Patterns and Mechanisms of Plant Community Assembly in an Industrially Degraded Ecosystem

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Contents

List of Tables

List of Figures

1. Introduction

For a long time, community ecology was a science primarily dealing with description of plant and animal associations (Keddy 1992). Over the past decades, it has developed towards becoming a predictive science. This is underlined by the current discussion of "assembly rules" for ecological communities (see Weiher & Keddy 1999a), which not only comprehends the description of community patterns, but also the processes and mechanisms leading to such patterns. Over the last 25 years, emerging concepts dealing with community assembly have been widely applied to a number of natural and semi-natural ecosystems, including wetlands (van der Valk 1981), forests (McCune & Allen 1985), dune communities (Houle 1996), cliff communities (Booth & Larson 1998, 2000) and grassland (Eriksson & Eriksson 1998). These concepts have also found their way into the restoration of such systems (see Keddy 1999 and Zedler 2000 for wetlands or Pywell et al. 2002 for grasslands).

However, this approach has rarely been applied to degraded land resulting from industrial activity, an anthropogenic ecosystem of growing importance, especially in densely-populated Europe (see Bradshaw & Chadwick 1980, Rebele & Dettmar 1996). Previous studies have been largely descriptive, including the vicinity of soda factories (e.g. Trzcinska-Tacik 1966, Dangien et al. 1974) and of magnesite factories (e.g. Kaleta 1975), fly ash heaps (e.g. Fischer 1976), chemical waste dumps (e.g. Klotz 1981), slag heaps (e.g. Punz 1989, Dettmar 1992), and the vicinity of phosphate fertiliser factories (Swieboda 1970, Heinrich 1984, Heinrich et al. 2001).
There are only a few studies of the vegetation of such sites extending beyond mere description. Examples for a more causal analytic approach, which has been advocated by Gemmell (1975), include the application of multivariate techniques to to infer causes and mechanisms of assembly (e.g. Wiegleb & Felinks 2001a,b), but there are also examples of a more experimental approach (e.g. Tischew & Mahn 1998).

This study addresses the processes of plant community assembly at a site adjacent to a former phosphorus-fertiliser factory. It is distinguished by a combination of both the descriptive and the experimental approach. The relevant concepts of community assembly are applied to the study of a number of factors thought to play a key role in governing successional dynamics and spatial patterns of vegetation at this industrial site. New insights into the mechanisms underlying the assembly of plant communities at such a site are thus provided.

2. The Steudnitz field site

2.1 Geography and solid geology

The field site (Figure 2.1) is a south-east facing slope situated near the village Steudnitz c. 10 km north of the town Jena on the western side of the Saale valley in the eastern part of Germany (51°01'N, 11°41'E). The Upper Buntsandstein base of the slope is covered by Triassic limestone. On the upper part of the slope there is a loess cover of c. 1-2 m thickness. The present study focuses on the lower slope, which ranges from 140-170 m above sea level, and is characterised by a slope angle of 35-40°. This part of the slope was strongly affected by the emissions of a fertiliser factory. Apart from a vegetation survey which is described in Chapter 6, most of the field investigations of this study were carried out near the factory (henceforth referred to as the proximal part). A soil and vegetation survey (Chapter 6) included also the distal part of the lower slope. The upper end of the lower slope is identified by a pronounced edge, beyond which the comparatively flat middle and upper parts of the slope (5-20° slope angle) extend up to 200 m above sea level.
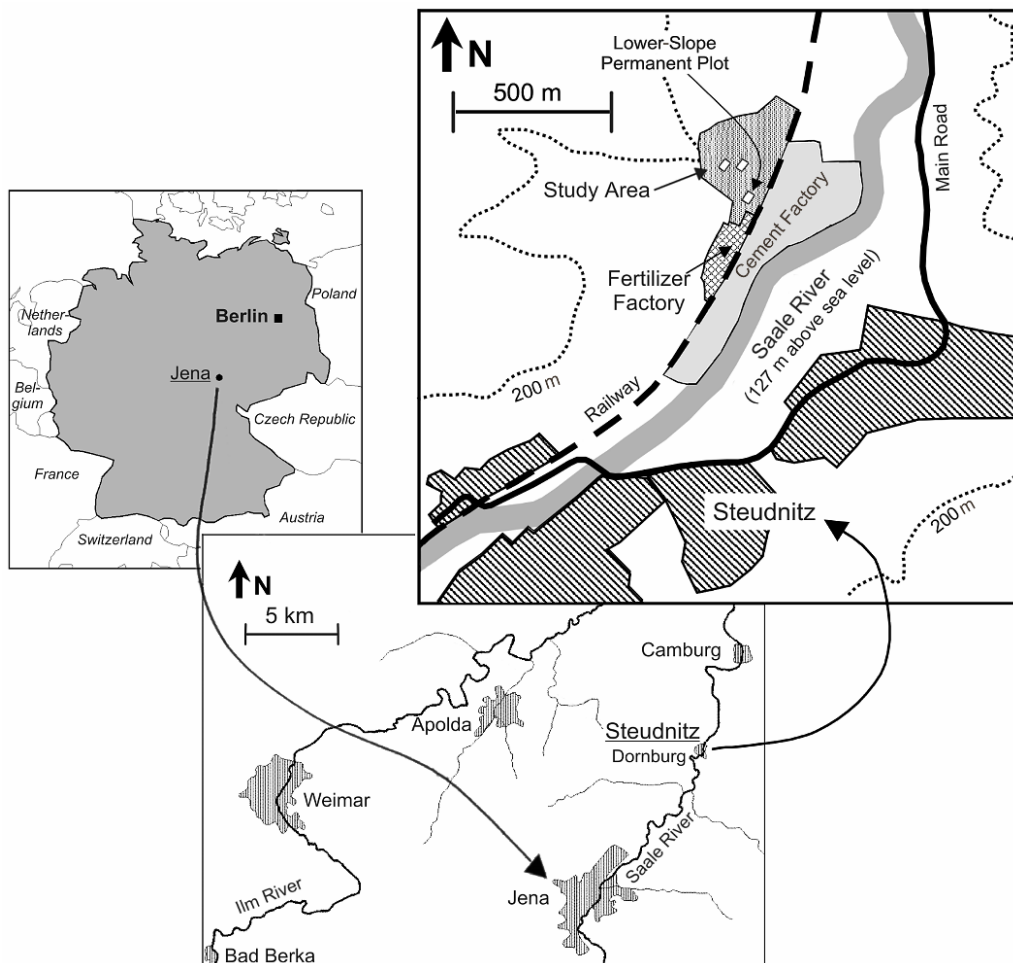
Figure 2.1. Map of the Steudnitz study area (from Heinrich et al. 2001, altered). The permanent plot on the lower slope is indicated by an arrow.

2.2 Climate

The climate in the middle Saale valley is warm and dry, as data from the University of Jena weather station show (Kluge & Müller-Westermeier 2000): the average annual precipitation for the period between 1966 and 1995 was 604 mm / year, the corresponding annual mean temperature was 9.5 °C. The precipitation maximum in the summer months is typical for the continental character of the regional climate (Heyer 1993). Between 1999 and 2002, when the present study was carried out, the temperatures were comparatively high, with annual means ranging between 10.1 °C (in 2001) and 11.1 °C (in 2000): the year 2000 was the year with highest annual mean temperature ever recorded in Jena. The annual amount of precipitation ranged from 541 mm in 2000 to 641 mm in 2001. The seasonal patterns of temperature and precipitation, based on long-term data (1966-1995), are outlined in Appendix 1, which also gives monthly values for the period between January 1999 and August 2002. The wind in the middle Saale valley blows predominantly from south and southwest.

2.3 Site history

Photographic evidence from the early 20th century indicates that the site was used at the time for vineyards and orchards. Between 1925 and 1942, and then again between 1945/46 and the mid-1950s cement was produced, the quarried limestone being used as a raw material (P. Hagenguth, personal communication). Subsequent large-scale production of Rhenania phosphate, a calcium sodium phosphate fertiliser (CaNaPO$_4$), began in 1957. In this process, phosphate rock, sodium carbonate and quartz sand were calcined in a rotary kiln at up to 1 200 °C (for details of the manufacturing process see Schmitz et al. 1980 or Young et al. 1985). Lignite and coal provided the energy for the production process. The original facility was closed down and replaced by a larger rotary kiln (Figure 2.2) in 1969/70. At peak production, c. 100 000 metric tonnes of Rhenania phosphate fertiliser were produced, equivalent to c. 25 000 metric tonnes of phosphorus pentoxide (P$_2$O$_5$). From 1969/70 until the late 1970s PK fertilisers were also produced: calcium sodium phosphate was mixed with potash, granulated in a drum by addition of water and then dried. Total production of these fertilisers was c. 50 000 metric tonnes. In April 1990, in the wake of reunification, the fertiliser factory was closed down. Cement and finely-ground limestone (for use as feed stuff additive for live-stock and as remedy for the acidification of forest soils caused by acid rain) are still produced in a cement factory at the site (Figure see 2.2).
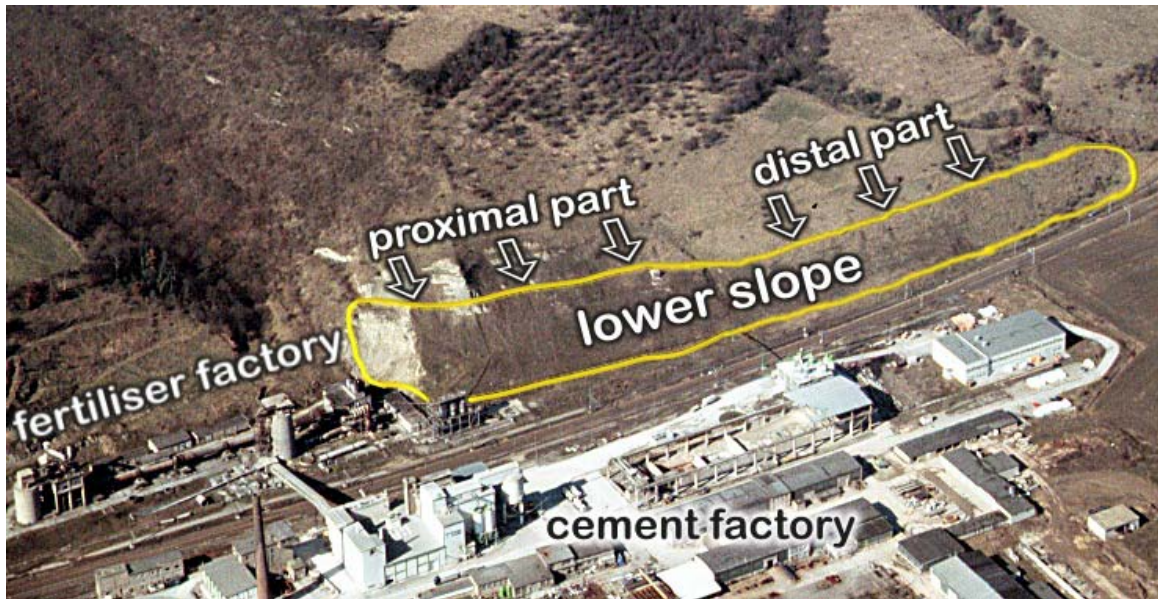
Figure 2.2. View of the field site, including the cement factory and the shut-down fertiliser factory with its rotary kiln of c. 100 m length (photo by W. Nerb). Field research for this study was mainly carried out in the proximal half of the lower slope, as pictured in the photo.

Figure 2.3. The proximal part of the lower slope in 1979 (photo by W. Heinrich).

2.4 Environmental impact of the fertiliser production at the Steudnitz site

Unlike cement production, fertiliser production had an enormous environmental impact in the vicinity of the factory, due to the alkaline dust particles emitted in the course of this production. It is estimated that from the chimneys alone, in peak years of fertiliser production, c. 3 000 metric tonnes of dust were emitted, and an additional c. 500 to 800 metric tonnes were released during the unloading of raw materials and the loading of end products (P. Hagenguth, personal communication). Between 1968 and the closure of the factory in 1990, local dust input was monitored by the 'Bezirkshygieneinstitut Gera', a regional authority dealing with issues of health and environment. In the immediate neighbourhood of the slope, monthly deposition during peak times of production could exceed 100 g/m² by far (Heinrich 1984). There were three main emission sources in the production process, the rotary kiln, the cooling drum, and the PK fertiliser facility, which accounted for 90 % of the dust emissions of the fertilizer factory (Vogler & Gebauer 1981). The raw materials rock phosphate and soda were emitted from the rotary kiln, whereas the other two facilities mainly emitted the end products, Rhenania phosphate and PK fertiliser. From the mid-1970s onwards, the dust emissions also contained a considerable amount of cadmium. At that time, Kola apatite, a rock phosphate from the Kola peninsula, USSR, was replaced by rock phosphate from North Africa (P. Hagenguth, personal communication). The cadmium content of the former is very low, whereas the latter is characterised by a very high cadmium content (McLaughlin et al. 1996). All three emission sources also emitted fluorine compounds, the fluorine being a component of both types of phosphate rock (McLaughlin et al. 1996, Rodin & Kosynkin 1999). Sulphur dioxide (SO_2) emissions from lignite-burning also played a considerable role (Vogler & Gebauer 1981). Sulphur trioxide (SO_3) and hydrochloric acid (HCl) are also mentioned in the literature (Heinrich 1984). Maximum pollution occurred between the end of the 1960s and 1980. With the termination of PK fertiliser production, pollution levels dropped to some extent.

The impact of the fertiliser production on the environment was already evident with tree death by the end of the 1950s. In the beginning, only the vegetation in the immediate vicinity of the fertiliser plant was affected: however, the zone of impact subsequently expanded (P. Hagenguth, personal communication), especially after the installation of the new rotary kiln at the end of the 1960s. The startling extent of these effects, which by then included the complete destruction also of the herbaceous vegetation, is depicted in Figure 2.3. The factory emissions, on a local scale, also affected agriculture. The fluorine compound emissions caused honeybees to die-off. Cattle suffered a high calf abortion rate. Hop plantations had to be relocated into unaffected areas (Vogler & Gebauer 1981). Orchards also suffered damage (Blechschmidt et al. 1984).

2.5 Soil conditions

Shallow skeletal rendzina soils with a poor water holding capacity are found at the lower slope study area. In the transition zone between the lower and the upper slope there are loess rendzina soils. Of special interest for the present study are the profound soil changes brought about by the fertiliser factory emissions. For some soil factors, these changes and the recovery after cessation of the emissions are well-documented. Table 2.1 summarises development in the proximal part of the lower slope for the period between 1990 and 1999.

Particularly noteworthy is the high initial total content of sodium indicating a high soil salinity at the time the fertiliser plant was shut down and its subsequent decrease by c. 50%. Soil pH at the time of factory closure was c. 9. The current value (c. 8) is only slightly higher than the pH of 7.0 to 7.5 found on comparable unpolluted soils in the region (Heinrich 1984). There was also a strong enrichment of the pollutants cadmium and fluorine in the top soil: cadmium levels were still high in 1999, however fluorine levels had markedly declined by then. This is due to the combination of high carbonate and phosphate levels with a high pH, leading to permanent cadmium fixation and immobilisation (McLaughlin et al. 1996) and, at the same time, favouring fluoride solubility (e.g. Larsen & Widdowson 1971). The gradients of cadmium, sodium and fluorine in soils in the vicinity of the fertiliser plant were investigated by Schäller (1987), Soldt & Einax (1998) and others. Maximum pollution levels were found north and northeast of the fertiliser factory (i.e. on the investigated slope), reflecting the wind conditions in the valley (see Section 2.2). Other changes caused by the emissions include exceedingly high levels of total and plant available phosphorus, and elevated levels of potassium over the entirety of the lower slope. The soil structure is also modified, due to the predominantly sand-grain-sized particles emitted (Metzner et al. 1997). This, in combination with the low level of organic matter and the slope aspect and topography, favours a quick drying of the soil after rainfall, particularly in summer. Due to the sparse vegetation cover at the proximal end of the slope during operation of the factory, organic carbon and total nitrogen contents are particulary low there. The situation in the distal part of the slope is different. There, a dense vegetation throughout the period of dust deposition allowed for the continuous retention of nitrogen in plant biomass. Other important aspects of soil chemistry such as salinity have not been included in analyses. Preliminary analysis of the composition of pollutant dust samples collected from sheltered locations at the factory site implies that levels of several additional elements and compounds were also elevated (Langer 2000, K. Metzner unpublished, M. Wagner unpublished). Results of dust composition analysis are summarised in Appendix 2. These data suggest that PO_4^{3-}, SO_4^{2-}, Cl^-, NO_3^- and K^+ were also integral in the initially very high soil salinity, in addition to the previously mentioned elevated levels of sodium (Na^+) and fluoride (F^-).

Table 2.1. Soil parameters (means ± standard deviation) from the years 1990 (1991), 1996 (1997) and 1999 in the proximal part of the Steudnitz lower slope (from Metzner et al. 1997, M. Wagner unpublished). Unless otherwise stated, n = 11 (1990-1996) or n = 24 (1999). * indicates values from 1991, ** indicates values from 1997 and n = 3, *** indicates n = 10. Unless otherwise indicated, total contents are given. Available contents of phosphorus and potassium are based on the CAL method (Schüller 1969). For heavy metals, limit values for soils with pH > 7 are given (EU Environment DG 2000).

Soil Factor		1990	1996	1999	proposed EU soil limit values
plant nutrients					
N	[%]	-	0.07 ± 0.07	0.11 ± 0.03	
P	[g × kg^{-1}]	83.9 ± 26.6 *	76.3 ± 26.3 **	-	
P (available)	[g × kg^{-1}]	-	8.6 ± 3.1 ***	4.4 ± 1.5	
K	[g × kg^{-1}]	6.7 ± 2.8	4.0 ± 1.2	4.9 ± 2.0	
K (available)	[mg × kg^{-1}]	-	281 ± 67	344 ± 137	
Mg	[g × kg^{-1}]	4.5 ± 1.0	4.0 ± 2.1	8.5 ± 2.4	
heavy metals					
Cd	[mg × kg^{-1}]	10.8 ± 7.9 *	7.8 ± 2.5	9.6 ± 4.3	1.5
Pb	[mg × kg^{-1}]	-	35.9 ± 6.4	20.9 ± 6.6	100
Cu	[mg × kg^{-1}]	-	18.6 ± 4.9	23.7 ± 5.8	100
Ni	[mg × kg^{-1}]	-	10.4 ± 2.2	13.8 ± 2.3	70
Cr	[mg × kg^{-1}]	-	10.6 ± 3.1	-	100
Zn	[mg × kg^{-1}]	-	57.9 ± 8.9	73.1 ± 11.4	200
other pollutants					
Na	[g × kg^{-1}]	16.1 ± 6.0	12.8 ± 5.5	7.9 ± 2.0	
F	[g × kg^{-1}]	8.2 ± 3.3	3.2 ± 0.9 **	-	
other soil parameters					
pH		9.14 ± 0.38	7.9 ± 0.10	8.09 ± 0.14	
sand	[%]	-	58	54	
silt	[%]	-	34	36	
clay	[%]	-	8	10	
organic C	[%]	-	3.7 ± 1.0	6.0 ± 0.6	

2.6 Previous investigations and the extent of earlier investigations on plant communities

This section gives an overview of previous ecological research on the impact of the fertiliser production in the Steudnitz area. It does not, however, provide an exhaustive list of all the works so far published.

Interest in the ecological and environmental implications of fertiliser production in Steudnitz first arose around 1980 (e.g. Peter 1979, Vogler & Gebauer 1981, Bährmann 1982). Heinrich's (1981a,b) review on the impact of air-borne pollution on ecosystems laid the foundations for a number of studies published in the 1980s, centring on the impact the emissions had on the slope ecosystem adjacent to the fertiliser factory. Most of this work dealt with the slope's insect fauna. Ecosystem functions were discussed by Schäller (1985), Heinrich & Schäller (1987) and Schäller et al. (1987). The plant communities were covered by the works of Heinrich (1984) and Marstaller (1987), the former dealing with higher plants and the latter with bryophytes.

Soil changes caused by the emissions were subject of a number of studies carried out after the factory closure. Temporal dynamics of the soil conditions were covered by Metzner et al. (1997). Soldt & Einax (1998) focused on spatial aspects of soil contamination. Langer & Günther (2001) described the lingering effects on the soil microbial community and its metabolic activity several years after cessation of the emissions.

Dying-off of the vegetation occurred in the immediate vicinity of the factory soon after fertiliser production began. Around 1980, vegetation on the slope showed a clear zonation, reflecting the spatial pollution gradient resulting from the more than two decades of emissions (Heinrich 1984). Closest to the factory, the lower slope was almost bare. Slightly further away from the factory, a near-monoculture of the halophytic grass *Puccinellia distans* (JACQ.) PARL., with scattered *Atriplex sagittata* BORKH. plants, covered the slope (nomenclature follows Rothmaler 2002). This was followed at the middle slope, and also in the distal part of the lower slope, by a similarly species-poor community dominated by the grass *Elytrigia repens* (L.) DESV. EX NEVSKI. Even further up on the slope, where pollutant input was negligible, was calcareous *Bromus erectus* HUDS. grassland. Such zonation more or less persisted until, in 1990, fertiliser production ceased. In that year, permanent plots were established on the lower, middle and upper slopes, in order to monitor vegetation changes to be expected in the course of ecosystem regeneration (Heinrich et al. 2001). Vegetation on each permanent plot (20 × 30 m, divided in 24 subplots of 5 × 5 m) was recorded in 1990 and all subsequent years by visual cover estimates, using the Braun-Blanquet scale (Braun-Blanquet 1964). Results are presented and analysed for the period 1990-1999 by Heinrich et al. (2001). In the proximal part of the lower slope, gradual natural amelioration of soil conditions, reflected in

Table 2.1 by a decrease in sodium and fluorine contents and a decrease in soil pH, allowed immigration of higher plants other than *Puccinellia distans* and *Atriplex sagittata*, and also of bryophytes (Figure 2.4).
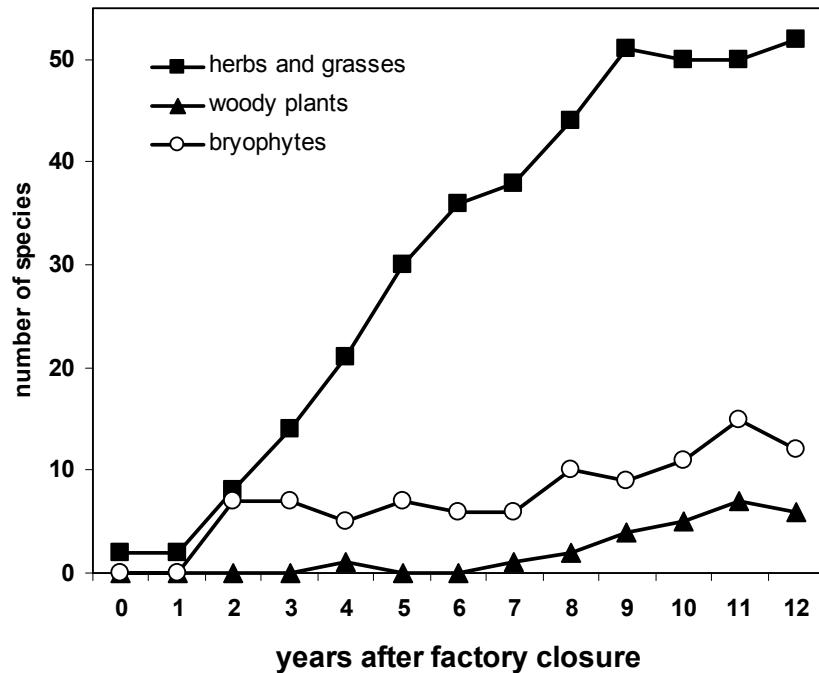
Figure 2.4. Development of plant species richness on the lower slope permanent plot at the Steudnitz field site after fertiliser factory closure in 1990 (data from Heinrich et al. 2001 and unpublished).

Subsequently, the species-poor *Puccinellia* community gave way to the assembly of a diverse ruderal plant community. The *Puccinellia distans* population collapsed, and at the same time, *A. sagittata* and *Artemisia vulgaris* L. achieved dominance (Heinrich et al. 2001). In 1997, woody plants gained a foothold on the lower slope. Currently, this part of the slope is dominated by two composite species, in spring by the annual *Senecio vernalis* WALDST. ET KIT., and in summer by *Picris hieracioides* L., which is perennial. In 2002, 58 species of higher plants (6 of them woody plants) and 12 broyphyte species were recorded on the lower slope permanent plot (Heinrich unpublished). In contrast, the distal end of the lower slope at present is still vegetated by a species-poor *Elytrigia repens* grassland.

In addition to the survey on permanent plots, vegetation also was recorded on two occasions along transects reaching from the bottom of the slope to the upper slope, in 1996 (Scholze 1997) and again in 1999 (Stephan 2001). Scholze (1997) analysed spatial vegetation patterns and correlated them with soil data used to characterise the gradient of pollution. Stephan (2001) repeated this three years later, along the same transects and using the same method, which allowed characterisation of the development between 1996 and 1999. The present thesis extends these previous works and puts the accumulated knowledge on the regeneration of this ecosystem into the context of environmental-filter concepts, which are outlined in Chapter 3.

3. The conceptual framework of this study: environmental-filter concepts

The question of what factors determine the composition and dynamics of ecological communities has been at the heart of ecology ever since it was established as a science. Questions associated with community assembly were already addressed in the early academic disputes on the nature of plant succession (e.g. Clements 1916, Cooper 1926, Gleason 1926). And in 1927, the animal ecologist Charles S. Elton coined the phrase **limited membership** of the community (Elton 1927). This all happened long before Jared Diamond (1975), in his study of bird communities on the Bismarck Archipelago in the southwest Pacific, coined the term **assembly rule**, invoking interspecific competition to explain apparent constraints on species combinations he had observed. Diamond's (1975) approach is restricted to the demonstration of non-random community patterns, and as such differs from current approaches.

3.1 Assembly rules

A direct descendant of Diamond's (1975) original approach on community assembly is the so-called **null model analysis**, which aims at the demonstration and analysis of non-random community patterns (see Gotelli & Graves 1996), which Diamond called assembly rules. Most community ecologists today use the term assembly rule for the specification of processes leading to such non-random patterns, although at present, different definitions of this term are used by different authors (Belyea & Lancaster 1999, Morin 1999, Weiher & Keddy 1999a): the major area of disagreement is as to whether the term should be used only for biotic constraints on community development or for other kinds of constraint too (Booth & Larson 1999).

A number of authors prescribe to the view that only biotic interactions may comprise assembly rules (Lawton 1987, Wilson 1999, Belyea & Lancaster 1999). Wilson and co-workers define assembly rules as "ecological restrictions on the observed patterns of species presence or abundance that are based on the presence or abundance of one or more other species or groups of species" (Wilson & Gitay 1995: 369). Wilson (1999) lists several examples of biotic assembly rules for higher plants, derived from interspecific competition, including **limiting similarity**, **guild proportionality** and **biomass constancy**. However, higher plants generally represent only one part of the community of organisms at a given site, and the restriction of a study to a part of a community can obscure higher-order patterns and dynamics that might be important for understanding lower-level phenomena (Samuels & Drake 1997). The potential importance of other functional groups of organisms in the assembly of plant communities as well as the need for further research on these aspects of community ecology is emphasised by several authors (e.g. Lawton 1987, Walker & Chapin 1987).

An alternative approach is advocated by Keddy and others (Keddy 1992, Weiher & Keddy 1999b, Booth & Larson 1999). According to these authors, assembly rules should include any constraint on the entry of species into the community. To make the previously descriptive soft science community ecology a hard science allowing for predictions, Keddy suggests the development of assembly rules based on species traits, including morphological, physiological or ecological features (Keddy 1992). For obtaining the necessary autecological data, he favours a screening approach (Keddy 1992). Numerous examples of this predictive approach based on screening methods can be found in the literature (e.g. Noble & Slatyer 1980, van der Valk 1981, Gaudet & Keddy 1988, Stockey & Hunt 1994, Diekmann & Falkengren-Grerup 2002). However, in the case of morphospecies consisting of a whole range of specialized genotypes, predictions based on autecological data from a different population (i.e. information extracted from the literature) might be unsound (for an elaboration of this problem see Harper 1982). Life-history typing and functional typing can be considered as variations of the screening theme. Advantages and disadvantages of certain plant life-history types under different environmental regimes are discussed at length in Crawley (1997a). A valid argument for the functional types approach is the fact that species traits are not acted upon independently from each other, since selective pressures act on integrated individuals (Gould & Lewontin 1979). An example widely used in Europe is the C-S-R classification of plant functional types, which is based on resource use and response to disturbance (Grime 1974, 1977).So far, c. 1 000 species of the British flora were classified according to these plant strategy types (R. Hunt, personal communication).

A third definition of assembly rule is based on the observation that different sequences of species invasion may lead to different outcomes in terms of community composition (e.g. Lockwood 1997, Samuels & Drake 1997). A number of studies using experimental microcosms (e.g. Drake 1991) or computer models (e.g. Lockwood et al. 1997) have demonstrated how the order of colonisation can induce so-called **priority effects** in simplified model systems. Advocates of the 'biotic interactions only' approach view priority effects as interactions between biotic mechanisms and dispersal constraints (Belyea & Lancaster 1999), masking actual biotic assembly rules (Lawton 1987). Young et al. (2001) critically discuss the limitations of the priority effects approach and question its applicability in real ecosystems, their judgement being based on the apparent lack of realism in mesocosm experiments and simulation models. Accordingly, they use the expression "assembly model" for this approach, and clearly discriminate between this term and "the related theory of assembly rules" (Young et al. 2001: 7).

3.2 Limited membership and environmental filters

Booth & Larson (1999) rightly point out that at the core of the current assembly rules discussion there are a number of topics which have already been debated over the last century. So does the

'biotic interactions only' approach to assembly rules have a lot in common with the concept of the realised niche of a species as opposed to its fundamental niche (Hutchinson 1957). And the 'any constraint' approach is reminiscent of the discussion of Elton's (1927) term limited membership in Roughgarden & Diamond (1986). Roughgarden & Diamond (1986) suggest three categories of causes for limited membership in ecological communities. These are (a) different capacities of candidate species to cope with the physico-chemical conditions of the environment, (b) dispersal limitations, and (c) species interactions. Advocates of the 'biotic interactions only' approach to assembly rules acknowledge the existence of categories (a) and (b) (Putman 1994, Belyea & Lancaster 1999), but call them external constraints, being fundamentally different from assembly rules (Belyea & Lancaster 1999).

While agreeing with the need for a rigorous, predictive approach to community ecology, including all kinds of constraints on community membership (see Keddy 1992), the approach chosen in this study is to leave the discussion about the exact definition of the term assembly rules to others (see Weiher & Keddy 1999a, Temperton et al. in press).

Instead, a different concept, based on **environmental filters**, was chosen for this study. It is not uncommon to characterise the different causes for limited membership as filters, through which applicant species have to pass in order to become members of a community (e.g. Keddy 1992, Diaz et al. 1998). The entirety of these applicant species often is referred to as **species pool** (for a review of the concept see Zobel et al. 1998). Zobel distinguishes between a **regional species pool** occurring in a certain region that is capable of coexisting in the target community and a smaller subset of species, the **local species pool**, able to migrate to the community relatively rapidly (Zobel 1997), by which he means within a few years.

In accordance with Roughgarden & Diamond's (1986) categories, a simple, conceptual, filter-model such as the one by Lambers et al. (1998) may consist of three types of filter (see Figure 3.1).

In this model, species from a regional pool of species have to pass through a series of filters to establish in the local vegetation. These filters are the **historical filter** (Can a species reach the site or is it already present in a dormant state?), the **abiotic filter** (Can the species cope with the physico-chemical conditions at the site?) and the **biotic filter** (Can the species cope with competitors, predators, herbivores and pathogens?). Several authors, including Diamond & Roughgarden (1986) and Lambers et al. (1998), acknowledge that there are interactions between different filter components that are important and need to be considered. Examples are the aforementioned priority effects, but also the co-determinination of community membership by environmental limits and species interactions (Roughgarden & Diamond 1986), the latter including both detrimental (e.g. competition) and beneficial (e.g. facilitation) interactions. To accommodate such interactions and potentially resulting feedback loops, a dynamic environmental filter model was developed by Fattorini & Halle (in press). Their model is depicted in Figure 3.2.
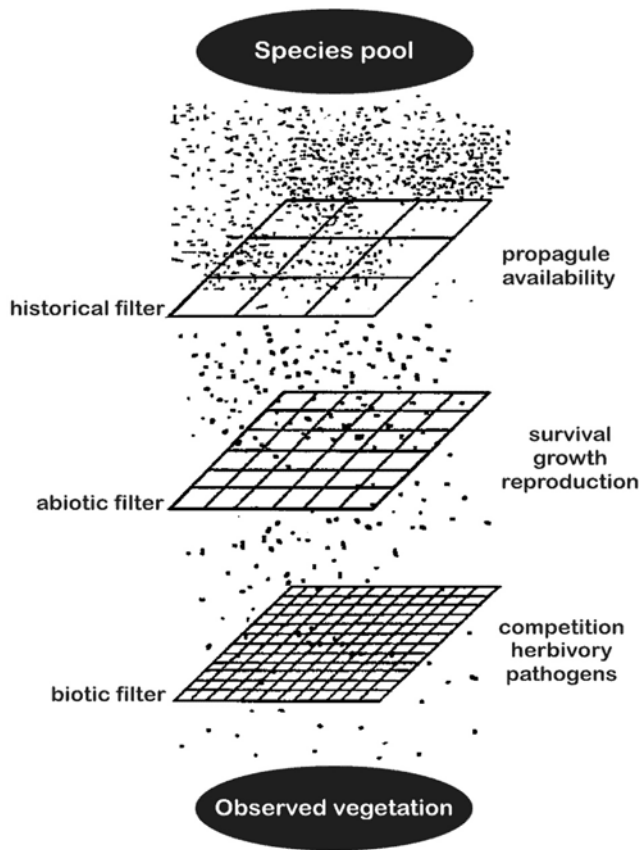
Figure 3.1. A simple filter model showing how a local plant community can be derived from a larger regional species pool (modified from Lambers et al. 1998).
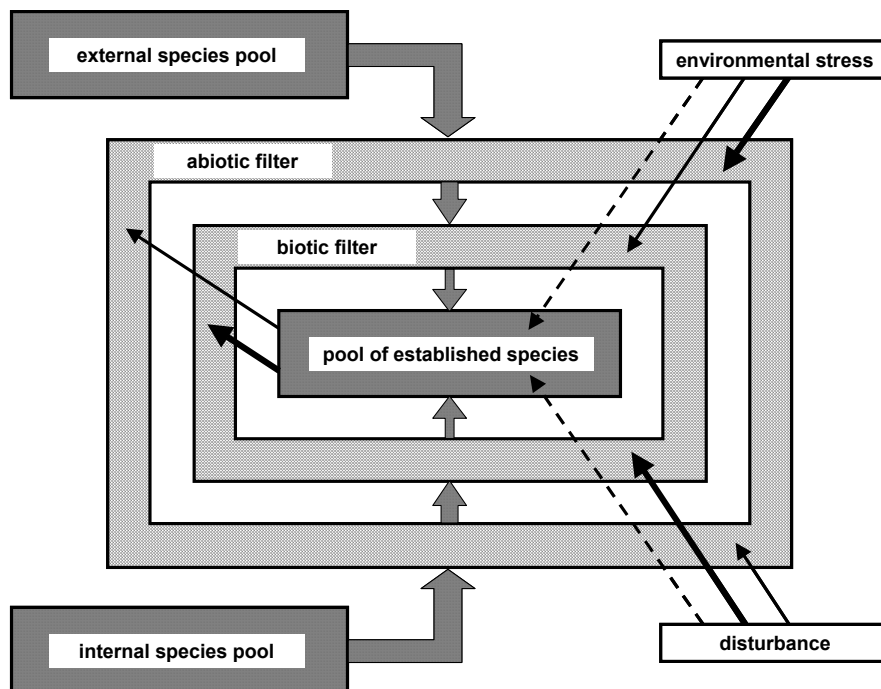
Figure 3.2. The dynamic environmental filter model by Fattorini & Halle (in press). This model includes feedback loops between the established community and different filters, thus emphasising the complexity of ecological assembly processes.

13

Since the focus of the present study is on isolated filter components rather than on interactions between different filters or filter components, the terminology used in this thesis is geared towards compliance with the simple environmental filter model by Lambers et al. (1998). To further investigate how environmental filters, past and present, may influence plant community development at the Steudnitz field site (Chapter 2), I conducted a number of studies, which are described fully in the following chapters. Chapter 4 deals with the influence of seed dispersal – a component of the historical filter – and of a gradual reduction in soil salinity – a component of the abiotic filter – on the order of colonisation. In Chapter 5, the soil seed bank at the site, another component of the historical filter, is described. Chapters 6 and 7 focus on the present role of the abiotic and biotic filter. In Chapter 6, a multivariate approach is used to link spatial vegetation patterns with underlying soil conditions. This analysis allows conclusions to be drawn regarding the current role of abiotic and biotic filter mechanisms and a comparison to be made between observed vegetation patterns and predictions based on life-history theory. In Chapter 7, changes in the plant community structure, induced by experimental nutrient addition, are interpreted in the context of biotic and abiotic filters. In Chapter 8, the final chapter of this thesis, all findings are summarised and discussed within the context of the environmental-filter concept.

