

An aerial photograph of a lush green landscape. In the foreground, there are dense green trees and a small, light-colored path or road. In the middle ground, a large, dense forest covers a hillside. In the background, a building with a red roof is visible, surrounded by more trees. The overall scene is a mix of natural forest and human-made structures.

Michaela Dölle

From arable field to forest:
Long-term studies
on permanent plots

Georg-August-University of Göttingen

"(...) the fundamental thesis, the source of all true progress in vegetational study - the universality of change. Any system which ignores, even partially, this fundamental fact is built upon sand."

(W.S. Cooper 1926)

From arable field to forest:

Long-term studies on permanent plots



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Michaela Dölle
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Erstgutachter: Prof. Dr. Wolfgang Schmidt, Abteilung Waldbau und Waldökologie
der gemäßigten Zonen, Fakultät für Forstwissenschaften und
Waldökologie, Georg-August-Universität Göttingen

Zweitgutachter: Prof. Dr. Friedrich Beese, Abteilung Ökopedologie der gemäßigten
Zonen, Fakultät für Forstwissenschaften und Waldökologie, Georg-
August-Universität Göttingen

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Cover picture: Overview of the study site southward sighted in September 2006
(Photo taken by M. Dölle).

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and especially for Paula!

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Summary

Abandonment of former intensively used agricultural land is a widespread phenomenon throughout Europe since the late 1960s approximately. The absence of disturbance by agricultural land management leads to fundamental changes in ecosystem properties such as soil chemical parameters and light conditions. Dramatic changes occur in the plant communities within relatively short time. One of the most important areas in ecology is to find those factors that drive successional changes.

The present study was carried out on a long-term permanent plot study site on old-field succession, located in the Experimental Botanical Garden of Göttingen University (Lower Saxony, Germany). It provides the distinctive feature of a real time series since 1968. In contrast to chronosequence studies, achieved by comparing different sites in various stages of succession, permanent plot studies do not run the risk of mixing age-related effects with site differences.

The present thesis covers the following main points:

- I. The structural and compositional changes of the plant community were investigated in the first study. Thereby the focus lay on plant species richness, target species for nature conservation, and the proportion of forest and open landscapes species.
- II. The dynamics of plant species composition during undisturbed old-field succession were analysed in the second study, to identify a successional pathway characterised by a sequence of different stages. Life history traits were considered to find main attributes of the successive stages.
- III. The third study examined changes in soil and light conditions to answer the questions how resources change over time and if differences in initial plot treatment have indirect, via different species compositions, lasting effects on resource availability.
- IV. To evaluate the potential contribution of the soil seed bank to the plant community composition on sites differing in successional age or disturbance intensity, in the fourth study, plant species richness, size and composition of the soil seed bank were investigated and compared with above-ground vegetation.

The total species richness significantly decreased during succession, but was always higher compared to technical afforestation of the same successional age. Open landscape species declined rapidly, whereas forest species showed a slow rate of establishment. The successional pathway consists of stages of differing vegetation composition and structure, characterised by specific life history traits. Early successional stages were characterized by a high proportion of species invasion, whereas with developing time species extinction increased.

Together with the changes in the plant community significant changes in ecosystem parameters occurred. Soil organic carbon accumulated, nitrogen showed redistribution from the lower to the upper soil, and the light indicator value decreased. The initial

treatment of the plots revealed a clear gradient regarding current tree species dominants, light and nutrient supply. The soil seed bank was mainly composed of early successional species of high disturbance habitats. Differences between seed bank composition and above-ground vegetation decreased with increasing disturbance intensity.

To sum up, a fundamental vegetation change took place within relatively short time periods. Plots changed from open annual or perennial vegetation into mixed pioneer forest stands. The occurrence of rare plant species and the comparatively high species richness throughout succession emphasize undisturbed succession as a process producing pioneer forest stands more or less free of charge and close-to-nature. The results shows that on the same site, on plots with different initial conditions different pathways may occur, but that they obviously converge with progress in time.

Light supply is the most decisive factor in the observed secondary succession. The induced differences, caused by the initial treatments, fundamentally determined the initial floristic composition. In consequence, the differences in vegetation development have sustainably influenced light availability, as well as litter pool and nutrient supply. Regeneration ability of an existing plant community dramatically decreases with increasing successional age and decreasing disturbance intensity. For many grassland and woodland species the present study underlines the importance of dispersal capacity, due to low seed accumulation in the soil. Since rare and target species were almost absent from the soil seed bank, their reappearance after local elimination or colonisation of a new site would be dependent on invasion from elsewhere.

To find general patterns, the long-term dataset was compared with other studies and main theories and concepts of vegetation succession were applied. Against the background that each additional description of a successional pathway may broaden our understanding of the process of succession in itself, the main focus was set on a descriptive approach. In order to find general concepts, such exact descriptions contribute considerably to an effective synthesis of the many divergent observations from many different ecosystems. Further on, this kind of specific observations of successional pathways and the gained knowledge of succession grow more and more to an irreplaceable supporting instrument for restoration ecologists, nature conservationists and any decision makers in the field of ecosystem management.

Zusammenfassung

Titel: Vom Acker zum Wald: Dauerflächenuntersuchungen zur Sukzession auf Ackerbrachen

Das Brachfallen von intensiv landwirtschaftlich genutzten Flächen ist seit Ende der 1960er Jahre in ganz Europa ein weitverbreitetes Phänomen. Fehlende Störungsregime der landwirtschaftlichen Nutzung haben dabei einschneidende Veränderungen der Umweltbedingungen zur Folge, die innerhalb relativ kurzer Zeiträume zu grundlegenden Veränderungen der Pflanzengemeinschaft führen. Solche Faktoren aufzudecken, die Veränderungen im Sukzessionsverlauf verursachen, ist eines der wichtigsten Felder ökologischer Forschung.

Untersuchungsobjekt der vorliegenden Arbeit ist ein Dauerflächenversuch zur Sukzession auf Ackerbrachen im Experimentellen Botanischen Garten der Universität Göttingen. Die Besonderheit dieses Langzeitversuchs ist das Bestehen einer echten Zeitreihe seit 1968. Im Vergleich zu Chronosequenzstudien, bei denen Flächen in unterschiedlichen Sukzessionsstadien miteinander verglichen werden, besteht bei Dauerflächen nicht die Schwierigkeit unterschiedlicher Standortbedingungen, die kaum von zeitbedingten Veränderungen getrennt werden können.

Folgende vier Schwerpunkte werden in der vorliegenden Arbeit anhand von vier Publikationen diskutiert:

- I. Die erste Studie untersucht die Veränderungen in der Struktur und Zusammensetzung der sukzessionalen Pflanzengemeinschaften. Hauptaugenmerk lag dabei auf Artenreichtum, Zielarten des Naturschutzes und den Anteilen typischer Wald- und Offenlandarten am Gesamtartenspektrum.
- II. Um den Sukzessionsverlauf in Phasen einzuteilen, wurde in einer zweiten Publikation die Dynamik der Pflanzengemeinschaft während ungestört ablaufender Sekundärsukzession analysiert. Spezifische Merkmale der Pflanzenarten wurden herangezogen, um die einzelnen Sukzessionsphasen zu charakterisieren.
- III. In einer dritten Studie wurden Veränderungen der Boden- und Lichtverhältnisse betrachtet. Dabei wurde untersucht, inwieweit sich Ressourcen im Laufe der Zeit verändern und ob sich Unterschiede in der Flächenbehandlung zu Beginn der Sukzession indirekt, über Unterschiede in der Baumartenzusammensetzung, nachhaltig auf das Ressourcenangebot auswirken.
- IV. Um den potentiellen Beitrag der Bodensamenbank zur Phytodiversität von Standorten unterschiedlichen Sukzessionsalters und unterschiedlicher Störungsintensität zu beurteilen, wurde in einer vierten Studie, die Zusammensetzung und Größe der Bodensamenbank untersucht.

Die Gesamtartenzahl zeigte eine signifikante Abnahme im Laufe der Sukzession, war aber stets deutlich höher im Vergleich zu aufgeforsteten Flächen gleichen Alters. Die Zahl typischer Offenlandarten nahm rasch ab, während sich typische Waldarten nur

langsam etablierten. Der Sukzessionsverlauf konnte klar in Phasen unterschiedlicher Vegetationszusammensetzung und -struktur unterteilt werden. Während der Sukzessionsbeginn durch einen hohen Anteil hinzukommender Arten charakterisiert war, nahmen mit zunehmendem Sukzessionsalter die Artenzahlen deutlich ab. Mit den Veränderungen der Pflanzengemeinschaft veränderten sich gleichzeitig wesentliche Ökosystemparameter: Organischer Kohlenstoff akkumulierte sich im Boden, Stickstoff zeigte eine Verlagerung von tieferen Bodenschichten in den Oberboden. Die unterschiedlichen Behandlungen der Flächen zu Beginn der Sekundärsukzession führten zu einem deutlichen Gradienten in der Baumartenzusammensetzung sowie der Licht- und Nährstoffversorgung. Die Bodensamenbank war im Wesentlichen aus Arten früher Sukzessionsstadien und gestörter Standorte aufgebaut. Mit zunehmender Störungsintensität verringerte sich der Unterschied in der Artenzusammensetzung zwischen Bodensamenbank und etablierter Vegetation.

