), and whether functionally similar species are more likely to locally exclude one another (the 'guild proportionality' model, see Herben *et al.* 2000).

There is also a need to explore the mechanistic bases of the local intra- and inter-specific interactions suggested by the phenomenological approach used in this thesis. In this context, there is much scope for integrating functional, demographic and spatial approaches using observational and experimental strategies (Fig. 6.2). For example, analysing differences in the physiological responses (e.g. photosynthesis, leaf water potentials) of *R. acetosella* individuals with different densities of conspecifics and heterospecifics in their local neighbourhoods (which could be altered by experimental removals), would allow to determine the way in which competitive and facilitative interactions actually affect plant performance. In this context, the experimental modification of available resource levels (e.g. water or nutrients) should also allow to explore which factors underlie plant-plant interactions.

Finally, as pointed out by Rees *et al.* (1996), to analyse how local spatial interactions influence population dynamics, it is important to develop empirically parameterised spatial models. For example, Colasanti and Grime (1993) have applied theoretically derived rules on resource capture, utilization and release to simulate succession and spatial structure dynamics using a cellular automata model (CAM). The approach used in Chapter 5 can be extended to construct empirically derived CAM transition rules, which could be used to model the effects of local interactions between ES and LS species on successional community dynamics. Moreover, the use of individual based simulation models has proved effective in integrating population dynamics with a physiological, mechanistic perspective on resource competition in a spatially explicit context. This kind of models have been successfully used to interpret patterns of community structure change during forest successions (see Shugart 1984; Botkin 1992; Pacala *et al.* 1996). An alternative approach has been applied by Tilman and co-workers to develop less complex, but more general resource competition models of succession on the basis of long-term studies in N limited herbaceous communities (see Tilman 1988; Tilman 1990). The success of both lines of research has depended on the integration of long-term observational, experimental and modelling programs guided by theory development and hypothesis testing. In my view, the implementation of this kind of long-term, integrated strategy is the main challenge ahead for research on plant succession in high mountain ecosystems (see Fig. 6.2).

Appendix A

(This appendix contains the Author's Proofs of a paper that expands on the work presented in Chapter 2: "*Sarmiento, L. Llambi, L.D., Escalona, A. and N. Marquez.*2002. *Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. Plant Ecology*". The final version of the paper has not been published yet. Hence, these Author's Proofs contain some minor typographic errors, indicated on the text, which will be corrected in the published version).

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Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes

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Abstract

Vegetation restoration during old-field succession was studied in an alpine Andean ecosystem (paramo). 123 plots with different fallow times (1 to 12 years) and 8 plots under natural vegetation were sampled. The results indicate that secondary succession in the paramo, like in other extreme environments, can be interpreted as an *autosuccession*: there are mainly changes in species relative abundance and little floristic relay (i.e. species turnover). Only a few herbaceous species, mostly introduced (e.g. *Rumex acetosella*), act as strict pioneers and strongly dominate the early stages. Then, they undergo a progressive decline, while native forbs (e.g. *Lupinus meridanus*) and grasses (e.g. *Vulpia myuros*) have their peak abundance in intermediate stages. The characteristic paramo life forms, sclerophilous shrubs (e.g. *Baccharis prunifolia*, *Hypericum laricifolium*) and giant rosettes (e.g. *Espeletia schultzii*), appear very early and gradually increase in abundance during succession, becoming dominant in the late stages and showing a dual behaviour, both as ruderal and stress tolerant species. The 1st axis of a Detrended Correspondence Analysis arranges the sites according to their fallow time. The 2nd and 3rd axes, associated with diverging pathways of regeneration, are correlated with topographic factors and physio-chemical soil characteristics. Hence, structural divergence between plots increases along succession as community composition starts to reflect the conditions of each site. We found evidence of a constant rate of succession during the first 12 years, contradicting the generally accepted hypothesis in the succession literature of a continous slow down up to the climax. Regeneration of vegetation physiognomy is relatively fast, questioning the prevailing idea of slow restoration in alpine ecosystems. However, 12 years of fallow are insufficient to attain the species richness of the natural paramo. Under the current trend of fallow length reduction observed in traditional potato cultivation in the Andes, our results raise doubts about the conservationist value of this management strategy.

Introduction

Knowledge of the mechanisms, rates and pathways of secondary succession is crucial for understanding the response of the vegetation to disturbance and to design strategies for ecosystem management and restoration. There are a number of generalizations in the literature on what to expect during plant secondary succession, including a successional increase in evenness, a high degree of predictability in the sequence of different life forms (Bazzaz 1996), a successional decline of introduced species (Pickett 1982; Vitousek 1986), and a decrease of the rate of succession as the system approaches its mature state (Myster and Pickett 1994). Other aspects, like the successional trend for species diversity, have generated substantial debate. Some authors (e.g. Odum (1969)) support the idea of a continuous increase in diversity, while others suggest there should be a "nearly universal decline" at late stages (e.g. Horn (1974)). Another important area of disagreement has been whether to expect convergence in community structure towards a single climax (as suggested by the classical ideas of Clements) or divergence along multiple alternative states of ecosystem development.

The study of succession has mostly been developed in temperate ecosystems, and in the case of the tropics, in lowland "old-field to forest" systems. Considerably less information is available on secondary succession in the highland tropics. The unique climate (low temperatures and no thermal seasons) and the treeless nature of tropical highland environments make them ideal for evaluating the generality of the expected trends discussed above. In other treeless ecosystems, like arctic and temperate alpine, attention has mainly been given to the study of primary succession in recently deglaciated areas (Matthews 1992). However, secondary succession proceeds at different rates and implies other mechanisms.

The Paramo is a tropical alpine ecosystem that occupies the upper belt of the Northern Andes (3000 to 4800 m). Giant caulescent rosettes, shrubs and bunch grasses dominate the vegetation. Most of the paramos are located in Venezuela, Colombia and Ecuador, and their flora is among the richest in the high mountains of the world (van der Hammen and Cleef 1986). Recently, the paramo has been subjected to an accelerated process of degradation and transformation, characterised by agricultural intensification and a continuous expansion of the agricultural frontier (Ferweda 1987; Luteyn 1992; Hofstede 1995; Hess 1990; Drost et al. 1999). The increasing human intervention, frequently involving long fallow agriculture, makes the study of secondary succession a priority for the preservation and management of this unique environment.

An important insight from recent theory, which can help in furthering the understanding of paramo succession, is to interpret vegetation development as a "vector", analysing both its rate and its directionality (Bakker et al. 1996). On the one hand, several authors agree that these high altitude ecosystems are fragile, showing slow rates of plant growth and regeneration after disturbances like fire and grazing (Janzen 1973; Horn 1989; Luteyn 1992; Hofstede et al. 1995). On the other hand, the possibility of multiple pathways of vegetation development has been emphasised in the mountain restoration context (Urbanska 1997). Apart from processes like random colonisation and non-linear species interactions, divergence in these highland systems could be due to the spatial heterogeneity of the environment, which would favour differentially the persistence of the arriving species. The high topographic and edaphic heterogeneity that characterises paramo environments (Llambí and Sarmiento 1998) offers a unique opportunity to analyse this issue. Nevertheless, very few detailed studies on vegetation dynamics in paramo old-field succession are available in the literature (but see Ferweda (1987) and Moreno and Mora-Osejo (1994)) and none have measured divergence and regeneration rates.

The objective of this study is to characterise old-field succession in a Venezuelan paramo, analysing the change in species richness and abundance and in the life-forms spectrums of the vegetation. Succession is evaluated in terms of whether it shows convergence or divergence and how this is related to environmental conditions. The rate of succession and the time necessary for the restoration of vegetation structure are also examined, evaluating the possible impact of fallow agriculture on paramo biodiversity.