4. Influence of seed dispersal capacity and seedling salt tolerance on order of colonisation

4.1 Introduction

Natural establishment processes on derelict land are known to display a high degree of stochasticity (e.g. Bradshaw 1987). Nevertheless, there is growing evidence that a disproportionately large number of plant species colonising industrially created habitats feature efficient mechnisms for long-range seed dispersal (e.g. Bradshaw 1983, Grime 1986). This suggests that poorly-dispersed species which are appropriately adapted to site conditions might be absent from a particular site owing to their inability to reach this site (Ash et al. 1994).

It has been pointed out that industrially created habitats resemble islands set in a solid sea (Gray 1982): they differ from their surroundings in soil chemistry and fertility and physical properties such as water supply. This was indeed the case for the Steudnitz field site. As mentioned in Chapter 2, recolonisation of the proximal part of the lower slope by a diverse flora began two years after the cessation of pollutant dust deposition, indicating the initial existence of an abiotic filter too strong to be overcome by species in the first year after factory closure. The main components of this filter may have been the high soil salinity and pH, which in subsequent years, as a result of leaching processes, declined to normal levels (see Chapter 2). This mitigation of the abiotic filter due to natural amelioration of soil conditions should have allowed for the gradual establishment of increasingly less tolerant species.

By now, the phase of rapid colonisation by species from the local species pool (*sensu* Zobel 1997) is more or less completed, as indicated by the levelling out of the lower-slope permanent-plot species richness curve at c. 50 species (see Figure 2.4). Due to Heinrich et al.'s (2001 and unpublished) permanent plot data, each species can be classified with respect to the time of their first appearance on the permanent plot. This chapter deals with the influence of seed dispersal capacity and of the gradual amelioration of soil conditions on the order of species colonisation at the Steudnitz field site. The former aspect is dealt with by investigating the question of whether plant species with a potential for long-distance dispersal, as conferred by a plumed seed morphology, appeared earlier in the vegetation. The latter aspect is exemplified by the salinity component, investigating the question of whether species with more salt-tolerant seedlings tended to colonise the site earlier. This chapter also examines whether there is a stronger correlation between seedling salt tolerance and order of colonisation for species with efficient long-distance dispersal than for those without. Such a stronger correlation for species featuring mechanisms for efficient dispersal might result from a higher probability of immediate colonisation once the conditions become suitable for colonisation (i.e. soil salinity falls below a species-specific critical threshold).

4.2 Methods

4.2.1 Role of dispersal type

Vegetation data from the Steudnitz lower slope permanent plot (Heinrich et al. 2001 and unpublished) were used as baseline data for the order of colonisation. All 80 species colonising the lower slope permanent plot between 1992 and 2002 were classified into two groups, according to the occurrence of a plumed seed morphology. A comprehensive seed morphology database (Müller-Schneider 1986) was used for this classification. For statistical analysis, species were ranked according to the first year of occurrence on the permanent plot, and a Mann-Whitney test was employed to test for significant group differences in the time of first appearance in the vegetation.

4.2.2 Role of seedling salt tolerance

4.2.2.1 Experimental design

The effects of salt stress on seed germination and on seedling radicle extension were tested under controlled conditions, using seeds of species recorded on the permanent plot which were locally collected in the respective field season and stored at room temperature for a period of several months. The intention was also to test effects of pH, but the use of buffer solutions produced toxicity problems, so pH effects were omitted. Salt stress was generated by using sodium chloride (NaCl) solutions of different concentrations.

The two species initially present in the permanent plot, *Puccinellia distans* and *Atriplex sagittata*, as well as 22 species colonising the site between 1992 and 1999 (12 species with plumed seeds and 10 without, see Appendix 3) were tested. Species from the pool of colonisers were chosen to represent the whole range from early colonisation in 1992 to late colonisation in 1999. For *Atriplex sagittata*, a species with dimorphic seeds (Mandák & Pyšek 2001a), only black seeds were tested, since in that year only a small number of brown seeds was produced by the plants. Seeds of two of the species, *A. sagittata* and *Chenopodium rubrum* L., were subjected to cold-moist stratification (five weeks in the dark at 5 °C) prior to the experiment to break dormancy. The stratification requirements of the two genera are documented in the ECOFLORA database (Fitter & Peat 1994). The experiment consisted of five different treatments, one distilled water control treatment and four different sodium chloride solution treatments, having osmotic potentials of -0.4, -0.8, -1.2 and -1.6 MPa respectively. The necessary calculations were carried out with the help of the computer programme SPMM (Michel & Radcliffe 1995). For each species and treatment there were four replicates. Each replicate consisted of 20-25 seeds of the respective species (see Appendix 3) sown into a 9 cm Petri dish containing two layers of Whatman™ No. 1 filter paper and 12 ml of the respective solution to moisten the filter paper. The Petri dishes were kept under a diurnal regime of 12 h day (light, 22 °C) and 12 h night

(dark, 14 °C), because daily temperature fluctuations of this magnitude are known to promote seed germination in a wide range of temperate species (Grime et al. 1981).

In order to keep the solute potentials constant, Petri dishes were sealed with Parafilm™ at the beginning and between counts, and at each count one quarter of the solution was replaced. Counts were carried out for the first time three days after the onset of the experiment, and then after 7, 14, 21, 28, 35, 42 and 49 days. On each occasion, the numbers of germinated seeds, seedlings with a radicle length ≥ 5 mm, and seedlings with a radicle length ≥ 10 mm were counted. Seedlings with a radicle length ≥ 10 mm were removed from the experiment.

4.2.2.2 Data analysis

A salt tolerance index (I_S) was calculated for each of the tested species in order to characterise salt tolerance at the early seedling stage:

$$I_s = \frac{1}{4} \times \left(\sum_{i=1}^{4} n_i \right) / n_c \qquad (4.1)$$

where n_i and n_c are the numbers of seedlings with ≥ 5 mm radicle extension for the four salt treatments and the control treatment, respectively. Therefore, a species completely insensitive to salt concentrations over the range tested will have an index value of close to 1.0, whereas a very sensitive species failing altogether even at the lowest salt concentration will have a value of zero. Strength of association between salt tolerance index I_s of a species and time needed for species establishment after factory closure was measured using Spearman rank correlation. This method is recommended when observations are in the form of indices, in which case the more strict assumptions of Pearson correlation are likely to be violated (Fowler et al. 1998). Significance of the correlation (at $P < 0.05$) was tested using the one-tailed test.

4.3 Results

Figure 4.1 shows the patterns of arrival of colonising species with plumed propagules (n = 24) and those without (n = 56) for the period from 1992 to 2002. Two thirds of the species with plumed propagules colonised the slope between 1992 and 1995, and only one species of this group colonised after 1999. In contrast, no such colonisation peak in the early 1990s existed for the group of species without plumed propagules (Figure 4.1). For this group, the rate of colonisation only marginally decreased with time. The Mann-Whitney test confirms that colonisation of the permanent plot by those species having plumed seeds occurred significantly earlier (two-tailed test, $P = 0.009$) than colonisation by species lacking this adaptation.
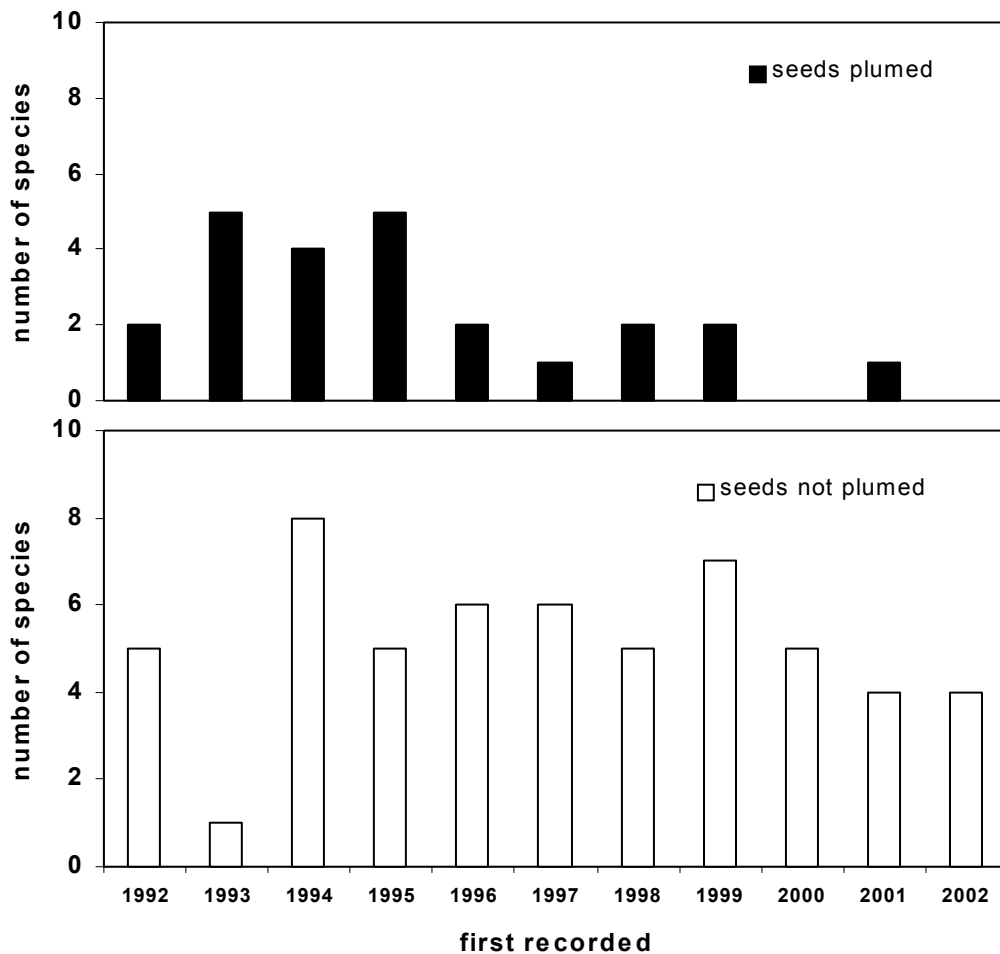
Figure 4.1. Total numbers of species colonising the Steudnitz lower slope permanent plot between 1992 and 2002, divided up into those with plumed propagules and those without (data from Heinrich et al. 2001 and unpublished, classification based on Müller-Schneider 1986).

Since the mechanism of seed dispersal seems to have influenced the order of colonisation at the slope, the Spearman rank correlation was used to establish a link between salt tolerance and time of colonisation for both groups of species separately, those with a plumed seed morphology and those without. Spearman rank correlation yielded very similar and significant (one-tailed test) correlation coefficients for both groups (plumed species: n = 12, r_s = -0.66, P = 0.010; species without plumed propagules: n = 10, r_s = -0.63, P = 0.026). A test for significant differences between the two correlation coefficients was not carried out. Due to both the difference between the two coefficients as well as the sample sizes being rather small, the power of such a test would have been very small (Zar 1999). The correlation between time of first appearance of a species and its seedling salt tolerance index I_S is visualised in Figure 4.2. The patterns displayed in this figure suggest that

salinity affected colonisation in the first few years after factory closure, including 1994. The resulting index values for each species are found in Appendix 3.
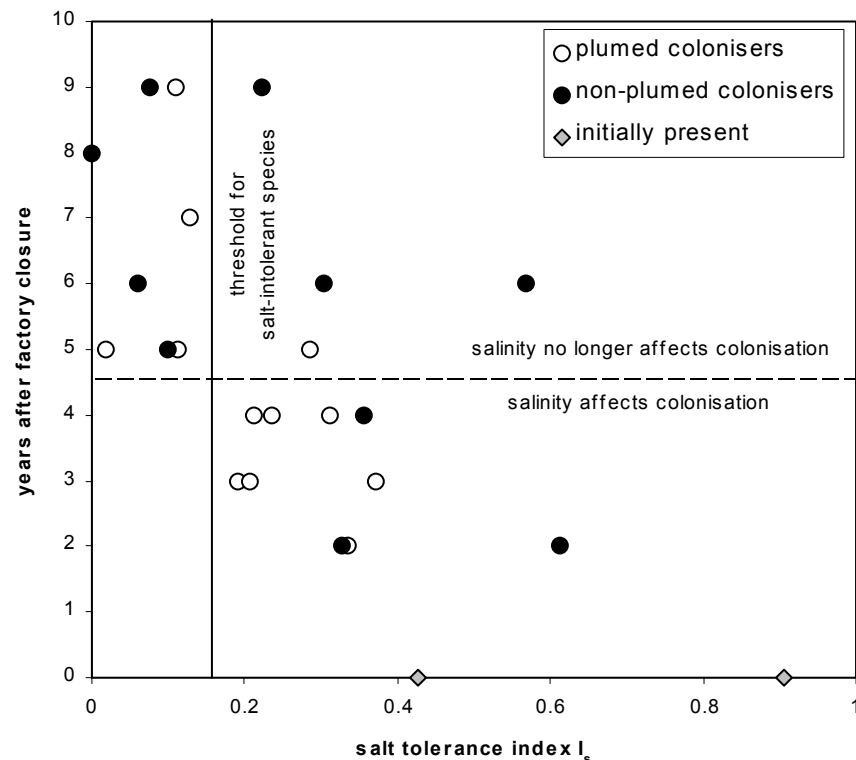
Figure 4.2. Scatter plot of time between factory closure and colonisation vs. seedling salt tolerance index I_S. The species initially present were *Puccinellia distans* ($I_S = 0.91$) and *Atriplex sagittata* ($I_S = 0.43$).

4.4 Discussion

4.4.1 The method used for salt tolerance characterisation

When interpreting the results of the Petri dish experiment, it must be kept in mind, that soil salinity at the field site was caused by a mixture of salts, including ions other than sodium and chloride. NaCl was selected for this study to allow comparison with results of other published work, the great majority of which also uses this salt.

It is not uncommon to use germination (defined as a visible protrusion of the radicle from the seed coat, see Kitajima & Fenner 2000) for the characterisation of salt tolerance (see Ungar 1995 and references therein). Indeed, several authors have found a correlation between germination response and salinity gradient in the field (e.g. Rozema 1975, Bakker et al. 1985, Mariko et al. 1992). Halophytes, on average, seem to be able to germinate at somewhat higher salinities than glycophytes (Ungar 1995). However, the relationship is not clear-cut. Seeds of a number of highly salt-tolerant plants exhibit osmotically induced dormancy (Ungar 1995). There is evidence that in both

glycophytes and halophytes germination is often controlled by osmotic potential in the surrounding medium, rather than by specific ion effects (Schratz 1934). This is confirmed by comparative experiments on the same species as in the present study, using either polyethylene glycol 6000 or NaCl for the simulation of corresponding osmotic potentials (data not shown). In contrast, ion toxicity mainly affects the subsequent process of seedling growth, thus lending support to Rozema's (1975) hypothesis that the ability of seedlings to tolerate salt stress is a much better measure for the characterization of salt tolerance than the ability to germinate.

Thus, in the present study counts of seedlings with radicles longer than 5 mm were used rather than germination rates. This is less arbitrary than it seems. In the distilled water control treatment, even in those species with the smallest seeds almost 100 % of the germinated seeds managed a radicle extension beyond 5 mm. In contrast, even low salinity levels cause necrosis of the radicle tip in a number of glycophytes almost immediately after the onset of germination, preventing any further root growth (data not shown). Therefore, seed size and seed reserves do not matter as much as one would expect. A comparison of the calculated salt tolerance index values with the relevant literature shows that the species with an I_s value > 0.35 are actually known to display some degree of salt tolerance in Central Europe (see Appendix 3). The only exception is *Bromus japonicus* Thunb., a rather large-seeded species which is typical for open ruderal habitats but rare in Germany (Rothmaler 2002). According to Cooper & Jean (2001), however, it is an abundant species in saline prairie habitats in the Northwestern Great Plains of North America. There, it is also found at saltwater blowout sites from the oil industries (Halvorson & Lang 1989). Overall, comparison with the literature therefore suggests that the calculated salt tolerance index could be useful for characterising salt tolerance in glycophytes. As the possibility of seed size exerting some influence on the results cannot altogether be ruled out, air-dry seed weights (determined by weighing of batches of 500 seeds from the local collections) are provided in Appendix 3.

4.4.2 Order of colonisation

Plumed-propagule species entered the plant community at the Steudnitz field site earlier than species without this dispersal adaptation. This study, like previous studies dealing with plant colonisation of industrially created habitats (e.g. Bradshaw 1983, Grime 1986, Ash et al. 1994), underlines the importance of efficient long-range dispersal in the early colonisation of derelict industrial sites. The same applies to plant community succession in other open sites (Fenner 1987a).

Unlike other studies this study deals with a secondary succession rather than with a primary succession, as the substrate of previous plant growth was not destroyed or removed by the disturbance caused by the nearby fertiliser production. Instead, it was covered by an additional layer of pollutant dust (see Chapter 2). At the onset of vegetation recovery, plant cover on the proximal part of the lower slope, comprising *Puccinellia distans*, already existed. It is generally agreed that

seed dispersal is less important in early secondary succession, compared to early primary succession (Walker & Chapin 1987). Yet, the secondary succession at the Steudnitz field site shares some characteristics with primary succession. Due to the extended period of deposition and the resulting accumulation of a pollutant dust layer at the soil surface, the seed bank of previously present species was either depleted over the three decades of dust deposition or buried too deeply to play a role after the cessation of dust deposition.

Order of colonisation was not only correlated with seed dispersal mode, but also with seedling salt tolerance, as shown by Spearman rank correlation. Figure 4.2 suggests that up to 1994 (i.e. four years after factory closure) salinity was an important component of the abiotic filter acting as a selective force upon species establishment, as only after five years the most salt-intolerant species were able to colonise. Spearman rank correlation coefficients were about equal for both plumed-propagule and non-plumed-propagule species. Assuming a higher probability of immediate colonisation of suitable sites (i.e. soil salinity falls below critical threshold) by plumed-propagule species, one would have expected a more predictable colonisation order - and therefore a better correlation – in this group compared to the group of non-plumed-propagule species. The data do not confirm this, as both groups had almost similar correlation coefficients. However, only a small subset of species was tested with respect to salt tolerance. In addition, due to the uneven distribution of plumed and non-plumed species over the temporal gradient, most of the early colonisers included in the salt tolerance experiment were plumed species, whereas most of the late colonisers were non-plumed species. Therefore, it might be difficult to establish a difference between the two groups.

The halophytic grass *Puccinellia distans* maintained its dominance until 1995 and then abruptly disappeared (see Chapter 2). This is most likely due to this species being outcompeted by colonising species. The complete collapse of the population in 1996 therefore indicates that salinity played no further role at the Steudnitz field site, especially as woody native species, which exhibit a very low salt tolerance (Brandes 1999), colonised the slope in the next year.

The abiotic filter probably played a more complex role in the early succession at the Steudnitz field site than that suggested by the clear correlation between seedling salt tolerance and order of colonisation. Both the modifying influence of soil pH decreasing in parallel with salinity and the role of potential nitrate enrichment during the period of dust deposition were not covered by this experiment. Subsequent chapters at least touch on the latter aspect. They also provide a detailed discussion on the role of other soil factors such as the poor moisture retention and the existing nutrient imbalance.

5. Soil seed bank

5.1 Introduction

The pool of species (*sensu* Zobel 1997, see Chapter 3 in this thesis) trying to establish themselves in a plant community at a given site contains species already present in a seed bank and species arriving from the outside via dispersal. The importance of seed dispersal mechanisms for patterns of plant community assembly at the Steudnitz field site was demonstrated in Chapter 4. The present chapter deals with those species present in the soil seed bank. In investigations of the seed rain at a given site, often only species from the local vegetation are detected. This is due to the near impossibility of detecting the more rare events of long-distance dispersal when using seed traps which commonly only cover a very minor fraction of the soil surface. In contrast to the seed rain, the seed flora in the soil is much less strongly correlated with the surface vegetation (Harper 1977) and often contains a number of species absent from the vegetation.

The study of seed banks as a starting point for explaining actual composition or dynamics of plant communities has been advocated by a number of authors. Published examples include studies from a variety of habitats, ranging from inland marsh vegetation (e.g. van der Valk & Davis 1978, Ungar & Riehl 1980) to cliff communities (Booth & Larson 2000). In such studies, exclusive occurrence of species in the seed bank but not in the vegetation is thought to indicate the existence of filter mechanisms preventing successful establishment of those species.

There are even instances in which knowledge of the seed bank, combined with information about a few other key features of the life history of those species present in the seed bank or vegetation, is considered sufficient for the construction of predictive models, such as van der Valk's (1981) quantitative model of wetland succession. Such a model would be helpful for predicting vegetation development at the Steudnitz field site, but although a plethora of seed bank persistence data for temperate European species have been compiled (Thompson et al. 1997), records for a given species often contradict each other and there are no records at all for many species occurring at the Steudnitz field site. Therefore, I determined the composition and vertical structure of the soil seed bank at the Steudnitz field site, to gain insight into seed bank persistence of species, and to determine what species were present in the seed bank but not in the vegetation. Knowledge of seed bank persistence of species facilitates interpretation of vegetation patterns, which are the subject of subsequent chapters in this thesis.

5.2 Methods

5.2.1 Sampling methods

Adjacent to Heinrich et al.'s (2001) lower slope permanent plot a 12×12 m plot was marked out with pegs in March 2000. Viable seed bank and vegetation within this plot were sampled in three successive years as outlined below. For this purpose, the 12×12 m plot was divided into 36 quadrats of 2×2 m. Yearly sampling of the soil seed bank of 12 randomly selected quadrats took place between 15 and 20 March 2000 through 2002 (before seed dispersal had begun in each year). Each quadrat was sampled only once in the three-year sampling period. In each quadrat, ten soil cores were extracted on a regular grid (one central row of four cores and two outer rows of three cores each), using a soil corer with a diameter of 4 cm. After removal of the litter layer, the cores were divided into segments of 0-2 cm, 2-5 cm and 5-10 cm, based on Thompson et al.'s (1997) recommendation of sampling at least two different layers. The shallow surface layer of 0-2 cm was included in the sampling design because, given the inability of many species to emerge from greater depths (Harper 1977), this better reflects the potential of regeneration from seeds in the absence of soil disturbance than the commonly employed sampling of a 0-5 cm surface layer. The ten segments for each depth collected in each 2×2 m quadrat were pooled. In each year, a total area of c. 1508 cm², corresponding to a soil volume of 15.08 dm³, was sampled. This is well above the recommendations given by Hutchings (1986), who recommended 1.0 to 1.2 dm³ of soil for grassland communities.

The pooled soil samples were concentrated using the bulk reduction method. This method promotes rapid and complete germination of the seeds of many species (ter Heerdt et al. 1996). The soil was washed through two sieves of 2.0 mm and 0.2 mm, respectively. By doing so, rhizomes and roots were eliminated from the samples, and the removal of coarse and very fine soil particles resulted in considerable bulk reduction. The samples were spread in trays into layers with a thickness of c. 5 mm, overlying a layer of heat-sterilised sand / standard potting soil mixture with a thickness of 30 mm. Within two days after sampling, samples were placed in a cold frame (in the University of Jena Botanical Garden). There, natural daily temperature fluctuations could promote germination (Thompson & Grime 1983, Poschlod 1991). The samples were covered with a fine gauze material, which allowed free gas and moisture exchange, but prevented contamination by wind-borne seeds. The effectiveness of the gauze was assessed by monitoring three control trays containing sand / potting soil mixture only. The trays were watered regularly, and checked for seedlings on a weekly basis. Seedlings were identified using the keys of Csapody (1968), Muller (1978) and Hanf (1999). If a seedling was not identifiable, it was transplanted into a flower-pot and grown until identification was possible. However, in each year a number of seedlings died between counts without being identified. In all three years, the experiment was terminated at the end of October, after

several weeks of no new seedlings emerging from the samples. Although some viable seeds may have remained in the soil samples beyond the experiment, the application of the concentration method should have resulted in complete germination of seeds of most species within the first 6 weeks of the experiment (see ter Heerdt et al. 1996).

Cover of species was estimated using a simplified percent-cover scale (less than 0.5 % were recorded as 0.25 %, between 0.5 and 10 % cover was recorded to the nearest percent, and values higher than 10 % were rounded to the nearest five percent). In each 2 × 2 m quadrat, the vegetation was sampled twice in each year, at the beginning of May and at the end of June.The higher of the two values was used for the calculation of the mean cover of a species.

5.2.2 Data analysis and seed bank classification

Among replicate samples of a particular year, there was a great deal of variation in the number of emerged seedlings of a given species. It was therefore not possible to make precise estimates of the seed bank density of individual species. Hence, no attempt was made to analyse the temporal seed bank dynamics of individual species.

Repeated measures analyses of variance (von Ende 2001) were performed in cases where samples could be matched. This was the case when different depths and years were compared simultaneously. When testing for differences in the mean number of seeds per unit volume and the mean number of seed bank species per pooled soil sample, depth was used as within-subjects factor, and year of sampling as between-subjects factor. In the latter case, two instead of three depths (0-5 cm, 5-10 cm) were used in order to avoid spurious results arising from different sample volumes. As indicated by Mauchly's test of sphericity (von Ende 2001), there was a sigificant departure from the sphericity assumption of repeated measures ANOVA for the mean number of seeds per unit volume (results not shown). Thus, Greenhouse-Geisser correction was applied for the correction of significance levels (von Ende 2001).

Temporal variation of species density in the vegetation was analysed using one-factorial analysis of variance. Since each quadrat was sampled in all three years, repeated measures analysis would have been possible, but this option would have prevented the use of *post hoc* tests. Also analysed by means of one-factorial ANOVA were the mean number of seed bank species per sample for the pooled profile and the mean number of seeds per sample for the pooled profile.
For both repeated measures and one-factorial ANOVA, numbers of seeds were log-transformed prior to analysis to normalise the data.

Seed bank type of the species found in the seed bank or vegetation was determined using the key proposed by Thompson et al. (1997), which is based on the presence or absence of a species in the vegetation as well as on the vertical distribution of its seeds in the soil. In this key, species are

classified into three categories: **transient** (persistent for less than one year), **short-term persistent** (persistent for one to five years), and **long-term persistent** (persistent for more than five years). Departing from the key, species were only classified if their calculated seed bank density was ≥ 20 seeds / m² or if they occurred in the vegetation of at least 25 % of the quadrats either in 2000 or in 2001. Species absent from the seed bank were not classified as transient if they occurred in the vegetation of fewer than 25 % of the quadrats in either year. In such a case, they might have been overlooked in the seed bank due to a low density or clumped distribution.

5.3 Results

5.3.1 Seed bank composition

Contaminants found among the control trays in 2000 were two seedlings of *Sonchus* spp. and two seedlings of *Oxalis* spp. Although there were no contaminants recorded in 2001, two more *Sonchus* spp. seedlings were found in the control trays in 2002. *Sonchus* spp. seedlings found in the samples were therefore excluded in spite of the sporadic appearance of *Sonchus oleraceus* L. and *Sonchus arvensis* L. throughout succession at the field site (see Heinrich et al. 2001).

Deducting *Sonchus* spp., 6493 seedlings emerged from the 36 pooled soil samples collected between 2000 and 2002, of which 6309 were identified and assigned to 26 different species (see Appendix 4).

Five species (*Puccinellia distans*, *Cerastium glutinosum* Fr., *Epilobium tetragonum* L., *Chenopodium rubrum* and *Atriplex sagittata*) constitute c. 88 % of the germinable seed bank, the bulk (62.5 %) being seeds of *P. distans* (see Figure 5.1).
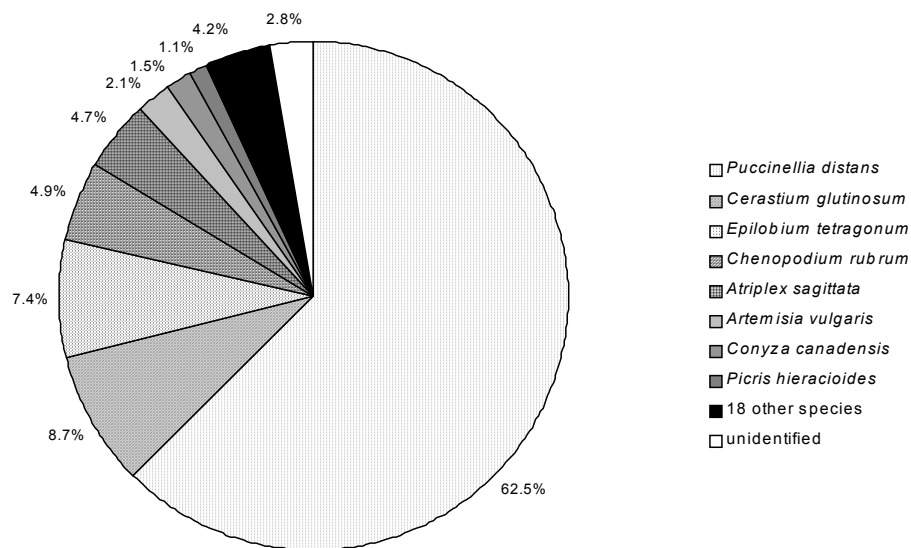
Figure 5.1. Soil seed bank composition (percent of total seeds in soil sampled from 0-10 cm depth) at the Steudnitz field site near the lower slope permanent plot of Heinrich et al. (2001). The pie chart is based on pooled data for 2000 – 2002.

Two of the most common species in the seed bank, *P. distans* and *C. rubrum*, did not occur in the vegetation during the study. Appendix 4 gives a detailed overview of the number of seedlings emerged in all three years. Appendix 5 lists the species that were found in the established vegetation in at least one year but not recorded as seedlings in any year.

Overall species total for vegetation and seed bank samples increased with time: The same trend was significant for the average number of species per 2 × 2 m vegetation quadrat and for the average number of species per seed bank sample (see Table 5.1).

Table 5.1. Number of species in the vegetation, seed bank density and number of species per seed bank sample (pooled 0-10 cm) for the years 2000-2002. Total numbers and means ± standard deviation (vegetation: n = 36; seed bank: n = 12) are given. One-factorial ANOVA *P*-values indicate significant differences between years. Superscripts indicate the identity of means that significantly differ from each other ($P < 0.05$), as indicated by a post-hoc Games-Howell test. Numbers of seeds were log-transformed prior to analysis.

	P	Year 2000	Year 2001	Year 2002	Total
Vegetation					
Species total		42	48	47	53
Species density / 4 m²	< 0.001	$14.6^b \pm 2.2$	$15.7^b \pm 2.8$	$18.2^a \pm 1.5$	
Seed bank					
Species total		20	21	24	26
Species density / soil sample	0.013	$8.3^b \pm 2.5$	$8.4^b \pm 2.4$	$11.2^a \pm 2.8$	
No. of seeds / m²	0.609	13 881 ± 9 138	13 018 ± 5 757	16 162 ± 7 296	

There were no significant differences in the number of seedlings emerged from the samples in different years (Table 5.1). Species density per sample was significantly lower in the 5-10 cm layer, compared to the 0-5 cm layer (Figure 5.2 and Table 5.2).
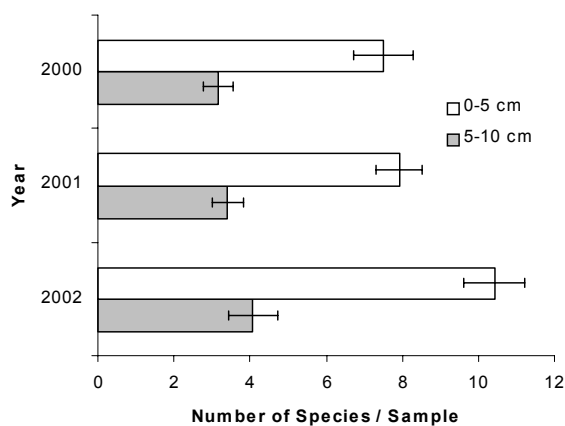
Figure 5.2. Mean species density in the soil seed bank near the lower slope permanent plot of Heinrich et al. (2001) for two depths (0-5 cm and 5-10 cm) over the course of three years. Error bars represent the standard error of the mean (n = 12).

26

As for pooled samples, the number of species per subsample significantly differed between years (Table 5.2). The number of seeds per unit volume (displayed in Figure 5.3 as number of seeds per dm³) also declined with increasing depth. This trend also was significant (Table 5.2).

Table 5.2. Summary of the repeated measures ANOVAs for average number of species per subsample (two depths: 0-5 cm, 5-10 cm) and average number of seeds per dm³ soil (three depths: 0-2 cm, 2-5 cm, 5-10 cm). In the latter case, degrees of freedom were Greenhouse-Geisser corrected. Depth was used as within-subjects factor, year of sampling was between-subjects factor. Significant results ($P < 0.05$) are indicated in bold. Numbers of seeds were log-transformed prior to analysis.

Parameter	Within-Subjects Effects	Between-Subjects Effects	d.f.	F	*P*
No. of species / subsample	Depth		1	135.35	**< 0.001**
	Depth × Year		2	2.17	0.130
	Error (Depth)		33		
		Intercept	1	439.28	**< 0.001**
		Year	2	4.15	**0.025**
		Error (Year)	33		
No. of seeds / dm³ soil	Depth		1.63 (2)	13.37	**< 0.001**
	Depth × Year		3.26 (4)	1.63	0.193
	Error (Depth)		53.74 (66)		
		Intercept	1	2153.89	**< 0.001**
		Year	2	0.62	0.543
		Error (Year)	33		
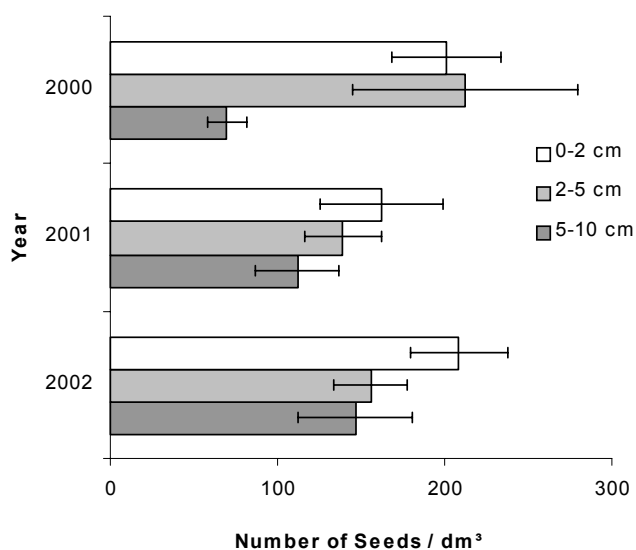
Figure 5.3. Vertical distribution of seeds in the soil seed bank near the lower slope permanent plot of Heinrich et al. (2001). over the course of three years. Error bars represent the standard error of the mean (n = 12).

5.3.2 Vertical profile and seed bank classification

The vertical seed distribution of species occurring at densities $\geq$ 20 seeds / m² is shown in Figure 5.4. Only one species, *Puccinellia distans*, had a higher density in both lower layers compared to the 0-2 cm surface layer. All other species, including *Chenopodium rubrum*, the only other species absent from the vegetation, had a higher density near the soil surface. Seeds of two species, *Inula conyzae* (GRIESS.) MEIKLE and *Senecio vulgaris* L., were almost exclusively found in the surface layer.
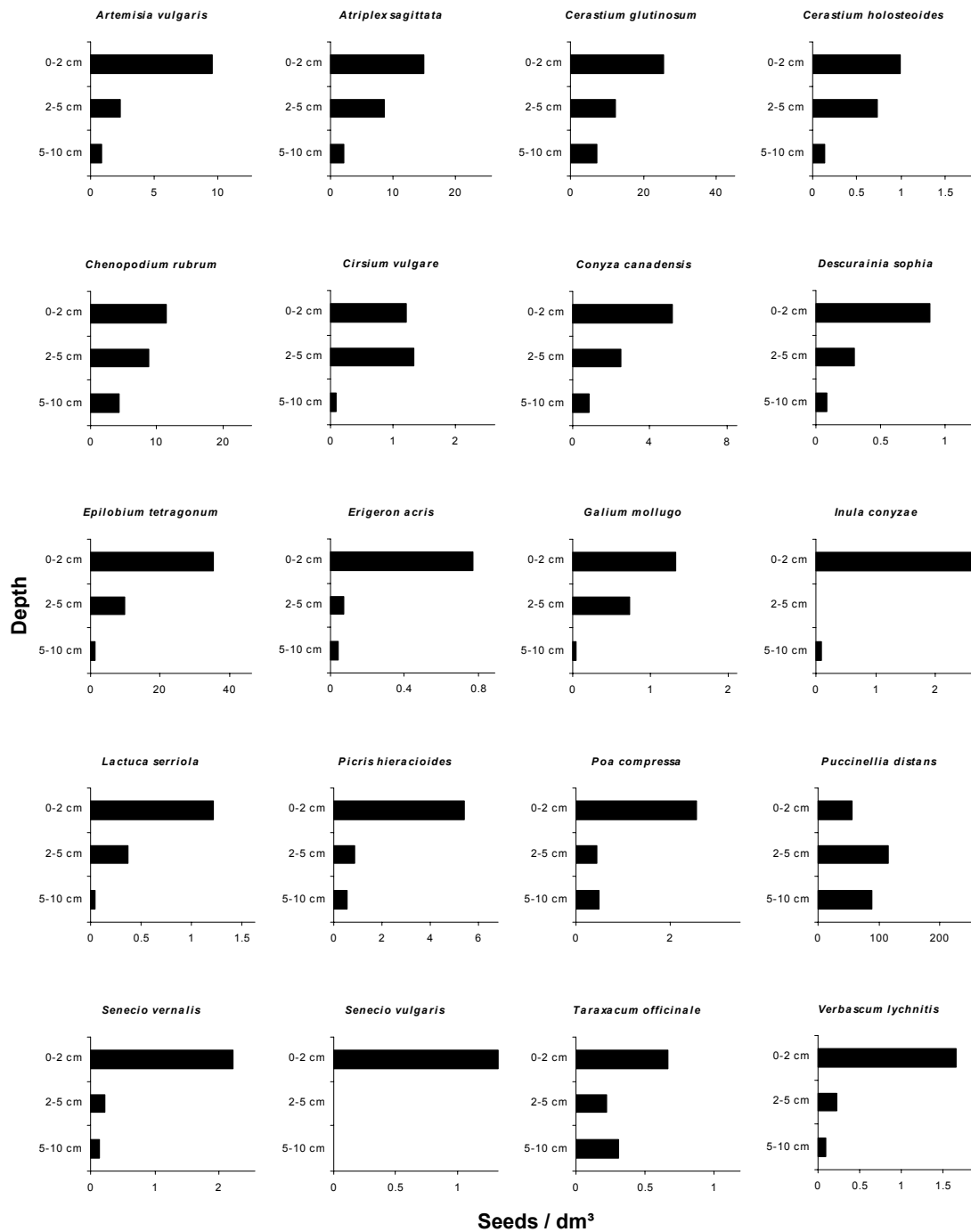
Figure 5.4. Depth distribution of the 20 most abundant species in the soil seed bank. To make the distributions comparable, total bar length was standardised for all graphs. Thus, although absolute scales differ, relative scales are the same.