Innerhalb relativ kurzer Zeit hat ein grundlegender Wandel der Vegetation stattgefunden; von krautiger Offenlandvegetation hin zu strukturreichen Pionierwäldern. Die vorliegende Arbeit zeigt, dass mit ungestörter Sekundärsukzession natürliche Prozesse ablaufen können und gleichzeitig die Möglichkeit zur kostenfreien Aufforstung besteht. Bedingt durch unterschiedliche Ausgangsbedingungen können auf gleichen Flächen unterschiedliche Sukzessionsabläufe auftreten, die sich jedoch im Laufe der Zeit angleichen.

Die beobachteten Entwicklungen zeigten deutlich, dass Licht ein entscheidender Faktor im Sukzessionsverlauf ist. Die durch die Behandlung der Flächen zu Beginn des Experiments hervorgerufenen Unterschiede haben grundlegend die initiale floristische Zusammensetzung der Flächen bestimmt. Daraus resultierend haben die voneinander abweichenden Vegetationsentwicklungen die Lichtverfügbarkeit im Bestand sowie Humusmenge und Nährstoffversorgung nachhaltig beeinflusst.

Die Analyse der Bodensamenbank ergab, dass die Erneuerungsfähigkeit einer bestehenden Pflanzengemeinschaft mit zunehmenden Sukzessionsalter und abnehmender Störungsintensität deutlich sinkt. Für viele Grünland- bzw. Waldarten, unterstreicht die vorliegende Arbeit die Bedeutung von Verbreitungsvektoren, da diese Arten im Allgemeinen eine geringe Kapazität aufweisen, Samen im Boden zu speichern. Gefährdete Arten bzw. Zielarten des Naturschutzes traten kaum in der Bodensamenbank auf. Daraus kann geschlussfolgert werden, dass deren Wiederauftreten oder die Neubesiedlung von Flächen einzig von der Einwanderung von außen abhängt.

Um allgemeine Muster und Strukturen zu erkennen, wurden die eigenen Daten mit zahlreichen anderen Untersuchungen zur Sekundärsukzession sowie Modellvorstellungen und Theorien zum Sukzessionsverlauf verglichen. Vor dem Hintergrund, dass jede einzelne exakte Beschreibung eines Sukzessionsverlaufs einen ganz

wesentlichen Beitrag zum Verständnis der ablaufenden Prozesse und zur Findung allgemeingültiger Konzepte leisten kann, stand der beschreibende Ansatz im Vordergrund. Desweiteren erlangen die Erkenntnisse aus beobachteten Sukzessionsverläufen in zunehmendem Maße bei der Restaurierung degradierter Ökosysteme, oder bei Fragen des Erhalts hoher Biodiversität von Ökosystemen, an Bedeutung.

List of abbreviations

ANOVA	Analysis of variance
C	Carbon
CaCO ₃	Calcium carbonate
CAP	Common Agricultural Policy
CEC	Commission of the European Community
DBH	Diameter at breast height (1.3 m above ground)
DCA	Detrended Correspondence Analysis
ECA	European Commission on Agriculture
EEC	European Economic Community
EU	European Union
FAO	Food and Agricultural Organization of the United Nations
ISA	Indicator Species Analysis
IV	Indicator value
N	Nitrogen
P	Phosphorus
<i>P</i>	Significance level
PAR	Photosynthetically Active Radiation
<i>r</i>	Correlation coefficient
SE	Standard error
SOC	Soil organic carbon

CHAPTER 1

General Introduction



Picture: Tree number one (*Betula pendula*). Identification mark from inventory in the 1970s (Photo taken by M. Dölle in June 2008).

1.1 Historical context

Like in any field of research, in order to understand the current advantages, it is necessary and essential to consider the historical background. Since I will hardly be able to present a complete summary of the development of successional theory and concepts, I rather give a brief overview over the main tendencies at this point. For more detailed information, I permit myself to refer to some comprehensive reviews of the field by MCINTOSH (1980, 1981), MILES (1987), GLENN-LEWIN et al. (1992) or HOBBS & WALKER (2007).

It seems appropriate to begin this part with MCINTOSH's (1980) formulation: *'Succession is one of the oldest, most basic, yet still in some ways, most confounded of ecological concepts. Since its formalisation (...) in the early 1900s, thousands of descriptions of, commentaries about and interpretations of succession have been published and extended inconclusive controversy has been generated. Withal, no effective synthesis of the divergent observations from many different ecosystems, terrestrial and aquatic, has produced a body of laws and theories which ecologists, generally have embraced.'*

The tendency of plant communities to change over time is for long noted and studied. Major contributors to the study of succession were COWLES (1899) with his study of changes in sand dune vegetation and CLEMENTS (1916) who first provided a historical description of succession research dating back to 1685. For the first half of the twentieth century, CLEMENTS' (1916) comprehensive theory of plant succession dominated the field and simultaneously provided for extensive controversy. In his **organismic concept** of succession, each successional series of a region tends to the same climax formation, as the endpoint and mature stage of plant succession. In his view each climax is able to reproduce itself, directional and irreversible. He defined succession as a sequence of plant communities marked by the change from lower to higher life-forms to the climax as an organic entity. An early critic of the Clementsian successional theory was GLEASON (1917, 1926, 1927), who stressed the unique, individualistic behaviour of plant species and the role of chance events. Another disputed aspect was CLEMENTS' assumption that all vegetation change in a particular region would converge to the same type of climax. TANSLEY (1935) underlined the importance of local factors, which may lead to different climax vegetation types.

Indicated by the results of numerous studies, our current view on the nature of community structure is close to the **individualistic concept** outlined by GLEASON (1926). But it took rather a long time until the scientific world paid attention to it and until a change away from the deterministic to more mechanistic and non-equilibrium approaches started. Even throughout more than the first half of the twentieth century successional research was characterised by the search for an universal explanation of succession. MARGALEF (1958, 1963) and ODUM (1969) were two main contributors

proposing general trends of succession, both of them held the idea that successional changes are largely the consequence of interactions within the community, with external influences playing minor roles.

Some authors contributed hypotheses that may all apply in varying degrees to any successional sequence. Representative only a few shall be named in the following. EGLER (1954) described the initial floristic composition model for succession in abandoned fields, what has been shown as an important factor that determines succession. EGLER noted that each species participating during old-field succession is present initially or colonises soon after abandonment, but achieves dominance at different stages according to their life history (Fig. 1.1). The successive establishment of new species in later stages he described with the relay floristic model.

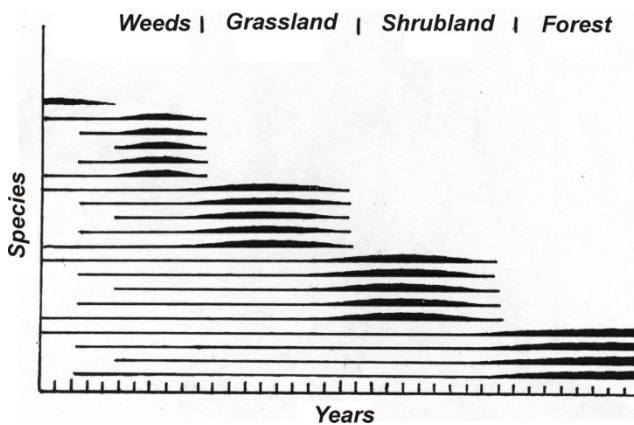


Fig. 1.1. EGLER's (1954) initial floristic composition model.

CONNELL & SLATYER (1977) stated three types of plant-to-plant interactions in their contribution about the mechanisms of succession: facilitation, tolerance, and inhibition. It is widely agreed, that the three models are not exclusive but can act together in the same succession process (BORNKAMM 1988). GRIME (1979) developed a triangular model interpreting succession related to various degrees of disturbance, stress, and competition. He concluded that changes in vegetation composition are a result of the strategy of the participating plant species. NOBLE & SLATYER (1980) proposed the use of 'vital attributes' of species which are crucial for their role in vegetation replacement processes. Another main contribution to successional theory is the work of TILMAN (1985, 1988). He emphasises the importance of competition in succession and with his resource ratio hypothesis he provided an important direction for succession research (Fig. 1.2). Later on and up to now research of vegetation dynamics was less concentrated on global explanations but was increasingly influenced by the search for site-specific information on the mechanisms, or direct causes of vegetation change. To conclude, I take advantage of MILES' (1987) regarding the search for a general concept of succession: '*(...) it is pointless to pursue the quest for*

the ecological grail of a single universal generalisation of succession that will be both useful and widely accepted.'

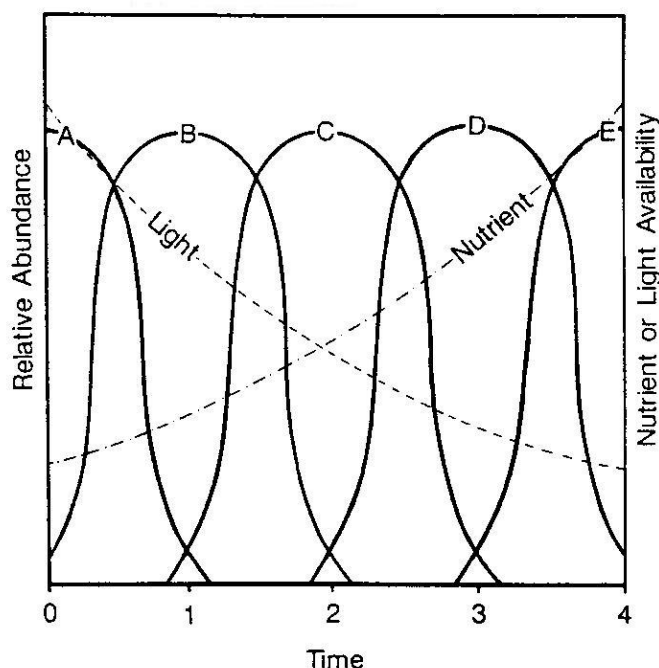


Fig. 1.2. Successional replacement of species (A-E) and changes in resource availabilities, defined in the resource ratio hypothesis of succession (TILMAN 1988).