Methodology

Study area

The study was carried out in the Páramo de Gavidia, located in the Sierra Nevada National Park, in the state of Mérida, at an altitude of 3200 to 3800 m a.s.l. The area is a narrow glacial valley, with well-drained inceptisols (*Ustic Humitropept*) of a sandy-loam texture, low pH (4.25 to 5.5), high organic matter levels (up to 20%) but low mineral nutrient contents (Llambí and Sarmiento 1998). Agriculture is practised on steep slopes and also on small colluvial and alluvial deposits in the valley bottom. The precipitation regime is unimodal, with a dry season between December and March and a peak of rainfall between June and July. The mean temperature ranges between 9 and 5 °C (with a higher frost frequency during the dry season) and the mean annual precipitation is 1300 mm. The land use system practised in the area is long fallow agriculture. Potatoes are grown during an agricultural phase lasting between 1 to 3 years. Agricultural practices include the incorporation of the successional vegetation as a green manure, mineral fertilisation with an average dose of 1.8 t ha^{-1} $year^{-1}$ of NPK and two to three ploughs per year. After the cultivation period, the fields are abandoned and the succession-restoration phase begins (Sarmiento et al. 1993). The current average fallow length is 4.6 years, but there is large variability, with times ranging from

2 to more than 15 years (Sarmiento et al. 2001). During the fallow period, fields are used for extensive cattle and horse grazing.

Plot selection

In mountain ecosystems, the study of secondary succession using synchronic methods (space for time substitution) is especially difficult due to the inherent heterogeneity of the environment. A large number of plots were selected in this study to attempt to differentiate the effects of time and spatial heterogeneity. We used a spatial database (Smith (1995), updated to the year 2000) which contains information on the fallow lengths of 1200 fields. This database also contains information for all the plots of attributes such as slope, area, aspect, elevation and distance to the valley bottom. 123 plots, between 1 and 12 years of fallow (repetitions per year: 12, 11, 12, 15, 16, 11, 10, 9, 7, 5, 4, 3), and 8 areas of never cultivated paramo (NCP) were selected. Fewer late successional plots were included as the database has no information on the exact fallow time for the oldest plots.

Sampling and data analysis

In each selected plot, the point-quadrate method was used to sample the vegetation (Greig-Smith 1983). A pin was placed vertically 100 times at random positions and the contacts with all species in 10 cm height intervals were recorded. All the vegetation relevées were carried out between 1996 and 1999, during the last part of the rainy season (September to November), when most of the species are in flower. This information was used to construct a matrix of species versus relevées.

A composite soil sample (0–20 cm) of each plot was collected from 10 random points and analysed for texture (Bouyocos method), total carbon (Walkley-Black), nitrogen (micro Kjeldalh), pH (measured in 1/1 soil water mixture using a pH meter) and CEC (measured after extraction with 1 M NH_4OAc at pH 7). An environmental matrix was constructed using the soil parameters and the other plot attributes extracted from the spatial database.

Richness was estimated as the total number of species recorded in each plot. Species abundance was calculated as the total number of contacts of each particular species by plot. Rank abundance diagrams were plotted for contrasting stages of succession as originally suggested by Whittaker (1972). The distribution of the abundance between the different life-forms was also analysed. Additionally, species were classified as native or introduced.

We performed a Detrended Correspondence Analysis (DCA) on the species vs. releveés matrix, using the CANOCO 4.02 software (Ter Braak and Smilauer 1999). The "detrending" was done by segments as suggested by Hill and Gauch (1980). To interpret the ordination we calculated Spearman's rank correlations of each axis with successional time and environmental variables.

The rate of succession has been understood in two ways in ecology: as the time it takes community structure to reach its climax stage, or as the year to year rate of change in the vegetation structure (Prach 1993). The first interpretation faces the difficulty of clearly defining what is considered to be the terminal stage. For the second interpretation, two main approaches have been proposed (Pickett 1982; Prach 1993; Myster and Pickett 1994; Donnegan and Rebertus 1999): 1) calculating an index of species turn-over (e.g. Sorensen's) between consecutive years, ignoring changes in species abundance or 2) calculating an index of community dissimilarity (e.g. Euclidean distance). The second approach was deemed the most promising in the case of the paramo, since our results indicate that succession is characterised by changes in species abundance more than species turnover. For the calculation we used two different methodologies, both based on calculating dissimilarity between all the plots of each fallow time and 1st year plots (called by Bakker et al. (1996) the *net rate of succession*). In one method we used chord distance (i.e. Euclidean distance on the normalized matrix, Orloci (1978)) as our dissimilarity index. For the other method, we used the distance in the DCA 1st axis scores, as this axis is strongly correlated to successional time (see results). A regression analysis was then carried out having time as the independent variable and our dissimilarity index as the predicted variable. The slope of the adjusted curve corresponds to the succession rate. To obtain an estimate of the time required for the system to reach a community structure similar to that of the never cultivated paramo an extrapolation of the adjusted function was performed, using the average distance between the 1st year plots and the NCP plots.

Successional divergence in species composition was analysed by comparing dissimilarity between all plots of a particular age (Christensen and Peet 1984). We used chord distance as our dissimilarity measure.

Results

In the 123 studied plots, 122 species of vascular plants were recorded. The best represented families were: Asteraceae, Poaceae and Rosaceae, with 32, 27 and 6 species respectively. In Table 1 the 44 most abundant species are ordered according to their relative abundance in succession (the same species included in the DCA diagrams). The following groups of species can be identified: a) Pioneers, such as *Rumex acetosella*, which is the most abundant species during the first 9 years of succession, showing a maximum of relative abundance during the 2nd year and a continuous decrease thereafter. Other species as *Erodium cicutarium*, also act as pioneers but show a faster decline. b) Mid-successionals, having their peak of abundance at intermediate stages (e.g. *Lupinus meridanus*). c) Late-successionals, showing their peak at the end of the study interval (e.g. *Baccharis prunifolia*). d) Dominant paramo species, a group that appears during the succession but has its maximum in the NCP (e.g. *Espeletia schultzii*). e) Exclusive paramo species, which do not appear during succession (e.g. *Calamagrostis effusa*).

It can be seen in Table 1 that most of the successional species can also be found in the NCP, with the exception of a few pioneers. Moreover, the majority of the species are present during the whole studied interval. Succession appears as a continous process of change in species abundance more than as a sequence of well defined successional stages.

Species richness doubles during the first four years of succession, passing from an average of 10 to 20 species per plot (Figure 1). Hereafter, the number of species stabilises, without any clear successional trend. After 12 years of succession, richness stays significantly lower than the average of 36 species measured for the NCP.

The rank abundance curves showed a tendency to flatten out as succession proceeds, reflecting the increase in the number of recorded species and the decrease in their relative dominance (Figure 2). Although the difference between the extremes (first year fallow and NCP) was clear, there were no clear differences between the rank abundance patterns for the intermediate years. This agrees with the asymptotic behaviour of richness seen in Figure 1.

The average relative abundance of the main life forms showed clear successional trends (Figure 3). Forbs presented a progressive decline, beginning with 80% of the total abundance in the first year of succession and attaining 33% by the 12th year. Simultaneously, shrubs and giant rosettes increased their abundance from less than 2% in the first year to 42% and 10% after 12 years respectively. Grasses did not show any successional tendency, representing on average 20% of the total plant abundance. After 12 years of succession the life form spectrum of the vegetation was very similar to that of the NCP, suggesting a relatively effective restoration of vegetation physiognomy.

There was a sharp decrease in the abundance of introduced species during succession, from 70% in the first year to 5.5% in year 12 (Figure 4). The most abundant of the introduced species was, by a large margin, *Rumex acetosella* (Table 1).

A clear successional progression can be seen in the ordination of the plots along the 1st DCA axis, with the early successional plots occupying the extreme left of the diagram and the NCP plots the right (Figure 5). A strong positive correlation between time and the scores on this 1st axis was found ($r = 0.85$, $p < 0.001$, Table 2). Nevertheless, an important overlap between plots of different ages occurred, indicating again the difficulty of defining discrete successional stages and suggesting that the rate of succession in not the same for all the plots.

The ordination scores of the species on the 1st axis were indicative of their changes in abundance in the successional sequence and corresponded very closely with the results in Table 1. The analysis of the 2nd axis indicated that there was a clear successional divergence, with a progressively greater dispersion of the sites from the left to the right extreme of the 1st axis. The 2nd axis was negatively correlated with the distance to the valley bottom and less significantly to the clay content (Table 2). The distance to the valley bottom can be related both to geomorphologic position and to grazing intensity, which is greater in lower areas due to the proximity of farmer houses. *Acaena elongata* is an example of a species that prefers the valley bottom, while species such as *Luzula racemosa* show a strong preference for the more distant zones.