Based on the criteria for seed bank classification (Thompson et al. 1997), 26 species which occurred in vegetation or seed bank were classified (Table 5.3).

Table 5.3. Seed bank persistence of 26 species occurring in the vegetation or soil seed bank at the Steudnitz field site. Persistence types after Thompson et al. (1997): Transient (T) = Seeds persist for less than one year; Short-term persistent (SP) = Seeds persist for c. 1-5 years; Long-term persistent (LP) = Seeds persist for at least 5 years. For comparison, records from Thompson et al. (1997) are given. In the case of *Cerastium glutinosum* and *C. holosteoides*, database records are for the aggregates C. *pumilum* agg. and *C. fontanum* agg., respectively. If available, additional information is given on a number of plant traits. Seed dispersal types based on data from Müller-Schneider (1986): WINDc = seeds small and shed from a capsule; WINDw = seeds winged or strongly flattened; WINDp = dispersule plumed or wrapped in wooly hairs; ANIMa = adhesive dispersal by means of animals; BALL = ballistic dispersal. Life history data is taken from Rothmaler (2002). In the case of *P. distans*, plants at the field site adopted an annual life-style (Heinrich et al. 2001).

Species	Persistence Type	Database (LP, SP, T)	Morphological Adaptation for Seed Dispersal	Life History Type
Chenopodium rubrum	LP	2, 5, 0	-	A
Puccinellia distans	LP	0, 1, 0	-	A (P)
Verbascum lychnitis	SP (LP?)	no records	WINDc	B
Artemisia vulgaris	SP	1, 7, 2	WINDc	P
Atriplex sagittata	SP	no record	WINDw	A
Cerastium glutinosum	SP	0, 0, 1	WINDc	A
Cerastium holosteoides	SP	15, 32, 23	WINDc	P
Cirsium vulgare	SP	1, 6, 11	WINDp	B
Conyza canadensis	SP	1, 6, 1	WINDp	A
Descurainia sophia	SP	0, 2, 0	WINDc	A
Epilobium tetragonum	SP	0, 3, 2	WINDp	P
Galium mollugo	SP	0, 3, 11	-	P
Picris hieracioides	SP	2, 1, 1	WINDp	P
Poa compressa	SP	0, 0, 2	WINDp?, ANIMa?	P
Taraxacum officinale	SP	8, 26, 38	WINDp	P
Erigeron acris	SP / T	0, 0, 1	WINDp	BP
Lactuca serriola	SP / T	1, 6, 1	WINDp	A
Senecio vernalis	SP / T	no record	WINDp	A
Bromus japonicus	T	no record	ANIMa	A
Carduus acanthoides	T	0, 0, 1	WINDp	B
Galium aparine	T	0, 9, 20	ANIMa	A
Inula conyzae	T	1, 0, 0	WINDp	BP
Poa angustifolia	T	0, 0, 1	ANIMa	P
Senecio vulgaris	T	6, 15, 7	WINDp	A
Thlaspi perfoliatum	T	no record	BALL	A
Veronica arvensis	T	0, 11, 12	BALL	A

Only two of the species, *P. distans* and *C. rubrum*, were classified as long-term persistent. The remainder were mostly classified as short-term persistent (13 spp.) or as transient (8 spp.). The three remaining species were classified as intermediate between short-term persistent and transient.

5.4 Discussion

5.4.1 Methodological aspects

According to Thompson et al.'s (1997) key, species absent from the seed bank but occurring in the vegetation should be classified as transient. In the current study, this classification was assigned only if a species was present in at least nine vegetation quadrats in 2000 or in 2001; species occurring in fewer quadrats were not classified. Rare seed bank species, due to a limited number of samples and a large degree of spatial heterogeneity in the soil, might simply have remained undetected. In the present study, this common phenomenon of spatial heterogeneity (e.g. Thompson 1986) is exemplified by the standard deviation of seed bank densities of individual species often being higher than their mean (Appendix 4). Apart from the occurrence of a species in the vegetation, a second criterion plays a role in Thompson et al.'s (1997) seed bank key: the presence and vertical distribution of seeds in the soil. In the key, the vertical distribution of seeds is indiscriminately used as evidence for a certain persistence type, regardless of the fact that the preceding dynamics of a species in the overlying vegetation might be influential for the depth distribution. In successional systems, this might lead to errors in determination of persistence types. Most of the species classified for the Steudnitz field site lacked pronounced directional changes of abundance in the vegetation. The only exception to this was the monocarpic perennial *Verbascum lychnitis* L., which increased strongly during the course of the study (see Section 5.4.3).

5.4.2 Seed bank composition and vertical distribution

Of the 53 species occurring in the vegetation, only 24 were also found in the seed bank. This is not surprising. At the time of the study, many of the species occurring at the site were rare or had just started to colonise the part of the slope that was sampled (see Appendix 5). Hence, it is reasonable to expect that seed bank densities of these species were low, and therefore many of them may have remained undetected. A formula provided by Thompson et al. (1997) allows estimation of the minimal density of seeds / m² required to have a 95 % chance of finding one seed of a species in a given year. In the current study, this density was calculated as 19.8 seeds / m^2. If the seed density of a species is assumed to remain constant over the three years, then the repeated sampling employed in the current study would allow for species with densities > 6.6 seeds / m^2 to be detected with a 95 % probability.

Both the number of species per soil sample and the number of species per vegetation quadrat increased with time. The same phenomenon was observed for the vegetation in the nutrient addition experiment described in Chapter 7, and the potential role of the spring 2000 drought in causing this pattern is discussed in more detail there. Despite regular watering, the drought factor may have contributed to the emergence of similar patterns in the seed bank samples. On the other hand, this increase of seed bank species richness with time might also be related to the higher probability towards the end of the study of detecting species in the seed bank that increased in the vegetation during the study.

The number of species (26) I found in the seed bank is similar to the number of species found in the seed bank of another temperate European grassland polluted with heavy metal. Near Prayon, Belgium, the seed bank of a grassland near an ore smelter contained 25 species (Meerts & Grommesch 2001). As in the present study, one tolerant grass species comprised most of the soil seed bank. In their study, 95 % of the soil seed bank was comprised of *Agrostis capillaris* L. seeds. In the present study, 62.5 % of the seed bank was comprised of *Puccinellia distans*. This species is no longer present in the vegetation at the Steudnitz site. An extended period of dominance, going back as far as the early 1980s (Heinrich 1984) and persisting until 1995 (Heinrich et al. 2001), allowed for the build-up of an enormous seed bank currently totalling c. 9 000 seeds / m² in the top 10 cm of soil (Appendix 4).

Total density of seeds declined with increasing depth: of the seeds sampled in the top 10 cm of soil, 62 % were found in the 0-5 cm layer. Such a decline with increasing depth is a widely known phenomenon, and is even more pronounced in other systems such as permanent grassland (Harper 1977). Species density also declined with increasing depth. This might partly be due to the seed production of many recent colonisers still increasing and their seeds not having had enough time yet to penetrate deeper into the soil.

All species present in the vegetation at the time of the study had higher seed densities near the soil surface, whereas the vanished *Puccinellia distans* had more seeds in subsurface layers (Figure 5.4). The only exception was *Chenopodium rubrum*, which colonised in 1992 and was lost from the vegetation three years later (see Heinrich et al. 2001). Seed density of this species was slightly higher in the surface layer than in subsurface layers. However, the decrease in seed density with increasing depth was less pronounced in this species, compared to those species present in the vegetation (Figure 5.4). A similar correlation between abundance of a species in the vegetation and its vertical distribution in the seed bank was found in other studies (e.g. Wagner et al. 2003).

5.4.3 Seed bank classification

The seed bank data base compiled by Thompson et al. (1997) contains only two records for the halophytic grass *Puccinellia distans*, one of them classifying the species as short-term persistent, the other one simply noting its presence in the seed bank. The current study clearly demonstrates the potential of this species to form a long-term persistent seed bank, especially so since there appears to be no sign of a decline in seed bank density over the duration of the study (Appendix 4).

Of the five species not included in Thompson et al.'s (1997) database, two species (*Verbascum lychnitis* and *Atriplex sagittata*) were classified as short-term persistent (Table 5.4). Another species, *Senecio vernalis*, was classified as intermediate between short-term persistent and transient. Finally, two species (*Bromus japonicus* and *Thlaspi perfoliatum* L.) were classified as (Table 5.4).

In the case of *V. lychnitis*, currently strongly increasing in the vegetation, the depth distribution criterion (Thompson et al. 1997) is not altogether reliable. For a species present in the vegetation to be defined as short-term persistent requires the seeds of this species to be present in both upper and lower soil layers, and to be more numerous in upper soil layers than in lower soil layers. In the case of strongly increasing species in successional systems incorporation of seeds into deeper soil layers might be offset by an increased input of freshly produced seeds into the surface soil. This might have been the case for *V. lychnitis*, the aboveground mean cover of which increased fourfold between 2000 and 2002, from 0.3 % to 1.2 % (see Appendix 4). Therefore, classification of this species as short-term persistent remains speculative, especially so since other *Verbascum* species have been found to be extremely long-term persistent: seeds of *Verbascum* spp. were still viable in the well-known burial experiment initiated by W.J. Beal after a period of 120 years (Telewski & Zeevaart 2002). Once the population at the Steudnitz field site has reached equilibrium, relatively more seeds might be found in deeper soil layers, which would then justify a classification as long-term persistent.

5.4.4 Soil seed bank and plant community assembly

Only two species currently absent from the vegetation have been found in the seed bank of the Steudnitz field site. These two species, *Chenopodium rubrum* and *Puccinellia distans*, were among the dominants of early succession at the site. *C. rubrum* was recorded between 1992 and 1994. In contrast, *Puccinellia distans*, a halophytic grass, was already preeminent at the lower slope during times of dust emission and continued to be so until 1995. Both species, although no longer occurring in the vegetation, are still among the most frequent species in the soil seed bank (Figure 5.1). This leaves the question as to why the two species no longer grow at the field site. The collapse of the population of *P. distans* and the disappearance of *C. rubrum* both more or less coincide with the first colonisation of the slope by salt-intolerant species (see Chapter 3). This implies that their disappearance might either be a direct or an indirect consequence of decreasing soil salinity. In the current study, seeds of both species readily germinated under non-saline conditions. At least in the case of *P. distans*, evidence exists of plants in experimental monocultures growing better in the

absence of salinity (Beyschlag et al. 1996). *P. distans* is generally described as a weak competitor (Beyschlag et al. 1996). It can therefore be regarded as one of the species described by Ellenberg (1954) as being restricted to sub-optimal conditions because there they are not out-competed by superior competitors. In the case of *C. rubrum*, raised soil salinity was shown to induce a significant increase in leaf succulence in a potted plant experiment (Kahles et al. 2002). It remains to be shown, however, whether this phenomenon is linked with a salt-induced increase in drought resistance. An increased drought resistance resulting from raised salinity is known for other members of the Chenopodiaceae (Marschner 1995). Since *C .rubrum* is a characteristic plant of disturbed nitrogen-rich habitats (Rothmaler 2002), it is also possible that this species was promoted by potentially higher levels of nitrate early on in succession that resulted from high nitrate content of the pollutant dust (see Chapter 2). There is some evidence that dark dormancy (Pons 1991) plays a role, because both species are known to have a light requirement for germination (Grime et al. 1981). Emergence of seedlings of both species at the Steudnitz field site after soil disturbance (M. Wagner, personal observation) also implies that dark dormancy, in the absence of disturbance, might play a role.

In an experiment investigating the potential light-filtering effects of a plant canopy on seed germination (Kahles et al. 2002), both species showed no sign of germination inhibition by far-red light. Germination percentages were, however, low in that experiment. The evidence is therefore not conclusive.

Other annuals found in the seed bank not only possess the capacity for dispersal in time (i.e. soil seed bank), but also the capacity for efficient dispersal in space, as indicated by seed morphological adaptations (see Table 5.4). In the case of one particular species occurring at high densities in the seed bank, *Atriplex sagittata*, different types of seed are produced, differing in their capacity for building up a seed bank and for being dispersed by wind or water (Mandák & Pyšek 2001b). This fact is commonly referred to as an explanation for the remarkable persistence of this species in successional vegetation (see Wißkirchen & Krause 1994), which was also observed at the Steudnitz field site. Apart from *Lactuca serriola* L., *A. sagittata* was the only species already found in 1992 which in 2002 was still present in the vegetation at high densities (see Heinrich et al. 2001). The rapid germination of non-dormant seeds in this species is supposed to confer a competitive advantage in the absence of disturbance, whereas in the case of disturbance dormant seeds from the seed bank supposedly provide a kind of 'insurance' against this disturbance (Wißkirchen & Krause 1994).

This study provided evidence that early successional species which have disappeared from the vegetation are still present in the seed bank. However, it remains unclear whether disappearance from the vegetation was primarily due to out-competing from later colonisers, i.e. due to biotic filtering. This seems likely for *P. distans*. In the case of *C. rubrum*, increased salinity or nitrate levels may have facilitated establishment early in succession. Subsequent reduction of nitrate or salinity levels may then have contributed to the disappearance of this species.

6. Spatial vegetation patterns and underlying soil gradients

6.1 Introduction

Previous studies of the successional vegetation at the Steudnitz lower slope were based on quadrat sizes of 1.5 × 1.5 m (Scholze 1997, Stephan 2001) and 5 × 5 m (Heinrich et al. 2001) and did not include the collection of any soil data. In addition, they were restricted to the proximal part of the lower slope and therefore made no use of the large-scale environmental gradient stretching across the whole of the lower slope. The study described here is distinguished by the employment of the collection of both vegetation and soil data on a small spatial scale. At the same time, the whole of the lower slope, including its distal end, is covered.

The central aim of this study is the assessment of the relative roles of environmental stress (*sensu* Grime 1979), a main component of the abiotic filter, and of competition, a main component of the biotic filter, in the formation of spatial vegetation patterns. Correlation of environmental gradients with patterns of species diversity provides a valuable tool for this task. According to the hump-backed model of species richness (Grime 1973), species density in herbaceous vegetation peaks at an intermediate level of productivity, expressed in terms of standing crop. In contrast, at low levels of productivity only a few species are assumed to being able to tolerate the effects of the disturbance or stress that has produced the low standing crop. At high levels of productivity, on the other hand, it is assumed that only a few species can tolerate the effects of competitive dominants. In the present study, the position of the peak in species density in relation to the sampled soil fertility gradient, taken as a correlate of productivity, should indicate the relative importance of both competition and abiotic stress in community assembly. A peak in species density somewhere near the middle of the sampled gradient would indicate that competition plays a prominent role as a filter at the high fertility end of the gradient, whereas stress would be more important at the low fertility end. In contrast, a monotonic negative relationship between soil fertility and species density over the entirety of the sampled gradient would suggest that competition is the dominant force in community assembly. Correspondingly, a monotonic positive relationship between fertility and species density would imply an outstanding role of abiotic stress.

A second aim of the study is to link the currently existing environmental gradients on a more general level with the success of different plant life-history types. This is done in order to find out whether in the investigated ecosystem plant life-history type is a species trait with a predictive value regarding plant community assembly (Keddy 1992, see also Chapter 3).
Subsidiary aims of the study are the investigation of interspecific associations between plants at the Steudnitz lower slope, the characterisation of the realised niches of the more common species in the investigated system, and a more detailed description of the large-scale soil gradients occurring at the lower slope, including the relation between different soil factors.

6.2 Methods

6.2.1 Field methods

In mid-June 2000, 140 quadrats of 1m² were randomly located at the lower slope of the Steudnitz field site (see Figure 2.3) and marked with pegs. Between 20 June and 30 June 2000, plant cover was recorded for each quadrat. Cover of individual species was visually estimated using the same simplified percent scale as in the seed bank study (Chapter 5). Slope orientation and slope angle were recorded, using a compass and a clinometer respectively. Both on 18 August 2000 and on 27 August 2000, soil moisture in each plot was measured using a Hydra Soil Moisture Probe (Stevens Vitel Inc., Chantilly, VA, USA). Both series of measurements were carried out under similar weather conditions (warm and sunny, no rainfall for $\geq$ 4 days). On both occasions, plot soil moisture was estimated by averaging the results of five measurements, arranged in a regular grid (one measurement in the centre and near each of the four corners of the quadrat). One series of measurements took c. 8 hours. To correct for effects of diurnal soil moisture fluctuations on the results, the second series of measurements was carried out in reverse order, and a soil moisture index, based on the moisture values of both series, was calculated for the ith quadrat using the formula:

$$I_{M(i)} = \{[(m_{1(i)} / m_{1(max)}) + (m_{2(i)} / m_{2(max)})] / 2\} \times 100 \qquad (6.1)$$

where $m_{1(i)}$ and $m_{2(i)}$ denote the soil moisture in the ith quadrat in the first and second series of measurements respectively; $m_{1(max)}$ and $m_{2(max)}$ stand for the maximum found in any quadrat during the respective series. Thus, the highest possible index value is 100.

Between 28 and 30 September 2000, soil sampling was carried out using a soil corer of 1 cm diameter. On each plot, the upper 10 cms of the soil profile were sampled by extracting 25 soil cores from a regular 5×5 grid. Soil cores for each plot were pooled prior to subsequent soil processing and analysis.

6.2.2 Soil analysis

Directly after collection in the field, samples were oven-dried for seven days at 30° C and then sieved with a 2 mm sieve, in order to separate gravel and fine-earth fractions. Sample total weight and the weight of the gravel fraction were determined, and percent by weight gravel content was calculated. Soil pH (10 g soil / 25 ml 0.1 M KCl) and electrical conductivity (EC), the latter measured from a 1:5 extract in water (20 g soil / 100 ml distilled water), were measured as described in Rowell (1997). Soil organic matter content was estimated from loss-on-ignition (L.O.I.). After oven-drying at 105 °C samples were repeatedly ignited at 430 °C until weight constancy was achieved. At this temperature, the presence of $CaCO_3$ in the samples does not affect the results (Davies 1974). The difference

between oven-dry weight and weight after the ignition procedure served as an estimate of organic matter content. Plant-available phosphorus and potassium, henceforth referred to as P_{CAL} and K_{CAL}, were extracted with the CAL method, using calcium lactate / calcium acetate as extractants (Schüller 1969). Total nitrogen (N_{total}) was determined with the method of Hendershot (1985). Total carbon was measured with an element analyser (Vario EL, Elementar Analysensysteme, Hanau, Germany). Soil organic C content was estimated via multiplication of the percent loss-on-ignition (L.O.I.) values by the factor 0.49 (the arithmetic mean of the range of organic C / organic matter ratios generally found in soils; Brady & Weil 2002). Estimated organic C content then was subtracted from total carbon content, giving rise to an estimate of mineral carbon (C_{min}) content.

6.2.3 Exploratory data analysis

Initially, soil data and vegetation data were analysed separately. Correlation between soil parameters was calculated and pairwise association between species was tested. This was followed by a joint analysis of soil and vegetation data, in order to explore interrelations between plant community structure and underlying soil conditions. This was done by means of direct ordination using Canonical Correspondence Analysis (CCA). Subsequently, General Linear Models were applied to the CCA model, to obtain regressions of a number of parameters in CCA ordination space.

6.2.3.1 Correlation between abiotic parameters

Data of ten environmental parameters (P_{CAL}, K_{CAL}, N_{total}, C_{min}, EC, pH, L.O.I., soil moisture, gravel content, slope angle) were tested for normal distribution by means of a one-Sample Kolmogorov-Smirnov test (two-tailed exact test by Monte Carlo simulation, 10000 permutations). Results (not shown) indicated a significant departure from the normality assumption in the case of K_{CAL}, N_{total}, C_{min}, gravel content and slope angle. The nonparametric method by Spearman was therefore used for the calculation of correlation coefficients (Zar 1999). Two-tailed tests were used for testing the significance of the correlations. Holm's sequential Bonferroni method (Holm 1979) was used for adjustment of the type I error rate, in order to limit the overall error rate.

6.2.3.2 Pairwise association between plant species

Pairwise association between species (Greig-Smith 1983) was tested using the two-sided version of the Fisher exact test. All possible pairwise combinations of the 16 most common species (occurring in ≥ 22 quadrats) were tested using presence / absence data. For each pair of species, numbers of separate and joint absences and occurences were arranged in a 2×2 contingency table. Preliminary analyses with simulated data showed that inclusion of those species occurring in fewer quadrats would have led to the testing of species pairs for which the limitations of the Fisher exact test would have precluded finding a significant negative association (Zar 1999). Type I error rate α was not adjusted for the number of comparisons, since in the case of species associations this would have led

to a much lower power of the tests, potentially causing a large number of pairwise associations to remain undetected (Sokal & Rohlf 1995). On the other hand, the strategy of not adjusting the error rate does lead to erroneous rejection of the null hypothesis in some of the tests. In the current context (120 pairwise comparisons, type I error rate of $\alpha = 0.05$), c. 6 out of 120 (= $\frac{1}{2} \times 16 \times 15$) tests can be expected to erroneously indicate a significant association on a chance basis. In addition to the Fisher exact test, Spearman's r was calculated as a measure of the strength of association.

6.2.3.3 Ordination

To prevent species with a large variance from unduly influencing the results, log-transformation of the species cover data was carried out prior to ordination (ter Braak & Šmilauer 1998). By logarithmic transformation, the presence / absence of species is emphasised, without completely neglecting quantitative aspects (Wildi 1986). Species occurring in fewer than four samples were excluded. Very rare species often are not accurately depicted in ordination diagrams. In addition, these species add considerable noise to multivariate data sets (Gauch 1982). For constrained ordination, Canonical Correspondence Analysis (CCA) was the method of choice, as indicated by the length of the longest gradient (4.09 units) in an initial Detrended Correspondence Analysis (ter Braak & Šmilauer 1998). The environmental data consisted of the same environmental variables as listed in Section 6.2.3.2. Four of the variables - K_{CAL}, N_{total}, C_{min}, and gravel content - had a right skewed distribution and were log-transformed (using the natural logarithm ln) prior to analysis (ter Braak & Šmilauer 1998). One variable, slope angle, had a left skewed distribution. This was remedied by transformation using the following formula:

$$\beta_{T(i)} = \exp (\beta_{(i)} / \beta_{(max)}) \qquad\qquad (6.2)$$

where $\beta_{T(i)}$ denotes the slope angle of a sample plot and $\beta_{(max)}$ stands for the maximum slope angle measured during the investigation.

In order to achieve an optimal CCA model, manual forward selection, in combination with partial Monte Carlo permutation tests (reduced model, 999 permutations), was used for step-wise inclusion of additional variables on the basis of maximum extra fit. Additional variables were included as long as their inclusion was associated with a significant ($P < 0.05$) increase in variance explained by the model. Significance of the axes of the resulting CCA model was tested using Monte Carlo permutation (1999 permutations under the reduced model). For the testing of higher axes the sample scores of all previous axes were specified as additional covariables (Lepš & Šmilauer 2000). Comparison with Correspondence Analysis (CA) allowed an overall assessment of the CCA model in terms of variance explained (ter Braak 1995).

Finally, several derived variables were linked with the explanatory variables of the model, among them community characteristics and proportionate cover of different life history types. Community characteristics included total cover of higher plants, total cover of bryophytes and two parameters of species diversity: species density / m² and evenness. As evenness measure, modified Hill's ratio $F_{2,1}$ was chosen (see Alatalo 1981). Proportionate cover of life history types was derived in two steps. First, each species was classified into one of five categories: annuals; monocarpic perennials, including biennial species; polycarpic grasses; polycarpic herbs; woody plants. Classification was based on Rothmaler (2002). In the case of two species, for which Rothmaler (2002) provided more than one option, classification was based on personal observation. Thus, *Inula conyzae* was classified as polycarpic perennial, and not as long-lived monocarpic species and *Torilis japonica* (HOUTT.) DC.was classified as biennial (i.e. as long-lived monocarpic plant), and not as annual. In a second step, total cover produced by each of the groups was standardised for each quadrat by division by total cover of all higher plants in that quadrat. In addition to the five above listed categories, a category of leguminous species (= members of the Fabaceae) was devised, comprising legume species already assigned to one of the other categories. All derived variables were included as passive variables and their patterns in ordination space were modelled by means of General Linear Model (GLM) regression techniques, as provided in the CanoDraw programme (ter Braak & Šmilauer 2002). Model selection was based on a stepwise selection procedure using the Akaike Information Criterion (AIC). By doing so, out of five candidate models (linear, quadratic, cubic; the latter two types with and without inclusion of an interaction term) the one with the best fit was chosen (ter Braak & Šmilauer 2002). The same regression techniques were applied to individual species recorded in at least 10 quadrats, to model their realised niche at the Steudnitz site.

6.3 Results

6.3.1 Correlation between abiotic parameters

27 out of 45 correlations were found to be significant after application of Holm's (1979) sequential Bonferroni procedure. The strongest positive correlation was found between gravel content and C_{min}. In turn, both of these parameters are strongly negatively correlated with P_{CAL}. Both P_{CAL} and N_{total} show a strong positive relationship with loss-on-ignition, and a less pronounced, but nevertheless significant negative correlation with soil pH. K_{CAL} is also positively correlated with loss-on-ignition, but not with soil pH. Soil pH - positively correlated with both gravel content and C_{min} - is negatively correlated not only with P_{CAL} and with N_{total}, but also with loss-on-ignition. Soil electrical conductivity is positively correlated with P_{CAL}, K_{CAL}, N_{total} and loss-on-ignition. Soil moisture is negatively correlated with slope angle, which in turn is positively correlated with gravel content. Spearman r values for all pairwise combinations are listed in Table 6.1.

Table 6.1. Spearman rank correlation coefficients for pairwise correlations between 10 abiotic parameters (9 soil parameters and slope angle). Significant correlations at the 5 % level (two-tailed test, sequential Bonferroni-adjustment) are highlighted.

	P_{CAL}	K_{CAL}	N_{total}	L.O.I.	C_{min}	pH	moisture	gravel	slope
conductivity	0.517	0.316	0.596	0.622	-0.451	-0.321	-0.174	-0.453	0.203
P_{CAL}		0.259	0.517	0.743	-0.891	-0.538	0.079	-0.807	-0.086
K_{CAL}			0.412	0.513	-0.184	-0.175	-0.232	-0.070	0.006
N_{total}				0.787	-0.320	-0.457	-0.206	-0.338	0.171
L.O.I.					-0.546	-0.562	-0.142	-0.540	0.013
C_{min}						0.501	-0.190	0.835	0.158
pH							-0.088	0.555	0.168
moisture								-0.224	-0.277
gravel									0.269

6.3.2 Pairwise association between plant species

Significant positive and negative associations detected by the association analysis are graphically displayed in Figure 6.1 as constellation diagrams (constructed according to Agnew 1961). At the 5 % level, 39 out of 120 pairwise associations were found to be significant. Of these, 31 were positive, and eight were negative associations. Strong positive associations were found among *Atriplex sagittata*, *Senecio vernalis* and *Lactuca serriola*, forming a triplet of species, and also among *Epilobium tetragonum*, *Artemisia vulgaris* and *Picris hieracioides*, forming another triplet (Figure 6.1). While there were no direct positive associations between these two groups of species, they are were linked with each other via *Cirsium vulgare* (SAVI) TEN., *Inula conyzae* and *Poa compressa*, all of which are positively associated with at least one member of each triplet. The strongest positive association was found between *Poa compressa* and *Bromus japonicus* (r = +0.654). Consequently, the negative associations of these two species were similar. Both were strongly negatively associated with *Elytrigia repens* and its associate species, *Cirsium arvense* (L.) SCOP. and *Galium aparine* L.. Another strong negative association was found between *Elytrigia repens* and *Artemisia vulgaris*. Of the eight significant negative associations, four did involve *E. repens*, the dominant species in the distal part of the lower slope.
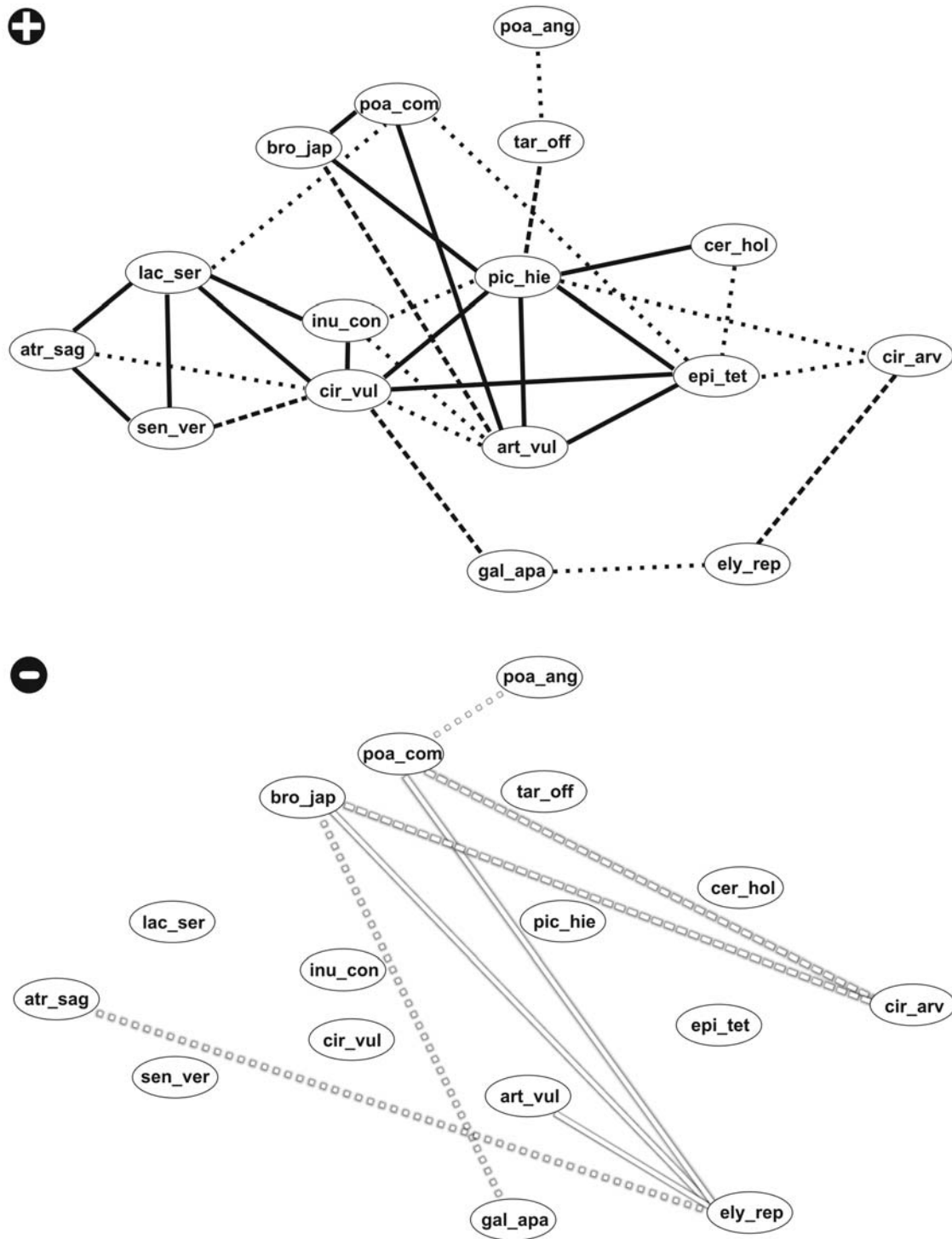
Figure 6.1. Constellation diagrams showing significant pairwise associations between the 16 most common species at the Steudnitz lower slope. Positive and negative associations are shown in the upper and lower diagram, respectively. Analysis was based on 140 randomly allocated sample quadrats (size: 1 m²). Line type indicates strength of the association (dotted line: $0.175 \leq r \leq 0.219$ and $0.01 \leq P \leq 0.05$; dashed line: $0.229 \leq r \leq 0.271$ and $0.001 \leq P \leq 0.01$; solid line: $r \geq 0.293$ and $P < 0.001$). For species abbreviations see Appendix 6.

6.3.3 Ordination

6.3.3.1 Canonical Correspondence Analysis (CCA)

Forward selection resulted in five environmental parameters being included into the CCA model as explanatory variables. These variables were slope angle, total nitrogen (N_{total}), electrical conductivity (EC), soil moisture and gravel content. The remaining parameters (L.O.I., C_{min}, pH, P_{CAL}, K_{CAL}), mainly due to correlation with already selected parameters, did not significantly increase the variance explained by the model. The quality of the chosen model is summarised in Table 6.2.

Table 6.2. Explanatory power of the Canonical Correspondence Analysis of the 140 lower slope 1 m² relevés. For comparison, values of the equivalent Correspondance Analysis are also presented. Significance levels, eigenvalues (EV) and percentage of the species variability explained are given for the first four axes. *P*-values were obtained by Monte Carlo permutation.

		CCA		CA	
	P	EV	% explained	EV	% explained
axis 1	< 0.001	0.289	5.7	0.433	8.6
axis 2)	< 0.001	0.130	2.6	0.286	5.6
axis 3	0.026	0.063	1.2	0.273	5.4
axis 4	0.088	0.052	1.1	0.258	5.1
all canonical axes		0.577	11.4	-	
sum of all EV		5.059		5.059	

The sum of canonical eigenvalues in the CCA is 0.577. This amounts to 11.4 % of the overall variability in the species data. In the CCA biplot of the first two axes (Figure 6.2), axis 1 is strongly correlated with soil factors indicating developmental status in terms of organic matter accumulation and nutrient availability. Sample plots on the right-hand side of the biplot are distinguished by a skeletal soil (i.e. high gravel content, low N and P levels and low organic matter content). Sample plots characterised by a high soil organic matter content and by high N and P levels are located on the left-hand side of the ordination diagram. The second CCA axis, in turn, is strongly correlated with volumetric soil water content after several days of drought and with slope angle. In spite of the third axis still being significant and the fourth axis being near-significant, these axes only explain a small fraction of variation in the species composition (Table 6.2) and are therefore not displayed.