1.2 Definitions

Vegetation succession is a multifaceted phenomenon (GLENN-LEWIN & VAN DER MAAREL 1992) and thus numerous definitions more or less deviate from each other and various typologies of vegetation dynamics as well as classifications of its patterns, processes, forces or mechanisms have been formulated.

GLEASON (1927) offered a very broad definition of **succession**: *'The successional phenomena of vegetation includes all types of vegetation change in time, whether they are merely fluctuating or produce a fundamental change in the association.'* And continuing *'...succession is an extraordinarily mobile phenomenon, whose processes are not to be stated as fixed laws, but only as general principles of exceedingly broad nature, and whose results need not and frequently do not ensue in any definitely predictable way.'*

Some other published examples are: *'The change in species composition, which occurs in a direct observable time span'* (FEOLI et al. 1975), and most general: *'(...) a sequence of something in time or place'* (MILES 1987), and also: *'(...) the change in species composition or community architecture of a site over time'* (PICKETT &

CADENASSO 2005), or '(...) *a directional non-seasonal cumulative change in the types of plant species that occupy a given area through time*' (PIDWIRNY 2006).

Succession begins when the vegetation of a certain area is partially or completely disturbed. GRIME (1979) defined **disturbance** as '*the mechanisms which limit the plant biomass by causing its partial or total destruction*'. Many different kinds of disturbance have been studied and its effects on successional process is dependent on its extent, a temporal dimension (season, frequency), and its magnitude (GLENN-LEWIN & VAN DER MAAREL 1992). Some common causes of disturbance are fire, wind storm, volcanic eruptions, logging, climate change, severe flooding, and agricultural land use. Most successions contain a number of **stages** that can be recognized by the combination of species that dominate at that point in succession (section 3.4.1). A **sere** is the successional process on a certain site at the whole, or the observed sequence of stages (GLENN-LEVIN & VAN DER MAAREL 1992). **Successional age** is to be considered as equivalent to time since last disturbance or in case of old-field succession to abandonment. Succession theoretically ends when changes in species composition no longer occur with time, and then the community is said to be a climax community.

The concept of a **climax** community assumes that the plants colonizing and establishing themselves in a given region can achieve a stable equilibrium. The idea that succession ends in the development of a climax community has had a long history in the fields of biogeography and ecology. CLEMENTS (1904, 1916) was one of the first supporting the idea. But more and more, scientists began viewing succession as a phenomenon that rarely attains stable equilibrium, related to the nature of disturbance, which acts on a great variety of spatial and temporal scales. But vegetational dynamics are as multifaceted as succession itself. Variations in vegetation composition in an equilibrium stage around a mean composition, induced by variations of environmental conditions (like growing season temperature or precipitation or slight disturbance on a short time scale) are known as **fluctuations**. In contrast to succession, which is a major compositional change, evident over decades or centuries, fluctuation is non permanent and comprises the natural temporal variations in plant abundance over short time periods (GLENN-LEWIN & VAN DER MAAREL 1992). However, like in most other fields there are smooth transitions between the various aspects of vegetation dynamics. Further distinctions can be made: fine-scale **gap dynamics**, especially important in forest ecosystems, highlight its mosaic structure as a result of treefall gaps. GRUBB (1977) emphasised the importance of such regeneration niche in community dynamics. **Patch dynamics** are closely related to the preceding with the main difference of being larger in size relative to the size of the community.

Two major categories of succession exist in theory: primary and secondary succession. In his empirical and analytical account on the causes of succession,

CLEMENTS (1904) clearly distinguished between **primary succession** on newly exposed surfaces which had never born vegetation before, and **secondary succession** where vegetation, on soils already developed had been damaged or destroyed. Examples of primary succession are lava flows, sand dunes or glacier retreat and for secondary, disturbance by severe windstorm or fire, or abandoned agricultural fields. Primary succession implies the absence of any parts of previous vegetation or seed or propagule bank as well as any developed soil, and is usually characterized by low fertility, especially in nitrogen. In secondary succession a developed soil is present and parts of previous vegetation, mainly seeds or seedlings and vegetative propagules exist. Thus for primary succession colonizing species have to immigrate from elsewhere, hence dispersal mechanisms and the distance of mature vegetation plays an overriding role.

However, primary and secondary succession represent extremes on a gradient of disturbance intensity. They probably form a continuum, what becomes apparent considering old-field succession. Arable fields usually provide at the time of abandonment bare soil, whereas grassland ecosystems bear a more or less complete vegetation cover. Thus the rate of succession fundamentally differs between grassland and arable field succession, but both are types on the secondary succession gradient.

A further distinction is made between progressive and retrogressive succession. **Progressive succession** is what is normally intended when we use the term succession. It implies a direction, and the process might be described as a series of successive stages (the sere) or a continuum from an initial to a mature community (climax). It is characterised by an increasing species diversity and biomass accumulation, increasing complexity, and floristic stability. **Retrogressive succession** is a succession where the community becomes simplistic and contains fewer species and less biomass over time. Retrogression is associated with long-term changes in environmental parameters such as soil leaching or water table elevation, causing severe stress.

In the same process of vegetation change, both progressive and retrogressive aspects may occur (BAKKER 1989). And since vegetation dynamics are characterised by a complexity of processes, patterns, and mechanisms, repeated disturbance is of major importance. For example in our study on undisturbed old-field succession, what can be clearly assigned to be progressive in terms of directionality, vegetational complexity and biomass accumulation, plant species diversity clearly increased during the first decades but later on the developing forest showed decreasing plant species richness (section 2.3.2).

An additional classification is made with the terms autogenic and allogenic succession. **Autogenic succession** is a succession where the vegetation change is a result of biotic interactions and biotic modification of the environment. It implies

internal forces and mechanisms, such as competition, and soil modification by plants. **Allogenic succession** is caused by a change in environmental conditions, or external forces which in turn influences the composition of the plant community. Long-term vegetation response to climate change is an example. And thus it becomes clear that both autogenic and allogenic forces act together in most successions. To label a successional series as a whole autogenic or allogenic would be misleading, but individual processes might (GLENN-LEWIN & VAN DER MAAREL 1992).

Using the term **undisturbed succession** in the following chapters, means the absence of any kind of agricultural treatment and that the sites are allowed to revegetate naturally.

Multiple mechanisms interact during vegetation succession. They may result on the one hand from the life-history characteristics of the participating plant species, and on the other hand from interactions between the plant species or with other environmental parameters. **Colonisation** is dependent on presence or immigration of propagules, specific characteristics of the propagules, and spatial patterns of the environment and existing vegetation. The **initial floristic composition** model proposed by EGLER (1954), indicates that the initial composition of plant species at a certain site largely determines the subsequent vegetation. But a complete, non-invasible initial floristic composition is one extreme, in most pathways additional successive colonisation is the normal case, described as **relay floristic** model. **Competition** for resources like light, nutrients or water determines largely the patterns of species replacement processes. It was TILMAN (1985, 1988) who mainly stated the importance of competition in succession (section 1.1). CONNELL & SLATYER (1977) summarised interactions between plant species during succession into the following three processes:

Facilitation is the mechanism when early successional species enable the establishment of later successional species, e.g. beech (*Fagus sylvatica*) and oak (*Quercus spec.*) can germinate in dark conditions under the pioneer tree canopy, but they need better light conditions for growing like in gaps, when pioneer tree species break down. **Inhibition** is the prevention of new species establishment by existing plants, e.g. the shade and litter accumulation in developed forests inhibit the establishment of early successional species. **Tolerance** describes a situation where neither inhibition, nor facilitation influences species establishment. These three processes of plant to plant interaction are not exclusive, they are mechanisms only separated in time which occur on the same site under participation of the same species.

1.3 Abandoned agricultural land

'Land abandonment is a process, whereby human control over land (e.g. agriculture) is given up and the land is left to nature' (FAO 2006).

Abandonment of agricultural land was an integrated instrument of land management and an essential measure for the regeneration of soil fertility until the end of the three-field crop rotation at the beginning of the 19th century. These fallow lands usually were of temporary character. But there was also permanent abandonment for several reasons, as for example marginal, less productive land, declining population development, or technical changes in land management practices (HÜPPE 1987).

Today, distinction is made between three categories of abandoned agricultural land: **Economical fallow land** mainly developed as a consequence of the progressive industrialisation of agricultural land use in the beginning of the 20th century, primarily characterised by the large scale production of synthetic fertiliser and continuous technical advances in land management. Consequently, less productive and marginal land was left to abandonment. This category mainly developed from the late 1960s, also referred to as 'social fallow land'. The second category, **obligatorily set-aside** was established by the European Union (EU) in 1988 as an instrument to delimitate agricultural overproduction. But in 2007 the EU minister of agriculture set the compensation for obligatorily set-aside to 0% as a reaction to the increasing tense situation at the grain trade (EU-COUNCIL 2007). Farmers are not obligated to till their set-aside land, however, at this point the obligatorily set-aside can pass over in **optional ecological set-aside**. This third category was established in the course of the Agenda 2000; the action program of the EU, concluded in March 1999, with the strengthening of the environmental measures of the CAP (Common agricultural policy) as one main point (EUROPEAN COMMISSION 1997). Farmers are entitled to direct payments for participation.