Divergence along the 3rd axis showed the opposite trend, with maximal dispersion in early successional stages (Figure 5). This axis was significantly correlated with many environmental variables as soil texture, pH, C and N content, absolute altitude above sea level and slope (Table 2) and can be interpreted as the more subtle response of plant species to the specific environmental conditions of the plots. In the 3rd axis *Lupinus meridanus* and *Senecio formosus* are

Table 1. Abbreviation of the 44 more abundant species names and their origin (N = native, I = introduced), life form and relative abundance along the succession and in the never cultivated paramo (NCP).

				Years in succession												
Species name	Abbre-viation	Origin	Life form	1	2	3	4	5	6	7	8	9	10	11	12	NCP
Poa annua L.	Poa ann	I	Grass	**2.8**	1.6	2.2	0.2	0.6	0.7	1.2	2.2	1.3	0.1	0.4	0.2	0.0
Erodium cicutarium L Hér.	Ero cic	I	Forb	1.3	**1.9**	0.3	0.2	0.1	0.1	0.0	0.2	0.2	0.0	0.0	0.2	0.0
Gnaphalium antennarioides D.C.	Gna ant	N	Forb	0.0	**1.6**	1.2	0.0	0.0	0.0	0.2	0.1	0.1	0.3	0.0	0.0	0.0
Rumex acetosella L.	Rum ace	I	Forb	52.8	**54.4**	45.3	30.9	21.0	22.1	19.6	19.3	15.7	12.6	14.8	7.2	1.1
Lachemilla moritziana Damm	Lac mor	N	Forb	8.7	**10.1**	8.0	6.1	5.6	5.2	5.6	5.2	2.8	3.6	5.8	1.2	0.3
Senecio formosus H.B.K.	Sen for	N	Forb	1.8	3.2	**7.8**	6.4	4.0	1.4	1.8	0.3	0.2	0.0	0.3	0.2	0.4
Conyza mima S.F. Blake	Con mim	N	Forb	0.5	0.8	**1.5**	0.3	0.6	0.4	0.3	0.5	0.2	0.2	2.2	0.0	0.2
Gnaphalium elegans Kunth	Gna ele	N	Forb	0.6	1.6	1.9	**2.7**	0.7	0.0	0.1	0.5	0.0	0.0	0.5	0.0	1.0
Gnaphalium meridanum Aristeg.	Gna mer	N	Forb	0.3	0.4	1.2	**1.7**	0.8	0.8	0.2	0.1	0.1	0.9	0.2	0.6	0.4
Bidens triplinervia H.B.K.	Bid tri	N	Forb	0.1	0.6	0.7	**0.7**	0.7	0.1	0.1	0.3	0.1	0.0	0.0	0.2	**1.4**
Gamochaeta americana (Mill.) Wedd.	Gam ame	N	Forb	1.8	0.6	0.4	**2.8**	2.6	2.2	1.1	2.1	0.2	2.1	0.5	0.5	0.3
Lupinus meridanus Moritz	Lup mer	N	Forb	4.6	3.1	1.4	2.2	**8.8**	4.6	1.7	0.3	0.5	2.5	3.2	0.3	0.6
Agrostis jahnii Luces	Agr jah	N	Grass	1.4	0.8	1.1	1.3	**2.7**	2.4	0.9	0.7	0.1	0.0	0.2	0.5	0.2
Calamagrostis pittieri Hack	Cal pit	I	Grass	0.2	0.0	0.5	1.1	**1.2**	0.0	0.3	0.0	0.3	0.4	0.4	0.0	1.1
Vulpia myuros (L.) C.C.Gmel.	Vul myu	N	Grass	9.9	11.3	10.5	15.5	**17.1**	11.4	12.8	13.3	12.8	14.1	7.1	2.6	0.4
Luzula racemosa Desv.	Luz rac	N	Grass	0.0	0.0	0.3	0.9	0.5	**1.4**	0.1	0.0	0.1	0.0	0.0	0.0	0.6
Acaena cylindristachya Ruiz & Pav.	Aca cyl	N	Forb	0.0	0.0	0.1	0.5	0.4	**0.6**	0.1	0.1	0.5	0.2	0.1	0.0	**1.5**
Geranium chamaense pittier.	Ger cha	N	Forb	0.9	0.4	1.4	1.3	2.2	**3.5**	2.0	2.0	0.9	0.5	0.1	2.3	0.0
Nassella mexicana (Hitchc.) R. W. Pohl	Nas mex	N	Grass	0.6	0.0	0.4	0.9	0.9	**1.8**	1.0	0.0	0.1	0.9	0.6	0.3	2.7
Stevia elatior H.B.K.	Ste ela	N	Forb	1.9	0.6	0.6	1.0	1.0	2.3	**5.3**	4.5	2.8	3.4	4.4	3.3	1.2
Oxalis sp.	Oxa sp.	N	Forb	0.0	0.5	0.1	0.4	0.0	0.1	0.4	**0.9**	0.2	0.1	0.3	0.2	0.3
Acaena elongata L.	Aca elo	N	Shrub	0.9	1.3	1.1	2.0	2.9	3.0	4.1	**7.7**	4.3	3.6	3.7	2.6	2.6
Agrostis trichodes (H.B.K.) Roem. & Schult.	Agr tri	N	Grass	0.3	0.2	0.5	0.9	0.9	0.4	1.5	2.0	**2.4**	0.1	0.7	0.3	0.2
Oenothera epilobifolia H.B.K.	Oen epi	N	Forb	0.1	0.4	1.3	1.5	1.9	1.3	1.4	1.8	1.4	**2.6**	0.8	0.8	0.4
Stevia lucida Lag.	Ste luc	N	Shrub	0.0	0.3	0.6	1.2	0.9	1.3	2.9	2.2	3.1	**6.6**	5.8	4.4	1.6
Sisyrinchium tinctorum Kunth	Sis tin	N	Forb	1.0	0.3	2.0	2.2	2.9	4.9	3.4	3.8	3.4	3.9	**6.7**	1.4	0.6
Baccharis prunifolia H.B.K.	Bac pru	N	Shrub	1.4	0.4	0.2	1.0	1.7	4.8	5.7	4.1	14.6	11.5	14.0	**23.5**	3.7
Noticastrum marginatum (Kunth) Cuatrec.	Not mar	N	Forb	0.2	0.0	0.0	0.5	0.6	0.8	0.3	1.3	1.9	5.7	6.8	**14.3**	1.2
Trisetum irazuense (Kuntze) Hitchc.	Tri ira	N	Grass	0.2	0.0	0.5	0.5	1.2	1.7	1.9	1.2	2.4	3.9	3.2	**8.6**	1.3
Ruilopezia floccose (Standl.) Cuatrec.	Rui flo	N	Rosette	0.0	0.0	0.0	0.1	0.0	0.1	0.4	0.5	0.0	0.2	0.0	0.0	**1.7**
Hypericum laricifolium Juss.	Hyp lar	N	Shrub	0.1	1.3	1.8	3.5	3.2	6.2	8.1	5.0	6.2	6.5	4.7	7.6	**9.9**
Orthosanthus chimboracensis (Kunth)	Ort chi	N	Forb	0.7	0.2	0.1	0.3	0.4	1.2	1.8	2.0	1.6	0.7	0.1	1.1	**2.1**
Bartsia laniflora Benth.	Bar lan	N	Forb	0.0	0.1	0.1	0.5	0.5	0.3	0.0	0.0	0.2	0.0	0.0	0.0	2.4
Hesperomeles obtusifolia (Pers.) Lindl.	Hes obt	N	Shrub	0.1	0.0	0.0	0.0	0.1	0.1	0.5	0.7	0.4	0.0	0.3	0.0	**1.4**
Espeletia schultzii Wedd.	Esp sch	N	Rosette	0.8	0.6	2.1	2.4	5.1	8.7	8.4	9.3	8.5	7.2	7.0	9.3	**11.7**
Agrostis subpatens (Hitchc)	Agr sub	N	Grass	0.0	0.0	0.0	0.5	0.1	0.0	0.1	0.0	0.4	1.2	0.3	0.5	**4.6**
Pernettya prostrata (Cav.) DC	Per pro	N	Shrub	0.2	0.0	0.1	0.2	0.0	0.0	1.3	0.7	3.7	0.9	0.3	1.4	**8.7**
Nassella linerifolia (Fourn.) Pohl	Nas lin	N	Grass	0.2	0.0	0.0	0.3	0.9	0.8	0.0	0.1	0.3	0.1	0.5	1.6	**2.5**
Arcytophyllum nitidum (H.B.K.) Schldl.	Arc nit	N	Shrub	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**2.6**
Calamagrostis effusa (H.B.K.) Steud	Cal eff	N	Grass	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**5.3**
Brachypodium mexicanum (Roem. & Schult.)	Bra mex	N	Grass	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**1.0**
Hypericum juniperinum Kunth	Hyp jun	N	Shrub	0.0	0.0	0.0	0.1	1.5	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.7
Conyza lasseriana Aristeg.	Con las	N	Forb	0.0	0.0	0.7	0.3	0.6	0.3	0.0	0.0	0.2	0.7	0.9	0.2	0.8
Bromus carinatus Hook & Arn	Bro car	N	Grass	0.9	0.2	0.4	0.0	0.8	0.0	0.0	0.3	0.6	0.9	0.9	0.3	0.0