Several species occur preferentially on dry nutrient-poor skeletal soil. This pattern is most pronounced for *Poa compressa*, *Bromus japonicus*, *Festuca rubra* L., *Verbascum lychnitis*, *Thlaspi perfoliatum* and *Anthemis tinctoria* L. (see Figure 6.2). Other species perform best on nitrogen-rich soil, including *Arrhenaterum elatius* (L.) BEAUV. EX J. PRESL ET C. PRESL, *Elytrigia repens*,
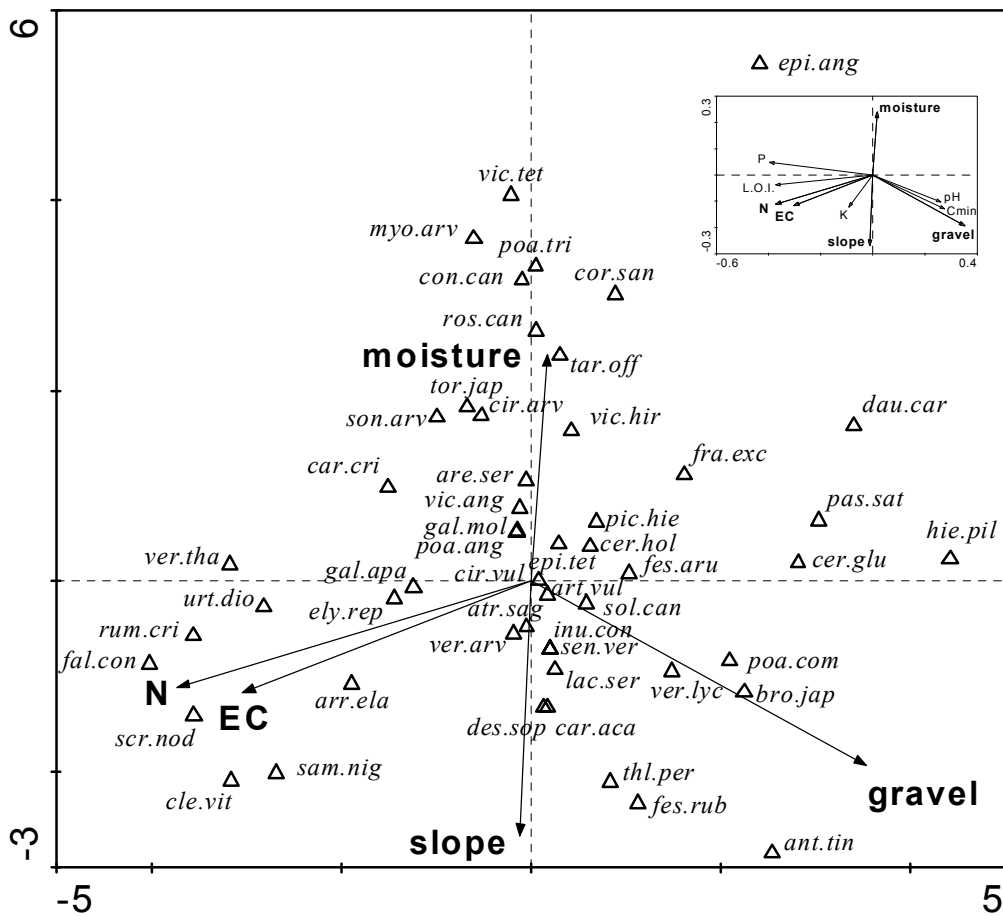
Figure 6.2. CCA species-environment biplot based on vegetation and soil data of 140 quadrats of 1 m² recorded on the Steudnitz field site. Only significant (forward selection, 1999 Monte Carlo permutations) explanatory variables are included. Explanatory variables are rescaled (× 10). The first two axes are shown, explaining 8.3 % of the species variability and 72.6 % of the species-environment relation. In the top right corner, variables not included by forward selection are shown as supplementary variables together with the explanatory variables. For species abbreviations see Appendix 6.

Galium aparine, Urtica dioica L., *Scrophularia nodosa* L., *Fallopia convolvulus* (L.) Á. LÖVE, *Rumex crispus* L., *Verbascum thapsus* L., the vine *Clematis vitalba* L. and the shrub *Sambucus nigra* L. (see Figure 6.2). Other woody species (*Rosa canina* L., *Cornus sanguinea* L., *Fraxinus excelsior* L.) primarily are located in the top half of the biplot, indicating a potential correlation with soil moisture. The same applies to a number of herbaceous species, including *Epilobium angustifolium* L., *Conyza canadensis* (L.) CRONQUIST, *Myosotis arvensis* (L.) HILL, *Taraxacum officinale* WEBER, *Vicia tetrasperma* (L.) SCHREB. and the grass *Poa trivialis* L. (Figure 6.2). Most of these species occur on the more level parts of the slope.

6.3.3.2 General Linear Models

Community Parameters

Community parameters vary significantly in CCA ordination space (Figure 6.3 and Appendix 7).
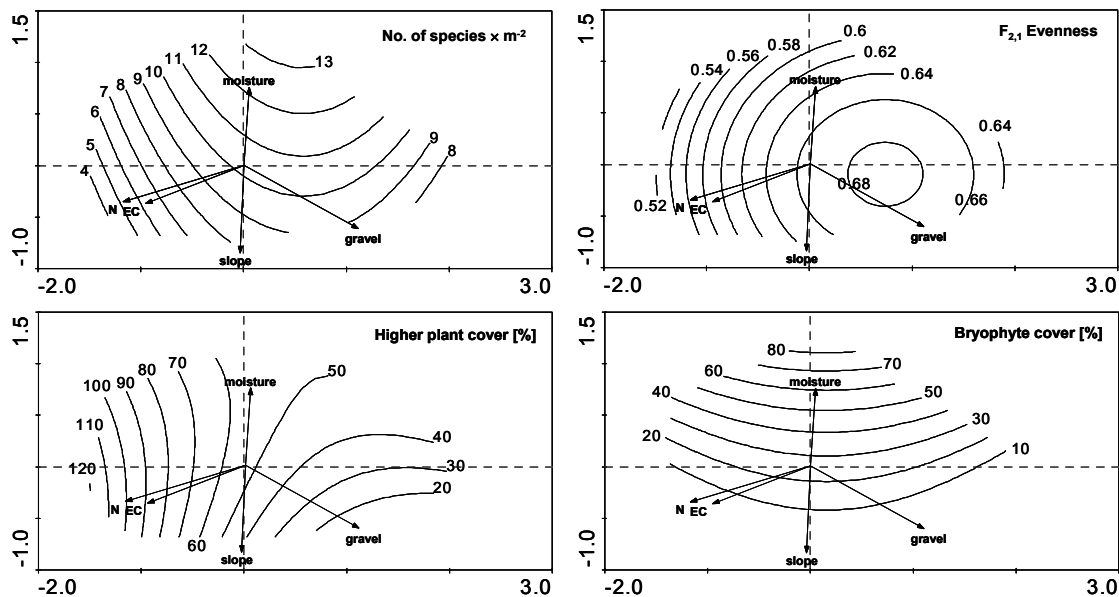
Figure 6.3. Modelled patterns of four community characteristics, overlayed with CCA explanatory variables. The GLM option of the CanoDraw programme was used, with model selection based on the Akaike Information Criterion (see text).

Species density varies both along the first and the second CCA axis. The highest number of species per m² is found in those plots with the highest soil moisture levels. Species density is somewhat lower under dry and nutrient-poor conditions. A particularly low species density is observed at high soil nitrogen levels. Under the latter conditions, evenness is low as well. Maximum evenness can be found at average soil moisture levels combined with below-average nutrient levels.

Higher-plant cover is lowest on nitrogen-poor soil prone to drying out. In contrast, high levels of soil moisture and, even more so, high levels of soil nitrogen are associated with a dense vegetation. Bryophyte total cover largely seems to be a function of soil moisture. Both parameters are positively correlated with each other.

Life history categories

Regression of the proportionate cover of life history types reveals distinct and highly significant (see Appendix 7) patterns in ordination space for all types (Figure 6.4).

Annual species on the whole play a much larger role on the steeper parts of the slope characerised by low soil moisture retention. Longer-lived monocarpic species, on the other hand, seem to be better adapted to nitrogen-poor conditions. Polycarpic herbs are most prominent under moist conditions,

with a secondary peak in dry nutrient-poor microhabitats. Polycarpic grasses are most prominent at high nitrogen levels whereas a secondary peak of relative abundance occurs under nitrogen-poor but not too dry conditions.Woody plants also exhibit a bimodal pattern, with one maximum at high nitrogen levels and another at high soil moisture levels. Legumes are excluded from the vegetation at the highest nitrogen levels and at the lowest soil moisture levels. They are most abundant under conditions of high soil moisture.
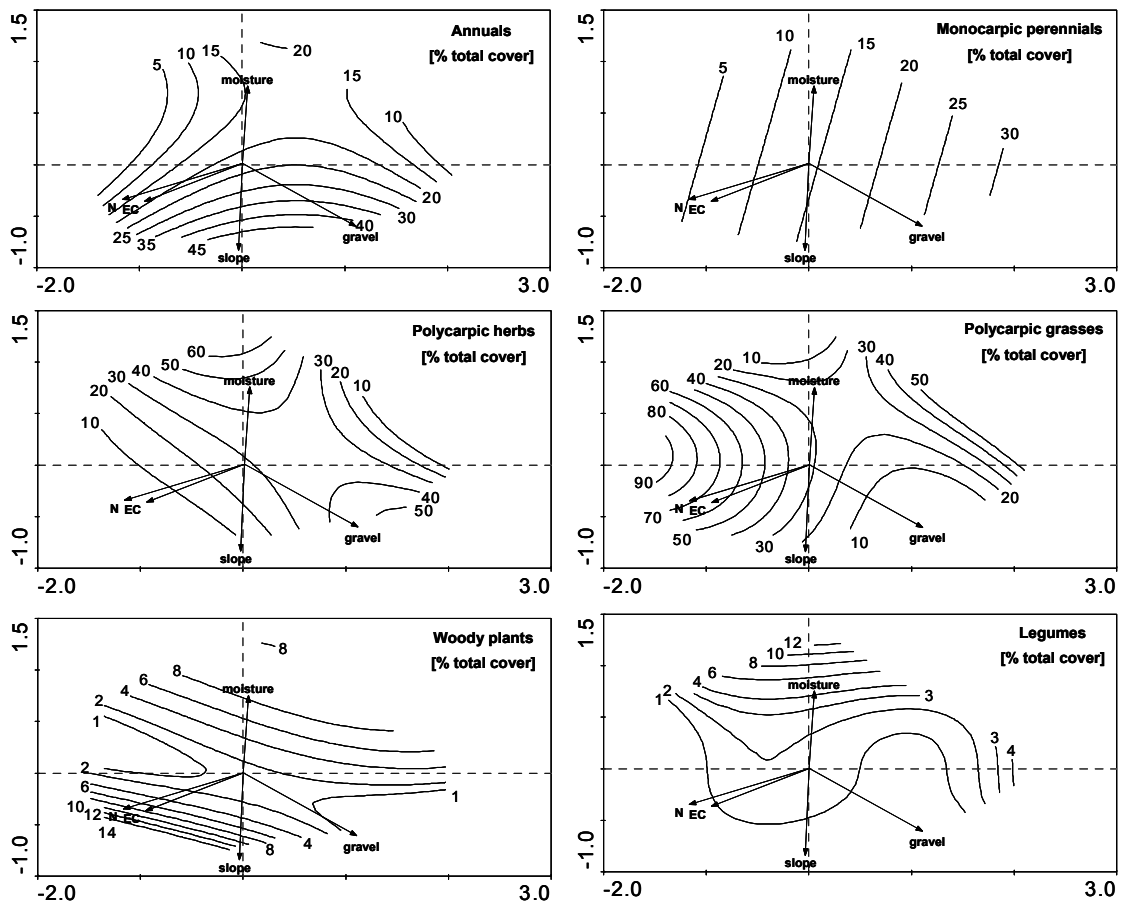
Figure 6.4. Modelled patterns of six different plant life-history categories, overlayed with CCA explanatory variables. The GLM option of the CanoDraw programme was used, with model selection based on the Akaike Information Criterion (see text).

Individual species

For 20 out of those 23 species occurring in at least ten sample quadrats, GLM regression resulted in a significant model (Appendix 8). These models are graphically summarised in Figure 6.5.

Individual patterns of most annual species are in good agreement with the patterns of the annual life-history type. This especially applies to the winter annuals *Lactuca serriola*, *Thlaspi perfoliatum* and *Senecio vernalis*. Patterns deviate slightly in the case of the summer annual *Atriplex sagittata* and the annual grass *Bromus japonicus*. Nevertheless, the centre of the realised niche of these species is
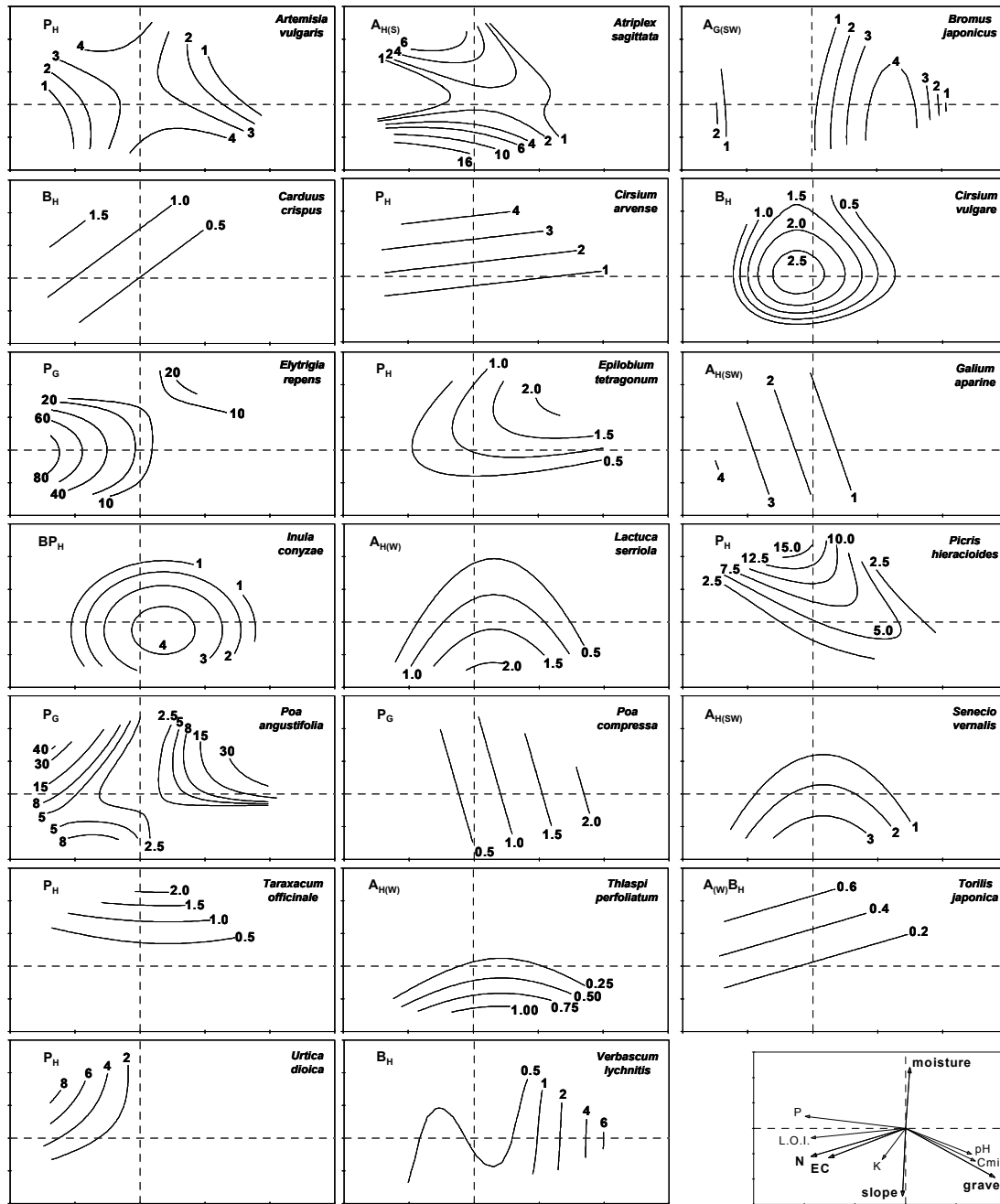
Figure 6.5. Modelled patterns of abundance in CCA ordination space of the most common species at the Steudnitz lower slope. The GLM option of the CanoDraw programme was used, with model selection based on the Akaike Information Criterion (see text). Only those species with models significantly better ($P < 0.05$) than the respective null model are displayed. Contour lines represent percent cover isolines. Additional information is given on life-span of species: A = annual, B = monocarpic biennial / perennial, P = polycarpic perennial. Subscript letters indicate whether a plant is a grass (G) or a herb (H). In the case of annuals, subscripts in parentheses indicate whether a plant is a summer annual (S) or a winter annual (W). Explanatory variables of the CCA model (printed in bold), along with those environmental variables not included into the CCA model, are illustrated in a separate diagram.

located in the lower part of the diagram, indicating a higher abundance on the drier parts of the slope. In the case of *A. sagittata*, the main peak of abundance coincides also with high levels of plant-available potassium. The annual *Galium aparine*, in turn, seems to be positively correlated with soil nitrogen levels. Another nitrophilous species, the polycarpic herb *Urtica dioica*, seems to be less strongly correlated with soil nitrogen and more linked to high levels of soil phosphorus and / or soil moisture.

A positive correlation with soil moisture is still more evident for other polycarpic herbs such as *Picris hieracioides*, *Cirsium arvense*, *Taraxacum officinale* and *Epilobium tetragonum*. Monocarpic perennials show a wider range of patterns. *Verbascum lychnitis* seems to conform best with the pattern of the monocarpic-perennial life-history type, being most abundant in nutrient-poor conditions. *Cirsium vulgare* and *Inula conyzae* are most abundant under 'average' environmental conditions, as indicated by peak occurrence in the centre of the graph. *Carduus crispus* L. and *Torilis japonica* are positively correlated with soil moisture and / or soil phosphorus levels. As for the perennial grasses, the main peak of this life-history type, occurring at high nitrogen levels, is largely due to the strong performance of *Elytrigia repens* under these conditions, whereas the secondary peak occurring under nutrient-poor but not too dry conditions is a result of *Poa angustifolia* L. performing relatively well under such conditions.

6.4 Discussion

6.4.1 Correlation between soil parameters

The strong positive correlation between gravel content and C_{min} is clear, given the underlying limestone geology of the slope: high C_{min} values of the field site soil reflect the high content of calcium carbonate ($CaCO_3$). Equally clear is the strong positive correlation between L.O.I. and N_{total}, since the great bulk of soil nitrogen (95 to 99 %, according to Brady & Weil 2002), is stored in organic compounds, and not in mineral form. The positive correlation of soil pH with C_{min} indicates that soil pH, initially being raised by the deposition of sodium-enriched pollutant dust (Chaper 2), is no longer consequent on this earlier deposition: the current pH of 7.3 to 8.5 is within the normal range for calcareous soils. According to Kissel et al. (1985), the pH of a soil will generally be in the range of 7.6 to 8.3 when its $CaCO_3$ content is > 2 % by weight. The strong positive correlation of soil EC with loss-on-ignition also indicates that soil salinity does no longer contribute to soil EC. Only in one quadrat was EC high enough (0.41 dS $\times$ m^{-1} in the 1:5 water extract) to indicate a raised salinity with potentially adverse effects for sensitive plants (Rowell 1997, Brady & Weil 2002), and the vegetation in this quadrat was dominated by the salt-tolerant *Atriplex sagittata* (65 % cover). The generally low EC is consistent with the low contents of an array of soluble ions found in the soil in 2002 (see Appendix 2). It is also in good accordance with the results of Chapter 5, demonstrating that even the most salt-sensitive plant species had begun to colonise the slope by the mid-1990s. The

negative correlation of P_{CAL} with C_{min} and with pH can be explained with inorganic P compounds being precipitated at high pH as less soluble or (even insoluble) calcium compounds (Brady & Weil 2002). It is noteworthy that this apparently now results in higher levels of plant-available phosphorus further away from the source of emission. The strong positive correlation of P_{CAL} with L.O.I. results from the tendency of phosphorus to be incorporated into the structures of organic compounds. This does not occur with potassium, in spite of this nutrient also playing numerous roles in plant and animal nutrition (Brady & Weil 2002). However, in spite of the correlation being weaker than the correlation between P_{CAL} and L.O.I., K_{CAL} is also positively correlated with loss-on-ignition.

6.4.2 Pairwise association between plant species

Execution of 120 statistical tests with a chosen significance level of $P = 0.05$ should result in about six erroneous rejections of the null hypothesis a on a chance basis. Rejection of the null hypothesis in the case of association analysis gives a significant association between two species. The actual number of significant associations found in this study was 39, which is markedly higher than 6, clearly implying non-random community patterns. When looking simultaneously at both positive and negative associations, none of the 16 species included in the analysis had fewer than two significant associations with other species.

31 of the 39 significant associations were positive. When interpreting this fact, the inherent limitations of the association analysis method must be kept in mind: the finding of an association itself does not allow for conclusions on the causal mechanism. Pairwise interspecific associations might not only be caused by direct interaction between the involved species, but also by the response of both species to a third species (Crawley 1997b) or to abiotic factors (Greig-Smith 1983). The results of association analysis also depend on the chosen quadrat size (Greig-Smith 1983). In the present study, the quadrat size was 1 m², with most species covering only a small percentage of the ground in most quadrats. Although smaller than in previous studies, the quadrat size used in the present study was still comparatively large. Thus, in this study, positive associations between species might well be attributable to a similarity in niche requirements. This does however not exclude the existence of facilitative plant-plant interactions at the site. Some evidence for facilitation at the Steudnitz site has been found in an experiment by Temperton & Zirr (in press), who tested for positive effects of *Picris hieracioides* rosettes on seedling emergence of 6 other species occurring at the slope. In the current study, the strong positive association between the annual species *Senecio vernalis*, *Lactuca serriola* and *Atriplex sagittata* on the one hand, and between the perennial species *Epilobium tetragonum*, *Artemisia vulgaris* and *Picris hieracioides* on the other hand, hints at the importance of the regeneration niche for the shaping of the realised niche of these species in the studied system.

Four out of eight significant negative associations involve *Elytrigia repens* (Figure 6.1). Dense stands of *E. repens* usually are characterised by high soil levels of nitrogen and phosphorus (see Figures 6.2 and 6.5), which, in the absence of interspecific competition, would presumably be beneficial for most of the species occurring at the slope. Thus, negative association of a species with *E. repens* most likely results from competitive exclusion of this species by *E. repens*, rather than from fundamental niche differences. *E. repens* is characterised by a marked tendency for lateral expansion and is classified as C / CR strategist within the CSR system of strategy types (Grime et al. 1988), indicating the high competitive ability of this species. The pronounced litter layer underneath this species at the Steudnitz field site (M. Wagner, personal observation) might prevent establishment of a number of species from seeds. *E. repens* is also negatively associated with *Artemisia vulgaris* and *Atriplex sagittata*, the two species which replaced *Puccinellia distans* as dominants on the more polluted parts of the lower slope a few years after dust emissions had ceased (see Chapter 2). The negative associations between *P. compressa* / *B. japonicus* and *Cirsium arvense* / *Galium aparine*, the latter pair of species being positively associated with *E. repens*, have to be interpreted differently. Neither *C. arvense* nor *G. aparine* are particularly dominant in the plots they occur in. Therefore, those negative associations most likely are not caused by direct interactions between the involved species, but are mediated by *E. repens*.

6.4.3 Canonical Correspondence Analysis

6.4.3.1 CCA model quality
The first two axes of the selected CCA model explain 8.3 % of the overall variability in the species data (Table 6.2). The first two axes in an unconstrained CA explain 14.2 % of the variation. Thus, the small percentage explained by the selected explanatory variables is not a result of the wrong factors being measured. It is rather due to a large stochastic component in the species data and / or the simultaneous influence of many factors. In spite of the small percentage explained by the first two axes, both of them are highly significant ($P < 0.001$), indicating suitability of the CCA model for drawing conclusions on the forces structuring the plant communities at the Steudnitz field site.

6.4.3.2 Main environmental gradients
Environmental gradients are a "powerful research tool" (Keddy 1991: 181), when used for the investigation of ecological community assembly. According to Keddy (1991) there are two basic types of environmental gradients: those that are spatially continuous and those that are not. The existence of the latter type is also accredited for by Crawley's statement that "apparently uniform areas actually consist of many, subtly different microhabitats" (Crawley 1997b: 484). The size of quadrats employed in a vegetation survey therefore is a vital consideration if a study aims at uncovering those less conspicuous small-scale microhabitat differences, in order to link them to the

realised niche of individual plant species. Both gradient types were retrieved by the Canonical Correspondence Analysis, indicating the suitability of the chosen quadrat size for detecting such small-scale microhabitat differences.

The first axis reflects the correlation of large-scale variation in plant community structure along with the complex pollution gradient extending between the proximal and the distal end of the lower slope. The second axis demonstrates that, on a smaller scale, variation in species composition is linked with soil moisture.

6.4.3.3 Abiotic vs. biotic filter

Within the context of this dissertation no experimental testing of the role of interpecific competition in plant community assembly was carried out. Nevertheless, some conclusions can be drawn based on patterns of species diversity in CCA ordination space. Interrelations between species density and the main environmental gradients at the Steudnitz field site (see Figure 6.3) are consistent with the hump-backed model of species richness (Grime 1973). High levels of productivity, as indicated by high vegetation-cover and high levels of soil nitrogen and phosphorus, seem to lead to the exclusion of a disproportionately large number of species. On the other hand, high stress levels caused by a low soil fertility also seem to lead to a reduction in species density. In agreement with the hump-backed model of species density, the highest species densities are found in quadrats characterised by intermediate levels of nitrogen and of plant-available phosphorus and by high soil moisture levels. Species density is somewhat lower in dry and in nutrient-poor microhabitats, and extremely low under conditions of high soil fertility. All told, these results indicate that in different parts of the slope either competition or stress predominates in the filtering of candidates from the pool of applicant species. Regarding stress, both nutrient stress and drought stress seem to play a role. The nutrient with the biggest influence on species density and composition most likely is nitrogen. Nitrogen varies much more along the first CCA axis than plant-available phosphorus,with the levels of the latter being raised considerably along the whole of the main environmental gradient.

The species density maximum at high moisture levels indicates that a number of species from the local species pool, due to a lack of drought tolerance, might be restricted to such conditions of a higher than average soil moisture. Similarly, several of the species present under nutrient-rich conditions might not be able to persist at low nutrient levels. This is very likely the case in the annual *Galium aparine*, the abundance of which clearly correlates with soil N levels (Figure 6.5). The strong positive response of this species to N addition is documented elsewhere (e.g. Pyšek & Lepš 1991, see also Chapter 7 in this dissertation). In the case of another nitrophilous species, *Urtica dioica*, patterns of occurrence (Figure 6.5) reflect as well the well-known preference of moist sites (Reif et al. 1985) and the known positive effects of high phosphate levels on growth (Pigott 1971). Patterns of occurrence of the summer annual *Atriplex sagitatta* (Figure 6.5) hint at the potential importance of

soil potassium for this species achieving the status of a dominant. This is underlined by similar findings in other studies (e.g. Wißkirchen & Krause 1994).

In contrast, the low species density at high levels of soil fertility (Figure 6.3) can be assumed to be a result of the competitive exclusion of a large number of species in the dense vegetation by *Elytrigia repens* (see Figure 6.5). The low evenness at the high-productivity end of the gradient (Figure 6.3) underlines the existence of a pronounced dominance hierarchy (see del Moral & Jones 2002).

6.4.3.4 Life history strategy – a trait with predictive value for assembly in this study?

GLM regressions of the proportionate cover of all life history categories without exception produced highly significant models (woody species: $P = 0.002$; all others: $P < 0.001$).

Modelled patterns of abundance of annual species (Figure 6.4) indicate an association with microhabitats characterised by great steepness and a tendency to dry out quickly after rainfall. The majority of annual species displayed in Figure 6.5 conform to this pattern, including *Atriplex sagittata*, *Lactuca serriola*, *Senecio vernalis*, *Thlaspi perfoliatum* and *Bromus japonicus*. *Veronica arvensis* L. and *Descurainia sophia* (L.) WEBB EX PRANTL might show similar distributional patterns, as indicated by their position in the CCA species-environment biplot (Figure 6.2), but data for these species are not sufficient to model their patterns of occurrence in ordination space individually. With the exception of the summer annual *A. sagittata* are all those annual species winter annuals (Rothmaler 2002). The importance of water supply at the seedling stage for differentiation in the regeneration niche has previously been pointed out for chalk grassland by Grubb (1977). The present system, in some aspects, including soil moisture regime, is edaphically similar to chalk grassland. According to Grubb, winter annuals are well adapted to the chalk grassland ecosystem, because they are past the susceptible seedling stage when the characteristic summer drought sets in (Grubb 1976). Because of the germination of winter annuals taking place soon after the drought, gaps created by the drought are preferably colonised by them, rather than by spring-germinating species. Hopkins (1978) likewise postulated that in chalk grasslands short-lived species should be more likely to escape severe drought stress as seeds and re-establish themselves in the greater proportion of bare areas caused by drought. A contrast between short-lived and perennial species is also emphasised by other authors. A promotion of monocarpic species by drought due to the debilitation of perennials has been found by Prince et al. (1985) and by Dunnett et al. (1998).

Apart from a life history compatible with the summer drought, several of the aforementioned annuals are known to possess morphological adaptations to drought in the adult stage. The root architecture of *L. serriola* is designed for maximising water capture in lower soil layers (Jackson 1995, Gallardo et al. 1996). The almost vertical orientation of *L. serriola* leaves in exposed habitats enhances photosynthesis during cooler periods in the morning and afternoon, simultaneously reducing water

loss and optimising water use efficiency (Werk & Ehleringer 1984, 1985). The wooly-pubescent leaf surface of *S. vernalis* (Rothmaler 2002) most likely serves a similar purpose.

Polycarpic herbs are in this study more common on those parts of the slope characterised by a high soil moisture (Figure 6.4). Examples include *Urtica dioica*, *Picris hieracioides*, *Cirsium arvense*, *Taraxacum officinale* and *Epilobium tetragonum* (Figure 6.5). At least one of these species. *P. hieracioides*, germinates in late spring (Muller 1978) and is therefore more likely to still being in the seedling stage when the summer drought sets in. Hence, this species depends on a more stable environment in terms of soil moisture.

The contrasting patterns of abundance for annuals and polycarpic herbs with respect to the drought-proneness of the microhabitat is in accordance with models of life history evolution such as the r / K concept (Pianka 1970) and the related CSR concept (Grime 1974, 1977). Soil moisture levels which are inadequately low for plant growth can result in both stress and disturbance (Grime 2001). According to Grime, vegetation disturbance by climate is "prevalent where conditions encouraging the establishment (but not the uninterrupted growth) of competitors alternate abruptly with seasons imposing severe stress" (Grime 2001: 81). This kind of climatic disturbance also operates at the Steudnitz field site. Presumably it is more pronounced on those parts of the slope which are most prone to drying out. Grime's (2001) statement that potentially fast-growing ephemeral plants are favoured under such circumstances is supported by the findings of this study and by several of the above mentioned studies (Hopkins 1978, Prince et al. 1985, Dunnett et al. 1998).

Monocarpic perennials are most abundant at the low-nitrogen end of the sampled gradient, with an intermediate tendency for soil to dry out (Figure 6.4). According to Hart (1977), monocarpic perennials do preferentially occur on sites of intermediate stability, in the present case exemplified by an intermediate tendency to dry out. Silvertown (1983) points out the importance of high survival of nonflowering rosettes for biennials in order to gain an advantage over annual plants. The species largely responsible for the observed overall patterns of relative abundance of monocarpic perennials (Figure 6.4), *Verbascum lychnitis* (Figure 6.5), is characterised by a deep tap root enabling the plant to obtain water deep in the subsoil even in times of severe drought (Kutschera & Lichtenegger 1992). Drought-related mortality of rosettes of this species should therefore be relatively low. According to Kelly (1985), the additional risk of death for a biennial during its second year of growth, compared to an annual, must be offset by the higher seed output made possible by the excess of resources accumulated during the second year. This might be especially important under the nitrogen-poor soil conditions characterising the proximal end of the lower slope.

Relative abundance of polycarpic grasses shows a bimodal distribution in CCA ordination space, with a main peak of abundance under nitrogen-rich conditions, and a secondary peak under nitrogen-poor and rather moist conditions (Figure 6.4). The secondary peak is largely due to *Poa*

angustifolia L., whereas the main peak is almost exclusively caused by the dominance of *Elytrigia repens* at high nitrogen levels. This fits with the assumption of higher nitrogen levels promoting the dominance of clonal species with a distinct potential for lateral expansion (de Kroon & Bobbink 1997), since *E. repens* represents such a species (Grime et al. 1988).

Soil moisture and soil nitrogen status seemingly also play a role in the establishment of woody plants and of leguminous herbaceous plants. With the notable exception of *Clematis vitalba* and *Sambucus nigra*, both of which preferentially occur on N-enriched soils, woody plants tend to occur mainly on sample plots characterised by high soil moisture. As a result, there is a bimodal pattern of woody plant abundance in ordination space (Figure 6.4). Preferred occurrence in quadrats with high soil moisture retention is most conspicuous in *Cornus sanguinea*, *Rosa canina*, and to a lesser extent, also in *Fraxinus excelsior* (Figure 6.2). Individuals were at the time of recording mostly seedlings and small saplings, making it unlikely that the high soil moisture is a result of, rather than a prerequisite for, the establishment of these taxa. These species are the exact opposite of fast-growing ephemerals, and therefore the results also are in agreement with life history theory. An overriding role of drought stress in controlling establishment of woody plants has also been found in related habitats, such as old-fields (e.g. deSteven 1991, McCarthy 1994, Berkowitz et al. 1995, Meiners et al. 2000). As in other studies (e.g. Dunne & Parker 1999), the spatial patterns of tree recruitment at the Steudnitz field site to some extent reflect local soil moisture variations.

In the case of leguminous species the apparent limitations imposed by drought cannot be explained in the same way. As annuals, occurrence of the most abundant legumes at the Steudnitz field site (*Vicia tetrasperma*, *Vicia hirsuta* (L.) GRAY, *Vicia angustifolia* L.) should in theory be promoted by disturbance. Limitation of legumes by drought has however been noted in other studies of plant community succession on nitrogen-poor soils, for example by Ritchie & Tilman (1995). In their study, a severe drought caused a dramatic decline in total legume biomass both in a successional old-field and a savanna, and it took several years for legume biomass to return to pre-disturbance levels (Ritchie & Tilman 1995). Optimum moisture in terms of realised niche is higher for the most common legumes at the site (*V. hirsuta* and *V. tetrasperma*, both characteristic for disturbed sites) than for typical chalk-grassland legumes absent from the slope but otherwise widespread in the region (e.g. *Anthyllis vulneraria* L., *Hippocrepis comosa* L., *Onobrychis viciifolia* SCOP.). This fact is illustrated by the higher Ellenberg moisture indicator values (4 and 5, respectively) for the former two species, compared to species of the latter group, characterised by the moisture value 3 (Ellenberg 1992). The distribution of legumes in the field with respect to drought might therefore simply be an artefact resulting from the absence of drought-tolerant chalk-grassland species. On the other hand, legumes might be more dependent on sufficient precipitation than members of other plant families, since this may be a critical prerequisite for the release of the characteristic hardseededness of legumes (Merou & Papanastasis 2000). For this reason, annual legumes might differ from other

annuals in terms of their realised niche. The performance of leguminous species on the middle slope is different from that on the lower slope. In recent years, *V. hirsuta* and *V. tetrasperma* thrived on the middle slope permanent plot (W. Heinrich, unpublished). On the deeper soils of the more level middle slope, drought stress is less pronounced. Here, the combination of high phosphorus levels with low nitrogen levels, shown in many previous studies in other systems to promote legumes (e.g. Willems et al. 1993, Kirkham et al. 1996, Brewer & Cralle 2003), provides optimum conditions for legumes.

The results of proportionate cover GLM regression models for different life-history categories are more or less in agreement with life history theory and the findings of previous studies on plant community composition. They also indicate that plant life history is a species trait with a predictive value regarding plant community assembly (*sensu* Keddy 1992) at the Steudnitz field site.

7. Nutrient imbalance and plant community structure: a nutrient addition experiment

7.1 Introduction

The potential importance of resource levels, in particular of soil nitrogen and moisture, for community assembly processes at the Steudnitz field site, was highlighted in the preceding chapter. This chapter deals in more detail with the influence of soil nutrients on plant community structure. Both excess and deficiency of soil nutrients can have a profound influence on the vegetation.

An increased supply of nutrients - brought about by processes such as natural succession, atmospheric pollution and extensive fertiliser use - can have pronounced effects on terrestrial ecosystems (Marrs & Gough 1989). Increased aerial deposition of nitrogen compounds (Brimblecombe & Stedman 1982) led to a disproportionate increase of soil nitrogen levels, causing nutrients to be available at excess levels in many ecosystems. This led to complex changes in community and ecosystem processes (e.g. Jefferies & Maron 1997), including in many cases an increased ecosystem productivity and shifts in plant species composition (e.g. Berendse et al. 1993). Such effects have commonly been explored in experiments simulating nitrogen deposition by means of fertiliser addition (see Eviner et al. 2000). In managed grasslands, a common result of these experiments seems to be an increased dominance of graminoid species (e.g. Thurston 1969, van Hecke et al. 1981, Ginzo et al. 1982, Heil & Diemont 1983, Bobbink et al. 1988, Bobbink 1991, Mountford et al. 1993). A shift towards graminoid species induced by N fertilisation could also be demonstrated in some unmanaged successional old field systems (e.g. Tilman 1987), but not in others (e.g. Goldberg & Miller 1990).

In contrast, in the case of nitrogen-poor soils it has been suggested that the successional sequence might be determined by the ability of different plant species to grow at low nitrogen levels in both the primary (e.g. Marrs & Bradshaw 1993) and secondary (e.g. Tilman 1986) types of succession.