Since the Neolithicum the natural landscape has been shaped by humans through agricultural activities in many ways. By the reason of this diversified land usage, our cultural landscape probably reached peak floristic biodiversity in the middle of the 19th century (ELLENBERG 1996). Low-intensity farming, in the form of livestock rearing and traditional cultivation methods, has created semi-natural habitats that now support a wider range of species than might otherwise be found in purely 'natural' climax vegetation. Species-rich grasslands, hay meadows, grazed wetlands and moorland habitats, are all examples of environmental assets associated with, or produced by, low-intensity agricultural land use. Today all over the world, the traditional farming systems largely has been given up for economical reasons and less productive, marginal land was left to abandonment (HOBBS & CRAMER 2007). Land abandonment drives landscape changes through secondary vegetation succession leading to shrub

encroachment and forest regrowth. This can dramatically cause losses of biodiversity on species and landscape level (EUROPEAN COMMISSION 1980). About half of the European network Natura 2000 sites designated under the Habitats and Species Directive are farmed habitats (EUROPEAN COMMISSION 1992). One main objective for maintaining biodiversity is to preserve the openness of the cultural landscape and impede undisturbed succession. This is only attainable by raising enormous financial support (EUROPEAN COMMISSION 2003). But beside the loss in biodiversity due to shrub and tree encroachment, undisturbed succession represents a highly natural process. And since the protection of natural processes is an integral part of nature conservational effort, undisturbed succession should receive more validation, particularly in comparison to technical afforestation.

1.4 Methods to study succession

The main goals in successional ecology are to describe successional pathways, to extract generalisations, and to identify the main driving forces of vegetation dynamics. Since ecological management and the management of natural areas is primarily the manipulation of succession (MILES 1987, LUKEN 1990), the understanding of vegetation dynamics derived from a large amount of experimental studies or direct field observations are of vital importance for applications.

Direct observations from **permanent plots** offer accurate data of the parameter of interest and thus allow a useful evaluation of the mechanisms, initial conditions and successional changes. The time-scale of a succession is long relative to any individuals career (VITOUSEK et al. 1989), and thus *'the establishment and initial sampling of such plots takes a large measure of unselfish forethought'* (BARBOUR et al. 1987). One has to accept the fact, that valuable results to assess the affects of succession will arise only many years in the future (LUKEN 1990). Thus many available data regarding vegetation dynamics during succession are based on **chronosequences** (Pickett 1989). In such space-for-time substitution vegetation data are taken from various different aged sites in similar environments. But since the importance of environmental conditions for the successional development, the assumption of environmental homogeneity (e.g. same soil conditions, site history, availability of propagules) can be misleading (MILES 1979, AUSTIN 1981). For a deeper understanding of successional changes and interpretation of successional processes permanent plot studies are of essential importance (AUSTIN 1981, PRACH 1990, SCHREIBER 1995, BAKKER et al. 1996)(also section 2.2 and 3.2).

Much of the research on secondary succession and the development of concepts of ecological succession has been done on old-fields (e.g. BILLINGS 1938, OOSTING 1942, BARD 1952, EGLER 1954, BAZZAZ 1975, SCHMIDT 1981, PICKETT 1982, TILMAN 1985, FIKE & NIERING 1999, HOOKER & COMPTON 2003, CRAMER & HOBBS 2007). Succession on **old-**

fields (agricultural land that has been abandoned and allowed to revegetate naturally) is assigned to secondary succession. On old-fields, a well developed soil and dependent on the management practice before, parts of the previous vegetation, mainly roots and a seed or a seedling bank are normally existent. In contrast to abandoned grassland, arable fields normally lack a closed vegetation cover in the beginning of the succession, and thus they are characterised by a high dynamic and turnover rate in the beginning (SCHMIDT 1981).

1.5 The Succession Experiment in the Experimental Botanical Garden of Göttingen University

The succession experiment in the Experimental Botanical Garden of Göttingen University started in 1968 on the initiative of Heinz Ellenberg. From this time up to now Wolfgang Schmidt hold the scientific supervision of the project, what means coordinating the continuously taking of vegetation relevées, and soil samples, the yearly mowing, ploughing and fertilising of the treatment plots and estimation of biomass pool as well as analysis of nutrient contents. It is an exemplary project for the study of long-term vegetation changes during secondary succession and since to my knowledge the longest direct report on old-field succession in Germany (Central Europe).

The experimental study site has a total size of 3450 m² and is divided into five main sections which differ in their initial treatment in 1968 (Fig.1.3):

section **I**: sterilised by heating,

section **II**: herbicide treatment,

section **III**, **IV**, and **V**: ploughing.

Each section is subdivided into four to five plots of differing yearly treatment. Since the regulation of the near by rivulet 'Lutter' at about 1930, the deep, calcareous, and fertile soil was intensively used for crop growing. For a detailed description of the study site I refer to SCHMIDT (1981).

Main subject of this thesis are the plots of undisturbed succession since 1968 (ID, IE, IID, IIID chapter 2, 3, and 4) and the plots of undisturbed succession since 1983 (IIA, IIB, IIC, IIIA, IIIB, IIIC)(chapter 3 and 4). For the study of the soil seed bank all plots of the study site were regarded (chapter 5). In order to find evident abbreviations for the considered plots, the plot labelling in the chapter 2-5 deviate from the purely systematically structure in Fig. 1.3 and also variates inbetween the chapters. This was mainly caused by the particular context of the papers.

1.6 Main objectives of the present thesis

The Succession Experiment described in the present work, was before intensively studied by Wolfgang Schmidt (e.g. SCHMIDT 1981, 1983, 1984, 1985, 1993, 1998, 2002, 2006).

This thesis shall be a contribution to carry forward the preceding work. Main focus was set on the plots of undisturbed succession. Four main points are discussed:

- I. The structural and compositional changes of the plant community were investigated in the first study. Thereby the focus lay on plant species richness, target species for nature conservation, and the proportion of forest and open landscapes species.
- II. The dynamics of plant species composition during undisturbed old-field succession were analysed in the second study, to identify a successional pathway characterised by a sequence of different stages. Life history traits were considered to find main attributes of the successive stages.
- III. To answer the questions how resources change over time and if differences in initial plot treatment have indirect, via differences in species composition, a lasting effect on resource availability, the third study examined changes in soil and light conditions.
- IV. To evaluate the potential contribution of the soil seed bank to the plant community composition on sites differing in successional age or disturbance intensity, in the fourth study, richness, size and composition of the soil seed bank were investigated.

The chapters 2 to 5 in this thesis each correspond to a paper, yet published or at least submitted for publishing in a scientific peer-reviewed journal. The differences in format of e.g. citations are caused by the guidelines of the particular journal and have been retained unchanged.

This thesis is largely build on data collected before I even could think about succession. Since 2003 all presented data are based upon own data collection. In the papers 2, 4 and 5 (Dölle & Schmidt; Allg. Forst- u. Jagdztg 2007, Dölle & Schmidt; Plant Ecology 2008, and Dölle & Schmidt; submitted 2008) Wolfgang Schmidt contributed to ideas and discussion, while I analysed the data and wrote the manuscript. In the paper 3 (Dölle, Bernhardt-Römermann, Parth & Schmidt; Flora 2008) Wolfgang Schmidt and Markus Bernhardt-Römermann contributed to ideas and discussion, Markus Bernhardt-Römermann and Andreas Parth contributed to the process of data analysis, while I was responsible for data analysis and writing the manuscript.