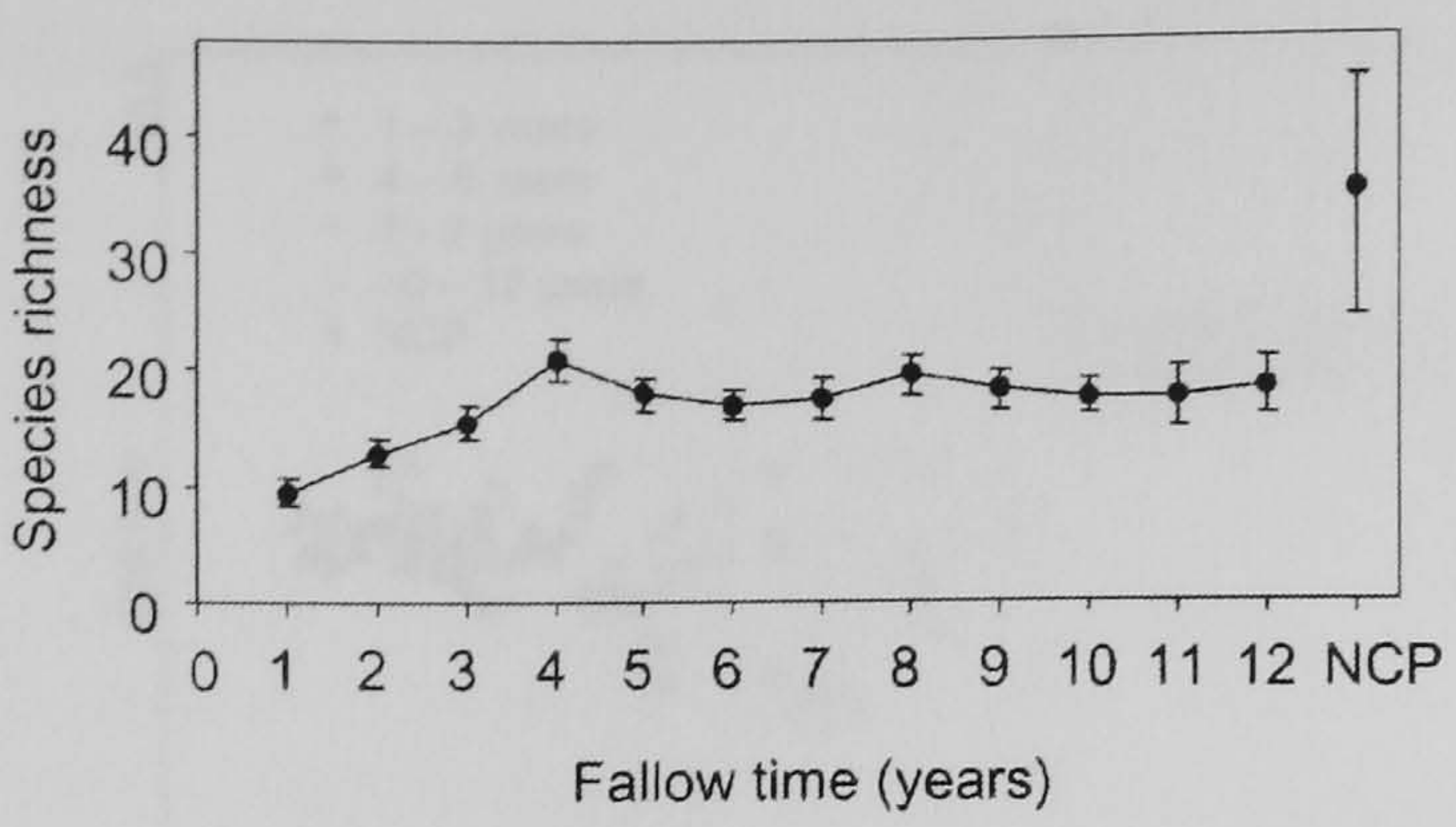

Figure 1. : Species richness by plot during the first 12 years of succession and in the never cultivated paramo (NCP). Mean ± standard error.