The proximal part of the lower slope at the Steudnitz field site is characterised by a combination of relatively low nitrogen levels with very high levels of total and extractable phosphorus and an above-average potassium content (see Chapter 2). At the same time, the vegetation is dominated by ruderal dicotyledonous herbs, with graminoid species only playing a subordinate role (see Chapter 6 and Heinrich et al. 2001). In contrast, dominance of the grass *Elytrigia repens* at the far end of the lower slope is associated with high levels of soil nitrogen (see Chapter 6). This chapter describes an experiment designed to find out whether the low relative abundance of grasses near the former fertiliser factory is due to the low local nitrogen levels, both in terms of (a) total levels and (b) relative levels when compared to levels of phosphorus and potassium. The experiment also allows conclusions to be made about the potential influence of nitrogen on successional patterns, as

suggested by the findings of the field survey described in Chapter 6. Consistency between the occurrence of plant species along the natural nitrogen gradient (illustrated in Figure 6.5) and their response to nitrogen addition (this chapter) would be evidence for such an influence. In addition, effects of different fertiliser treatments on above-ground primary production are investigated, allowing for a discussion of nutrient limitation at the community level. Finally, treatment-dependent changes of evenness and species richness, the latter broken down in colonisation and extinction events, can be quantified. The results might provide clues to problems such as whether nitrophilous plants are barred from colonisation of this part of the slope by the low present day nitrogen levels or whether the addition of nitrogen increases interspecific competition.

7.2 Methods

7.2.1 Experimental design

Treatments were established in a row of six contiguous complete blocks, oriented perpendicularly to the slope. Each block consisted of four square plots of 2×2 m (Figure 7.1).
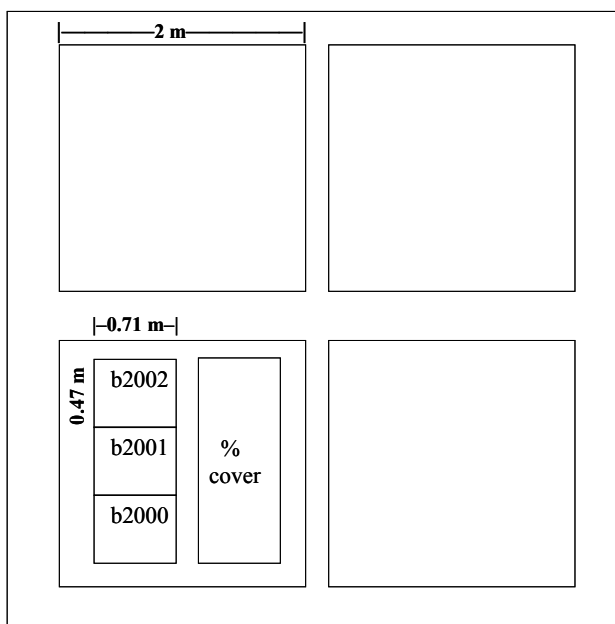
Figure 7.1. Design of an experimental block in the nutrient addition experiment, consisting of 4 treatment plots. Subplots are shown for one treatment plot: b2000, b2001 and b2002 denote the areas sampled for aboveground biomass in the respective year, and the 1 m² subplot for visual cover estimates is also indicated. Further details in the text.

Because the area available for experimentation on this part of the lower slope was limited, there was no within-block replication of single treatments. Treatments were: (a) addition of nitrogen (N); (b) addition of nitrogen, phosphorus and potassium (henceforth referred to as NPK treatment); (c) addition of micronutrients; (d) no fertiliser addition (= control treatment). Details are given in Table 7.1. The blocks were set up in September 1999. Due to the experimental site being a slope, slow-release fertilisers (Osmocote™ and Scotts Micromax™) were used and timing of their application

55

(mid-March in the years 2000 to 2002) was chosen to coincide with the onset of the growing season, to minimise losses due to leaching, whilst maximising uptake of the applied nutrients by the vegetation (Eviner et al. 2000).

Table 7.1. Summary of the different treatments applied in the fertiliser addition experiment.

Treatment	Fertiliser Type	Nutrients added / yr × m²	Remarks
NPK	Osmocote™ 17-10-12	8.5 g N, 5 g P, 6 g K	slow-release pellets; active ingredients: ammonium nitrate, potassium sulphate, ammonium phosphates, calcium phosphates
N	Osmocote™ 23-0-0	8.5 g N	slow-release pellets; active ingredient: ammonium nitrate
micronutrients	Scotts Micromax™	6 g S, 0.05 g B, 0.25 g Cu, 6 g Fe, 1.25 g Mn, 0.025 g Mo, 0.5 g Zn	fine powder
control	-	-	-

The N and NPK treatments were randomly allocated to the lower plots within each block, whereas the micronutrients and control treatments were randomly allocated to the upper plots. This was done in order to avoid spurious effects resulting from nitrogen leaching downwards from N or NPK plots into plots of the other types. The upper and lower rows were separated by a strip of 0.5 m, and the vegetation of upper row plots and lower row plots was similar in composition. Because of the powdery character of the micronutrient fertiliser, fertilisers were distributed under windless conditions. Vegetation sampling was carried out in two different ways. Standing biomass was harvested from a 47 cm x 71 cm subplot (equalling 1/3 m²) located on the left-hand side of each treatment plot in the first week of July in the years 2000 to 2002. Each year, a different subplot was used (Figure 7.1). Vegetation was cut at ground level using scissors. Samples were stored in closed plastic bags in a 5 °C cold-storage chamber and processed within 48 hours. Standing dead material from the previous year was removed, and the live material was sorted to species level, dried to constant weight at 80 °C in a drying chamber, and weighed. Two species, *Cerastium glutinosum* and *Cerastium holosteoides* FR. EM. HYL., were pooled as they were not clearly distinguishable that late in the year. Non-destructive sampling of the vegetation was carried out by estimating the percent cover of all species in rectangles of 1 m² located on the right-hand side of the treatment plots (Figure 7.1). The same simplified percent cover scale as in the seed bank study (see Chapter 5) was used. In each year, cover estimates were carried out both at the beginning of May and in mid-July. By doing

so, the inclusion of early species, such as *Erophila verna* (L.) CHEVALL., was ensured. For species recorded on both occasions, the higher of the two cover values was used in subsequent data analysis. No baseline data of the vegetation was collected prior to the first imposition of the experimental treatments; however, baseline data were collected for soil parameters. The soil was sampled to a depth of 10 cm prior to the onset of the experiment in October 1999. Sampling was repeated at the beginning of March 2002, just before the third annual fertiliser application. On both occasions a soil corer of 1 cm diameter was used for extracting 25 soil cores - laid out in a regular 5×5 grid - from each treatment plot. Soil cores for each treatment plot were pooled prior to soil analysis. Soil pH, loss-on-ignition (L.O.I.), plant-available P (P_{CAL}) and K (K_{CAL}) and total N (N_{total}) were determined using the methods described in Chapter 6. A summary of the results is provided in Appendix 9.

7.2.2 Data analysis

7.2.2.1 Univariate community characteristics

Univariate community characteristics were analysed using a repeated measures General Linear Model (GLM), in order to test (a) for significant differences between years, and (b) for significant differences between the responses to the various treatments.

Community characteristics included cover and biomass totals as well as the portion made up by graminoids for both above-ground biomass and plant cover. For both data sets, measures of plant species diversity were calculated. Whereas the most popular diversity indices are difficult to interpret because they incorporate both species richness and relative abundance of the component species at the same time (Magurran 1988), the approach used in this study aims at avoiding these difficulties. Separate measures for both components of diversity were used. Treatment effects on species richness were assessed via the calculation of species density (i.e. number of species per m²). Equality of species abundances was measured by computing the modified Hill's ratio recommended by Alatalo (1981). This index is one of several evenness indices largely uncorrelated with species richness. It focuses on the more common species within a community and therefore is robust with respect to rare species (Alatalo 1981).

In the repeated measures GLM, time (three levels) was used as within-subjects factor. Treatment and block identity were analysed as between-subjects factors. An important assumption for the use of GLMs is the homogeneity of within-group variances (Quinn & Keough 2002). As indicated by Levene's test, this assumption was not fulfilled. Therefore, parameters were power transformed. The spread-versus-level option in SPSS (SPSS Inc. 1999) allows for each parameter separately to estimate the optimal power for a transformation to stabilise variances. Transformation did not improve variance homogeneity in the case of cover subplot species density. Therefore, untransformed data were used for analysis of this parameter. For repeated measures analysis, another

important assumption is the sphericity of the variance-covariance matrix (von Ende 2001, Quinn & Keough 2002). As indicated by Mauchly's test of sphericity (von Ende 2001), there was a significant departure from this assumption in the case of several parameters (results not shown). Thus, Greenhouse-Geisser correction was applied for the correction of significance levels (von Ende 2001). Because of the lack of within-block replication, all repeated measures GLMs were based on the assumption of the absence of treatment by block interactions. The corresponding interaction term therefore was not included in the model (Quinn & Keough 2002). In the case of significance of the within-subjects factor time or its interaction with block identity or treatment type, the sum of squares was partitioned in order to test whether the trend was significantly linear or significantly quadratic (or both).

7.2.2.2 Species-specific response and community response

Analysis on the species level was carried out for the most common species, occurring in ≥ 24 of the 72 (= 24 treatment plots x 3 years) samples gathered in 2000-2002, using repeated measure GLM as described in the previous section. While power transformation resulted in a considerable stabilisation of within-group variances for a number of species especially in the cover data set, improvement was only marginal for the biomass data.

Since most of the species exhibited treatment-independent temporal trends, multivariate analysis of the complete cover and biomass data sets was carried out as well. Inclusion of appropriate covariables in multivariate analysis allows for the elimination of treatment-independent temporal effects and for clearer illustration of treatment effects. In a species declining during succession, a positive treatment effect might manifest itself in an attenuated population decline compared to the control. In contrast, if a species increases during succession, a positive effect might be expressed as a stronger increase. In the ordination diagram, these two scenarios cannot be distinguished. Net differences between treatments are illustrated irrespective of the underlying general tendencies. On the other hand, summarising three years' data in such a model makes this method unsuitable for the detection of transient non-linear species dynamics (which can occur in experiments very similar to this one, see Tilman 1987). This means that a species increasing between the first and the second year of the experiment and then again decreasing to initial levels is depicted in exactly the same way as a species not exhibiting any dynamics at all. The combined use of both the repeated measures GLM and the multivariate analysis should result in an increased understanding of the system.

For the multivariate analyses, species occurring in less than 10 % of the 72 samples were eliminated from the data sets. Rare species add noise to multivariate data sets (Gauch 1982). Also, they often are not accurately depicted in ordination diagrams. Thus, 24 species remained in the percent cover data set and 20 species in the biomass data set. Since the duration of the experiment seemed too short for a considerable number of extinction and colonisation events to occur, the analysis focused on treatment-induced cover changes of the species which were initially present. Therefore, data were not

transformed prior to analysis. Partial Redundancy Analysis (pRDA) in the CANOCO package (ter Braak & Šmilauer 1998) was used for both the biomass data and the cover data, as the species composition in the plots was rather homogeneous (Lepš & Šmilauer 2000). The appropriateness of the linear model was also indicated by the length of the longest gradient in an initial Detrended Correspondence Analysis being lower than 3.0 in both cases (biomass data: 2.544, percent cover data: 2.833; see ter Braak & Šmilauer 1998). As I was most interested in the effects of particular treatments on community composition, the corresponding interactions of treatments with time were used as explanatory variables in the analysis (Lepš & Šmilauer 2000). Plot identity, time, and time × block interaction were included as covariables. The inclusion of plot identity (coded as dummy variables) secures that only the changes within each plot were analysed by the pRDA. Because of the inclusion of time as a covariable, the revealed trends have to be seen as relative to the average trend in the community (Lepš & Šmilauer 2000). Values for this covariable ranged from 1 to 3 for the years 2000 to 2002, respectively. In such a model, plots of different treatments are assumed to already differ slightly in vegetation composition in the summer of 2000 as a result of the March 2000 fertiliser application. Based on this, the model fits the linear increase in difference over time. The time × block interaction was included in order to remove the effect of block on dynamics (J. Lepš, personal communication). In order to test for treatment-dependent shifts in species composition, significance of the first axis was tested using Monte Carlo permutation (9999 permutations under the reduced model). After specifying the sample scores of axis 1 as additional covariable (Lepš & Šmilauer 2000), the significance of the second axis was also tested. Permutations were restricted according to the experimental design and the investigated hypothesis. Therefore, individual treatment plots were defined as whole-plots, each whole-plot consisting of three split-plots (corresponding to the three years). While the whole-plots were permuted at random within each complete block, the split-plots of each whole-plot were kept together. Eigenvalues were compared with those of Principal Components Analysis (PCA) of the same data (ter Braak 1995).

7.3 Results

7.3.1 Univariate community characteristics

Biomass data

Above-ground biomass differed significantly between years (Table 7.2). There was a general increase in biomass over time (Figure 7.2a). The highly significant time × treatment interaction term indicates that the magnitude of this increase depended on the treatment. Figure 7.2a shows that the increase was much larger on the plots fertilised with N or NPK fertilisers. Standing biomass on the control plots was a mere 25 % higher in 2001 and 2002, compared with 2000. In contrast, biomass on the N plots roughly doubled from c. 150 g × m^{-2} to c. 300 g × m^{-2}. Third year biomass on the NPK

Table 7.2. Repeated measures GLM results for the univariate plant community parameters collected in the nutrient addition experiment. Due to a lack of within-block replication, no treatment × block interaction was included in the model. Prior to analysis, homogeneity of within-group variances was improved by power transformation for all parameters apart from the number species per cover subplot. Potential violation of the sphericity assumption of repeated measures GLM was taken into consideration by applying a Greenhouse-Geisser correction. Uncorrected degrees of freedom were $d.f._{TIME} = 2$, $d.f._{TIME \times BLOCK} = 10$, $d.f._{TIME \times TREATMENT} = 6$, $d.f._{ERROR} = 30$. Significant P-values ($P < 0.05$) are indicated by bold style. In this case, superscript letters L and Q denote significant linear and quadratic within-subject contrasts.

Parameter	Within-Subjects Effects	biomass data			cover data		
		d.f.	F	*P*	d.f.	F	*P*
biomass	Time	1.87	39.17	**< 0.001**[LQ]	1.98	84.97	**< 0.001**[LQ]
/ cover	Time × Block	9.33	1.03	0.445	9.87	1.38	0.238
total	Time × Treatment	5.60	7.49	**< 0.001**[L]	5.92	17.73	**< 0.001**[LQ]
	Error	27.98			29.62		
proportion	Time	1.71	27.13	**< 0.001**[L]	1.56	39.25	**< 0.001**[LQ]
of grass	Time × Block	8.57	2.20	0.059	7.81	2.54	**0.039**[L]
[%]	Time × Treatment	5.14	4.16	**0.006**[LQ]	4.68	3.02	**0.032**[Q]
	Error	25.71			23.42		
number of	Time	1.97	54.08	**< 0.001**[L]	1.75	3.78	**0.041**[L]
species /	Time × Block	9.85	0.59	0.807	8.76	1.56	0.179
subplot	Time × Treatment	5.91	0.83	0.552	5.26	2.87	**0.032**[L]
	Error	29.56			26.29		
modified	Time	1.69	0.48	0.592	1.75	3.22	0.062
Hill's ratio	Time × Block	8.43	1.06	0.423	8.75	0.62	0.769
evenness	Time × Treatment	5.06	0.90	0.497	5.25	0.45	0.819
	Error	25.30			26.26		

plots was even higher (c. 375 g × m^{-2}), although differences between N and NPK plots are not significant (Figure 7.2a). Remarkably, effects of the N and NPK treatments only manifest themselves from the second year onwards. The percentage of grass biomass did also differ significantly between years (Table 7.2). Again, there was a significant time × treatment interaction. Figure 7.2b illustrates the general increase of the relative contribution of grasses to aboveground primary production. It also shows that the significant time by treatment interaction is largely due to the disproportionately large relative increase on the N plots between year two and year three of the experiment. Third year grass biomass on N plots amounted to 49 % of total plant biomass, compared to 8 % in the first year.
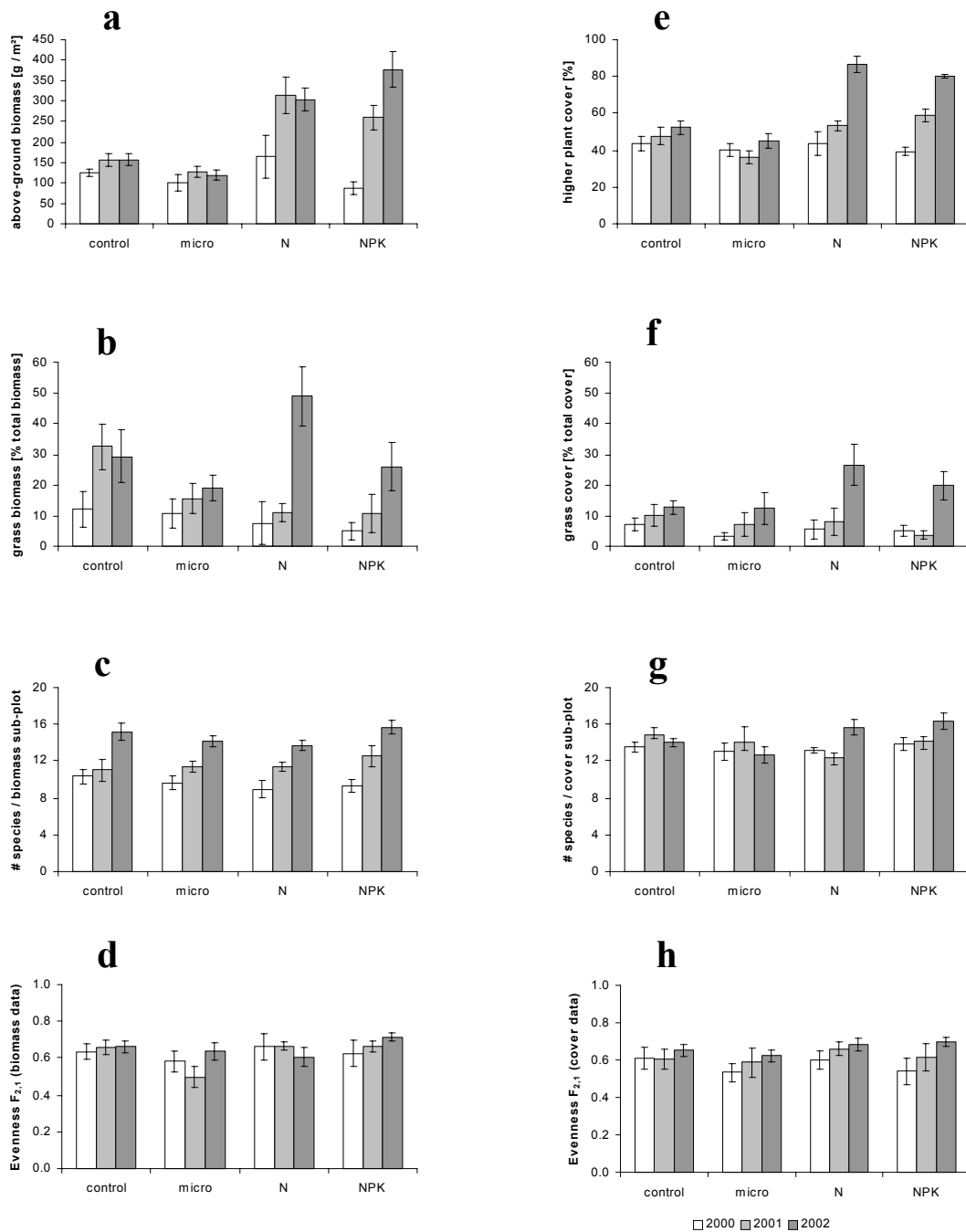
Figure 7.2. Univariate community characteristics for the treatments of the nutrient addition experiment. For the period from 2000 to 2002 the means are shown (error bars represent 1 S.E.M.). From the top to the bottom the following parameters are illustrated for the biomass data: (a) total biomass, (b) percentage of grasses, (c) species density per subplot, (d) modified Hill's ratio evenness (Alatalo 1981). The same parameters are shown for the cover data (e-h). Treatments were: control = no fertiliser addition; micro = addition of micronutrients; N = nitrogen addition; NPK = addition of nitrogen, phosphorus and potassium.

At the same time, this increase was smallest (from 9 % to 19 %) on the micronutrient plots. Unlike the N treatment, the NPK treatment in the third year yielded a percentage of grass biomass not markedly different from the one found on the untreated controls (Figure 7.2b).

Species density on the biomass subplots increased steadily and significantly (Table 7.2) over time (Figure 7.2c). The extent of this increase did not vary significantly between treatments. Species density per 1/3 m² totalled between 9 and 10 species in 2000 and between 14 and 16 species in 2002. Modified Hill's ratio evenness did slightly decrease on N plots and slightly increase in the other treatments (Figure 7.3d). There were however no significant linear trends (Table 7.2).

Cover data

As indicated by the repeated measures GLM (Table 7.2), total plant cover differed significantly between years. An increase with time was observed (Figure 7.2e). In good consistency with the biomass data, this increase was small in the micronutrient and control treatments and pronounced in the N and NPK treatments. In the first year, total cover ranged between 40 and 45 % irrespective of treatment. In 2002, the third year of the experiment, average total plant cover was > 80 % on the N and NPK plots, whereas on the micronutrient and control plots it was around 50 %. This difference is reflected in the highly significant time by treatment interaction (Table 7.2). The contribution of grass species to total plant cover differed significantly between years, increasing with time in all treatments (Figure 7.2f). Due to this increase being more pronounced on the N and NPK plots, the time by treatment interaction is also significant. As in the biomass data, the relative contribution of grasses increased enormously on the N and NPK plots between the second and the third year (Figure 7.2f).

The mean number of species recorded on a 1 m² cover subplot differed significantly among years (Table 7.2) and in general was higher in 2002 than in 2000. In contrast to species density on the 1/3 m² biomass subplots, the magnitude of this increase differed significantly between treatments, as reflected in the significant time × treatment interaction. The increase was small on the control plots (13.5 species / m² to 14.0 species / m²), and on the micronutrient plots species density even was marginally lower in 2002 than in 2000. In contrast, there was a pronounced increase in species density on the N and NPK plots (from between 13 and 14 species / m² to c. 16 species / m²). A tendency of modified Hill's ratio evenness on cover subplots to increase with time fell short of significance ($F = 3.22$, d.f. $= 1.75$, $P = 0.062$).

7.3.2 Species-specific response and community response

Summarised results of the repeated measures GLMs are shown in Table 7.3. For conciseness, between-subjects effects are not reported in this table. Whenever required, they are referred to in the text.

Table 7.3. Repeated measures GLM results for cover and biomass data of the plant species most common in the nutrient addition experiment (≥ 24 out of 72 subplots). Due to a lack of within-block replication, no treatment × block interaction was included in the model. Power transformed data were used (see text). Potential violation of the sphericity assumption of repeated measures GLM was taken into consideration by applying a Greenhouse-Geisser correction. Uncorrected degrees of freedom were d.f.$_{TIME}$ = 2, d.f.$_{TIME \times BLOCK}$ = 10, d.f.$_{TIME \times TREATMENT}$ = 6, d.f.$_{ERROR}$ = 30. Significant P values ($P < 0.05$) are indicated by bold style. In this case, superscript letters L and Q denote significant linear and quadratic within-subject contrasts.

Species	Within-Subjects Effects	biomass data			cover data		
		d.f.	F	P	d.f.	F	P
Artemisia vulgaris	Time	1.95	1.81	0.183	1.32	9.53	**0.003**^{LQ}
	Time x Block	9.73	0.56	0.829	6.61	3.12	**0.023**^{Q}
	Time x Treatment	5.84	2.35	0.058	3.97	10.22	**< 0.001**^{LQ}
	Error	29.20			19.83		
Atriplex sagittata	Time	1.74	34.63	**< 0.001**^{LQ}	1.50	37.46	**< 0.001**^{LQ}
	Time x Block	8.69	2.90	**0.017**^{Q}	7.50	6.84	**< 0.001**^{LQ}
	Time x Treatment	5.21	1.11	0.379	4.50	1.49	0.236
	Error	26.06			22.51		
Bromus japonicus	Time	1.39	47.24	**< 0.001**^{L}	1.38	47.14	**< 0.001**^{LQ}
	Time x Block	6.96	3.01	**0.024**^{Q}	6.89	3.72	**0.009**^{L}
	Time x Treatment	4.18	10.41	**< 0.001**^{LQ}	4.13	7.50	**< 0.001**^{LQ}
	Error	20.88			20.66		
Cerastium spp.	Time	1.60	16.93	**< 0.001**^{L}	-	-	-
	Time x Block	7.98	3.14	**0.014**^{L}	-	-	-
	Time x Treatment	4.79	1.04	0.415	-	-	-
	Error	23.94			-		
Cerastium glutinosum	Time	-	-	-	1.72	3.23	0.063
	Time x Block	-	-	-	8.59	1.50	0.203
	Time x Treatment	-	-	-	5.16	0.36	0.873
	Error	-			25.78		
Cerastium holosteoides	Time	-	-	-	1.22	7.82	**0.009**^{LQ}
	Time x Block	-	-	-	6.08	1.98	0.121
	Time x Treatment	-	-	-	3.65	0.66	0.613
	Error	-			18.23		
Cirsium vulgare	Time	1.42	4.27	**0.039**^{Q}	1.40	7.43	**0.007**^{LQ}
	Time x Block	7.11	2.16	0.079	6.99	1.15	0.373
	Time x Treatment	4.26	1.44	0.254	4.19	1.05	0.409
	Error	21.32			20.96		
Conyza canadensis	Time	1.02	12.96	**0.002**^{LQ}	-	-	-
	Time x Block	5.08	1.24	0.341	-	-	-
	Time x Treatment	3.05	0.85	0.491	-	-	-
	Error	15.24			-		
Epilobium tetragonum	Time	1.21	12.24	**0.002**^{LQ}	1.19	11.54	**0.002**^{Q}
	Time x Block	6.05	1.83	0.149	5.93	1.90	0.137
	Time x Treatment	3.63	4.03	**0.019**^{LQ}	3.56	4.86	**0.009**^{LQ}
	Error	22.70			17.78		

Table 7.3 (continued)

Species	Within-Subjects Effects	biomass data			cover data		
		d.f.	F	*P*	d.f.	F	*P*
Galium aparine	Time	-	-	-	1.49	4.44	**0.033**[Q]
	Time x Block	-	-	-	7.43	1.79	0.136
	Time x Treatment	-	-	-	4.46	5.83	**0.002**[L]
	Error	-			22.28		
Inula conyzae	Time	1.37	5.88	**0.017**[L]	1.97	23.58	**< 0.001**[L]
	Time x Block	6.85	0.83	0.569	9.86	1.79	0.108
	Time x Treatment	5.77	0.86	0.507	5.92	3.13	**0.017**[L]
	Error	20.54			29.59		
Lactuca serriola	Time	1.47	12.16	**< 0.001**[L]	1.98	5.27	**0.011**[L]
	Time x Block	7.33	1.87	0.122	9.88	1.83	0.099
	Time x Treatment	4.40	2.56	0.063	5.93	2.46	**0.048**[L]
	Error	21.99			29.63		
Picris hieracioides	Time	1.42	9.30	**0.003**[Q]	1.91	3.91	**0.033**[Q]
	Time x Block	7.09	0.87	0,549	9.53	1.61	0.156
	Time x Treatment	4.26	1.32	0.296	5.72	3.37	**0.013**[Q]
	Error	21.28			28.58		
Poa angustifolia	Time	1.63	2.99	0.078	1.36	2.33	0.136
	Time x Block	8.14	0.97	0.481	6.80	0.96	0.483
	Time x Treatment	4.88	0.58	0.708	4.08	0.67	0.621
	Error	24.42			20.41		
Poa compressa	Time	1.92	3.17	0.059	1.64	7.61	**0.004**[L]
	Time x Block	9.61	0.64	0.760	8.22	1.08	0.409
	Time x Treatment	5.76	0.78	0.587	4.93	2.18	0.090
	Error	28.82			24.67		
Senecio vernalis	Time	1.89	2.85	0.077	1.37	3.80	0.053
	Time x Block	9.46	3.10	**0.009**[L]	6.85	3.94	**0.007**[L]
	Time x Treatment	5.68	1.80	0.138	4.11	1.31	0.297
	Error	28.39			20.56		
Taraxacum officinale	Time	1.64	12.69	**< 0.001**[L]	1.95	14.30	**< 0.001**[LQ]
	Time x Block	8.20	0.82	0.596	9.77	1.29	0.284
	Time x Treatment	4.92	1.45	0.241	5.86	0.69	0.659
	Error	24.61			29.30		
Verbascum lychnitis	Time	1.82	7.26	**0.004**[L]	1.80	35.25	**< 0.001**[L]
	Time x Block	9.11	2.26	**0.048**[Q]	9.01	1.47	0.211
	Time x Treatment	5.47	1.61	0.187	5.41	0.70	0.639
	Error	27.33			27.04		

The treatment responses of individual species are illustrated in Figure 7.3 for the biomass data and in Figure 7.4 for the cover data. Overall, both the cover and biomass data of a species yielded very similar results in most cases. The GLM results for both the cover and biomass data indicate that almost all common species, perhaps with the exception of the perennial grass *Poa angustifolia*, are subject to treatment-independent temporal dynamics (Table 7.3).
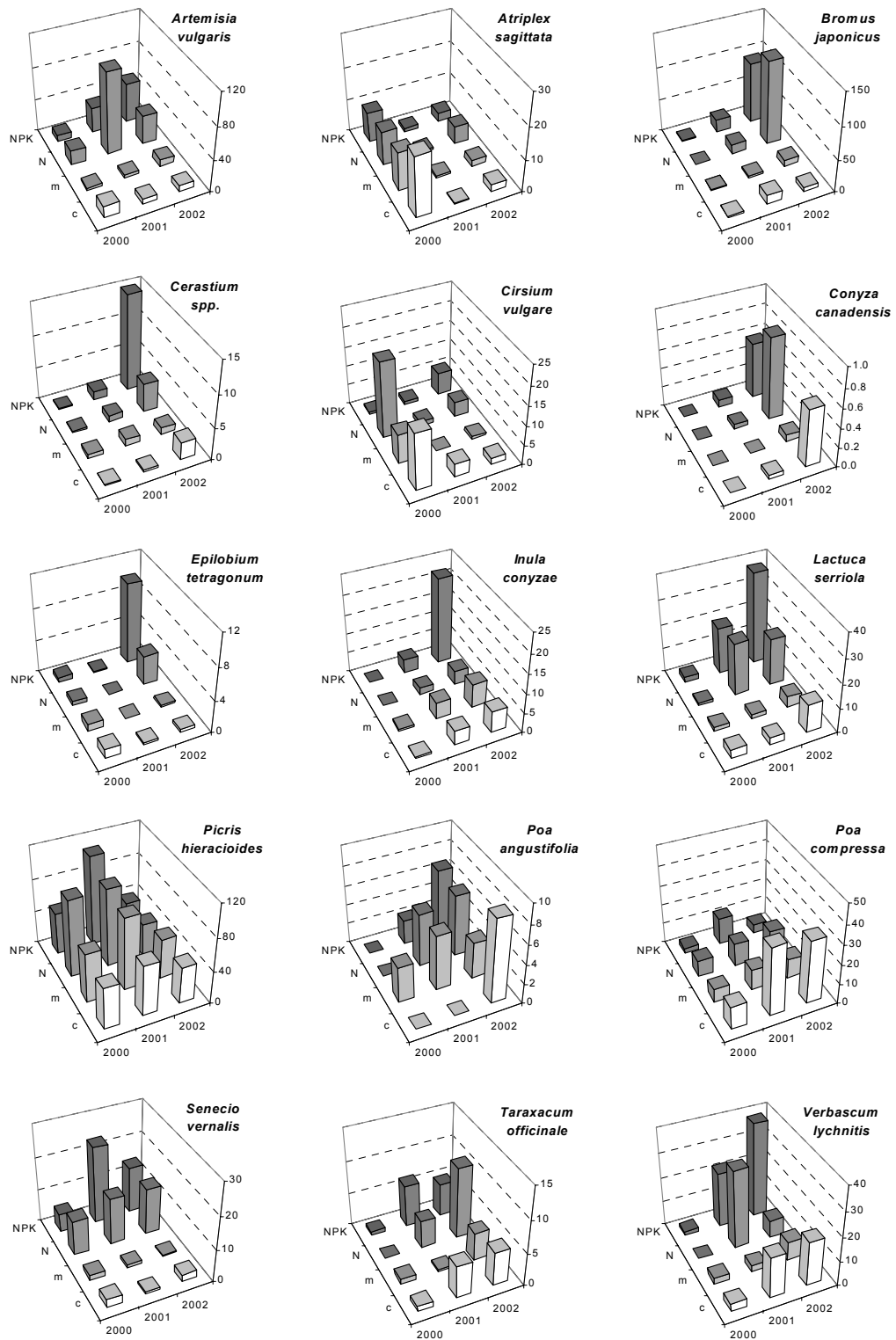
Figure 7.3. Mean annual above-ground biomass [g × m²] of the most common species in the biomass subplots of the nutrient addition epxeriment. Treatments are: c = unfertilised control; m = micronutrient addition; N = nitrogen addition; NPK = addition of nitrogen, phosphorus and potassium.

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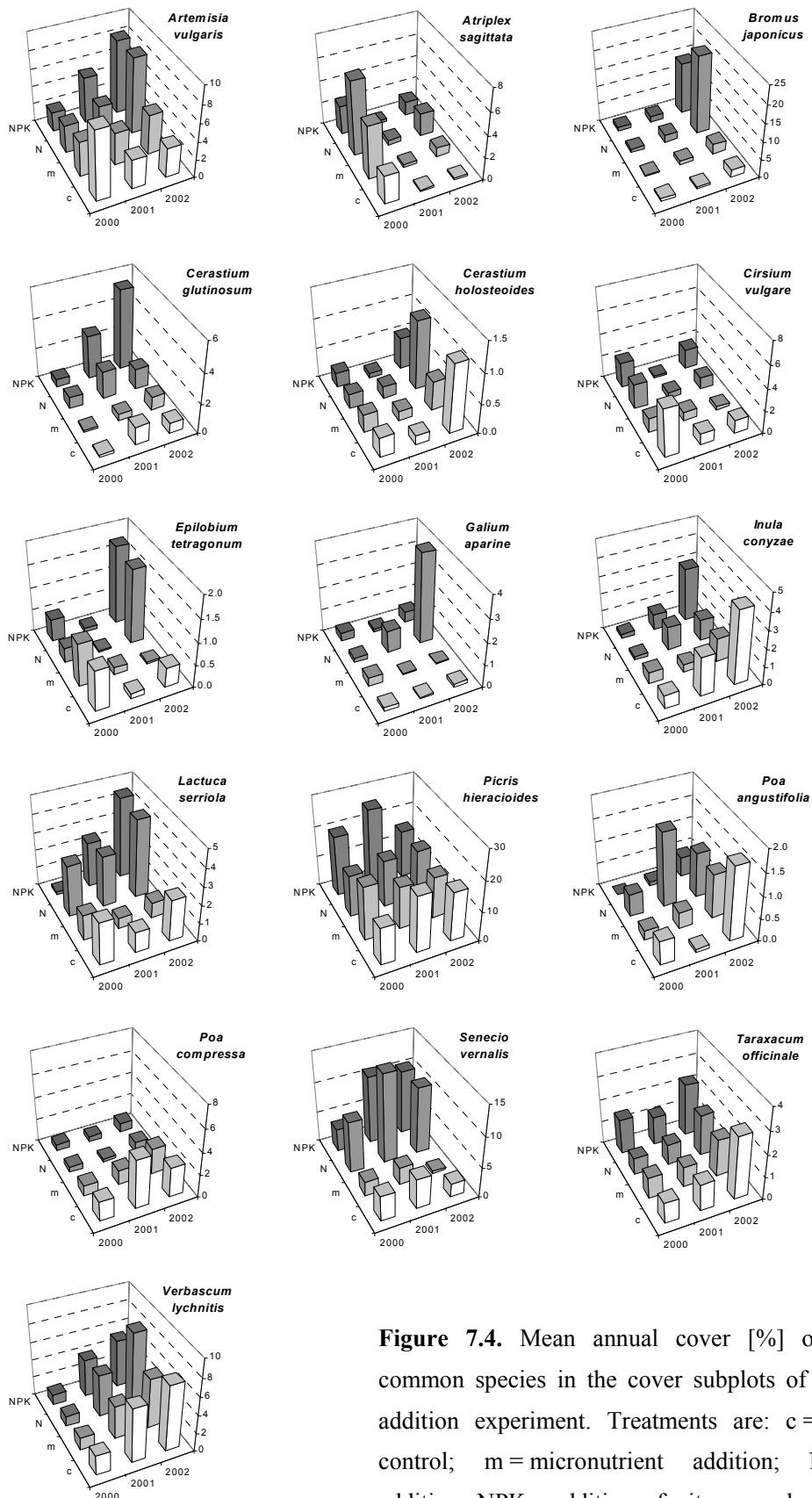
Figure 7.4. Mean annual cover [%] of the most common species in the cover subplots of the nutrient addition experiment. Treatments are: c = unfertilised control; m = micronutrient addition; N = nitrogen addition; NPK = addition of nitrogen, phosphorus and potassium.