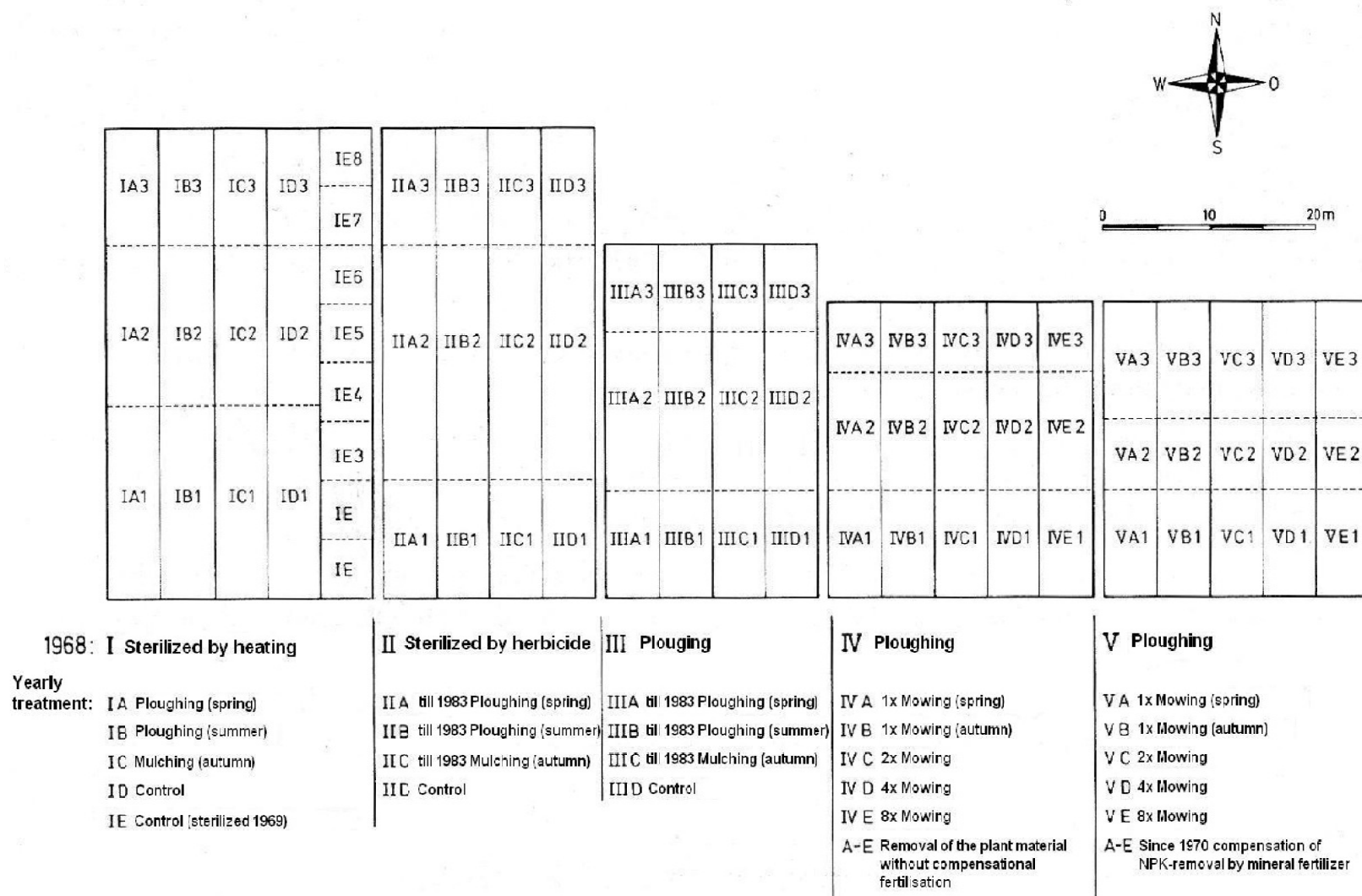


Fig. 1.3. Experimental setup of the Succession Experiment in the Experimental Botanical Garden of Göttingen University (modified according to SCHMIDT 1981).

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CHAPTER 2

Changes in plant species diversity during thirty-six years of undisturbed old-field succession

Dölle, M. & Schmidt, W. (2007)

Allgemeine Forst- und Jagdzeitung 178: 225-232



Large picture: View in the crown canopy of a plot of undisturbed succession since 36 years. Small picture: Beech sapling (*Fagus sylvatica*) in the understory (Photos taken by M. Dölle).

Key words – Schlagwörter

afforestation; forest species; long-term study; open landscape species; permanent plots; red list species; succession.

natürliche Wiederbewaldung; typische Waldarten; echte Zeitreihe; Offenlandarten; Dauerflächen; Rote-Liste-Arten; Sukzession.

2.1 Introduction

Set-aside is the most common way of “management” of fallow agricultural land in Europe. In many cases political and socio-economic reasons strongly determine the development of abandoned land. Since the mid-1960s, agricultural overproduction in Germany and in many other European countries has led to a system of supporting abandonment which costs several hundred millions of Euros per year (EUROPEAN COMMISSION 2003). It includes subsidies for afforestation in areas with a lower share of forested sites or on less productive marginal sites (Council Regulation (EC) No 1257/1999). Furthermore, afforestation is also used as a compensational measure countering negative anthropogenic impacts on landscape.

Evidently land abandonment plainly affects habitat shift with important consequences for biodiversity (POSCHLOD *et al.* 2005, PYKÄLÄ *et al.* 2005, STRIJKER 2005), as ecosystem functioning and therefore species numbers are altered during succession. Current knowledge about undisturbed vegetation development, especially colonization of woody plants on abandoned fields, is mostly based on short-term observations in a few restricted areas or indirectly on space-for-time substitution (PICKETT 1982, VANKAT & CARSON 1991). However, such substitutions, achieved by comparing different sites in various stages of succession, are often not useful for explaining general mechanisms and pathways of undisturbed vegetation development (SCHMIDT 1975, SCHREIBER 1995). Various investigations showed that the complexity of undisturbed succession following agricultural abandonment makes a general prediction on how succession proceeds difficult (PICKETT 1982, SCHREIBER 1995, FIKE & NIERING 1999). Long-term studies on permanent plots are essential both for a better understanding of the mechanisms of succession and of the change in species composition during succession. BAKKER *et al.* (1996), PRACH (1990), and ROSENTHAL & MÜLLER (2005) emphasized the importance of such long-term ecological studies. These studies alone offer invaluable insights into the complex processes of vegetation change. In the case of old-field succession only a few studies are available that offer continuous datasets extending from the beginning of the set-aside beyond the first ten years (PICKETT 1982, FIKE & NIERING 1999).

Additionally, undisturbed succession as a dynamical and “natural” way of afforesting abandoned land is rarely considered (KLEIN 1997, REIF 1997). Since 1995 technical afforestation and successional afforestation are equal before the German

law. It seems reasonable that there is a causal relationship between scarcely investigated forests resulting from undisturbed succession on former arable land and the low acceptance of undisturbed succession for afforestation.

In this study, patterns and processes of forest regeneration were investigated on permanent plots during undisturbed succession on formerly arable fields since 1968. On the basis of this dataset, covering about 36 years of undisturbed old-field succession, plant species diversity as a key parameter characterizing ecosystems (LOREAU *et al.* 2002) was intensively investigated. Diversity of plant communities was measured as species richness (α -diversity sensu WHITTAKER (1977)) and evenness (HAEUPLER 1982, MAGURRAN 2004). Each stage in vegetation succession is marked by certain groups of plant species, as there are winners and loser in each stage and a more or less continuous process of structural change is taking place. The current study documents the replacement of old-field herbaceous plant communities by pioneer forest stands. Plant species diversity and dynamics of target species (e.g. Red List species, species typical to open landscapes) which occur in different stages of undisturbed secondary succession as well as the general vegetation structure are selected to describe the change.

In this study on the effects of shrub and tree colonization we addressed the following questions:

- (1) Is the total number of plant species affected by increasing shrub and tree colonization?
- (2) Are target species for nature conservation (many are species typical to open landscapes) decreasing during succession? Do plant species typical to closed forests invade at the expense of species typical to open landscapes?
- (3) Does the presence or absence of the soil seed bank in the beginning of the successional seres considerably influence the development of the plant community at later stages?

2.2 Material and methods

2.2.1 Study area and experimental design

All plots of the current study are part of a 3450 m² experimental field located in the New Botanical Garden of Göttingen University, Lower Saxony, Germany (180 m a.s.l., 51°34'0"N, 9°56'60"E; mean annual temperature: 8.5°C; average annual rainfall: 635 mm). Initiated by Heinz Ellenberg, the experiment was set up on a former arable field cultivated until 1968 on deep, calcareous and fertile soil (alluvial loamy brown earth). Regional forest vegetation is dominated by *Fagus sylvatica* (Fagion sylvaticae) which is the natural vegetation type (BOHN *et al.* 2003).

The vegetation development was studied on four permanent plots of undisturbed succession since 1968/1969. The initial treatment at the beginning of the experiment

differed in all four plots. In two plots, the soil was sterilized by heating to a depth of 30 cm (S_1 , S_2 each 200 m²). A third plot was ploughed 20 cm deep and treated by herbicide (H_1 : 200 m²). The fourth plot was just ploughed 20 cm deep (C_1 : 150 m²). The plot C_1 (control) corresponds to the natural conditions of an abandoned arable field with undisturbed soil seed bank. In the plots S_1 and S_2 (sterilized) all living parts of former vegetation (including soil seed bank) were destroyed. The herbicide (H_1) treatment destroyed all parts of above ground vegetation, but had marginal effects on the soil seed bank. All treatments were implemented in summer 1968, except plot S_2 which was sterilized by heating in spring of the following year. Here the timing of the start was varied in order to differentiate the impact of the initial condition (year, season) on vegetation development (SCHMIDT 1981, 1983, 1993).

The plots S_1 , H_1 and C_1 are each subdivided into three subplots, plot S_2 into eight subplots. A more detailed description of the study site and methods are given in SCHMIDT (1981, 1993).

2.2.2 Vegetation sampling

Vegetation relevés included records of the percentage cover of all vascular plant species and were conducted twice per year in the beginning and once per year since trees have started to dominate. From 1968 until 1993 vegetation was recorded annually, thereafter vegetation relevés were conducted in 1995, 1999, 2004 and 2005. In 1989 and 2005 all ramets of woody plants in the tree (>5 m) and shrub layer (0.5-5 m) within the entire plot area were counted. In 1994 and 2005 woody ramets were counted also in the herb layer (<0.5 m height) within a subplot consisting a core area 2 m right and left from the centre line. No differentiation was made between generative saplings and clonal shoots. Nomenclature follows WISSKIRCHEN & HAEUPLER (1998).

2.2.3 Data analysis

Species richness considers the number of vascular plant species occurring per plot and time period. Evenness, as a parameter independent of species number, describes the degree of uniform distribution (MAGURRAN 2004). To evaluate the "quality" of species richness, at first, the degree of vulnerability (risk of extinction) was estimated by the Red List for hillsides and mountains of Lower Saxony (GARVE 2004). Additionally, the list of forest plants of hillsides and mountains in Germany (SCHMIDT *et al.* 2003) was used as a basis to ecologically characterize the plant species, in regard whether they are closely tied to forests or more or less common in open landscapes. Evaluation was done on the basis of species lists (qualitative) or on the basis of coverage (quantitative). Values of subplots were divided into one dataset per year.