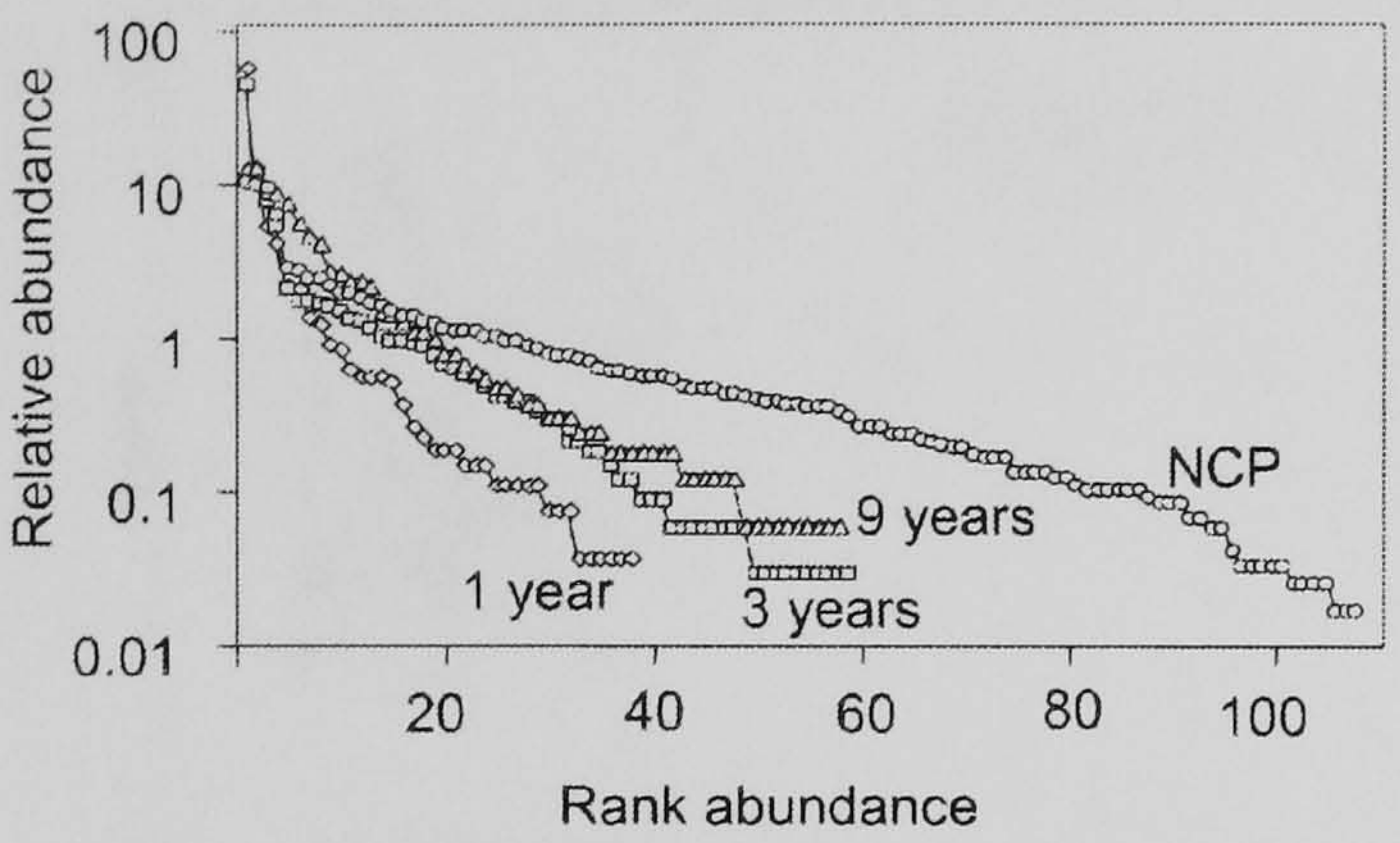

Figure 2. : Rank abundance diagrams for 1, 3 and 9 years of succession and for the never cultivated paramo (NCP). For each fallow age the average abundance of the species in all the sampled plots was considered. The y axis is on a logarithmic scale.

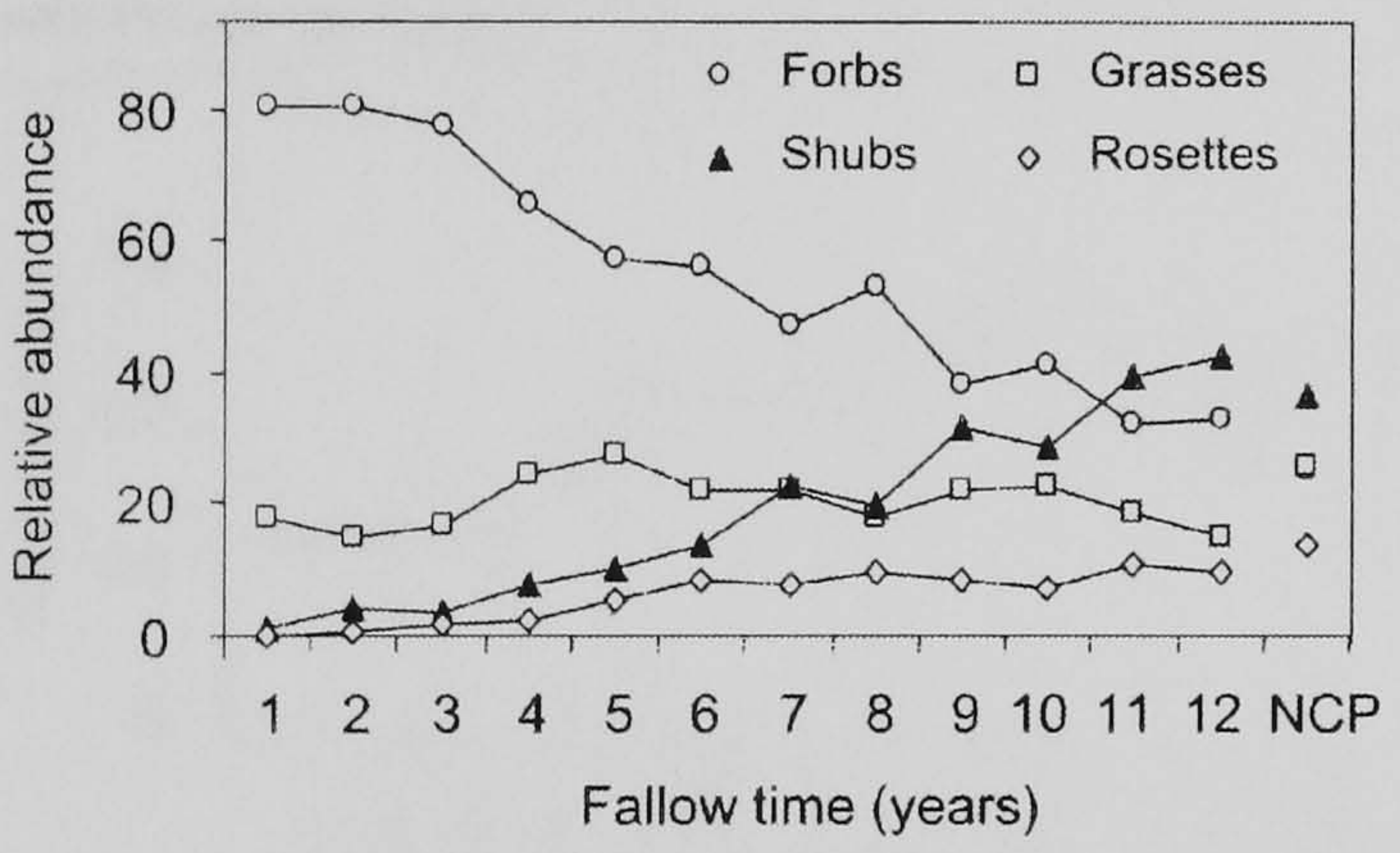

Figure 3. : Relative abundance of the different life forms along succession.

examples of intermediate species in opposite extremes, with *L. meridanus* preferring sites with high pH, C, N and clay content.

The quantification of the successional rate is presented in Figure 6. The two methods used indicated the same trend: a linear regression provided a very good fit to the floristic distance between the first year plots and subsequent years, indicating a constant rate