This tendency was most pronounced in two annual species which were largely unaffected by treatments, *Atriplex sagittata* and *Conyza canadensis*. *C. canadensis* was virtually absent in 2000 and in 2001, but quite abundant in 2002 (Figure 7.3). In contrast, *A. sagittata* was most abundant in 2000 and much less abundant in 2001 and 2002 (Figures 7.3 and 7.4). Dynamics of the biennial *Cirsium vulgare* were very similar to those of *A. sagittata*, but less pronounced. A number of species significantly increased in abundance largely uninfluenced by treatment (Table 7.3). The tendency was most clear in the polycarpic perennials *Poa compressa* and *Taraxacum officinale* and the monocarpic perennial *Verbascum lychnitis* (Figures 7.3 and 7.4). Another group of species is characterised by a pronounced treatment-dependent response as illustrated by a significant time × treatment interaction. Among them are the annual grass *Bromus japonicus*, the annual herbs *Lactuca serriola* and *Galium aparine* and the polycarpic perennials *Epilobium tetragonum* and *Artemisia vulgaris* (Table 7.3). In the case of *B. japonicus*, there is a strong positive response to N and NPK addition which seems to be slightly more pronounced in the N treatment (Figures 7.3 and 7.4). Patterns are very similar for *G. aparine* (Figure 7.4). In the case of *L. serriola*, the increase seems to be stronger with the addition of NPK fertiliser. For the annual herb *Senecio vernalis*, the time × treatment interaction of both the biomass and cover data is non-significant (Table 7.3). Nevertheless, there is a consistent difference between treatments, indicated by a highly significant treatment effect (biomass: F = 13.29, d.f. = 3, $P < 0.001$; cover: F = 13.48, d.f. = 3, $P < 0.001$). Post-hoc Games Howell tests reveal that average biomass of *S. vernalis* is significantly ($P < 0.05$) lower on control and micronutrient plots, compared to N and NPK plots. The percent cover also was significantly lower on micronutrient but not on control plots, compared to N and NPK plots.

A summary of both the partial Redundancy Analyses (pRDA) and the Principal Components Analyses (PCA) is provided in Table 7.4, and pRDA results are graphically displayed in Figure 7.5.

Table 7.4. Summary of partial Redundancy Analyses and Principal Components Analyses of biomass and percent cover data from the nutrient addition experiment. Abbreviations as follows: EV = axis eigenvalue; % = percentage of species variability explained by axis; F = F-ratio; P = corresponding probability value, obtained by Monte Carlo permutation test (9 999 permutations); Subscripts indicate axis number (except for EV_U = sum of unconstrained eigenvalues).

Analysis	Data Set	EV_1	EV_2	$\%_1$	$\%_2$	EV_U	F_1	P_1	F_2	P_2
partial RDA	biomass	0.065	0.013	14.2	2.9	0.455	2.76	< 0.001	1.37	0.274
partial RDA	% cover	0.053	0.014	16.1	4.3	0.331	3.66	< 0.001	2.10	0.147
PCA	biomass	0.358	0.232	35.8	23.2	1.000	-	-	-	-
PCA	% cover	0.312	0.214	31.2	21.4	1.000	-	-	-	-
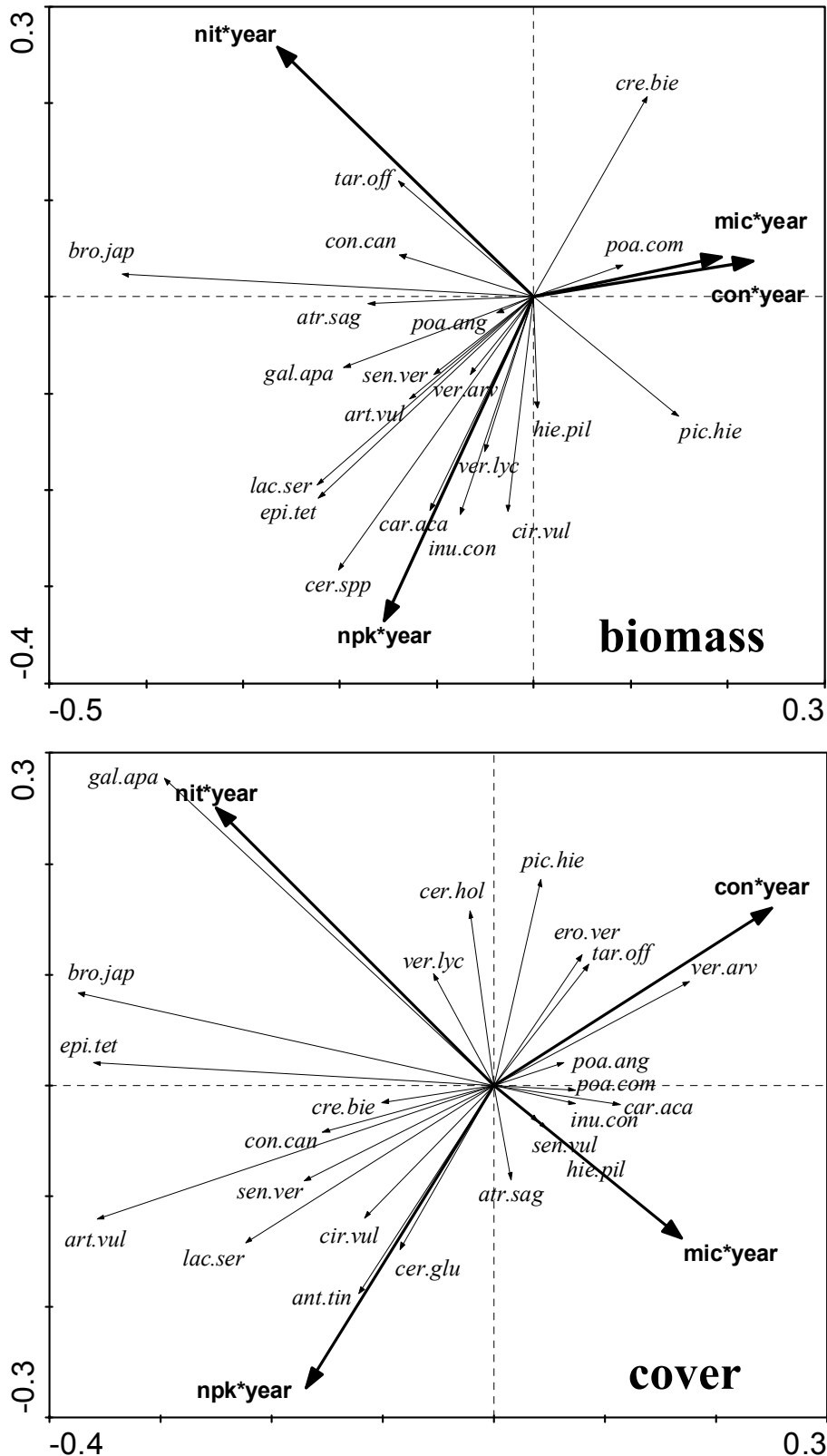
Figure 7.5. Biplots showing the first two axes of partial Redundancy Analyses of the nutrient addition experiment. Both biomass and cover data were analysed separately. Explanatory variables are treatment × time interactions (nit*year = nitrogen addition, npk*year = addition of NPK fertiliser, mic*year = micronutrient addition, con*year = unfertilised control). The first two axes explain 17.1 % (biomass data) and 20.4 % (cover data) of the species variability, respectively. For species abbreviations see Appendix 6.

Eigenvalues for the first two axes of the partial RDAs are well below those of the PCAs. This is not surprising given the large fraction of variance removed by the covariables used in the partial RDAs (55 % in the biomass data set, 67 % in the cover data set). Nevertheless, the first pRDA axis explains between 14 and 16 percent of the remaining variation, and Monte Carlo permutation tests yield highly significant results for the first pRDA axis.

Orientation of explanatory variable vectors is quite similar with respect to the first pRDA axis in both analyses. In both cases, the N × year and NPK × year vectors point towards the left-hand side, and the micronutrient × year and control × year vectors point towards the right-hand side (Figure 7.5). The N × year and NPK × year vectors have the highest scores - with opposite algebraic signs - on the second pRDA axis. However, the second axis, as indicated by Monte Carlo tests, was non-significant in both cases.

Among the displayed species, those with (a) a more or less identical response in both pRDAs, or (b) with an exceptionally good fit to the explanatory variables in at least one pRDA, indicated by the length of the species vector, deserve attention. An equally strong promotion by both the N and the NPK treatment is indicated for *Epilobium tetragonum*. In the case of *Bromus japonicus*, one of the most strongly responding species, the N treatment seems to be slightly more beneficial. In contrast, *Lactuca serriola*, *Artemisia vulgaris*, *Cirsium vulgare* and *Senecio vernalis* seem to respond more strongly to the NPK treatment. In the cover-based pRDA, but not in the biomass-based pRDA, *Galium aparine* shows a much more pronounced reaction to N than to NPK fertilisation. Species lacking a clear positive response to N or NPK fertilisation include the perennial herb *Picris hieracioides* and the grasses *Poa compressa* and *Poa angustifolia*.

7.4 Discussion

7.4.1 Nutrient limitation

Above-ground biomass strongly increased in the second year both in the N and NPK treatments. This increase was of a similar magnitude in both treatments, implying that the net primary productivity (NPP) of the extant plant community is primarily limited by nitrogen. Third year values were slightly higher on the NPK plots (377 g × m^{-2}), compared to the N plots (302 g × m^{-2}) This difference, due to large within-treatment variability, is however not significant. Continuation of the experiment, planned within the context of a mycorrhizal experiment (V. Blanke, personal communication), might provide more conclusive evidence as to whether this difference indicates a secondary nutrient limitation by one of the other macronutrients once the nitrogen limitation is eliminated. If this is the case then the difference in above-ground primary productivity will persist.

Interestingly, the c. 150 g × m^2 above-ground biomass measured on the unfertilised control plots are about 50 % lower than the values obtained in 1980 from a *Puccinellia distans* stand on the most

degraded part of the slope (Heinrich 1984), in spite of the then used method (clipping at ground level and drying at 80 °C; H.-U. Peter, personal communication) being very similar to the method used in this study. The productivity levels reported by Heinrich (1984) are even higher than those found in a study where monocultures of *P. distans* was grown in experimental field plots under non-limiting water and nutrient conditions (see Beyschlag et al. 1992). This implies that at that time nitrogen was not a limiting nutrient. A likely explanation is that nitrate contained in the pollutant dust (see Appendix 2) may have prevented nitrogen limitation to occur during the period of dust deposition. The current nitrogen limitation however, for a number of reasons, is reasonable. The occurrence of nitrogen limitation is widespread in terrestrial ecosystems (Vitousek & Howarth 1991). Nitrogen retention within ecosystems is dominated by biological processes such as plant uptake and microbial immobilisation (Vitousek & Howarth 1991). Obstruction of these processes usually results in mobilisation and increased losses of nitrogen via leaching, denitrification, and erosion (e.g. Vitousek & Matson 1985). The study area, the proximal part of the lower slope, was partially devoid of vegetation between the early 1980s and the time of factory closure (Heinrich et al. 2001), and soil microbial biomass is still reduced in the more polluted part of the slope (Langer & Günther 2001). Hence, more than three decades of pollutant dust deposition may have hindered nitrogen retention processes and this may be the main reason for the observed low levels of soil nitrogen, in spite of the potential input of nitrate resulting from earlier deposition. The same deposition process caused phosphorus (the other main nutrient commonly limiting NPP in terrestrial systems; see Koerselman & Meuleman 1996) to be strongly enriched.

The absence of a growth response by the plant community in the first year calls for an explanation. Biological immobilisation of the first dose of nitrogen by the soil microbial community might have played a minor role in this delay of a growth response. Chapin et al. (1986) characterise the soil microbial community as powerful competitors for added nutrients and recommend large nutrient additions that are sufficient to saturate chemical and microbial immobilization processes. However, the nitrogen addition rates in the N and NPK treatments of this study ($8.5 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$) were only slightly lower than the 10 to 20 $\text{g} \times \text{m}^{-2}$ recommended for achieving a quick response (Eviner et al. 2000): thus, temporary immobilisation of the added nitrogen by the soil microbial community cannot have overridingly contributed to the delayed response. This is also supported by the fact that no accumulation of nitrogen in the soil was observed in response to N or NPK fertiliser addition (see Appendix 9). A more convincing explanation for the lack of response in the first year may be provided by the below-average spring 2000 rainfall. The relatively small difference in control plot primary production between the rainfall-deficient year, 2000, and the years 2001 and 2002 should not be taken as evidence for a subordinate role of the water factor. Rather, a co-limitation of primary production by both water supply and nitrogen supply seems a likely explanation for the observed patterns. Remedy of just one factor might have only a small impact, explaining the small response to

added nitrogen in the particularly rain-deficient year 2000 and the small response to increased rainfall on the control plots in the subsequent years which were characterised by high rainfall. Such a co-limitation by water and nitrogen commonly occurs in grasslands in arid climatic regions (e.g. Kirchner 1977, Lauenroth et al. 1978, Fisher et al. 1988). Furthermore, co-limitation by water and a mineral nutrient has also been found in the temperate climatic region, including the co-limitation of primary productivity by nitrogen and water in a 1st year old-field community in Michigan (Goldberg & Miller 1990) and the co-limitation of seedling growth by phosphorus and water in a calcareous grassland in England (Grime & Curtis 1976). A negative effect of drought on nitrogen fertiliser effectiveness has also been observed in a long-term study on successional old-fields, where aboveground biomass was correlated with rate of N addition in all years but 1988, the year of a severe drought (Tilman 1993).

7.4.2 Species-specific response to treatments

Repeated measures GLMs of individual species responses illustrate that abundance of most species varies significantly between years irrespective of fertiliser application. Particularly strong fluctuations were observed in the case of the biennial *Cirsium vulgare* and the annuals *Atriplex sagittata* and *Conyza canadensis*. The former two species showed peak abundance in the dry summer of 2000, whereas the latter species peaked in 2002, a year characterised by above-average rainfall. This pattern is consistent with the occurrence of *A. sagittata* and *C.vulgare* in microhabitats prone to drying out and of *C. canadensis* in microhabitats with a better soil moisture retention (see Chapter 6, Figures 6.2 and 6.5). In contrast, those species characterised by a steady and treatment-independent increase in abundance (*Poa compressa*, *Taraxacum officinale* and *Verbascum lychnitis*) were perennials. It is not surprising that annual and biennial species, abundance of which strongly depends on environmental conditions during establishment, show irregular patterns of abundance with time. In contrast, the steady increase of the above mentioned perennials irrespective of treatment suggests that none of these species has yet reached its equilibrium density.

A number of species show a pronounced response to N and NPK fertilisers. The perennials *Artemisia vulgaris* and *Epilobium tetragonum* responded primarily by means of a strongly increased shoot growth (M. Wagner, personal observation). The annuals *Galium aparine, Bromus japonicus, Senecio vernalis* and *Lactuca serriola*, which seemed to more permanently benefit from the N and NPK fertiliser addition, seemingly responded not only with increased growth, but also via a numerical response due to increased seed set (M. Wagner, personal observation) or reduced mortality.

These effects were most evident in the case of *G. aparine*, which grew much bigger on N and NPK plots (M. Wagner, personal observation), and also colonised three N cover subplots where it previously was absent, although, at the same time, the number of subplots of other treatments inhabited by *G. aparine* declined. Strong promotion of this species by nitrogen fertilization has also

been demonstrated for arable fields (e.g. Koch 1957, Pyšek & Lepš 1991, Gerowitt 1999). At the Steunitz field site there is a strong positive relationship between the abundance of *G. aparine* and soil nitrogen level (Chapter 6, Figure 6.5). The low abundance in the proximal part of the lower slope may be ascribed to low levels of soil nitrogen. The scarcity of nitrogen in this case seems to act as a component of the abiotic filter. The same might hold true for other species, such as *Urtica dioica* L. and *Elytrigia repens* (see Figure 6.5). A prominent ecological feature of *G. aparine* is its capacity for adhesive seed dispersal by means of humans or animals. Other species confined to more nitrogen-rich soils at the slope might not yet have colonised the N or NPK plots for a lack of similarly efficient dispersal mechanisms.

In the case of of *Bromus japonicus*, a dramatic increase in abundance resulting from nitrogen fertilisation has previously been documented for North American rangeland plant communities (Hewlett et al. 1981). Whereas effects of the N and NPK additions on community net primary productivity NPP became visible in the second year (Figure 7.2), the pronounced increase of *B. japonicus* occurred mainly in the third year (Figures 7.3 and 7.4). This suggests that the increased third year biomass / cover of this species primarily resulted from an increase in population size due to an increased seed production in the second year. The higher abundance of *B. japonicus* on those parts of the slope characterised by low nitrogen levels (see Figure 6.5), in combination with the strong negative association between *B. japonicus* and *E. repens* (= the dominant species in the more nitrogen-rich part of the slope), suggests that competitive exclusion of *B. japonicus* by *E. repens* plays an important role in the patterns of occurrence of *B. japonicus* at the field site. The current increase in abundance of this species might be regarded as a transient phenomenon, which is expected to disappear with the advanced colonisation of the treatment plots by competitive species.

The only species with a marked positive response to N / NPK addition in the first year of the experiment was *Senecio vernalis*. Unlike the other species positively responding to N addition in the current experiment, *S. vernalis* finishes its life cycle well before the onset of the summer drought, which was most extreme in the first year of the experiment (see Apendix 1).

In summary, patterns of individual species' responses lend support to the hypothesis that soil water and soil nitrogen are co-limiting the growth of plants at the field site.

7.4.3 Changes in community structure

The timing of the fertiliser application (mid-March) and the type of fertiliser used in the N and NPK treatments (Osmocote™ slow-release fertilisers with an average duration of release of 5 to 6 months) should have resulted in seasonal N supply patterns resembling the seasonal patterns of the N mineralisation rate in unmanipulated temperate soils (see Davy & Taylor 1974). Seasonal N supply patterns on N-manipulated plots and control plots should thus be more or less similar and treatment

effects on community composition should not be the product of differences in temporal N availability patterns.

The results of the multivariate analysis showed a significant influence of the applied treatments on plant community structure, indicated by highly significant pRDA 1st axes (Table 7.4). The prominent role of nitrogen is underlined by the similar orientation of both the N × year vector and the NPK × year vector with respect to the first axis (Figure 7.5), and by the fact that the second axis in both pRDAs falls short of significance.

The shift in community composition induced by application of nitrogen alone was slightly more pronounced compared to the application of all three macronutrients together. This is indicated by the higher absolute value of the 1st axis score in the case of the the N × year vector, compared to the NPK × year vector (Figure 7.5). A somewhat larger effect of N addition compared to NPK addition was found with respect to the relative contribution of grasses to total biomass / cover (Figure 7.2). These observations are in accordance with hypotheses emphasising the role of resource ratios (e.g. Tilman 1985, Braakhekke & Hooftman 1999), as the addition of the limiting nutrient nitrogen on its own results in a larger alteration of macronutrient ratios compared to the simultaneous addition of all macronutrients. In this study, most of the effect was accounted for by the annual grass *Bromus japonicus*. The absence of perennial grasses characterised by a marked tendency for lateral expansion and a known positive response to N fertilization was probably a prerequiste for the strong increase of *B. japonicus* in response to N addition in this study. The perennial grasses present on the experimental plots studied here, *Poa angustifolia* and *P. compressa*, lack the tendency for nitrogen-mediated clonal expansion. In contrast, *Elytrigia repens*, known for its positive response to nitrogen fertilisation (e.g. Tilman 1987, Story et al. 1989), is a dominant species at the distal end of the lower slope, but absent from the experimental plots studied here.

Average number of species increased markedly on the small (1/3 m²) biomass subplots. A similarly significant but much smaller increase was observed on the larger (1 m²) cover subplots (Figure 7.2 and Table 7.2). The more pronounced increase on the smaller subplot type indicates that it did at least partly result from the spread of existing species, leading to the homogenisation of an initially heterogeneous vegetation. Similar phenomena have been observed in other successional systems (e.g. del Moral & Jones 2002). The general increase in species richness during the experiment might, in part, be an artefact of the extraordinarily dry weather in the first year of the experiment. The 2000 drought might have caused the temporary disappearance of a number of species. Due to a lack of comparative data for 1999, this hypothesis cannot be evaluated. An immediate drop in species richness caused by severe drought followed by an increase in species richness in subsequent years is known from other systems, such as old-field plant communities (Tilman & El Haddi 1992), which are structurally very similar to this system.

The magnitude of increase in species density on the cover subplots was treatment-dependent. The increase was more pronounced in the N and NPK treatments than in the control and micronutrient treatments (Figure 7.2). Tilman (1993) points out the importance of the duration of a particular study in assessing the effects of fertiliser addition on plant diversity. A transient increase in species richness after fertilisation has been observed in old-field successional communities (e.g. Tilman 1987, Carson & Barrett 1988). Tilman (1993) ascribes this effect to nitrogen-dependent germination of seed bank species. In this study, only a few species accounted for the more pronounced increase in species richness on N and NPK plots. The raw data (not shown) indicates that this stronger increase was caused to a large extent by a few species only, and was not only a result from species actively colonising more NPK and N plots, compared to control and micronutrient plots, but also of species being less likely to disappear from N / NPK fertilised plots. Two species, *Atriplex sagittata* and *Epilobium tetragonum*, disappeared from the vegetation of a remarkably large number of control and micronutrient plots, but from relatively few of the N and NPK plots. Two other species, *Poa angustifolia* and *Conyza canadensis*, managed to invade more previously unoccupied N / NPK plots than control and micronutrient plots. The same holds true for *Galium aparine* on N plots, compared to the other three treatments. All of these species, *P. angustifolia* and *G. aparine* excepted, more or less regularly occur in the seed bank of the field site (Chapter 5). Furthermore, for at least two of these four species, stimulation of germination by nitrate is known from the literature: the germination of G. aparine is markedly stimulated by application of potassium nitrate (Froud-Williams 1985); in the case of *A. sagittata*, the germination of the more common, small black seed type, which is characterised by a high degree of dormancy, is stimulated by moderate amounts of nitrate (Mandák & Pyšek 2001a). Thus, the mechanism postulated by Tilman (1993) might also play a role in the present study.

The tendency of cover subplot evenness to increase with time (Figure 7.2) fell short of significance (Table 7.2). Observed patterns of evenness and species density imply that the application of N or NPK fertilisers has not yet induced the development of dominance hierarchies or the competitive exclusion of species. This underlines the conclusions drawn in Chapter 6 that abiotic stress at present plays a more important role on this part of the slope than biotic factors. Stephan (2001) has come to similar conclusions in her study.

There is evidence from this experiment that the scarcity of nitrogen in the proximal part of the lower slope affects some species more than others and that severity of the summer drought also plays a role in the abiotic filtering of plant species. Thus, this experiment has produced experimental evidence in support of those abiotic filter mechanisms postulated in the preceding chapter.

8. Conclusions and directions for future research

The research presented in this dissertation illustrates the complex dynamics of plant community assembly in an ecosystem degraded by industrial activities but in the process of regeneration. A diverse array of factors, here referred to as "environmental filters", is involved in this assembly process. Most of these environmental filters vary in importance over different timescales and along existing spatial gradients The subject is complicated, as the overall result is more than its constitutuent parts: there are complex interactions between different environmental filters. Ecologists increasingly realise this fact (see Fattorini & Halle in press). This study does not give a complete account of these filter components and their interactions. Instead, a number of filters or filter components, deemed important at the study site in the past or at present, were selected for investigation. In this final chapter, the role of these factors at the Steudnitz site is discussed, some general remarks on the role of stress in assembly processes on derelict industrial land are made, and directions for future research are proposed.

8.1 Plant community assembly at the Steudnitz site

8.1.1 Early colonisation and priority effects

During early colonisation of the lower slope, which was simultaneous with the amelioration of site conditions after closure of the fertiliser factory, no attempt was made to study seed rain originating beyond the site, seed bank composition at the site, or the plants growing in the vicinity of the site. In this study the role of the historical filter in early colonisation of the Steudnitz lower slope could therefore only be assessed indirectly. An existing permanent plot allowed an indirect assessment of the role of dispersal processes. Classification of all colonising species into two groups, according to their seed morphology, revealed that colonisation of species with a "plumed" seed morphology occurred earlier than colonisation by other species. This trend was shown to be highly significant in Chapter 3, despite the assumed stochastic nature of natural establishment processes on derelict land (e.g. Bradshaw 1987). Similar results have been obtained for the colonisation of spoil heaps in Britain (Grime 1986). At present, most of the suitable species from the local species pool *sensu* Zobel (1997) seem to have colonised the site already, as indicated by the number of species occurring at the site over recent years remaining more or less constant (see Figure 2.4).

Salt tolerance of the incoming species also played a role, as demonstrated in Chapter 3 by the correlation between the seedling salt tolerance of 22 species and the time of their first appearance in the vegetation of the permanent plot. The first species colonising the site were characterised by an above average tolerance to salinity. In the current study, the correlation between time of first appearance and perceived salt tolerance was equally strong for both the species with a plumed seed morphology and those without. A difference between the groups would have been expected on the

grounds of a postulated higher probability for plumed-propagule species to immediately colonise sites becoming suitable as a result of decreasing soil salinity. However, only a small subset of species was tested with respect to salt tolerance. Also, due to the uneven distribution of plumed and non-plumed species over the temporal gradient, early colonisers were mainly represented by plumed-propagule species, and late colonisers mainly by non-plumed-propagule species.

The high concentration of nitrate in pollutant dust samples (K. Metzner unpublished and M. Wagner unpublished, see Appendix 2) implies that nitrate might also have played a role in early plant community assembly. Two lines of evidence support this assumption. One is the high above-ground primary productivity measured during times of dust deposition in those *Puccinellia distans* stands dominating the most degraded part of the slope (Heinrich 1984), compared to the currently low, nitrogen-limited, primary production on the same part of the slope (see Chapter 7). The second line of evidence is the abrupt disappearance of *Chenopodium rubrum* following peak abundance in 1994 (Heinrich et al. 2001). *Chenopodium rubrum* is a nitrophilous species characteristic of disturbed sites (Rothmaler 2002) and still present at high density in the seed bank (see Chapter 5). A dependance of *C. rubrum* on high nitrate levels, in the light of the presently low soil levels (Appendix 2) of this ion, would provide an explanation for the abrupt disappearance of this plant species. *Puccinellia distans*, despite being the most abundant species in the soil seed bank (Chapter 5), also no longer occurs in the vegetation. Disappearance from the vegetation was much less abrupt for this species (see Heinrich et al. 2001), implying that outcompetition by other species might have been the main reason for disappearance of this species at the field site. In both species, dark dormancy is likely to contribute to inhibition of recruitment from the seed bank and continued persistence in the seed bank at high densities (see Chapter 5). Seedlings of both species emerged at the field site after soil disturbance (M. Wagner, personal observation).

In this study, priority effects resulting from an interaction between the historical filter and the biotic filter were not investigated. Such effects, which can lead to founder-controlled communities, are occasionally discussed in the context of natural revegetation of derelict industrial land (e.g. Mahn & Tischew 1995). Priority effects are most conspicuous in those cases where a species already present inhibits (*sensu* Connell & Slatyer 1977) colonisation by other species. Tall perennial species, with a strong tendency to expand by means of clonal growth and to build up a thick litter layer, are best geared for such an inhibition of their competitors (Grime 1979). One such species is the grass *Calamagrostis epigejos* (L.) ROTH which forms monospecific stands in lignite mining sites (Jakob et al. 1996). In the present study, succession at the distal end of the lower slope is arrested by dense stands of a different perennial grass, *Elytrigia repens*. In the immediate vicinity of the former fertiliser factory, where the lower slope permanent plot is located, this species only plays a minor role. In fact, none of the early colonisers on this part of the slope can be characterised as having a

high potential for lateral expansion. Therefore, persistent priority effects in this part of the slope, if they have occurred at all, were probably quite subtle.

8.1.2 Currently-operating environmental filters

Canonical Corresponence Analysis, in combination with subsequent GLM regression modelling of patterns of species diversity, indicates that both the abiotic filter and the biotic filter currently have an influence on plant community assembly at the site (Chapter 6). This is in good agreement with the findings of Stephan (2001). Based on CSR strategy types, she concluded that adjacent to the fertiliser factory abiotic stress was more important on the lower slope, whereas competition played a larger role on the upper slope (Stephan 2001). In the present study, there is evidence for a major role of competition at the distal end of the lower slope, where species density is low in spite of abiotic conditions being favourable for plant growth. This presumably is due to the competitive exclusion of other species by *E. repens*.

In contrast, species composition of the vegetation in the proximal part of the lower slope seems to be primarily determined by the abiotic filter. There is some evidence that colonisation by nitrophilous species such as *Galium aparine* might be inhibited by low levels of soil nitrogen there (Chapter 7). A strong influence of nitrogen level on the abundance of species could be demonstrated in a nutrient addition experiment (Chapter 7). A number of species, among them *Bromus japonicus*, *Epilobium tetragonum*, *Lactuca serriola* and *Galium aparine*, responded positively to the addition of nitrogen, whereas other species were more or less unaffected (Figure 7.5). In the case of *E. tetragonum* and *B. japonicus*, this seems surprising, since both of these species mainly occur on the more nitrogen-poor parts of the slope (Figure 6.5). Absence of superior competitors, such as *Elytrigia repens*, from the experimental plots might be responsible for this positive response, illustrating that the realised niche of a species is defined by the identity of co-occurring species. In the absence of *E. repens*, *B. japonicus* seems to be able to occupy a wider realised niche. A strong increase of *B. japonicus* following nitrogen addition is also known from other systems (Hewlett et al. 1981). The GLM regression of this species, exhibiting a secondary maximum at higher nitrogen levels, also hints at this potential (see Figure 6.5).

The influence of soil moisture on species composition, in the absence of evidence resulting from experimental manipulation of this factor, is best reflected in the CCA results. Axis 2 of the CCA model is strongly related to soil moisture (Figure 6.2), and correlation of this axis with the occurrence of a number of plant life history types is in good agreement with life history theory (see Chapter 6). Slope areas characterised by particularly low soil moisture levels are distinguished by a high cover of annual species, most of which are winter annuals. Winter annuals, as opposed to summer annuals, are capable of early colonisation of those gaps resulting from the summer drought. At the same time, it is ensured that the particularly vulnerable seedling stage is passed before the

onset of the next summer drought. In contrast, longer-lived perennial herbs and woody species are more predominant in areas characterised by a less extreme soil moisture regime. These results are in agreement with life history theory and the findings of previous studies (see Chapter 6). They also indicate that plant life history can be used as a trait with a predictive value regarding plant community assembly (*sensu* Keddy 1992) at the Steudnitz field site.

8.2 Abiotic stress and plant community assembly in industrial ecosystems

The Steudnitz site, like many other derelict industrial sites, was characterised by conditions for plant growth initially being markedly adverse. Grime (1979) defines such conditions limiting the production of biomass as stress. In contrast, he refers to the removal of existing biomass as disturbance. The high stress levels that plants are exposed to on derelict industrial land are not always linked to soil toxicity, as it was the case in this study. In the absence of toxicity, early stages of plant colonisation of freshly created raw substrates regularly are influenced by the low levels of available resources, including soil nutrients (e.g. Marrs & Bradshaw 1993).

In the present study, the overall pattern of early plant colonisation could largely be explained without reference to biotic interactions (see Chapter 4). An approach including abiotic constraints on the entry of species into plant communities, such as the one advocated by Keddy (1992), seems to be more useful in the context of this and other studies on derelict industrial land characterised by high levels of stress *sensu* Grime (1979). Keddy suggests that one should base predictions about community assembly on species traits, which "could include morphological, physiological or ecological features" (Keddy 1992: 159). This was also the approach used in Chapter 4, using a morphological trait (adaptation to long-distance seed dispersal) and a physiological trait (salt tolerance at the early seedling stage).

Measuring the stress tolerance of seedlings is an easy method of characterisation, and it also is likely to be an appropriate one. As put by Angevine & Chabot (1979: 189), "the germination of seeds and subsequent early growth of seedlings are not only essential phases of the life cycle of all higher plants, but represent periods of maximum vulnerability to physical changes in the environment and minimal potential for homeostatic response or physiological retrenchment."
This is one of the reasons why mortality risk usually is much higher in the early post-germination stage, compared to later stages in the life-cycle (Fenner 1987b), and why the regeneration niche is so important for the species composition of plant communities (see Grubb 1977). Therefore, the bottleneck for species colonisation in stressful habitats could lie with the ability of seedlings to withstand the adverse abiotic conditions in such habitats.

The importance of stress tolerance for community assembly is best illustrated in systems where stress levels change over time. Short-term extremes of environmental conditions can cause the species composition of communities to undergo selection, reflecting the different capacities of species to

withstand these extremes. Examples from non-industrial systems include the dependance of floodplain meadow species composition on the duration of the spring flood (Eliashevich 1982), and of dry grassland community structure on the extent of droughts in summer (Hopkins 1978, Ellenberg 1996). In the present study, it was the order of colonisation which was influenced by the gradual amelioration of soil conditions provided by the leaching process. Also, as in dry grassland, the pronounced climatic between-year variation over the duration of the study seemed to have had an influence on community composition (see Chapter 7). Climatic variation might also be relevant in other industrial ecosystems characterised by high average levels of drought stress.

The importance of stress levels for community composition was previously pointed out in Grime's (1979) conceptual model, providing an explanation for the relationship between total biomass and species density found in herbaceous vegetation by Al-Mufti et al. (1977). In this so-called "hump-backed" model of species density, community membership in productive habitats is restricted by competition for light, and membership in unproductive habitats is restricted mainly by extreme conditions of stress and / or disturbance. Grime's model and more recent models, specifying the relative importance of facilitation along stress gradients (Belcher et al. 1995, Callaway & Walker 1997, Brooker & Callaghan 1998, Bruno et al. 2003), can be amalgamated into a simple conceptual community assembly model summarising how the relative importance of the abiotic stress filter, interspecific facilitation and competition could vary along a stress gradient (Figure 8.1).
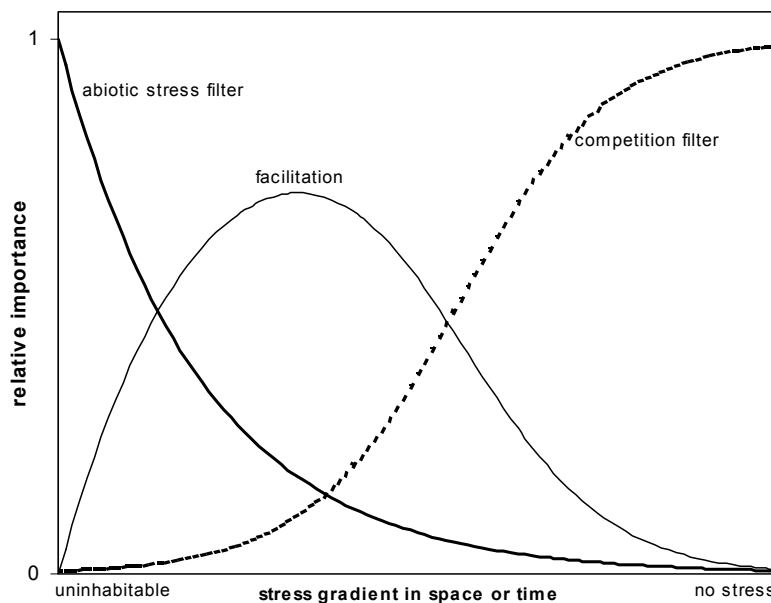
Figure 8.1. Conceptual model of the relative importance of the abiotic stress filter and of plant-plant interactions (facilitation) and competition) for plant community assembly along a hypothetical stress gradient (from Wagner in press).

Exact curve shapes would depend on the identity or combination of stress factors particular to a system. The abiotic environment does not only have a direct effect on community assembly via the abiotic stress filter, it also has indirect effects through the modulation of biotic interactions: the relative competitive ability of the involved species depends on the abiotic environment, and so does the strength of facilitative interactions (e.g. Bruno et al. 2003). The model does not incorporate other factors such as disturbance, life history processes, and interactions with other biota (for these factors see Walker & Chapin 1987). However, it can be used to illustrate how the importance of various filter components during the development / recovery of industrial ecosystems varies over time. At the beginning, when stress levels are high, abiotic stress is the overriding factor in plant community assembly. The time span required for development of a mature ecosystem development varies, depending on the nature and initial levels of toxicity and resource deficiency. In this study, salinity was a major component of the abiotic filter for the first 5 years of the regeneration process (Chapter 4). In other industrial systems, ecosystem development might be arrested for a much longer time, sometimes for centuries. Examples include areas contaminated by heavy metals and some mine-spoil substrates characterised by continuous production of acidity due to pyrite oxidation (Bradshaw & Chadwick 1980).

At the Steudnitz site, there is some evidence that facilitation currently plays some role in the proximal part of the lower slope (Temperton & Zirr in press), whereas competition is not that relevant (Chapter 7 and Stephan 2001). In contrast, in the distal part of the lower slope, the ecosystem is more developed, and competitive exclusion of other species by *Elytrigia repens* seems to be a predominant force in the structuring of the plant community. The conceptual model shown in figure 8.1 therefore can be used for the illustration of both spatial gradients of degradation and temporal processes of ecosystem recovery.

8.3 Directions for future research

Due to the multitude of factors influencing plant community assembly at the Steudnitz site, this study can only provide a starting point for investigating the underlying mechanisms. Current, ongoing research is concentrated on the role of mycorrhizae in alleviating the effects of abiotic stress caused by nitrogen limitation and drought stress (V. Blanke, personal communication). Future research could, for example, focus on the further investigation of the role of soil moisture, and the correlation of soil moisture levels with plant life history types should be verified experimentally. Research on the role of biotic filters and on interactions between both biotic and abiotic filters is strongly advocated.