The annual datasets were compiled into four decades to facilitate a quick overview over the successional pathway:

- I. 1969-1978 (S_1 , H_1 , C_1), 1970-1979 (S_2) – 1st to 10th year
- II. 1979-1988 (S_1 , H_1 , C_1), 1980-1989 (S_2) – 11th to 20th year
- III. 1989-1998 (S_1 , H_1 , C_1), 1990-1999 (S_2) – 21st to 30th year
- IV. 1999-2005 (S_1 , H_1 , C_1), 2000-2005 (S_2) – 31st to 36th (35th) year.

In addition to the methods of descriptive statistics (mean, standard error), the Kruskal-Wallis-H-test ($p < 0.05$) was applied as a non-parametric test to compare among the four decades, since a normal distribution was not given.

2.3 Results

2.3.1 Vegetation structure

Plots changed from initial open herbaceous annual plant communities to perennial herb and grassland communities then to shrub thickets and finally to pioneer forest communities. After five years, the first woody species reached shrub layer height (>0.5 m), and two decades after the initial survey, the first trees grew up to tree layer height of 5 m. The established pioneer forest stands now exhibit a closed tree canopy reaching up to 22 m. All plots show a similar development of coverage for the different vegetation layers (Fig. 2.1). The herb layers had the highest coverage in the first and second decade. On the control plot (C_1) peak herb layer coverage was found in the first decade. Within the last time period, herbaceous cover of all plots decreased to means between 12 % and 28 %. Currently all plots feature a dense multilayered shrub stratum with 45 % to 60 % of coverage. The dense tree stands cover 70 % to 100 % with 5200 – 8000 stems per ha. Predominant species in the tree layer in terms of both density and coverage are *Salix caprea*, *Betula pendula* and *Fraxinus excelsior* (Fig.2.2). Stem density of *S. caprea* and *B. pendula* in the tree layers decreased, whereas that of *F. excelsior* increased during the last 15 years. All plots show a similar composition of woody species in the herb layers. Overall *F. excelsior* is the tree species with the highest density of saplings. The dominant shrub species is *Cornus sanguinea*; *Crataegus monogyna* and *Viburnum opulus* are subdominant. Nine tree species and 11 shrub species occur in much lower frequencies. The tree layer showed significant differences in tree species dominance between the different plots. Especially *B. pendula* is absent in the control plot (C_1) while it is the dominant species in plot S_2 with 53 % stem density. Twenty years after abandonment *F. excelsior* was represented only in the tree layer of the control plot (C_1).

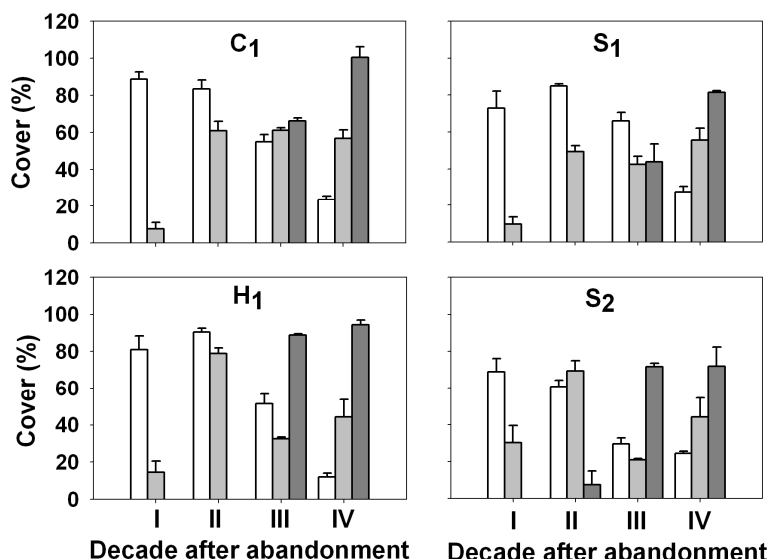


Fig. 2.1. Mean cover (%) of the vegetation subdivided into herb layer (<0.5 m; white bars), shrub layer (0.5 – 5 m; grey bars), and tree layer (>5 m; dark grey bars) with standard error for each period of time for the four study plots.

Mittlerer Deckungsgrad (%) der Vegetation der vier Versuchsstreifen unterteilt in Krautschicht (<0,5 m; weiße Balken), Strauchschicht (0,5 – 5 m; graue Balken) und Baumschicht (>5 m; dunkelgraue Balken) (\pm Standardfehler) in den vier Dekaden.

Fifteen years later it is also part of the tree layer of plot S₁ and H₁. Stem density of *B. pendula* decreased during that time. At least two of the tree species which build the today's tree layer germinated in the first year of abandonment and were continuously recorded. In the plots S₁ and S₂ *B. pendula*, *F. excelsior*, and *S. caprea* were continuously recorded, in S₂ *Acer platanoides* and *Acer pseudoplatanus* additionally. In plot H₁ *S. caprea* and *A. platanoides* and in plot C₁ *F. excelsior* and *A. platanoides* occur since 1969. All of these species are wind dispersed and occur in close vicinity. Animal dispersed tree species, with tall and heavy seeds, like *Quercus robur* and *F. sylvatica* were recorded at earliest in the second decade.

2.3.2 Diversity

The total species number in the first decade ranges between 52 and 63 per plot (Fig. 2.3). In all plots, total species number decreased significantly from the first decade to the fourth, or in case of the plots sterilized by heating (S₁, S₂) second and fourth. For the shrub and tree layers, a continuous increase in species number over time was recorded. All plots show the highest evenness values for the total stand in the first decade and a slight decrease in at least one of the following decades (Fig. 2.3). Evenness in the herb layer was lowest in the second decade. At this time, herb layer coverage was dominated by a few competitive species like *Solidago canadensis* or *Calamagrostis epigejos*.

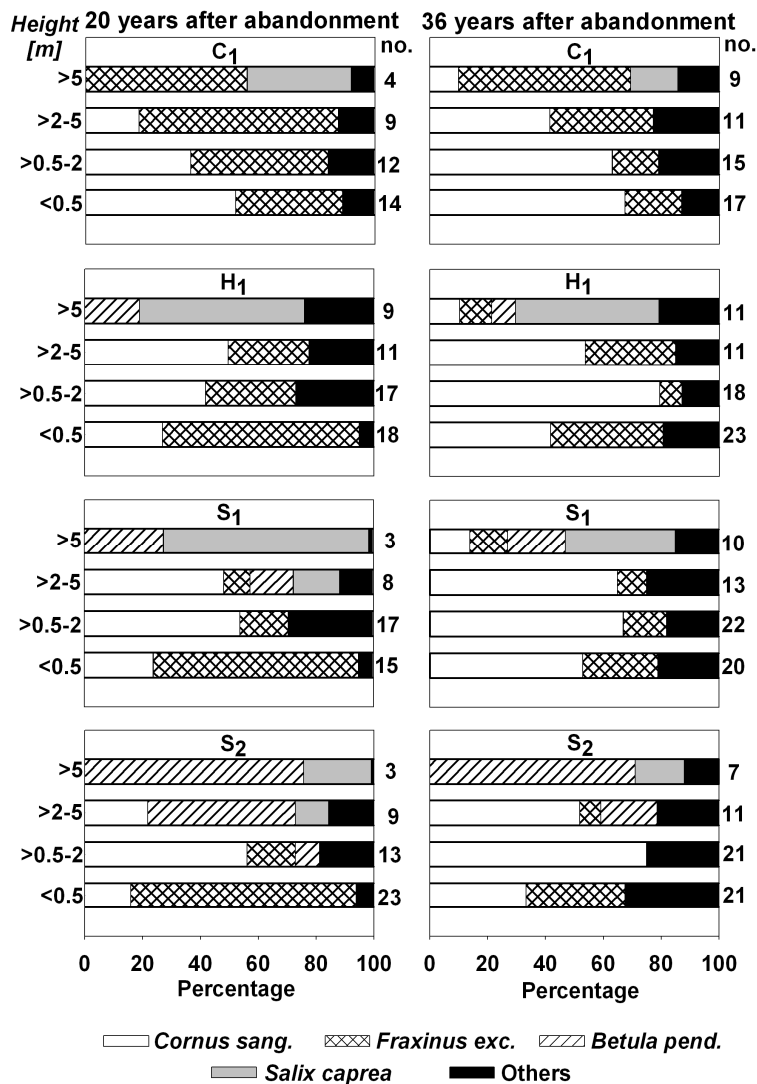


Fig. 2.2. Species richness and percentage of numbers of dominant woody species in herb layer (<0.5 m), in lower (>0.5 – 2 m) and upper (>2 – 5 m) shrub layer and in tree layer (> 5 m) for the four study plots 20 and 36 years after abandonment.

Artenzahl und prozentualer Anteil (Individuenzahl) der Hauptbaumarten in der Krautschicht (<0,5 m), der unteren (>0,5 – 2 m) und oberen (>2 – 5 m) Strauchschicht und der Baumschicht (>5 m) auf den vier Versuchstreifen jeweils 20 und 36 Jahre nach Brachfallen.