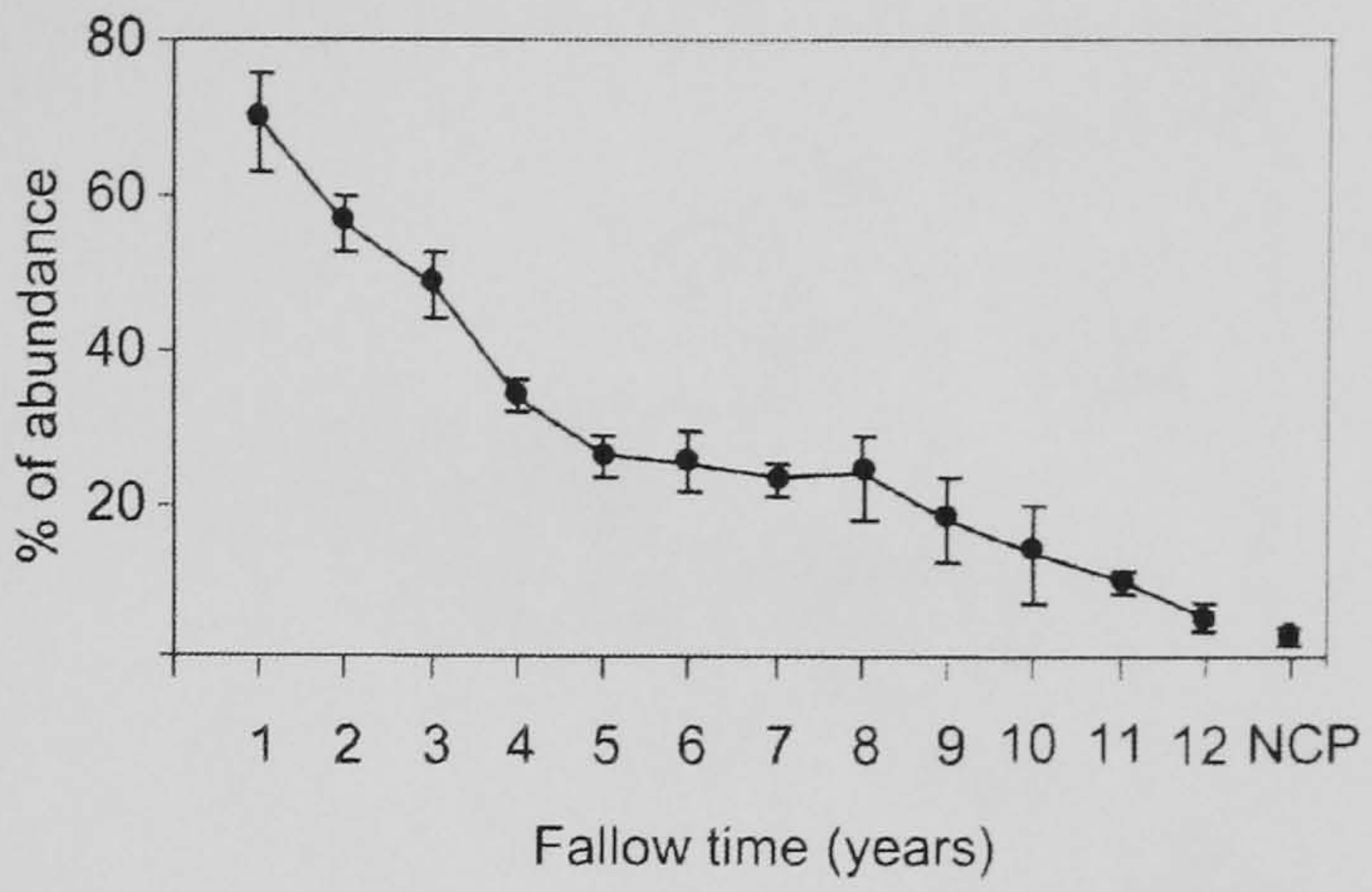

Figure 4. : Percent of the total abundance represented by introduced species along the succession and in the never cultivated paramo (NCP). Mean ± standard error.

Table 2. Spearman rank correlations between environmental variables and the DCA axis scores of the sites. Significant correlations ($p < 0.05$) are indicated with an asterisk.

	1st Axe	2nd Axe	3rd Axe
Time[1]	0,85*	0,15	0,17
Sand	–0,12	0,13	–0,44*
Clay	0,24*	–0,25*	0,48*
Silt	–0,03	0,03	0,15
pH	0,18	–0,15	0,46*
%C	0,12	–0,01	–0,58*
%N	0,12	–0,04	–0,51*
C/N	0,10	0,12	–0,46*
CEC	0,09	0,12	–0,37*
Altitude	–0,12	–0,06	–0,54*
Slope	0.04	0.07	0.34*
Aspect	–0.1	–0.00	0.04
Dist. to the Valley bottom	0.03	–0.41*	–0.04

[1] Correlations with time were calculated excluding the natural paramo in the DCA ordination.

of succession (represented by the slope of the line). Assuming that the rate remains constant after 12 years, and extrapolating to the differences in community structure observed between first year plots and the NCP, the time necessary to reach the community structure of the NCP is estimated to be 30 years.

The analysis of divergence using chord distance showed a moderate increase in community heterogeneity along succession. The chord distance at the end of the studied interval attained levels similar to those found in the NCP (Figure 7). The high standard error of chord distances in plots with 11 and 12 years was the result of the lower number of plots included in these late stages of succession.

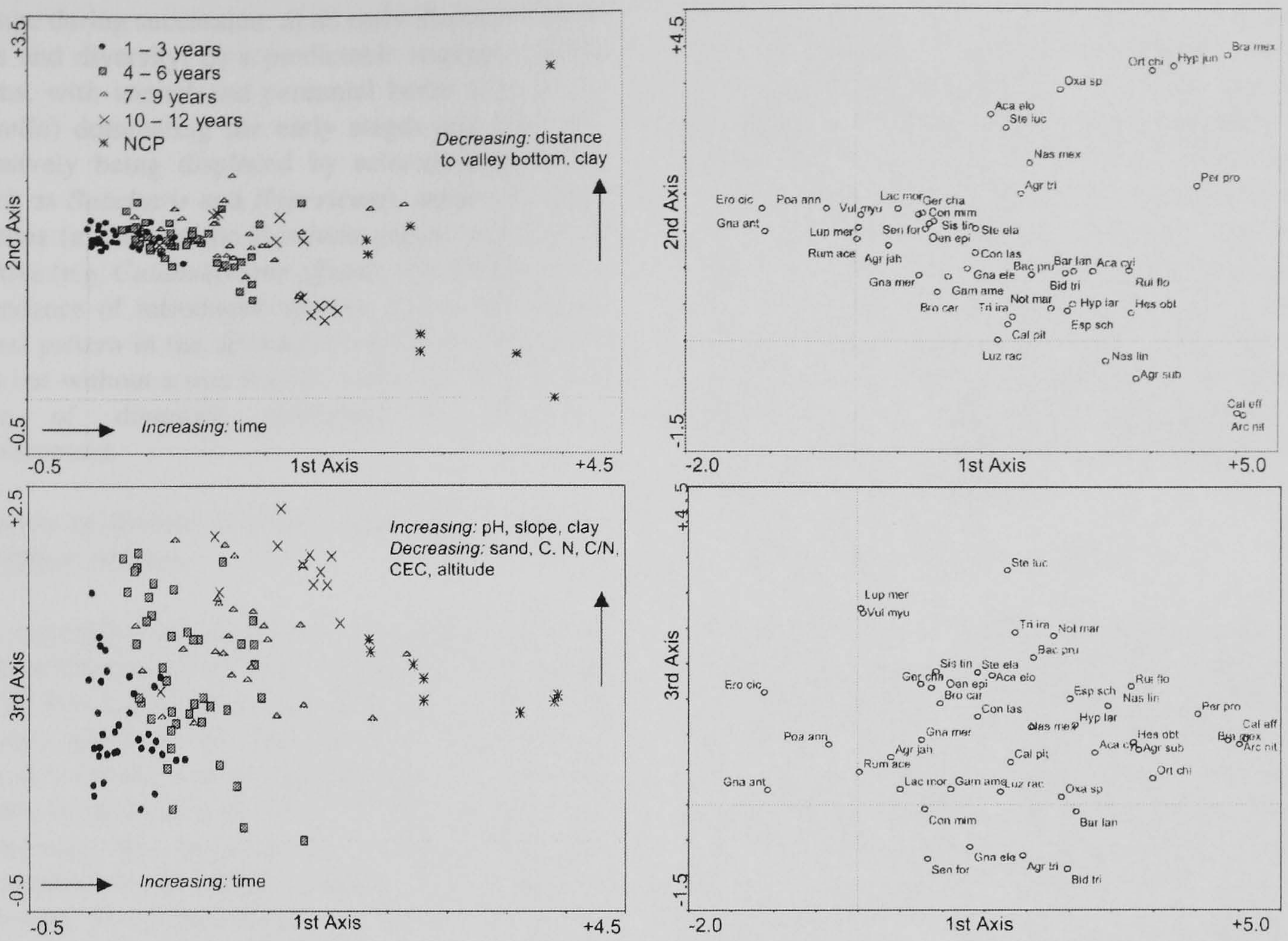

Figure 5. : DCA ordination diagrams of sites and species using the 1st vs. the 2nd axis and the 1st vs. the 3rd axis. Only the 44 more abundant species are shown for greater clarity. The eigenvalues for the three first axes were 0.587, 0.348 and 0.217 respectively. For species abbreviations see Table 1.