Understanding of the processes underlying the vegetation patterns at the Steudnitz site could also be furthered by the development of simulation models. Processes relevant for assembly could be incorporated in such models and tested with respect to their suitability for generating patterns similar

to those observed in the field. This thesis, for a number of reasons, might provide the foundations for such a line of research: in addition to providing a description of vegetation patterns and their correlation with environmental variables, it has also generated hypotheses which are testable through simulation, and data that can be used in the parameterisation of simulation models.

Summary

Industrially degraded land is an anthropogenic ecosystem of growing importance. In spite of a large number of studies describing the vegetation of such sites, mechanisms of plant community assembly are still poorly understood. To gain insights into these mechanisms, this study combines descriptive and experimental approaches within the context of recently developed environmental-filter concepts. The study was carried out at the Steudnitz field site, which is the lower part of a calcareous slope degraded by deposition of alkaline dust emitted during operation (1957-1990) of an adjacent fertiliser factory. The influence of environmental filters on temporal patterns of colonisation and spatial vegetation patterns was investigated in four separate experiments.

Order of colonisation

- The species colonising the site after factory closure were classified according to whether they disperse by plumed propagules. Seedling salt tolerance was determined for a subset of species.
- Plumed-propagule species entered the community earlier than species without this adaptation.
- Early-successional species also were characterised by a high seedling salt tolerance. Up to 1994, salinity acted as a selective force upon species establishment.

Soil seed bank

- The soil seed bank was sampled in all three years of the study. 24 of the 53 species occurring in the vegetation were also found in the seed bank.
- Two species no longer occurring in the vegetation, the halophytic grass *Puccinellia distans* and the herb *Chenopodium rubrum*, were also found in the seed bank in large numbers. Potential reasons for their disappearance from the vegetation are increased competition from late colonisers and, in the case of the nitrophilous *C. rubrum*, leaching-out of the nitrate supplied by previous dust deposition from the fertiliser factory.
- Seed bank persistence type was determined for 26 species, including five species for which no previous information on persistence was available.

Spatial vegetation patterns

- Vegetation patterns were investigated by recording the visual cover of plant species in randomly located 1 m² quadrats. Field measurements included slope angle and soil moisture. Soil pH, electrical conductivity, organic matter content, total nitrogen, and plant-available phosphorus and potassium were determined.
- Salinity and pH have returned to normal levels, whereas levels of plant-available phosphorus are still raised throughout the site. In the proximal part of the site P-availability is somewhat reduced by higher pH and carbonate levels, leading to permanent phosphorus fixation.
- Thirty-one significant interspecific associations were positive, and eight were negative. Strong positive associations occurred between species with similar life histories. Half of the sigificant

negative associations involved *Elytrigia repens*, a perennial grass with a marked tendency for clonal expansion which dominates the vegetation in the distal part of the site.

- Soil nitrogen and moisture play a major role in the structuring of plant communities. The soil underneath the species-poor *Elytrigia* grassland is characterised by high nitrogen levels and a high organic matter content. The ruderal communities of the proximal part of the slope occur on skeletal, nitrogen-poor soil. Soil moisture, which is related to small-scale variation in species composition, is negatively correlated with slope angle and varies independently of the large-scale pollution gradient.

- Annual species, most of them being winter annuals which complete their life cycle before the onset of the summer drought and which in autumn are able to quickly colonise gaps created by the summer drought, are associated with microhabitats characterised by a great steepness and a tendency to dry out quickly after rainfall. Polycarpic herbs, woody species and legumes are more abundant on those parts of the slope characterised by a high soil moisture. Monocarpic perennials are most abundant at the low-nutrient end of the sampled gradient. Polycarpic grasses peak in abundance under nitrogen-rich conditions, fitting with the assumption of high nitrogen levels promoting dominance of species characterised by clonal expansion. Life history in this study is a trait with predictive value for community assembly.

- Patterns of species density, evenness and higher plant total cover indicate that abiotic stress is more important for community assembly in the more degraded part of the site, whereas competitive exclusion by *Elytrigia repens* is more important at the distal end of the slope.

Nutrient addition

- Effects of experimental nutrient addition were assessed over the course of three years using sorted biomass and visual cover techniques.

- At present, above-ground primary productivity is co-limited by soil moisture and nitrogen.

- Increased soil nitrogen levels affects plant community structure in the thort term by strongly promoting a number of species: *Galium aparine*, *Bromus japonicus*, *Epilobium tetragonum*, *Senecio vernalis*, *Artemisia vulgaris*, *Lactuca serriola*.

- Patterns of species diversity indicate that those changes in community structure so far do not result from competitive exclusion.

Overall, dispersal limitations and salinity levels were major factors influencing the order of colonisation in the first few years after factory closure. At present there is still a strong abiotic filter acting upon species establishment and performance. This filter is mainly due to plant stress resulting from low levels of soil moisture and, in the proximal part of the lower slope, low soil nitrogen. The results of the study fit well with a conceptual model describing the relative roles of the abiotic filter and of competition along temporal and spatial stress gradients.

Zusammenfassung

Industriell beeinträchtigte Flächen sind anthropogene Ökosysteme von wachsender Bedeutung. Obwohl eine große Zahl deskriptiver Studien der Vegetation solcher Standorte existiert, ist wenig über Mechanismen des Zusammentretens solcher Pflanzengemeinschaften bekannt. Eine möglichen Erklärungsansatz bieten Umweltfiler-Modelle, die hier zur Interpretation einer Kombination von beschreibenden und experimentellen Arbeiten herangezogen werden. Untersuchungsgebiet war der untere Abschnitt eines Muschelkalk-Hanges, welcher durch Einträge alkalischer Stäube aus einer nahegelegenen Kunstdünger-Fabrik (1957-1990) beeinträchtigt wurde. Der Einfluss von Umweltfiltern auf die zeitliche Abfolge von Besiedlungsprozessen und auf räumliche Vegetationsmuster wurde in vier separaten Studien untersucht.

Reihenfolge der Besiedlung

- Die Arten, welche sich nach Stillegung der Fabrik ansiedelten, wurden hinsichtlich ihrer Diasporenmorphologie klassifiziert. Für einen Teil der Arten wurde die Salztoleranz der Keimlinge bestimmt.
- Arten mit pappusartigen Anhängen an den Diasporen, die sie zur Fernausbreitung befähigen, siedelten sich rascher an als Arten ohne diese Anpassung.
- Frühe Arten zeichneten sich durch überdurchschnittlich hohe Salztoleranz im Keimlings-Stadium aus. Bis 1994 wurden Etablierungsprozesse durch Bodensalinität beeinflusst.

Diasporenbank

- Die Diasporenbank in 0-10 cm Bodentiefe wurde über drei Jahre erfasst. 24 von 53 in der Vegetation vorkommenden Arten wurden auch in der Diasporenbank nachgewiesen.
- Zwei aus der Vegetation verschwundene Arten, *Puccinellia distans* und *Chenopodium rubrum*, traten gehäuft in der Diasporenbank auf. Möglicher Grund für das Verschwinden dieser Arten ist verstärkte Konkurrenz durch später aufgetretene Arten. Insbesondere bei der nitrophilen Art *C. rubrum* mag auch ein Rückgang von Nitrat im Boden, welches bis 1990 durch Staubeintrag erhöht gewesen sein dürfte, zum Verschwinden beigetragen haben.
- Persistenz in der Diasporenbank wurde für 26 Arten bestimmt (darunter fünf Arten, für die zuvor keine entsprechende Information bekannt war).

Räumliche Vegetationsmuster

- In 140 zufällig verteilten Quadraten von 1 m² Fläche wurde die Deckung der vorkommenden Pflanzenarten aufgenommen. Hangneigung und Bodenfeuchte wurden *in situ* gemessen. Bodenanalysen beeinhalteten Bestimmung von pH, elektrischer Leitfähigleit, organischer Substanz und von N (Gesamtgehalt) sowie von P und K (pflanzenverfügbare Gehalte).
- Salinität und pH sind nicht mehr erhöht. Pflanzenverfügbarer Phosphor ist noch immer im gesamten UG erhöht. Nahe der Fabrik ist die P-Verfügbarkeit etwas geringer. Dies liegt an Fixierungsprozessen, die durch hohe Carbonat-Gehalte und den höheren pH-Wert begünstigt werden.
- Einunddreißig paarweise Arten-Assoziationen waren signifikant positiv. Starke positive Assoziationen traten auf zwischen Arten mit einer ähnlichen Lebensgeschichte. An vier der acht

signifikanten negativen Assoziationen war die Quecke *Elytrigia repens* beteiligt, ein ausdauerndes Gras mit einem ausgeprägten Hang zur klonalen Ausbreitung, welches teilweise Dominanzbestände bildet.

- Stickstoff und Bodenfeuchte spielen eine große Rolle für das Verteilungsmuster von Pflanzenarten am Hang. Artenarme *Elytrigia*-Bestände zeichnen sich durch hohe Bodenstickstoff-Werte aus. Diversere ruderale Pflanzengemeinschaften in Fabriknähe treten auf rohen, durch Stickstoff-Armut gekennzeichneten, Böden auf. Die Bodenfeuchte, welche die kleinräumige Vegetationszusammensetzung beeinflusst, ist negativ mit der Hangneigung korreliert und variiert unabhängig vom großräumigen Belastungs-Gradienten.

- Annuelle Arten, insbesondere Winterannuelle, welche ihren Lebenszyklus vor Beginn der Sommertrockenheit abschließen und in der Lage sind trockenheitsbedingte Lücken im Herbst rasch zu besiedeln, kommen vor allem in steilen, zur raschen Austrocknung tendierenden Hangbereichen vor. Iteropare krautige Pflanzen, Gehölze und Leguminosen kommen gehäuft in feuchteren Hangbereichen vor. Semelpare mehrjährige Kräuter sind am häufigsten in nährstoffarmeren Bereichen zu finden. Ausdauernde Gräser dominieren bei hohen Bodenstickstoff-Werten, was mit der Annahme übereinstimmt, dass zur raschen klonalen Ausbreitung befähigte Arten unter solchen Bedingungen zur Dominanz gelangen. Lebensgeschichte erweist sich im Rahmen dieser Studie als geeigneter Parameter zur Vorhersage der Zusammensetzung von Pflanzengemeinschaften.

- Muster des Artenreichtums, der Evenness und der Gesamtdeckung höherer Pflanzen zeigen an, dass im stärker beeinträchtigen Teil des UG's abiotischer Stress einen größeren Einfluß auf die Artenzusammensetzung hat, während in anderen Bereichen Konkurrenzausschluß durch die Quecke eine größere Rolle spielt.

Düngeversuch

- Die Auswirkungen experimenteller Nährstoffzufuhr wurden über den Zeitraum von drei Jahren untersucht, indem Deckung und Biomasse der Arten erfasst wurden.
- Gegenwärtig ist die Primärproduktion durch Stickstoff und Bodenfeuchtigkeit limitiert.
- Erhöhte N-Verfügbarkeit wirkt sich kurzfristig auf die Struktur der Artengemeinschaft aus, indem einige Arten stark gefördert werden: insbesondere sind dies *Galium aparine*, *Bromus japonicus*, *Epilobium tetragonum*, *Senecio vernalis*, *Artemisia vulgaris* und *Lactuca serriola*.
- Diversitäts-Muster zeigen an dass diese Änderungen der Pflanzengemeinschafts-Struktur nicht das Resultat von Konkurrenzausschluß-Prozessen sind.

Während unterschiedliche Ausbreitungsfähigkeit und Salztoleranz der Arten die Reihenfolge der Besiedlung in den ersten Jahren nach Werkstillegung beeinflussten, werden gegenwärtige Besiedlungsprozesse vor allem durch abiotischen Trockenstress (im werksnahen Bereich auch durch N-Mangel-Stress) beeinflusst. Die Ergebnisse der Arbeit lassen sich mit einem konzeptionellen Modell vereinbaren, welches die relative Rolle von abiotischem Filters und von Konkurrenz entlang zeitlicher und räumlicher Stress-Gradienten beschreibt.

References

Agnew, A.D.Q. 1961. The ecology of *Juncus effusus* L. in North Wales. *Journal of Ecology* **49**: 83-102.

Alatalo, R.V. 1981. Problems in the measurement of evenness in ecology. *Oikos* **37**: 199-204.

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* **65**: 759-791.

Angevine, M.W. & Chabot, B.F. 1979. Seed germination syndromes in higher plants. In: *Topics in Plant Population Biology* (eds. Solbrig, O.T., Jain, S., Johnson, G.B. & Raven, P.H.), pp. 188-206. Columbia University Press, New York.

Ash, H.J., Gemmell, R.P. & Bradshaw, A.D. 1994. The introduction of native plant species on industrial waste heaps: a test of immigration and other factors affecting primary succession. *Journal of Applied Ecology* **31**: 74-84.

Bährmann, R. 1982. Zum Vorkommen sogenannter halophiler Dipteren-Arten in einem industriell belasteten Immissionsgebiet. *Entomologische Nachrichten und Berichte* **26**: 75-78.

Bakker, J.P., Dijkstra, M. & Russchen, P.T. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. *New Phytologist* **101**: 291-308.

Belcher, J.W., Keddy, P.A. & Twolan-Strutt L. 1995. Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology* **83**: 673-682.

Belyea, L.R. & Lancaster, J. 1999. Assembly rules within a contingent ecology. *Oikos* **86**: 402-416.

Berendse, F., Aerts, R. & Bobbink, R. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In *Landscape Ecology of a Stressed Environment* (eds. Vos, C.C. & Opdam, P.), pp. 104-121. Chapman & Hall, London.

Berkowitz, A.R., Canham, C.D. & Kelly, V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology* **76**: 1156-1168.

Beyschlag, W., Ryel, R.J. & Ullmann, I. 1992. Experimental and modelling studies of competition for light in roadside grasses.*Botanica Acta* **105**: 285-291.

Beyschlag, W., Ryel, R.J., Ullmann, I. & Eckstein, J. 1996. Experimental studies on the competitive balance between two Central European roadside grasses with different growth forms. II. Controlled experiments on the influence of soil depth, salinity and allelopathy. *Botanica Acta* **109**: 449-455.

Blechschmidt, K., Gebauer, H.J., Naumann, J., Peter, H.-U., Rotter, I. & Vogler, J. 1984. Auswirkungen industrieller Prozesse auf die Umwelt – Vorschläge zur Verhinderung und Beseitigung von Umweltschäden. *Nachrichten: Mensch – Umwelt* **12**: 57-60.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* **28**: 28-41.

Bobbink, R., Bik, L. & Willems, J.H. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. *Acta Botanica Neerlandica* **37**: 231-242.

Booth, B.D. & Larson, D.W. 1998. The role of seed rain in determining the assembly of a cliff community. *Journal of Vegetation Science* **9**: 657-668.

Booth, B.D. & Larson, D.W. 1999. Impact of language, history, and choice of system on the study of assembly rules. In *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds. Weiher, E. & Keddy, P.), pp. 206-229. Cambridge University Press, Cambridge.

Booth, B.D. & Larson, D.W. 2000. Constraints on the assembly of cliff communities at the seed bank stage. *Ecoscience* **7**: 326-335.

Braakhekke, W.G. & Hooftman, D.A.P. 1999. The resource balance hypothesis of plant species diversity in grassland. *Journal of Vegetation Science* **10**: 187-200.

Bradshaw, A.D. 1983. The reconstruction of ecosystems. *Journal of Applied Ecology* **20**: 1-17.

Bradshaw, A.D. 1987. The reclamation of derelict land and the ecology of ecosystems. In *Restoration Ecology – A Synthetic Approach to Ecological Research* (eds. Jordan, W.R., III., Gilpin, M.E. & Aber, J.D.), pp. 53-74. Cambridge University Press, Cambridge.

Bradshaw, A.D. & Chadwick, M.J. 1980. *The Restoration of Land – The Ecology and Reclamation of Derelict and Degraded Land.* Blackwell, Oxford.

Brady, N.C. & Weil, R.R. 2002. *The Nature and Properties of Soils*. 13th edition. Prentice Hall, Upper Saddle River.

Brandes, D. 1999. Flora und Vegetation salzbeeinflusster Habitate im Binnenland - eine Einführung. In *Vegetation salzbeeinflusster Habitate im Binnenland* (ed. Brandes, D.), pp. 7-12. Universitätsbibliothek TU Braunschweig, Braunschweig.

Braun-Blanquet, J. 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde.* 3rd edition. Springer, Berlin.

Brewer, J.S. & Cralle, S.P. 2003. Phosphorus addition reduces invasion of a longleaf pine savanna (Southeastern USA) by a non-indigenous grass (*Imperata cylindrica*). *Plant Ecology* **167**: 237-245.

Brimblecombe, P. & Stedman, D.H. 1982. Historical evidence for a dramatic increase in the nitrate component of acid rain. *Nature* **298**: 460-461.

Brooker, R.W. & Callaghan, T.V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**: 196-207.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**: 119-125.

Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**: 1958-1965.

Carson, W.P. & Barrett, G.W. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology* **69**: 984-994.

Chapin, F.S., III., Vitousek, P.M. & van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* **127**: 48-58.

Clements. F.E. 1916. *Plant Succession. An Analysis of the Development of Vegetation.* Carnegie Institute, Washington, Publication 242.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**: 1119-1144.

Cooper S.V. & Jean C. 2001. *Wildlife succession in plant communities natural to the Alkali Creek vicinity, Charles M. Russell National Wildlife Refuge, Montana.* Report to the U.S. Fish and Wildlife Service. Montana Natural Heritage Program, Helena.

Cooper, W.S. 1926. The fundamentals of vegetation change. *Ecology* **7**: 391-413.

Crawley, M.J. 1997a. Life history and environment. In *Plant Ecology* (ed. Crawley, M.J.), pp. 73-131. Blackwell, Oxford.

Crawley, M.J. 1997b. The structure of plant communities. In *Plant Ecology*, 2nd edition (ed. Crawley, M.J.), pp. 475-531. Blackwell, Oxford.

Csapody, V. 1968. *Keimlingsbestimmungsbuch der Dikotyledonen.* Akademiai Kiado, Budapest.

Dangien, B., Hayon, J.-C. & Pelt, J.-M. 1974. Analyse phytosociologique de la végétation halophile d'origine industrielle de la basse vallee de la Meurthe. *Documents Phytosociologiques* **5**: 1-41.

Davies, B.E. 1974. Loss-on-ignition as an estimate of soil organic matter. *Soil Science Society of America Proceedings* **38**: 150-151.

Davy, A.J. & Taylor, K. 1974. Seasonal patterns of nitrogen availability in contrasting soils in the Chiltern Hills. *Journal of Ecology* **62**: 793-807.

de Kroon, H. & Bobbink, R. 1997. Clonal plant dominance under elevated nitrogen deposition, with special reference to Brachypodium pinnatum in chalk grassland. In *The Ecology and Evolution of Clonal Plants* (eds. de Kroon, H. & van Groenendael, J.), pp. 359-379. Backhuys, Leiden.

del Moral, R. & Jones, C. 2002. Vegetation development on pumice at Mount St. Helens, USA. *Plant Ecology* **162**: 9-22.

deSteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession – seedling survival and growth. *Ecology* **72**: 1076-1088.

Dettmar, J. 1992. *Industrietypische Flora und Vegetation in Ruhrgebiet.* Dissertationes Botanicae 191. Cramer, Berlin.

Diamond, J.M. 1975. Assembly of species communities. In *Ecology and Evolution of Communities* (eds. Cody, M.L. & Diamond, J.M.), pp. 342-444. Belknap, Harvard.

Diaz, S., Cabido, M. & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**: 113-122.

Diekmann, M. & Falkengren-Grerup, U. 2002. Prediction of species response to atmospheric nitrogen deposition by means of ecological measures and life history traits. *Journal of Ecology* **90**: 108-120.

Dunne, J.A. & Parker, V.T. 1999. Species-mediated soil moisture availability and patchy establishment of Pseudotsuga menziesii in chaparral. *Oecologia* **119**: 36-45.

Dunnett, N.P., Willis, A.J., Hunt, R. & Grime, J.P. 1998. A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology* **86**: 610-623.

Eliashevich, N.V. 1982. Year-to-year variability of floodplain meadows. *The Soviet Journal of Ecology* **12**: 147-155.

Ellenberg, H. 1954. Über einige Fortschritte der kausalen Vegetationskunde. *Vegetatio* **5/6**: 199-211.

Ellenberg, H. 1992. Zeigerwerte der Gefäßpflanzen (ohne Rubus). *In Zeigerwerte von Pflanzen in Mitteleuropa*, 2nd edition (eds. Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D.), pp. 9-166. Scripta Geobotanica 18. Golze, Göttingen.

Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer, Stuttgart.

Elton, C.S. 1927. *Animal Ecology.* Sidgwick & Jackson, London.

Environment Directorate-General of the EU. 2000. *Working Document on Sludge.* 3rd draft, Brussels, 27 April 2000.

Eriksson, O. & Eriksson, A. 1998. Effects of arrival order and seed size on germination of grassland plants: Are there assembly rules during recruitment? *Ecological Research* **13**: 229-239.

Eviner, V.T., Chapin, F.S., III. & Vaughn, C.E. 2000. Nutrient manipulations in terrestrial ecosystems. In *Methods in Ecosystem Science* (eds. Sala, O.E., Jackson, R.B., Mooney, H.A. & Howarth, R.W.), pp. 291-307. Springer, New York.

Fattorini, M. & Halle, S. In press. The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance? In *Assembly Rules and Restoration Ecology - Bridging the Gap Between Theory and Practice.* (eds. Temperton, V.M.,Nuttle, T.J., Hobbs, R.J. & Halle, S.). Island Press, Washington.

Fenner, M. 1987a. Seed characteristics in relation to succession. In *Colonization, Succession and Stability* (eds. Gray, A.J., Crawley, M.J. & Edwards, P.J.), pp. 103-114. Blackwell, Oxford.

Fenner, M. 1987b. Seedlings. *New Phytologist* **106 (Supplement)**: 35-47.

Fischer, W. 1976. Beobachtungen über die Vegetationsentwicklung auf Ascheaufschüttungen im Berliner Gebiet. *Naturschutzarbeit in Berlin und Brandenburg* **12**: 2-9.

Fisher, F.M., Zak, J.C., Cunningham, G.L. & Whitford, W.G. 1988. Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *Journal of Range Management* **41**: 387-391.

Fitter, A.H. & Peat, H.J. 1994. The ecological flora database. *Journal of Ecology* **82**: 415-425.

Fowler, J., Cohen, L. & Jarvis, J. 1998. *Practical Statistics for Field Biology.* Wiley, Chichester.

Froud-Williams, R.J. 1985. The biology of cleavers (*Galium aparine*). *Aspects of Applied Biology* **9**: 189-195.

Gallardo, M., Jackson, L.E. & Thompson, R.B. 1996. Shoot and root physiological responses to localized zones of soil moisture in cultivated and wild lettuce (*Lactuca* spp.). *Plant, Cell and Environment* **19**: 1169-1178.

Gauch, H.G. 1982. *Multivariate Analysis in Community Ecology.* Cambridge University Press, New York.

Gaudet, C.L. & Keddy, P.A. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242-243.

Gemmell, R.P. 1975. The importance of chemical toxin detection and substrate factor interactions in the reclamation of unusual toxic sites. In *The Ecology of Resource Degradation and Renewal* (eds. Chadwick, M.J. & Goodman, G.T.), pp. 385-403. Blackwell, Oxford.

Gerowitt, B. 1999. Zum Einfluß der Stickstoffdüngung auf die Populationsdynamik annueller Unkräuter im Ackerbau. *Mitteilungen der Gesellschaft für Pflanzenbauwissenschaften* **12**: 63-64.

Ginzo, H.D., Collantes, M. & Caso, O.H. 1982. Fertilization of a native grassland in the 'Depresión del Rio Salado', Province of Buenos Aires: herbage dry matter accumulation and botanical composition. *Journal of Range Management* **35**: 35-39.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26.

Goldberg, D.E. & Miller, T.E. 1990. Effects of different resource additions on species diversity in an annual plant community. *Ecology* **71**: 213-225.

Gotelli, N.J. & Graves, G.R. 1996. *Null Models in Ecology.* Smithsonian Institution Press, Washington.

Gould, S.J. & Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. *Proceedings of the Royal Society of London Series B* **205**: 581-598.

Gray, H. 1982. Plant dispersal and colonisation. In *Ecology of Quarries* (ed. Davis, B.N.K.), pp. 27-31. Institute of Terrestrial Ecology, Cambridge.

Greig-Smith, P. 1983. *Quantitative Plant Ecology.* 3rd edition. Blackwell, Oxford.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**: 344-347.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature **250**: 26-31.

Grime, J.P. 1977. Evidence for the existence of three primary strategies and its relevance to ecological and evolutionary theory. *American Naturalist* **111**: 1169-1194.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.* Wiley, Chichester.

Grime, J.P. 1986. The circumstances and characteristics of spoil colonization within a local flora. *Philosophical Transactions of the Royal Society of London, Series B* **314**: 637-654.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties.* 2nd edition. Wiley, Chichester.

Grime, J.P. & Curtis, A.V. 1976. The interaction of drought and mineral nutrient stress in calcareous grassland. *Journal of Ecology* **64**: 975-988.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. & Shaw, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**: 1017-1059.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative Plant Ecology: a Functional Approach to Common British Species.* Unwin Hyman, London.

Grubb, P.J. 1976. A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biological Conservation* **10**: 53-76.

Grubb, P.J. 1977. The maintentance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**: 107-145.

Halvorson G.A. & Lang K.J. 1989. Revegetation of a salt water blowout site. *Journal of Range Management* **42**: 61-65.

Hanf, M. 1999. Ackerunkräuter Europas mit ihren Keimlingen und Samen. 4th edition. BLV Verlagsgesellschaft, München.

Harper, J.L. 1977. *Population Biology of Plants.* Academic Press, London.

Harper, J.L. 1982. After description. In *The Plant Community as a Working Organism* (ed. Newman, E.I.), pp. 11-25. Blackwell, Oxford.

Hart, R. 1977. Why are biennials so few? *American Naturalist* **111**: 792-799.

Heil, G.W. & Diemont, W.H. 1983. Raised nutrient levels change heathland into grassland. *Vegetatio* **53**: 113-120.

Heinrich, W. 1981a. Über den Einfluß von Luftverunreinigungen auf Ökosysteme. I. Literaturübersicht. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* **30**: 621-634.

Heinrich, W. 1981b. Über den Einfluß von Luftverunreinigungen auf Ökosysteme. II. Literaturzusammenstellung. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* **30**: 635-644.

Heinrich, W. 1984. Über den Einfluß von Luftverunreinigungen auf Ökosysteme. III. Beobachtungen im Immissionsgebiet eines Düngemittelwerkes. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* **33**: 251-289.

Heinrich, W. & Schäller, G. 1987. Veränderungen von Ökosystemstrukturen im Einflussbereich eines Düngemittelwerkes. Über den Einfluß von Luftverunreinigungen auf Ökosysteme XI. *Hercynia N.F.* **24**: 328-334.

Heinrich, W., Perner, J. & Marstaller, R. 2001. Regeneration und Sekundärsukzession – 10 Jahre Dauerflächenuntersuchungen im Immissionsgebiet eines ehemaligen Düngemittelwerkes. *Zeitschrift für Ökologie und Naturschutz* **9**: 237-253.

Hendershot, W.H. 1985. An inexpensive block digester for nitrogen determination in soil samples. *Communications in Soil Science and Plant Analysis* **16**: 1271-1278.

Hewlett, D.B., Johnson, J.R., Butterfield, R.I. & Mosley, V.K. 1981. Japanese brome response to atrazine in combination with nitrogen fertilizer in the mixed prairie. *Journal of Range Management* **34**: 22-25.

Heyer, E. 1993. *Witterung und Klima.* 9th edition. Teubner, Stuttgart.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**: 65-70.

Hopkins, B. 1978. The effects of the 1976 drought on chalk grassland in Sussex, England. *Biological Conservation* **14**: 1-12.

Houle, G. 1996. Environmental filters and seedling recruitment on a coastal dune in subarctic Quebec (Canada). *Canadian Journal of Botany* **74**: 1507-1513.

Hutchings, M.J. 1986. Plant population biology. In *Methods in Plant Ecology*, 2nd edition (eds. Moore, P.D. & Chapman, S.B.), pp. 377-435. Blackwell, Oxford.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* **22**: 415-457.

Jackson, L.E. 1995. Root architecture in cultivated and wild lettuce (*Lactuca* spp.). *Plant, Cell and Environment* **18**: 885-894.

Jakob, S., Tischew, S. & Mahn, E.-G. 1996. Zur Rolle von *Calamagrostis epigejos* (L.) ROTH in den Sandtrockenrasen des Braunkohlentagebaues „Goitsche" (bei Delitzsch). *Verhandlungen der Gesellschaft für Ökologie* **26**: 797-805.

Jefferies, R.L. & Maron, J.L. 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends in Ecology and Evolution* **12**: 74-78.

Kahles, A., Kanter, F., Salido López, M., Schuster, A. & Schneider, N. 2002. Das Verschwinden zweier salztoleranter Arten von einem industriellen Offenland: Ist Konkurrenzausschluss die ganze Wahrheit? Unpublished Report, Friedrich Schiller University, Jena.

Kaleta, M. 1975. Vegetacné pomery v oblasti Jelšavy so zretel'om na imisné podmienky [in Slovak with English summary:Vegetational circumstances in the region of Jelsava with respects to the conditions of emissions]. *Quaestiones Geobiologicae* **17**: 1-131.

Keddy, P.A. 1991. Working with heterogeneity: an operator's guide to environmental gradients. In *Ecological Heterogeneity* (eds. Kolasa, J. & Pickett, S.T.A.), pp. 181-201. Springer, New York.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**: 157-164.

Keddy, P.A. 1999. Wetland restoration: the potential for assembly rules in the service of conservation. *Wetlands* **19**: 716-732.

Kelly, D. 1985. Why are biennials so maligned? *American Naturalist* **125**: 473-479.

Kirchner, T.B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology* **58**: 1334-1344.

Kirkham, F.W., Mountford, J.O. & Wilkins, R.J. 1996. The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. *Journal of Applied Ecology* **33**: 1013-1029.

Kissel, D.E., Sander, D.H. & Ellis, R., Jr. 1985. Fertilizer-plant interactions in alkaline soils. In *Fertilizer Technology and Use*, 3rd edition (ed. Engelstad, O.P.), pp. 153-196. Soil Science Society of America, Madison.

Kitajima, K. & Fenner, M. 2000. Ecology of seedling regeneration. In *Seeds: The Ecology of Regeneration in Plant Communities* (ed. Fenner, M.), pp. 331-359. CAB International, Wallingford.

Klotz, S. 1981. Pflanzensoziologische Untersuchungen an einer Kalkhydratdeponie bei Knapendorf, Kr. Merseburg. *Wissenschaftliche Zeitschrift der Universität Halle* 30: 55-76.

Kluge, G. & Müller-Westermeier, G. 2000. *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena.* Berichte des Deutschen Wetterdienstes 213. Deutscher Wetterdienst, Offenbach.

Koch, F. 1957. Die Unkrautgemeinschaften der deutschen Dauerdüngungsversuche auf Ackerland. *Bayerisches Landwirtschaftliches Jahrbuch* **34**: 403-457.

Koerselman, W. & Meuleman, A.F.M. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* **33**: 1441-1450.

Kutschera, L. & Lichtenegger, E. 1992. *Wurzelatlas mitteleuropäischer Grünlandpflanzen. Band 2: Pteridophyta und Dicotyledoneae (Magnoliopsida). Teil I: Morphologie, Anatomie, Ökologie, Verbreitung, Soziologie, Wirtschaft.* Gustav Fischer, Stuttgart.

Lambers, H., Chapin, F.S., III & Pons, T.L. 1998. *Plant Physiological Ecology.* Springer, New York.

Langer, U. 2000. *Bodenbiologische Zustandsanalyse eines Grasland-Ökosystems im Emissionsgebiet des ehemaligen Phosphat-Düngemittelwerkes Steudnitz anhand ausgewählter chemisch-physikalischer und mikrobiologischer Parameter.* PhD Thesis, Friedrich Schiller University, Jena.

Langer, U. & Günther, T. 2001. Effects of alkaline dust deposits from phosphate fertilizer production on microbial biomass and enzyme activities in grassland soils. *Environmental Pollution* **112**: 321-327.

Larsen, S. & Widdowson, A.E. 1971. Soil fluorine. *Journal of Soil Science* **22**: 210-221.

Lauenroth, W.K., Dodd, J.L. & Sims, P.L. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* **36**: 211-222.

Lawton, J.H. 1987. Are there assembly rules for successional communities? In *Colonization, Succession and Stability* (eds. Gray, A.J., Crawley, M.J. & Edwards, P.J.), pp. 225-244. Blackwell, Oxford.

Lepš, J. & Šmilauer, P. 2000. *Multivariate Analysis of Ecological Data.* Faculty of Biological Sciences, University of South Bohemia, Ceské Budejovice.

Lockwood, J.L. 1997. An alternative to succession – assembly rules offer guide to restoration efforts. *Restoration & Management Notes* **15**: 45-50.

Lockwood, J.L., Powell, R.D., Nott, M.P. & Pimm, S.L. 1997. Assembling ecological communities in time and space. *Oikos* **80**: 549-553.

Magurran, A.E. 1988. *Ecological Diversity and its Measurement.* Princeton University Press, Princeton.

Mahn. E.-G. & Tischew, S. 1995. Spontane und gelenkte Sukzessionen in Braunkohlentagebauen – eine Alternative zu traditionellen Rekultivierungsmaßnahmen? *Verhandlungen der Gesellschaft für Ökologie* **24**: 585-592.

Mandák, B. & Pyšek, P. 2001a. The effects of light quality, nitrate concentration and presence of bracteoles on germination of different fruit types in the heterocarpous *Atriplex sagittata*. *Journal of Ecology* **89**: 149-158.

Mandák, B. & Pyšek, P. 2001b. Fruit dispersal and seed banks in *Atriplex sagittata*: the role of heterocarpy. *Journal of Ecology* **89**: 159-165.

Mariko, S., Kachi, N., Ishikawa, S.-I. & Furukawa, A. 1992. Germination ecology of coastal plants in relation to salt environment. *Ecological Research* **7**: 225-233.

Marrs, R.H. & Bradshaw, A.D. 1993. Primary succession on man-made wastes: The importance of resource acquisition. In *Primary Succession on Land* (eds. Miles, J. & Walton D.W.H.), pp. 221-248. Blackwell, Oxford.

Marrs, R.H. & Gough, M.W. 1989. Soil fertility – a potential problem for habitat restoration. In *Biological Habitat Reconstruction* (ed. Buckley, G.P.), pp. 29-44. Wiley, Chichester.

Marschner, H. 1995. *Mineral Nutrition of Higher Plants.* 2nd edition. Academic Press, London.

Marstaller, R. 1987. Zur Beeinflussung einiger Moosgesellschaften durch Luftverunreinigung. 26. Beitrag zur Moosvegetation Thüringens. *Hercynia N.F.* **24**: 279-297.

McCarthy, B.C. 1994. Experimental studies of hickory recruitment in a wooded hedgerow and forest. *Bulletin of the Torrey Botanical Club* **121**: 240-250.

McCune, B. & Allen, T.F.H. 1985. Will similar forests develop on similar sites? *Canadian Journal of Botany* **63**: 367-376.

McLaughlin, M.J., Tiller, K.G., Naidu, R. & Stevens, D.P. 1996. Review: the behaviour and environmental impact of contaminants in fertilizers. *Australian Journal of Soil Research* **34**: 1-54.

Meerts, P. & Grommesch, C. 2001. Soil seed bank in a heavy-metal polluted grassland at Prayon (Belgium). *Plant Ecology* **155**: 35-45.

Meiners, S.J., Handel, S.N. & Pickett, S.T.A. 2000. Tree seedling establishment under insect herbivory: edge effects and interannual variation. *Plant Ecology* **151**: 161-170.

Merou, T. & Papanastasis, V.P. 2000. Germination pattern of certain annual legumes in a sub-humid Mediterranean environment of Macedonia, Greece. In *Legumes for Mediterranean Forage Crops, Pastures and Alternative Uses* (ed. Sulas, L.), pp. 343-347. CIHEAM-IAMZ, Sassar.

Metzner, K., Friedrich, Y. & Schäller, G. 1997. Bodenparameter eines Immissionsgebietes vor und nach der Schließung eines Düngemittelwerkes (1979 - 1997). *Beiträge zur Ökologie* **3**: 51-75.

Michel, B.E. & Radcliffe, D. 1995. A computer program relating solute potential to solution composition for five solutes. *Agronomy Journal* **87**: 126-130.

Morin, P.J. 1999. *Community Ecology.* Blackwell, Massachusetts.

Mountford, J.O., Lakhani, K.H. & Kirkham, F.W. 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *Journal of Applied Ecology* **30**: 321-332.

Müller-Schneider, P. 1986. Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel* **85**: 1-263.

Muller, F.M. 1978. *Seedlings of the North-Western European Lowland. A Flora of Seedlings.* Junk, The Hague.

Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**: 5-21.