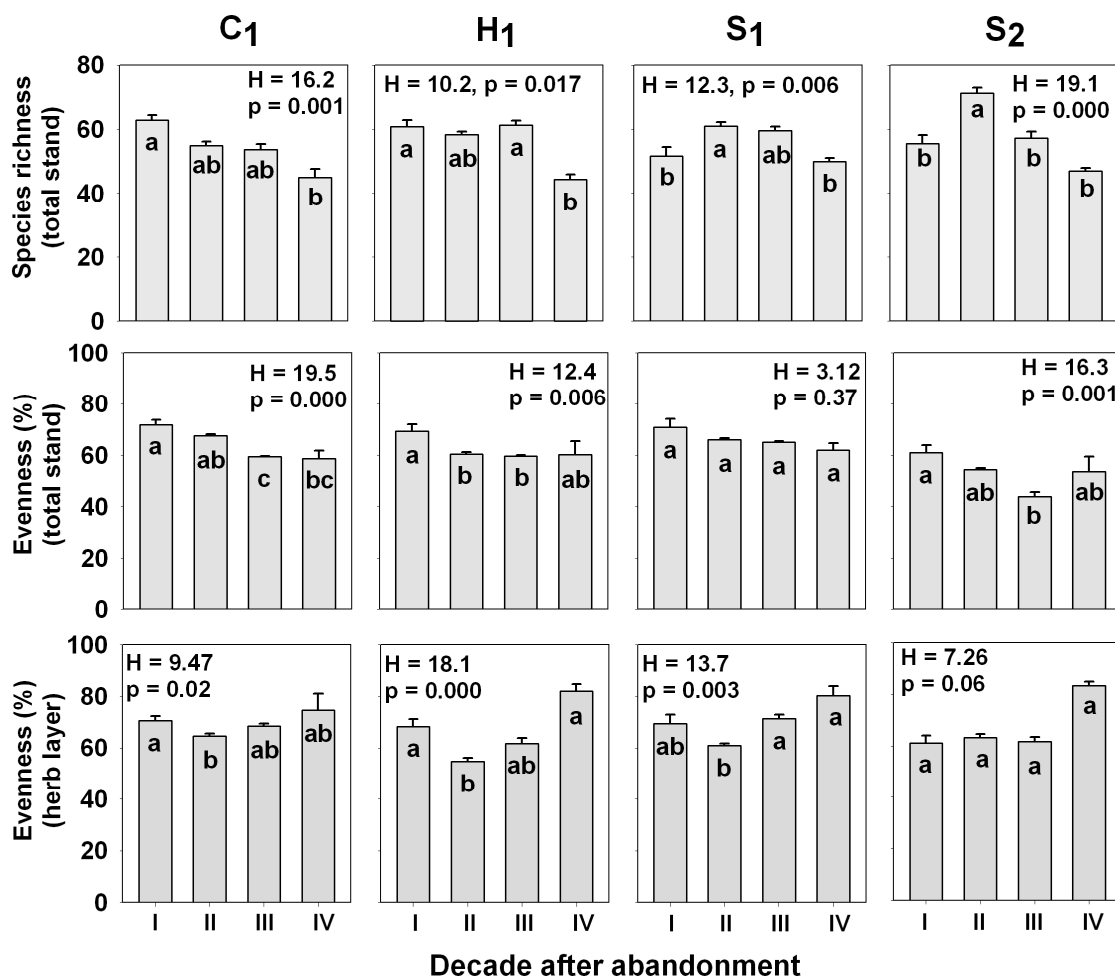


Fig. 2.3. Species richness and evenness for total stand (herb-, shrub- and tree layer) and for herb layer for each period of time for the four study plots. Means (\pm standard error) which do not share the same letter significantly differ within one diagram (Kruskal-Wallis-H-test, $p < 0.05$).

Gesamtartenzahl sowie Evenness für alle Schichten und für die Krautschicht der vier Versuchsstreifen in den vier Dekaden. Signifikante Unterschiede zwischen den Mittelwerten (\pm Standardfehler) innerhalb eines Diagramms sind durch verschiedene Kleinbuchstaben gekennzeichnet (Kruskal-Wallis-H-Test, $p < 0.05$).

2.3.3 Species characteristics

In all plots, the mean number of light demanding species that are typical to open landscapes decreased immediately after the first decade (Fig. 2.4). Today almost no open landscape species are left. The numbers and coverage of plant species growing mainly in the open landscapes but occasionally in forests also decreased, however less rapidly. Shade tolerant species predominantly growing in closed forests show a slow increase in their numbers and only contribute to a small part of total coverage. Twelve species (up to six per plot) that are predominantly growing in closed forests established themselves to date. According to ROTHMALER (2002), most of these species (*Brachypodium sylvaticum*, *Carex sylvatica*, *Daphne mezereum*, *Galium odoratum*, *G. sylvaticum*, *Lonicera xylosteum*, *Melica uniflora*, *Milium effusum*) are mainly dispersed

by animals over longer distances. Furthermore *Cephalanthera damasonium* and *Dryopteris filix-mas* as wind-dispersed species and *Campanula trachelium* and *Lathyrus vernus* with none specific dispersal vector for longer distances established.

Endangered species according to the Red List of hillsides and mountains for Lower Saxony (GARVE 2004) occurred primarily in the first and second decade. They were mainly annual weeds of arable land (Table 2.1). Four species particularly protected by law but not graded as endangered, occurred on the study site (*C. damasonium*, *D. mezereum*, *Digitalis lutea*, *Listera ovata*). They mainly appeared in the third and fourth decade.

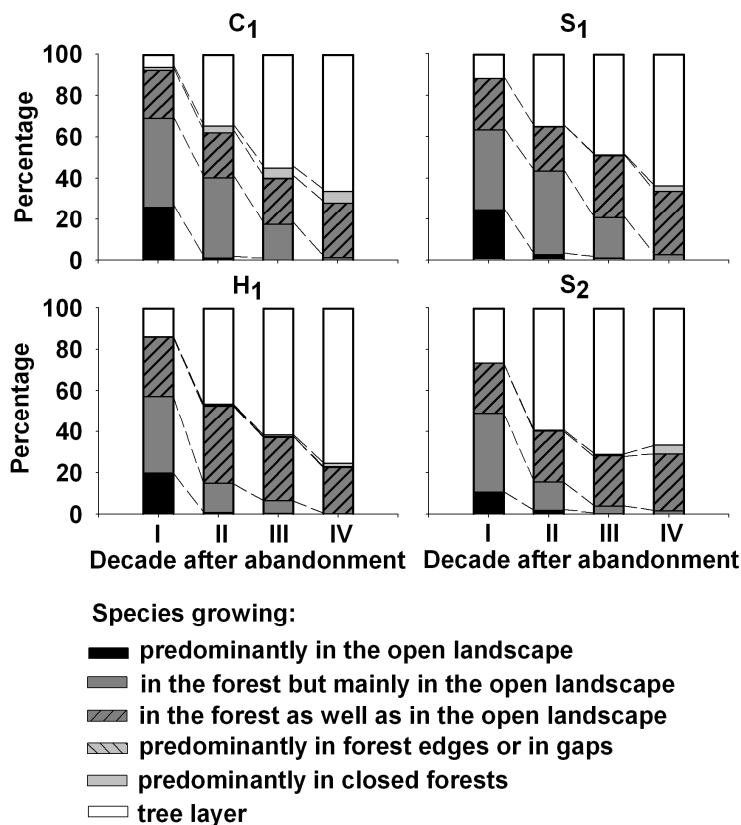


Fig. 2.4. Mean percentage of coverage of plants typical to forests and open landscapes (according to SCHMIDT *et al.* 2003) for the four study plots within the four time periods.

Prozentualer Deckungsgradanteil typischer Wald- und Offenlandarten (nach SCHMIDT *et al.* 2003) am Gesamtdeckungsgrad der Vegetation der vier Versuchsstreifen innerhalb der vier Dekaden.

Tab. 2.1. Endangered species, according to the Red List of hillsides and mountains for Lower Saxony (GARVE 2004), with degree of endangering (1=threatened with extinction, 2=highly endangered, 3=endangered, V=warning list, §=particularly protected by law, but not graded as endangered), their occurrence on the study plots during the four time periods and no. of endangered or protected and total no. of species per time period.

Gefährdete Pflanzenarten nach der Roten Liste für das Hügel- und Bergland in Niedersachsen (GARVE 2004), mit dem Grad der Gefährdung (1=vom Aussterben bedroht, 2=stark gefährdet, 3=gefährdet, V=Vorwarnliste, §=besonders geschützt, nicht eingestuft als gefährdet) und deren Vorkommen auf den Versuchsstreifen während des Sukzessionszeitraums.

	Degree of endangering	Decade			
		I	II	III	IV
Endangered species					
<i>Hieracium schultesii</i>	1	-	S ₁ , H ₁	-	-
<i>Campanula glomerata</i>	2	-	H ₁	-	-
<i>Bromus arvensis</i>	3	C ₁ , H ₁	-	-	-
<i>Cornus mas</i>	3	-	S ₁	-	-
<i>Euphrasia rostkoviana</i>	3	S ₁ , H ₁ , C ₁	C ₁ , S ₁ , H ₁ , S ₂	-	-
<i>Ranunculus nemorosus</i>	3	-	S ₂	-	-
<i>Sherardia arvensis</i>	3	C ₁ , S ₁ , S ₂	-	-	-
<i>Silene noctiflora</i>	3	C ₁ , H ₁	-	-	-
<i>Tanacetum corymbosum</i>	3	H ₁	H ₁	H ₁	-
<i>Valerianella dentata</i>	3	C ₁ , H ₁	-	-	-
<i>Euphorbia exigua</i>	V	H ₁	-	-	-
<i>Rhinanthus angustifolius</i>	V	H ₁	H ₁	-	-
<i>Verbena officinalis</i>	V	H ₁	-	-	-
Protected species					
<i>Daphne mezereum</i>	§	-	-	C ₁	C ₁ , H ₁ , S ₂
<i>Digitalis lutea</i>	§	-	H ₁	C ₁ , H ₁	H ₁
<i>Cephalanthera damasonium</i>	§	-	S ₂	S ₂	C ₁ , S ₁ , H ₁ , S ₂
<i>Listera ovata</i>	§	-	-	-	S ₁
Total number of endangered/ protected species		9/ 0	7/ 2	1/ 3	0/ 4
Total number of vascular plant species		172	154	120	94

2.4 Discussion

A fundamental vegetation change took place within the study site over the 36 years of undisturbed old-field succession. The total species richness decreased distinctly with increasing shrub and tree colonization. Such trends are well documented in various studies on abandoned grassland (e.g. SCHREIBER & SCHIEFER 1985, BAKKER 1989, POSCHLOD *et al.* 1998, DIERSCHKE 2003, PYKÄLÄ *et al.* 2005). Studies that extend beyond the first stages of succession on abandoned old-fields also confirm this trend (e.g. PICKETT 1982, INOUE *et al.* 1987, FIKE & NIERING 1999).