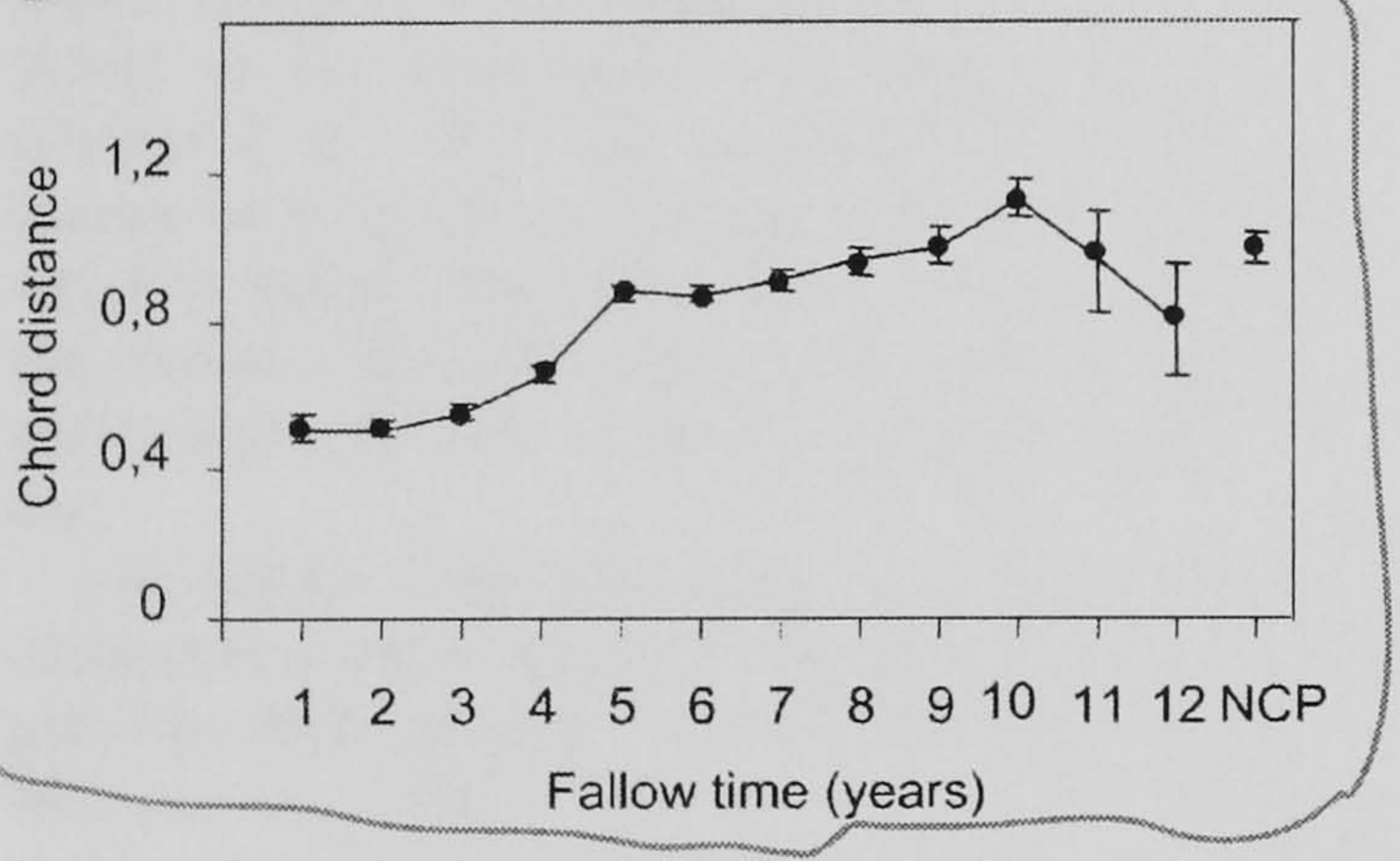

Figure 6. Successional rate calculated as a) the difference between average 1st year DCA scores for the 1st axis and subsequent years and b) average chord distance between 1st and subsequent years.

Discussion

Based on the results of this and other studies on long fallow agriculture in the paramo (Ferweda 1987; Moreno and Mora-Osejo 1994; Jaimes 2000), we can identify a set of common patterns for vegetation

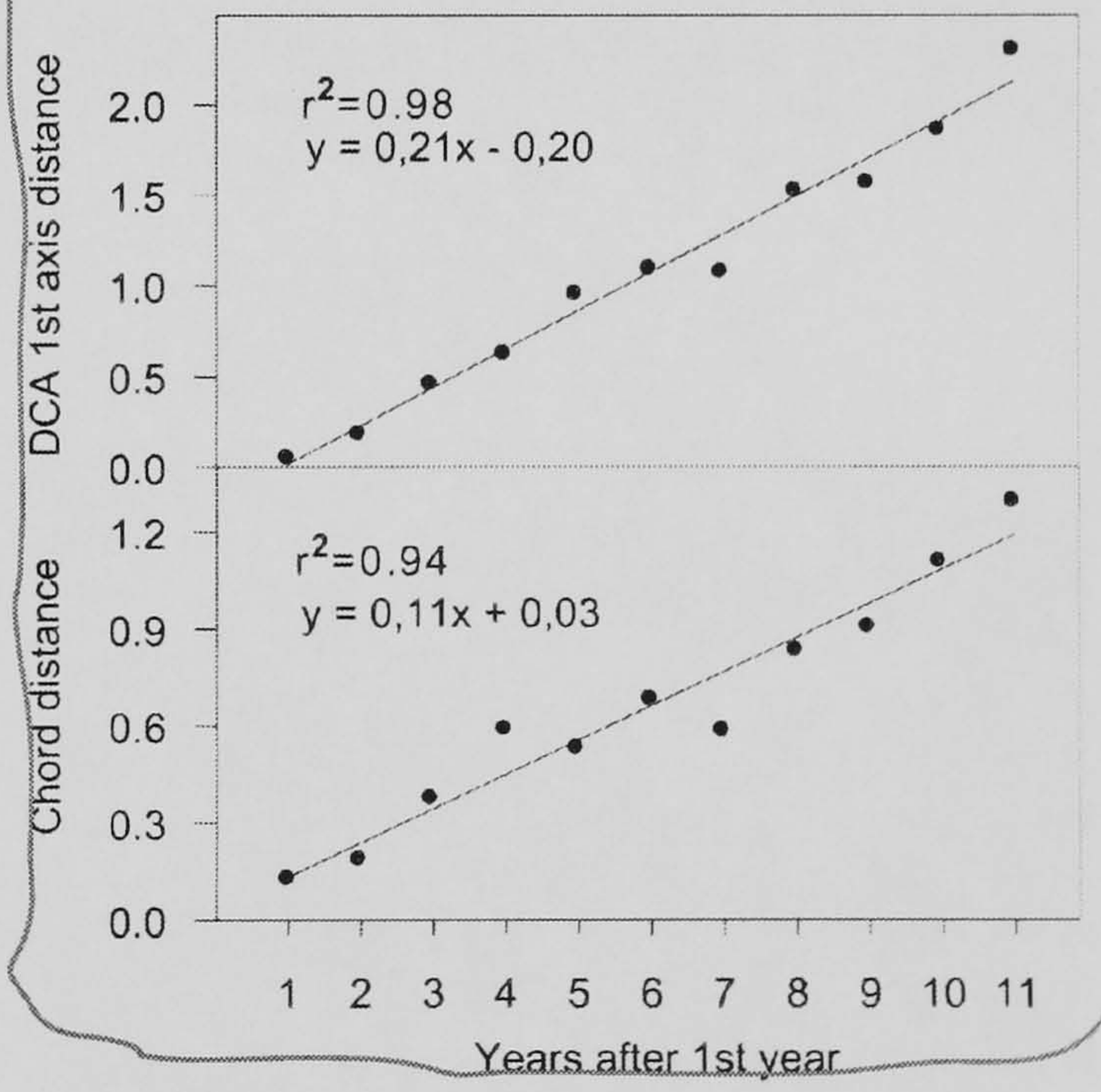

Figure 7. : Successional divergence calculated as the dissimilarity between plots of the same fallow age using chord distance as a dissimilarity index. Mean ± standard error.

change during succession: a) an early increase of richness and diversity; b) a predictable sequence of life forms, with annual and perennial herbs (e.g. *R. acetosella*) dominating the early stages and then progressively being displaced by sclerophilous shrubs (such as *Baccharis* and *Hypericum*), caulescent giant rosettes (mainly of the *Espeletia* genus) and tussock grasses (e.g. *Calamagrostis effusa*); c) a decline in the abundance of introduced species; d) a clear successional pattern in the abundance of the dominant species but without a true floristic relay and e) the existence of divergent pathways in vegetation development.