Peter, H.-U. 1979. Insekten als Indikatoren für anthropogene Einflüsse. *Nachrichten: Mensch – Umwelt* **7**: 135-140.

Pianka, E.R. 1970. On r- and K-selection. *American Naturalist* **104**: 592-597.

Pigott, C.D. 1971. Analysis of the response of *Urtica dioica* to phosphate. *New Phytologist* **70**: 953-966.

Pons, T.L. 1991. Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Functional Ecology* **5**: 669-675.

Poschlod, P. 1991. Diasporenbanken in Böden – Grundlagen und Bedeutung. In *Populationsbiologie der Pflanzen* (eds. Schmid, B. & Stöcklin, J.), pp. 15-35. Birkhäuser, Basel.

Prince, S.D., Carter, R.N. & Dancy, K.J. 1985. The geographical distribution of prickly lettuce (Lactuca serriola). II. Characteristics of populations near its distribution limit in Britain. *Journal of Ecology* **73**: 39-48.

Punz, W. 1989. Zur Vegetation von Hochofenschlacken. *Linzer Biologische Beiträge* **21**: 211-228.

Putman, R.J. 1994. *Community Ecology.* Chapman & Hall, London.

Pyšek, P. & Lepš, J. 1991. Response of a weed community to nitrogen fertilization: a multivariate analysis. *Journal of Vegetation Science* **2**: 237-244.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology* **39**: 294-309.

Quinn, G.P. & Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists.* Cambridge University Press, Cambridge.

Rebele, F. & Dettmar, J. 1996. *Industriebrachen – Ökologie und Management.* Ulmer, Stuttgart.

Reif, A., Teckelmann, M. & Schulze, E.-D. 1985. Die Standortamplitude der Großen Brennessel (*Urtica dioica* L.) – eine Auswertung vegetationskundlicher Aufnahmen auf der Grundlage der Ellenbergschen Zeigerwerte. *Flora* **176**: 365-382.

Rich, T.C.G. 1991. *Crucifers of Great Britain and Ireland.* Botanical Society of the British Isles, London.

Ritchie, M.E. & Tilman, D. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* **76**: 2648-2655.

Rodin, V. & Kosynkin, V. 1999. *Fluoride production from phosphate raw material treatment in Russia.* Unpulished Report, IFA Technical Sub-committee and Committee Meeting, 15-17 September 1999, Novgorod, Russia.

Rothmaler, W. 2002. *Exkursionsflora von Deutschland. Bd. 4. Gefäßpflanzen: kritischer Band.* (eds. Jäger, E.J. & Werner, K.). Spektrum, Heidelberg.

Roughgarden, J.& Diamond, J. 1986. Overview: the role of species interactions in community ecology. In *Community Ecology* (eds. Diamond, J. & Case, T.J.), pp. 333-343. Harper & Row, New York.

Rowell, D.L. 1997. *Bodenkunde: Untersuchungsmethoden und ihre Anwendung.* Springer, Berlin.

Rozema, J. 1975. The influence of salinity, inundation and temperature on the germination of some halophytes and nonhalophytes. *Oecologia Plantarum* **2**: 367-380.

Samuels, C.L. & Drake, J.A. 1997. Divergent perspectives on community convergence. *Trends in Ecology and Evolution* **12**: 427-432.

Schäller, G. 1985. Untersuchungen zur Struktur und Funktion von naturnahen und immissionsbelasteten Grasland-Ökosystemen. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* **34**: 475-489.

Schäller, G. 1987. *Nutzungskonzeption für immissionsgeschädigte Grasland-Ökosysteme (Immissionsgebiet des Düngemittelwerkes Steudnitz).* Unpublished Research Report, Friedrich Schiller University, Jena.

Schäller, G., Bährmann, R., Heinrich, W., Sander, F. & Voigt, W. 1987. Über den Einfluß von Luftverunreinigungen auf Ökosysteme. XII. Untersuchungen zur Stabilität und Belastbarkeit von Grasland-Ökosystemen. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* **36**: 323-338.

Scheffer, F. & Schachtschabel, P. 1992. *Lehrbuch der Bodenkunde.* 13th edition. Enke, Stuttgart.

Schmitz, J., Merz, A. & Kaspers, H. 1980. Verfahrenstechnische Untersuchungen an einem Rhenania-Phosphat-Drehofen mit radioaktiven Indikatoren. *Chemie-Technik* **9**: 229-236.

Scholze, A. 1997. *Raummuster der Vegetation eines Rasenökosystems als Spiegelbild der Regeneration nach massiver Störung durch ein Phosphatdüngemittelwerk.* Diploma Thesis, Friedrich Schiller University, Jena.

Schratz, E. 1934. Beiträge zur Biologie der Halophyten. I. Zur Keimungsphysiologie. *Jahrbücher für Wissenschaftliche Botanik* **80**: 112-142.

Schüller, H. 1969. Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates im Boden. *Zeitschrift für Pflanzenernährung und Bodenkunde* **123**: 48-63.

Silvertown, J.W. 1983. Why are biennials sometimes not so few? *American Naturalist* **121**: 448-453.

Sokal, R.R. & Rohlf, F.J. 1995. *Biometry – The Principles and Practice of Statistics in Biological Research.* 3rd edition. Freeman, New York.

Soldt, U. & Einax, J.W. 1998. Statistische Aus- und Bewertung immissionsbedingter Bodenbelastungen. Fallstudie des Altstandortes Dorndorf-Steudnitz (Thüringen). *UWSF – Zeitschrift für Umweltchemie und Ökotoxikologie* **10**: 23-29.

SPSS Inc. 1999. *SPSS for Windows Base System User's Guide Release 10.0.* SPSS Inc., Chicago.

Stephan, K. 2001. *Succession and C-S-R functional types in a perturbed grassland ecosystem.* Diploma Thesis, Friedrich Schiller University, Jena.

Stockey, A. & Hunt, R. 1994. Predicting secondary succession in wetland mesocosms on the basis of autecological information on seeds and seedlings. *Journal of Applied Ecology* **31**: 543-559.

Story, J.M., Boggs, K.W. & Graham, D.R. 1989. Effects of nitrogen fertilization on spotted knapweed and competing vegetation in western Montana. *Journal of Range Management* **42**: 222-225.

Swieboda, M. 1970. Wplyw przemyslowych zanieczyszczen powietrza na roslinnosc w otoczeniu fabryki supertomasyny "Bonarka" w Krakowie [in Polish with English summary: The influence of industrial air pollution on the vegetation in the vicinity of the "Bonarka" factory of silicophosphate fertilizers in Cracow]. *Ochrona przyrody* **35**: 161-220.

Telewski, F.W. & Zeevaart, J.A.D. 2002. The 120-yr period for Dr. Beal's seed viability experiment. *American Journal of Botany* **89**: 1285-1288.

Temperton, V.M. & Zirr, K. in press. Order of arrival and availability of safe sites – an example of their importance for plant community assembly in stressed ecosystems. . In *Assembly Rules and Restoration Ecology - Bridging the Gap Between Theory and Practice* (eds. Temperton, V.M., Nuttle, T.J., Hobbs, R.J. & Halle, S.). Island Press, Washington.

Temperton, V.M., Nuttle, T.J., Hobbs, R.J. & Halle, S. in press (eds.). *Assembly Rules and Restoration Ecology - Bridging the Gap Between Theory and Practice.* Island Press, Washington.

ter Braak, C.J.F. 1995. Ordination. In *Data Analysis in Community and Landscape Ecology* (eds. Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R.), pp. 91-173. Cambridge University Press, Cambridge.

ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4).* Microcomputer Power, Ithaca.

ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5).* Microcomputer Power, Ithaca.

ter Heerdt, G.J.N., Verweij, G.L., Bekker, R.M. & Bakker, J.P. 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10**: 144-151.

Thompson, K. 1986. Small scale heterogeneity in the seed bank of an acidic grassland. *Journal of Ecology* **74**: 733-738.

Thompson, K. & Grime, J.P. 1983. A comparative study of germination responses to diurnally-fluctuating temperatures. *Journal of Applied Ecology* **20**: 141-156.

Thompson, K., Bakker, J.P. & Bekker, R.M. 1997. *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity.* Cambridge University Press, Cambridge.

Thurston, J.M. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland and on the yield of hay. In *Ecological Aspects of the Mineral Nutrition of Plants* (ed. Rorison, I.H.), pp. 3-10. Blackwell, Oxford.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* **125**: 827-852.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* **67**: 555-563.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* **57**: 189-214.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* **74**: 2179-2191.

Tilman, D. & El Haddi, A. 1992. Drought and biodiversity in grasslands. *Oecologia* **89**: 257-264.

Tischew, S. & Mahn, E.-G. 1998. Ursachen räumlicher und zeitlicher Differenzierungsprozesse von Silbergrasfluren und Sandtrockenrasen auf Flächen des mitteldeutschen Braunkohlentagebaus – Grundlagen für Renaturierungskonzepte. *Verhandlungen der Gesellschaft für Ökologie* **28**: 307-317.

Trzcinská-Tacik, H. 1966. Flora i roslinnosc zwalów Krakowskich Zakladów Sodowych [in Polish with English summary: Flora and vegetation of the spoil mounds of the Cracow Soda Factory]. *Fragmenta Floristica et Geobotanica* **12**: 243-318.

Underwood, A.J. 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance.* Cambridge University Press, Cambridge.

Ungar, I.A. 1995. Seed germination and seed-bank ecology in halophytes. In *Seed development and germination* (eds. Kigel, J. & Galili, G.), pp. 599-628. Marcel Dekker, New York.

Ungar, I.A. & Riehl, T.E. 1980. The effect of seed reserves on species composition in zonal halophyte communities. *Botanical Gazette* **141**: 447-452.

van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* **62**: 688-696.

van der Valk, A.G. & Davis, C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**: 322-335.

van Hecke, P., Impens, I. & Behaeghe, T.J. 1981. Temporal variation of species composition and species diversity in permanent grassland plots with different fertilizer treatments. *Vegetatio* **47**: 221-232.

Vitousek, P.M. & Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**: 87-115.

Vitousek, P.M. & Matson, P.A. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* **66**: 1360-1376.

Vogler, J. & Gebauer, H.J. 1981. Analyse der Auswirkungen der industriellen Produktion auf die Umwelt – dargestellt am Beispiel des VEB Chemiewerk Coswig / Betriebsteil Steudnitz. *Nachrichten: Mensch – Umwelt* **9**: 65-69.

von Ende, C.N. 2001. Repeated-measures analysis: growth and other time-dependent measures. In *Design and Analysis of Ecological Experiments*, 2nd edition (eds. Scheiner, S.M. & Gurevich, J.G.), pp. 134-157. Chapman & Hall, New York.

Wagner, M. in press. Plant community assembly in extreme habitats: a case study on the roles of seed dispersal capacity and seedling salt tolerance. In *Assembly Rules and Restoration Ecology - Bridging the Gap Between Theory and Practice* (eds. Temperton, V.M., Nuttle, T.J., Hobbs, R.J. & Halle, S.). Island Press, Washington.

Wagner, M., Poschlod, P. & Setchfield, R.P. 2003. Soil seed bank in managed and abandoned semi-natural meadows in Soomaa National Park, Estonia. *Annales Botanici Fennici* **40**: 87-100.

Walker, L.R. & Chapin, F.S., III. 1987. Interactions among processes controlling successional change. *Oikos* **50**: 131-135.

Weiher, E. & Keddy, P. 1999a (eds.). *Ecological Assembly rules – Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.

Weiher, E. & Keddy, P. 1999b. Assembly rules as general constraints on community composition. In *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds. Weiher, E. & Keddy, P.), pp. 251-271. Cambridge University Press, Cambridge.

Werk, K.S. & Ehleringer, J. 1984. Non-random leaf orientation in *Lactuca serriola* L. *Plant, Cell and Environment* **7**: 81-87.

Werk, K.S. & Ehleringer, J. 1985. Photosynthetic characteristics of *Lactuca serriola* L. *Plant, Cell and Environment* **8**: 345-350.

Wiegleb, G. & Felinks, B. 2001a. Predictability of early stages of primary succession in post-mining landscapes of Lower Lusatia, Germany. *Applied Vegetation Science* **4**: 5-18.

Wiegleb, G. & Felinks, B. 2001b. Primary succession in post-mining landscapes of Lower Lusatia – chance or necessity? *Ecological Engineering* **17**: 199-217.

Wildi, O. 1986. Analyse vegetationskundlicher Daten: Theorie und Einsatz statistischer Methoden. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel* **90**: 1-226.

Willems, J.H., Peet, R.K. & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* **4**: 203-212.

Wilson, J.B. 1999. Assembly rules in plant communities. In *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds. Weiher, E. & Keddy, P.), pp. 130-164. Cambridge University Press, Cambridge.

Wilson, J.B. & Gitay, H. 1995. Limitations to species coexistence: evidence for competition from field observations, using a patch model. *Journal of Vegetation Science* 6: 369-376.

Wißkirchen, R. & Krause, S. 1994. Zur Verbreitung und Ökologie von *Atriplex sagittata* BORKH. (Glanz-Melde) im nördlichen Rheinland. *Tuexenia* **14**: 425-444.

Young, R.D., Westfall, D.G. & Colliver, G.W. 1985. Production, marketing, and use of phosphorus fertilizers. In *Fertilizer Technology and Use* (ed. Engelstad, O.P.), pp. 323-376. Soil Science Society of America, Madison.

Young, T.P., Chase, J.M. & Huddleston, R.T. 2001. Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration* **19**: 5-18.

Zar, J.H. 1999. *Biostatistical Analysis*. 4th edition. Prentice Hall, Upper Saddle River.

Zedler, J.B. 2000. Progress in wetland restoration ecology. *Trends in Ecology and Evolution* **15**: 402-407.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence. *Trends in Ecology and Evolution* **12**: 266-269.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, ist determination and significance for community restoration. *Applied Vegetation Science* **1**: 55-66.

Appendices

Appendix 1. Air temperature and precipitation data of the University of Jena weather station. Monthly and annual values for the period of this study (1999 - 2002) and a reference period (1966 – 1995) are given.

	1999	2000	2001	2002	1966-1995
Air temperature [°C]					
annual mean	10.4	11.1	10.1	-	9.5
mean April to June	13.7	15.3	13.1	14.0	12.9
January	4.0	2.0	1.6	1.9	1.0
February	1.6	5.3	3.5	6.2	1.5
March	6.3	6.6	5.2	6.3	5.0
April	9.6	11.7	8.6	8.5	8.5
May	15.1	15.9	15.3	15.1	13.6
June	16.3	18.4	15.5	18.4	16.6
July	19.9	16.8	19.7	19.2	18.6
August	17.5	19.1	19.8	19.8	17.8
September	17.3	15.0	13.0	-	14.1
October	9.7	11.8	13.0	-	9.8
November	4.5	6.8	5.0	-	5.0
December	3.5	3.8	0.7	-	2.2
Precipitation [mm]					
annual amount	582.2	540.7	640.9	-	603.8
April to June	151.1	104.9	136.6	141.7	190.8
January	25.9	35.8	19.9	20.2	36.9
February	46.4	47.9	26.2	67.9	33.5
March	41.2	87.2	90.8	50.0	45.7
April	29.9	34.3	30.6	34.2	54.4
May	54.7	33.7	45.7	62.4	60.0
June	66.5	36.9	60.3	45.1	76.3
July	108.9	59.7	127.1	58.3	59.2
August	67.3	70.2	27.0	121.3	65.5
September	15.1	56.1	48.5	-	43.9
October	15.5	29.4	33.2	-	41.4
November	71.4	28.1	72.0	-	42.3
December	39.4	21.4	59.6	-	44.6

Appendix 2. Composition of dust samples from sheltered locations within the factory premises. Samples were collected in 1997 (Langer 2000 and K. Metzner, unpublished) and in 2000 (M. Wagner, unpublished). Metzner collected and separately analysed 11 samples from all over the site, Langer and Wagner pooled their samples prior to analysis. Data for a soil sample collected in 2002 are provided for comparison.

Factor	Metzner (n=11)		Wagner (n=1)	Langer (n=1)	soil in 2002
	median	range	value	value	
pH	10.4	8.6 – 11.1	-	9.3	
texture					
sand [%]	34 (mean: 43)	2 – 85	-	-	
silt [%]	14 (mean: 28)	7 – 73	-	-	
clay [%]	22 (mean: 29)	1 – 71	-	-	
anions (soluble)					
PO_4^{3-} [mg x kg^{-1}]	36 000	0 – 105 900	11 790	1 940	18
SO_4^{2-} [mg x kg^{-1}]	13 940	460 – 96 950	22 400	-	22
F^- [mg x kg^{-1}]	3 670	50 – 15 280	1 710	300	5
Cl^- [mg x kg^{-1}]	1 170	200 – 23 360	2 100	-	25
NO_3^- [mg x kg^{-1}]	570	160 – 2 160	540	-	28
cations (soluble)					
Na^+ [mg x kg^{-1}]	-	-	58 020	123 000	140
K^+ [mg x kg^{-1}]	-	-	600	610	15
Ca^{2+} [mg x kg^{-1}]	-	-	160	11	52
Mg^{2+} [mg x kg^{-1}]	-	-	58	37.5	3
elements (total)					
Na [mg x kg^{-1}]	76 400	24 210 – 104 450	-	188 000	
K [mg x kg^{-1}]	820	500 – 9 460	-	2 700	
Ca [mg x kg^{-1}]	94 380	49 600 – 174 850	-	151 000	
Mg [mg x kg^{-1}]	3 370	860 – 8 250	-	4 700	
F [mg x kg^{-1}]	-	-	-	5 300	
P [mg x kg^{-1}]	-	-	-	53 000	
Cd [mg x kg^{-1}]	4	1 – 29	-	250	
Zn [mg x kg^{-1}]	220	160 – 540	-	120	
Mn [mg x kg^{-1}]	-	-	-	100	
Pb [mg x kg^{-1}]	48	8 – 150	-	82	
Ni [mg x kg^{-1}]	20	0.3 – 81	-	-	
Cr [mg x kg^{-1}]	-	-	-	68	
Cu [mg x kg^{-1}]	30	11 – 170	-	17	
As [mg x kg^{-1}]	-	-	-	2	

Appendix 3 List of species tested for seedling salt tolerance in Petri dish experiments. Results are summarised as salt tolerance index values. Unless otherwise indicated, 25 seeds were used per replicate. Information is given on seed morphology (Müller-Schneider 1986) and year of first occurrence (Heinrich et al. 2001). Information on pre-germination treatments and seed selection under remarks. Evidence from the literature for salt tolerance is given. Air-dry seed weight based on batches of 500 seeds.

Species	First year	Plumed (yes / no)	Remarks	Seed weight [mg]	Salt tolerance index	Evidence from the literature for salt tolerance
Atriplex sagittata	1990	no	only black seeds, stratified	1.40	0.43	slightly salt-tolerant (Brandes 1999)
Puccinellia distans	1990	no	glumes removed	0.23	0.91	halophyte (Ellenberg 1992)
Artemisia vulgaris	1992	no		0.13	0.33	
Chenopodium rubrum	1992	no	stratified	0.11	0.61	slightly salt- tolerant (Ellenberg 1992)
Lactuca serriola	1992	yes		0.57	0.34	
Erigeron acris	1993	yes		0.09	0.19	
Senecio vulgaris	1993	yes		0.22	0.21	
Taraxacum officinale	1993	yes	20 seeds / replicate	0.68	0.37	slightly salt-tolerant (Ellenberg 1992)
Cirsium vulgare	1994	yes		2.67	0.31	
Conyza canadensis	1994	yes		0.04	0.24	
Lepidium ruderale	1994	no		0.07	0.36	slightly salt-tolerant (Rich 1991, Brandes 1999)
Senecio vernalis	1994	yes		0.21	0.21	
Arenaria serpyllifolia	1995	no		0.03	0.10	
Epilobium tetragonum	1995	yes	20 seeds / replicate	0.07	0.02	
Inula conyzae	1995	yes		0.23	0.11	
Picris hieracioides	1995	yes	20 seeds / replicate	0.64	0.29	
Achillea millefolium	1996	no		0.18	0.30	
Bromus japonicus	1996	no	20 seeds / replicate	2.55	0.57	frequent in saline US prairie (Cooper & Jean 2001)
Verbascum lychnitis	1996	no	20 seeds / replicate	0.08	0.06	
Solidago canadensis	1997	yes		0.07	0.13	
Erophila verna	1998	no		0.02	0.00	
Anthemis tinctoria	1999	no	20 seeds / replicate	0.44	0.22	
Hieracium piloselloides	1999	yes		0.23	0.11	
Thlaspi perfoliatum	1999	no		0.08	0.08	

A3

Appendix 4. Composition of the seed bank in a quadrat of 12 m side length adjacent to Heinrich et al.'s (2001) lower slope permanent plot. Vegetation over values represent 3 yr. means (2000– 2002), mean cover in single years in brackets. Seed bank density / m² is given for single years (means ± standard deviation) and averaged for the 3 yr. period. For the 3 yr. average, additional information on the depth distribution is included in brackets. – indicates absence from the vegetation / seed bank.

Taxa	Vegetation % cover 3 yr. mean (2000, 2001, 2002)	Seed bank density / m² over the sampled profile			
		2000 [mean ± s.d.]	2001 [mean ± s.d.]	2002 [mean ± s.d.]	3yr. mean (in 0–2 cm, 2–5cm, 5–10cm)
Arenaria serpyllifolia	0.4 (0.2, 0.3, 0.5)	-	-	13 ± 31	4 (2, 0, 2)
Artemisia vulgaris	5.0 (8.9, 3.8, 2.3)	226 ± 354	318 ± 265	358 ± 255	301 (190, 69, 42)
Atriplex sagittata	1.4 (3.4, 0.1, 0.7)	902 ± 788	226 ± 211	876 ± 560	668 (301, 261, 106)
Capsella bursa-pastoris	<0.05 (<0.05, <0.05, <0.05)	7 ± 23	7 ± 23	7 ± 23	7 (2, 4, 0)
Carduus acanthoides	0.1 (0.1, 0.2, 0.1)	-	-	27 ± 71	9 (0, 9, 0)
Cerastium glutinosum	1.2 (1.4, 1.0, 1.0)	471 ± 1 631	1 485 ± 4 947	1 777 ± 4 357	1 244 (511, 367, 367)
Cerastium holosteoides	0.1 (0.1, 0.2, <0.05)	40 ± 54	86 ± 146	20 ± 49	49 (20, 22, 7)
Chenopodium album	-	7 ± 23	7 ± 23	-	4 (2, 2, 0)
Chenopodium rubrum	-	603 ± 1 224	670 ± 1 437	829 ± 1 913	701 (228, 261, 212)
Cirsium vulgare	1.8 (3.8, 0.5, 1.1)	40 ± 80	73 ± 104	93 ± 117	69 (24, 40, 4)
Conyza canadensis	<0.05 (-, <0.05, 0.1)	146 ± 155	66 ± 95	451 ± 542	221 (103, 75, 42)
Descurainia sophia	<0.05 (0.1, <0.05, <0.05)	53 ± 62	7 ± 23	33 ± 53	31 (18, 9, 4)
Epilobium tetragonum	0.8 (2.0, 0.2, 0.3)	1 472 ± 1907	995 ± 881	736 ± 856	1 068 (705, 294, 69)
Erigeron acris	0.6 (0.3, 0.7, 0.8)	-	-	60 ± 97	20 (16, 2, 2)
Galium mollugo	0.1 (0.1, 0.1, 0.2)	-	152 ± 528	-	51 (27, 22, 2)
Inula conyzae	7.6 (7.3, 7.2, 8.2)	13 ± 31	-	159 ± 186	58 (53, 0, 4)
Lactuca serriola	2.1 (2.0, 2.5, 1.7)	33 ± 72	46 ± 63	33 ± 72	38 (24, 11, 2)
Picris hieracioides	8.6 (10.4, 7.5, 7.8)	33 ± 53	100 ± 144	352 ± 379	161 (108, 27, 27)
Poa angustifolia	0.6 (0.8, 0.5, 0.6)	13 ± 31	-	13 ± 46	9 (4, 4, 0)
Poa compressa	2.6 (3.8, 2.2, 1.7)	86 ± 154	7 ± 23	173 ± 206	88 (51, 13, 24)
Puccinellia distans	-	9 589 ± 7 854	8 130 ± 5 406	9 211 ± 7 571	8 977 (1 112, 3 455, 4 410)
Senecio vernalis	4.6 (6.5, 4.9, 2.5)	20 ± 36	7 ± 23	146 ± 191	58 (44, 7, 7)
Senecio vulgaris	<0.05 (-, 0.1, -)	27 ± 52	40 ± 63	13 ± 31	27 (27, 0, 0)
Solidago canadensis	0.2 (0.2, 0.1, 0.1)	-	13 ± 31	7 ± 23	7 (2, 2, 2)
Taraxacum officinale	0.5 (0.3, 0.3, 0.8)	47 ± 72	46 ± 93	13 ± 31	35 (13, 7, 16)
Verbascum lychnitis	0.7 (0.3, 0.6, 1.2)	-	33 ± 53	100 ± 132	44 (33, 7, 4)
unidentified dicots		40 ± 72	351 ± 129	345 ± 226	245 (128, 58, 60)
unidentified Poaceae		13 ± 31	153 ± 205	318 ± 315	161 (62, 44, 55)
Total		13 881	13 018	16 162	14 355 (3 812, 5 072, 5 472)

Appendix 5. List of species present in the vegetation of the seed bank plot which were not found in the seed bank in any year. Species are listed in alphabetical order. In brackets information on percent cover: 3 yr. mean value given in bold, followed by values for the single years 2000, 2001 and 2002. – indicates absence from the vegetation in a given year.

Acer campestre (**< 0.05** | < 0.05, < 0.05, < 0.05), *Anthemis tinctoria* (**0.1** | < 0.05, 0.1, 0.3), *Bromus erectus* (**< 0.05** | -, -, < 0.05), *Bromus japonicus* (**0.9** | 0.8, 0.9, 0.9), *Carduus crispus* (**< 0.05** | -, < 0.05, -), *Cirsium arvense* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Cornus sanguinea* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Crepis biennis* (**< 0.05** | -, < 0.05, 0.1), *Daucus carota* (**0.1** | -, < 0.05, 0.2), *Elytrigia repens* (**0.2** | 0.2, 0.2, 0.2), *Erophila verna* (**< 0.05** | < 0.05, < 0.05, -), *Falcaroa vulgaris* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Festuca rubra* (**< 0.05** | -, < 0.05, < 0.05), *Fraxinus excelsior* (**0.1**, < 0.05, 0.1, 0.1), *Galium aparine* (**0.1** | 0.2, 0.1, < 0.05), *Geum urbanum* (**< 0.05** | -, -, < 0.05), *Hieracium piloselloides* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Lepidium ruderale* (**< 0.05** | < 0.05, -, -), *Myosotis arvensis* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Poa nemoralis* (**< 0.05** | < 0.05, -, -), *Prunus avium* (**< 0.05** | -, < 0.05, -), *Rosa canina* (**0.2** | 0.2, 0.1, 0.2), *Saxifraga tridactylites* (**0.1** | < 0.05, < 0.05, 0.2), *Sedum maximum* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Torilis japonica* (**< 0.05** | < 0.05, < 0.05, < 0.05), *Trifolium campestre* (**0.1** | -, 0.1, 0-3), *Veronica arvensis* (**0.1** | < 0.05, 0.1, 0.1), *Vicia angustifolia* (**0.1** | < 0.05, < 0.05, 0.2), *Vicia tetrasperma* (**< 0.05** | -, -, < 0.05)

Appendix 6. Abbreviations of species used in constellation diagrams (Chapter 6) and ordination biplots (Chapters 6 and 7).

Anthemis tinctoria	ant.tin		*Hieracium piloselloides*	hie.pil	
Arenaria serpyllifolia	are.ser		*Inula conyzae*	inu.con	inu_con
Arrhenaterum elatius	arr.ela		*Lactuca serriola*	lac.ser	lac_ser
Artemisia vulgaris	art.vul	art_vul	*Myosotis arvensis*	myo.arv	
Atriplex sagittata	atr.sag	atr_sag	*Pastinaca sativa*	pas.sat	
Bromus japonicus	bro.jap	bro_jap	*Picris hieracioides*	pic.hie	pic_hie
Carduus acanthoides	car.aca		*Poa angustifolia*	poa.ang	poa_ang
Carduus crispus	car.cri		*Poa compressa*	poa.com	poa_com
Cerastium glutinosum	cer.glu		*Poa trivialis*	poa.tri	
Cerastium holosteoides	cer.hol	cer_hol	*Rosa canina*	ros.can	
Cirsium arvense	cir.arv	cir_arv	*Rumex crispus*	rum.cri	
Cirsium vulgare	cir.vul	cir_vul	*Sambucus nigra*	sam.nig	
Clematis vitalba	cle.vit		*Scrophularia nodosa*	scr.nod	
Conyza canadensis	con.can		*Senecio vernalis*	sen.ver	sen_ver
Cornus sanguinea	cor.san		*Senecio vulgaris*	sen.vul	
Crepis biennis	cre.bie		*Solidago canadensis*	sol.can	
Daucus carota	dau.car		*Sonchus arvensis*	son.arv	
Descurainia sophia	des.sop		*Taraxacum officinale*	tar.off	tar_off
Elytrigia repens	ely.rep	ely_rep	*Thlaspi perfoliatum*	thl.per	
Epilobium angustifolium	epi.ang		*Torilis japonica*	tor.jap	
Epilobium tetragonum	epi.tet	epi_tet	*Urtica dioica*	urt.dio	
Erophila verna	ero.ver		*Verbascum lychnitis*	ver.lyc	
Fallopia convolvulus	fal.con		*Verbascum thapsus*	ver.tha	
Festuca arundinacea	fes.aru		*Veronica arvensis*	ver.arv	
Festuca rubra	fes.rub		*Vicia angustifolia*	vic.ang	
Fraxinus excelsior	fra.exc		*Vicia hirsuta*	vic.hir	
Galium aparine	gal.apa	gal_apa	*Vicia tetrasperma*	vic.tet	
Galium mollugo	gal.mol				

Appendix 7. Summary of GLM regression models selected for pattern of species density, evenness, total cover of higher plants and of bryophytes, proportional cover of six plant life history categories. The type of the selected model is indicated (L = linear; Q = quadratic without interaction term; C = cubic without interaction term; Q_I = quadratic with interaction term; C_I = cubic with interaction term) and fitted model quality is summarised on the basis of a deviance-based F-ratio test (ter Braak & Šmilauer 2002). Further details in the text.

Modelled Parameter	Unit	Selected model	Null model d.f.	Model residual d.f.	F-ratio	*P*
Species Density	no. $\times$ m^{-2}	Q	139	135	17.34	< 0.000001
Evenness	$F_{2,1}$ Ratio (Alatalo1981)	Q	139	135	3.53	0.008979
Higher Plant Cover	%	Q_I	139	134	46.47	< 0.000001
Moss Cover	%	Q	139	135	21.78	< 0.000001
Annuals	% Higher Plant Cover	Q	139	135	8.48	0.000004
Monocarpic Perennials	% Higher Plant Cover	L	139	137	12.13	0.000014
Polycarpic Herbs	% Higher Plant Cover	C_I	139	130	9.17	< 0.000001
Polycarpic Grasses	% Higher Plant Cover	C_I	139	130	13.73	< 0.000001
Woody Plants	% Higher Plant Cover	C_I	139	130	3.15	0.001786
Legumes	% Higher Plant Cover	C	139	133	4.42	0.000414

Appendix 8. Summary of GLM regression models selected for patterns of abundance of individual species, expressed as percent cover. Only the most common species occurring in ≥ 10 quadrats are included in the analysis. The type of the selected model is indicated (N = null model; L = linear; Q = quadratic without interaction term; C = cubic without interaction term; Q_I = quadratic with interaction term; C_I = cubic with interaction term) and fitted model quality is summarised on the basis of a deviance-based F-ratio test (ter Braak & Šmilauer 2002). Species for which model significance could not be achieved by any model are highlighted by bold script. Further details in the text.

Modelled Species	Number of occurrences	Selected model	Null model d.f.	Model residual d.f.	F-ratio	*P*
Artemisia vulgaris	109	Q_I	139	134	2.48	0.035213
Elytrigia repens	90	C_I	139	130	19.53	< 0.000001
Epilobium tetragonum	84	Q_I	139	134	4.22	0.001345
Inula conyzae	82	Q	139	135	3.63	0.007705
Lactuca serriola	82	Q	139	135	7.08	0.000033
Cirsium vulgare	78	C	139	133	3.58	0.002530
Picris hieracioides	74	C_I	139	130	6.63	< 0.000001
Atriplex sagittata	73	C_I	139	130	4.69	0.000021
Galium aparine	62	L	139	137	6.22	0.002593
Senecio vernalis	56	Q	139	135	3.70	0.006794
Poa compressa	45	L	139	137	5.58	0.004695
Bromus japonicus	44	C	139	133	6.41	0.000006
Poa angustifolia	42	C_I	139	130	4.76	0.000018
Cerastium holosteoides	**30**	**N**	**139**	-	-	-
Cirsium arvense	29	L	139	137	4.12	0.08301
Taraxacum officinale	22	Q	139	135	6.53	0.000078
Verbascum lychnitis	18	C	139	133	5.11	0.000095
Carduus crispus	17	L	139	137	4.00	0.020471
Thlaspi perfoliatum	17	Q	139	135	2.92	0.023530
Torilis japonica	16	L	139	137	3.92	0.022127
Urtica dioica	11	Q_I	139	134	3.45	0.005745
Sonchus arvensis	**10**	**N**	**139**	-	-	-
Vicia hirsuta	**10**	**N**	**139**	-	-	-

Appendix 9. Soil parameters for the treatments of the nutrient addition experiment. Means ± standard deviation are given (n = 6).

	control		micronutrients		N		NPK	
	1999	**2002**	**1999**	**2002**	**1999**	**2002**	**1999**	**2002**
pH	8.09 ± 0.13	7.94 ± 0.07	8.03 ± 0.13	7.97 ± 0.14	8.21 ± 0.14	7.97 ± 0.09	8.05 ± 0.13	7.88 ± 0.06
L.O.I. [%]	6.26 ± 0.27	6.48 ± 0.99	5.76 ± 0.85	5.74 ± 1.39	6.03 ± 0.41	6.39 ± 0.66	5.97 ± 0.81	5.99 ± 0.86
N_{total} [%]	0.12 ± 0.03	0.12 ± 0.05	0.10 ± 0.02	0.11 ± 0.04	0.12 ± 0.03	0.13 ± 0.04	0.11 ± 0.03	0.13 ± 0.06
P_{CAL} [g × kg^{-1}]	4.14 ± 1.41	4.51 ± 1.78	3.69 ± 1.17	2.94 ± 1.38	4.75 ± 0.98	5.14 ± 1.78	5.09 ± 2.22	4.44 ± 2.69
K_{CAL} [g × kg^{-1}]	0.34 ± 0.15	0.33 ± 0.15	0.28 ± 0.14	0.32 ± 0.23	0.40 ± 0.12	0.43 ± 0.12	0.35 ± 0.14	0.44 ± 0.14

Acknowledgements

Selbständigkeitserklärung

Ich erkläre hiermit, daß ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe

Jena, am 28. Juli 2003

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Markus Wagner

Curriculum Vitae

Personal Details

Name:	Markus Wagner
Date and Place of Birth:	06 Dec. 1970 in Baden-Baden, Germany
Nationality:	German
Marital Status:	unmarried

Education

1991-1994	Vordiplom, (= Intermediate Degree) Biology, Karlsruhe University, Germany
1994-1999	Diploma ('Sehr Gut'), Biology, Marburg University, Germany Thesis: Comparative studies of the vegetation and seed bank of managed and abandoned meadows in Soomaa National park, Estonia
1996-1997	Erasmus exchange student at Imperial College, London, UK
1999-2003	PhD at the Institute of Ecology, Jena University

Job Experience

1995, 1996, 1998	Monitoring of the population dynamics of *Dactylorhiza fuchsii* (Orchidaceae) in a grassland (Prof. P. Poschlod, Department of Biology, Marburg University)
1997	Leader of a field assistant team in experiments on the influence of nutrient addition, liming and herbivory on grassland vegetation (Silwood Park, UK) and involvement in a study on the relationship between vegetation productivity and Soay sheep population dynamics (St. Kilda, Outer Hebrides) (Dr. G. Edwards and Prof. M.J. Crawley, Imperial College at Silwood Park)
2002, 2003	Botanical survey of semi-natural Thuringian grasslands for a project investigating the relationship between biodiversity and ecosystem functioning in grassland ecosystems"; field work in artificially assembled grasslands in a project on the role of biodiversity for element cycling and trophic interactions. (Prof. W.W. Weisser, Institut of Ecology, Jena University)

Publications

Wagner, M., Poschlod, P., Setchfield, R.P. 2003. Soil seed bank in managed and abandoned semi-natural meadows in Soomaa National Park. *Annales Botanici Fennici* **40**, 87-100.

Wagner, M. 2004 in press. Plant community assembly in extreme habitats: a case study on the roles of seed dispersal capacity and seedling salt tolerance. In *Assembly Rules and Restoration Ecology - Bridging the Gap Between Theory and Practice* (eds. Temperton, V.M., Nuttle, T.J., Hobbs, R.J. & Halle, S.). Island Press, Washington.