Patterns of diversity and the conservation value of the fallow strategy

The asymptotic behaviour showed by species richness early in the succession, with a stabilisation in a number of species far below that in the never cultivated paramo, questions the value of long fallow agriculture as a strategy for the conservation of paramo diversity (Sarmiento et al. 2001). This is especially true considering that the dominant species during early succession are all foreign invaders. The asymptotic behaviour of richness makes it difficult to asses the fallow time that would be necessary for a complete restoration (if it is ever achieved).

Our results contradict the generalisation of a higher diversity at intermediate successional stages linked to the intermediate disturbance hypothesis (Collins et al. 1995). The complete competitive exclusion of early species from late successional stages which is behind these predictions, does not occur in the paramo. Moreover, many of the rare mature paramo species are slow in re-colonizing the fallow areas.

Our results support the general tendency for early succession to show relatively vertical rank abundance patterns, which reflect low evenness (Bazzaz 1996; Wilson et al. 1996).

Life forms dynamics and their life history underpinning

In the context of the alpine tropics, a unique set of adaptations confer competitive advantage to life forms like the giant rosette and the sclerophilous shrub, which show a remarkable degree of convergence between the Andes and the mountains of East Africa (Hedberg and Hedberg 1979; Hedberg 1992). These life forms present morphological and ecophysiological adaptations to low temperature, extreme daily temperature fluctuations, water stress and nutrient deficit (Goldstein et al. 1984; Monasterio and Sarmiento 1991; Squeo et al. 1991; Rada 1993; Meinzer et al. 1994). Our results show that dominant shrub and rosette species are able to colonise from early stages of succession, presenting characteristics of *ruderal* and *stress tolerant* species (*sensu* Grime (1987)). However, as a result of trade-offs with their adaptations to the extreme conditions of the paramo, these species show relatively low photosynthesis and growth rates (Rada 1993). Hence, their abundance increases slowly in succession.

The decline of the introduced species

The colonisation ability of the introduced herb *R. acetosella*, has been related (among other factors) to its dual clonal and sexual reproductive strategy (Escarre and Houssard 1989). This species was introduced in the Venezuelan paramos as a weed of wheat by the Spanish Conquerors (Salgado-Labouriau and Schubert 1977). The clear successional decline of the introduced species could be related to the strong environmental filters of the paramo environment. In the climatically more extreme case of the Venezuelan super-paramo (above 4100 m) permanent plot studies have not found re-colonization by *R. acetosella* after disturbance (Smith and Young 1987). Interestingly, endemic fast growing forbs that are able to show explosive colonization, like *L. meridanus*, only have their abundance peaks after 4 or 5 years.

Patterns of species abundance: paramo regeneration as an autosuccession

Successional dynamics in which changes in abundance more than species replacement are the driving force have been termed *autosuccession* by Muller (1952) and *demographic succession* by Urbanska (1997). These and other authors (e.g. MacMahon (1981) and Svoboda and Henry (1987)) have proposed that in extreme environments (e.g. tundra and deserts), where few adaptive strategies are possible, succession is characterised by the progressive colonisation by the climax species without a real species replacement. Muller (1952) classified autosuccession as selective or non-selective, depending on the existence of a particular order in species colonisation. Paramo succession can be considered as a selective autosuccession, with the exception of the foreign species that act as colonisers and disappear during succession. Late species become established from early stages and increase in relative importance by virtue of *vital attributes* (*sensu* Noble and Slatyer (1980), see Vargas-Rios (1997) application of the approach to paramo post-fire succession) that allow them to *tolerate* as juveniles (sensu Connell and Slatyer (1977)) the high abundance of early ruderal species and to competitively displace them as they grow later in succession. The importance of competition as a mechanism explaining the decline of early species is suggested by their long persistence tails, since the alternative hypothesis of a decline caused by changes in environmental conditions is less compatible with this kind of incomplete exclusion (see Pickett (1982)).

Successional divergence and environmental heterogeneity

The pattern of successional divergence found in this study could be linked to the heterogeneity that is characteristic of these mountain environments. Divergence can be partially explained by the distance of the plots to the valley bottom, a variable that could be related to grazing pressure. The role of grazing intensity is supported by the fact that *Acaena elongata*, a species dispersed by cattle (Molinillo and Bremen 1993), is associated with small distances to the valley bottom on the 2nd axis of the ordination. Absolute altitude as an explanatory factor for divergence is probably linked to the identity of the natural vegetation surrounding the plots. The importance of surrounding vegetation in determining alternative succession pathways has been shown by del del Moral (1995) and Tsuyuzaki (1995) in primary mountain succession. In our case, a more dense shrub matrix, dominated by species like *B. prunifolia* and *S. lucida*, is found at low altitudes, coinciding with a higher abundance of these species in the low fallow plots.

The lower heterogeneity in community structure in the early succession stages is linked to the strong dominance of *R. acetosella*. Its ruderal habit ensures a universal presence at this stage, probably making its colonisation less dependent on local abundance.

In the mountain context, Rikhari et al. (1993) have associated divergent pathways of succession with differences in slope and soil depth between plots. Moreno and Mora-Osejo (1994) were able to link different pathways to fire and grazing intensity, while Ferweda (1987) associated them with differences in slope and altitude. Herben et al. (1993) suggested that this kind of individualistic or multiple pathway response could be the result of non-linearities linked with processes such as small scale spatial interactions between species.

Succession rates: slow and slowing down?

Our results of a constant rate of succession contradict the generally accepted hypothesis of a continuous slow down from initial stages to the "climax" (Shugart and Hett 1973; Armesto et al. 1991; Myster and Pickett 1994). While Brown and Southwood (1987) found a constant rate of species turnover, other authors have found a non-monotonic decrease in the rate of succession (Prach 1993) or a cyclic behaviour (Donnegan and Rebertus 1999).

The early rate of succession in our system seems to be determined by the constant decline of introduced species and the increase in abundance of the dominant paramo species as individuals slowly gain biomass. However, we could expect that later in succession, as community composition approaches a stable climax state (if it ever does), there could be a lower rate of succession. Hence, our figure of about 30 years for the regeneration of the paramo structure, assuming a constant rate, could be an underestimate.

Nevertheless, if we compare this estimation with physiognomic regeneration times calculated for forest ecosystems, which range from hundreds to thousands of years (MacMahon 1981), paramo succession seems relatively fast (partially as a result of the longer mean generation time for most trees compared to paramo species). This suggests we should be cautious about the accepted wisdom that vegetation regeneration in alpine environments is a very slow process (e.g. Billings (1973)), which has also found its echo in the paramo literature (e.g. Janzen (1973) and Smith and Young (1987), Horn (1989), Vargas-Rios (1997), Luteyn (1992)).

However, it is important to consider that the fast regeneration of paramo physiognomy does not imply a fast restoration of plant diversity or other ecosystem properties like soil organic matter (see Llambí and Sarmiento (1998)). Hence, our perception of the conservation value of the fallow strategy will depend on the importance we attach to these different properties of the ecosystem and their roles in the maintenance of the environmental services that we expect the paramo to provide.

Alternatives for management

Some alternative management practices emphasizing the conservation of paramo biodiversity can be suggested. Fallow agriculture, under the current trend of a reduction in fallow times, appears to be an inappropriate strategy from this perspective: it maintains large areas in successional stages that are less diverse than the mature ecosystem. This could contribute to the loss of a number of rare paramo species that are slow in recolonizing fallow areas. A possibility to speed up restoration would be to increase the abundance in early succession of some of the late or intermediate species. For example, the active planting of the fast growing *Lupinus meridanus* (a nitrogen fixer) in the first years of succession could improve the soil nitrogen status and accelerate the reinvasion of other species, a possibility that is being tested at the moment. Nevertheless, the intensification of agriculture seems to be the best alternative to reduce the total area under cultivation while maintaining production levels and improving biodiversity, given that representative natural areas are set aside for protection (Sarmiento et al. 2002). The selection of the areas to be protected must consider the high heterogeneity of paramo vegetation and the divergence in vegetation structure and composition associated with this heterogeneity. Another factor to be evaluated is the impact of grazing practices, which is likely to have a pronounced effect on vegetation structure and on successional patterns, pathways and rates.

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