However, compared with similar forest stands, the species richness on our site, today ranging from 44 to 50 vascular plant species per 200 m², is still remarkably high, even if we assume an overestimation because of edge effects. DIERSCHKE (1989) gives mean species numbers in species-rich European beech forests between 21 and 32 per stand, and SCHMIDT (2005) reports on average 17 higher plant species per 314 m² in unmanaged forests on limestone (*Hordelymo-Fagetum*). The species richness reported here is also far higher than the richness found on technically afforested sites (FISCHER 1998, POSCHLOD *et al.* 1998, WISKOW 1999). FISCHER (1998) has reported for afforested (acidic, but limed) sites two years after plantation only up to 21 vascular plant species per 90 m² on control plots. WISKOW (1999) reports for nutrient-rich afforested sites one year after plantation on average 29 vascular plant species per 100 m².

A shift from pioneer to later successional tree species took place in the herb layer. Seedlings and saplings of *Betula pendula* and *Salix caprea* are now absent, whereas later successional tree species like *Carpinus betulus*, *Prunus avium*, *Quercus robur* and *Fagus sylvatica* established themselves. High seedling and sapling recruitment of *Fraxinus excelsior* in the herb and shrub layer and an increasing proportion in the tree layer indicate a future dominance of *F. excelsior*. The increasing convergence in woody species composition on the four plots leads to the assumption that there is a trend toward one terminal forest stage. All treatment plots show approximately the same trend, indicating that the initial treatment of the plots did not lead to differences in the long-term vegetation development.

The main driving force for the change in species composition might be the lower availability of light caused by increasingly closing stand canopy. PYKÄLÄ *et al.* (2005) showed that an increasing density of trees has a negative effect on total species richness, and an increase of solar radiation was positively correlated with richness variables.

The decreasing evenness for the total stands, parallel to the decreasing total species richness, confirms the assumption of decreasing species diversity with increasing tree growth. Considering only the herb layer, a tendency toward a more equally distributed community is observable with progress in time.

With progressive shrub and tree colonization, a turnover in species composition took place. Light demanding plant communities were replaced by woody vegetation. Endangered species went extinct. The slow rate of establishment of typical closed forest species on the site may be due to limited seed source in the close vicinity and especially limited dispersal vectors of these species. Various investigations showed that species richness is affected by dispersability in space and time (POSCHLOD *et al.* 1998, STAMPFLI & ZEITER 1999). Only a few forest herb species have seeds which are transported over longer distances by wind, water, or animals (BONN & POSCHLOD 1998). Therefore, dispersability seems to be a key factor limiting the colonization of forest plant species (SINGLETON *et al.* 2001, VERHEYEN & HERMY 2001, VERHEYEN *et al.* 2003). Besides seed availability, recruitment limitation might be a prime factor limiting colonization success (GRUBB 1977, MAYER 2003, ZEITER *et al.* 2006). Colonization success may be affected by the physical barrier of the litter layer or by well developed herbal vegetation, which prevents the roots of seedlings from reaching the mineral soil (VELLEND *et al.* 2000). A fast growing annual community in the first years after abandonment on the control plot (C₁) dominated by *Papaver rhoeas* inhibited the initial recruitment of tree seedlings (absence of *B. pendula*). It seems that *B. pendula* (with a large number of small and light, wind-dispersed seeds) has a very narrow "window" through which it can enter a successional system (GROSS 1980). The occurrence of the most current tree layer species on the plots, already in the first year after set-aside, supports EGLER's (1954) initial floristic composition model which suggests that many of the late-successional species may be present initially or soon after abandonment. Most plant species find optimal conditions for germination at this stage (open top-soil). The initial condition seems to be crucial for the further development of the plant community (SCHMIDT 1983) and possibly determines the future stand structure (HARD 1976). The main plant colonization window seems to be open in the early successional stage (*B. pendula*). Nevertheless, the continuous increase of cumulative species richness indicates that subsequent colonization windows are present in the later stages as well (BARTHA *et al.* 2003). Thus, the recruitment of plants may be either or both limited by the availability of seeds or suitable microsites (ERIKSSON & EHRLÉN 1992, ERIKSSON 2000, TURNBULL *et al.* 2000). Some authors (BORNKAMM & HENNIG 1982, KRUMBIEGEL *et al.* 1995, PRACH & PYŠEK 2001) state, that on eutrophic sites, only a few plant species (above all *Calamagrostis epigejos*, *S. canadensis* or *Urtica dioica*) quickly form dominant stands, which inhibit the further development of trees. Our results do not support these observations. Even on plots with well-developed perennial herb-/grassland phases, with temporary dominance of *S. canadensis*, tree growth was not restricted.

To summarize our results, even without "active intervention" former agricultural land developed into species-rich pioneer forest stands within a relative short time

period. We conclude that afforestation by planting on comparable sites is not necessary. Our results indicate that with undisturbed succession as a natural process, traditional targets of nature conservation, i.e. diversity and rarity, are not necessarily lost. The occurrence of rare plant species (endangered or especially protected by law (GARVE 2004)) and the comparatively high species richness of vascular plants throughout all time periods emphasize this conclusion. Undisturbed succession combines several advantages of the goal of multiplying forests with nature- and landscape conservational aspects. The protection of natural processes ("naturalness") (STURM 1993, PLACHTER 1996) should be an integral part of the nature conservational effort. PRACH & PYŠEK (2001) and HODAČOVÁ & PRACH (2003) emphasize that the resulting vegetation on spontaneous succession usually exhibits a higher diversity and higher natural value than the one of technically restored sites. Additionally, several problems connected with traditional plantations, like high costs and risks, are cut to a minimum (LEIBUNDGUT 1982). Spontaneous succession offers pioneer forest stands more or less free of charge and close-to-nature. Our study supports the appraisal of REIF (1997) that there are neither economical nor ecological reasons to prefer afforestation by planting over natural succession. Clearly, undisturbed succession might not be the only solution for landscape and biodiversity conservation; however we regard it as a viable alternative as a low-input management.

2.5 Abstract

This long-term permanent plot study describes the patterns and process of forest restoration by spontaneous succession on former agricultural land. In 1968, initiated by Heinz Ellenberg, an experimental study site was set up on an arable field in the New Botanical Garden of Göttingen University (Germany). At the beginning of the experiment the study plots were either sterilized by heating or by applying herbicides (to eliminate soil seed bank) or were ploughed only (soil seed bank present) and subsequently left to themselves. Species richness was continuously recorded. Density of shrub and tree species was counted 20 and 36 years after abandonment. A fundamental vegetation change took place within the study plots during the 36 years of abandonment. On all plots, undisturbed succession has lead to a change from open annual vegetation into mixed pioneer forest stands; or in other words, from a profoundly affected agricultural land-use system towards an ecosystem much more close to nature. The species-rich pioneer forests with a closed tree canopy established themselves irrespective of whether the initial soil seed bank was left intact or not. Dominant tree layer species are *Salix caprea*, *Fraxinus excelsior* and *Betula pendula*, reaching up to 22 m in height. The species-rich shrub layers cover 45 – 60 %, with *Cornus sanguinea* and *F. excelsior* being the dominant species. We determined a clear decrease in total plant species richness over time. While plant species typical to open

landscapes disappeared nearly completely, typical herb layer species to closed forests increased rather slowly during the 36 years of old-field succession.

2.6 Zusammenfassung

Titel: Veränderung der Phytodiversität während 36 Jahren ungestört ablaufender Sukzession auf Ackerbrachen

Der hier beschriebene Dauerflächenversuch wurde 1968, auf Initiative von Heinz Ellenberg, auf einem ehemaligen Acker im Neuen Botanischen Garten der Universität Göttingen (Deutschland) eingerichtet. Die ungestörte Vegetationsentwicklung (progressive Sekundärsukzession) wurde auf vier Versuchsstreifen untersucht, die sich in ihrer Behandlung zu Beginn des Experiments unterscheiden. Sie wurden entweder hitzesterilisiert oder einer Herbizidbehandlung unterzogen (Eliminierung von Vegetation und Bodensamenbank) oder nur gepflügt (Bodensamenbank ungestört) und anschließend sich selbst überlassen. Vegetationsaufnahmen (Artlisten mit Deckungsgradschätzung) liegen kontinuierlich seit Beginn des Experiments vor. Eine intensive Gehölzinventur wurde 20 und 36 Jahre nach Brachfallen durchgeführt. Wesentliches Ziel der vorliegenden Arbeit ist die Beschreibung der Entwicklung von Pflanzenartendiversität und der Dynamik sogenannter Zielarten des Naturschutzes (wie z.B. Rote-Liste-Arten und typische Offenlandarten) sowie der Vegetationsstruktur während des Beobachtungszeitraums. Auf allen Teilflächen hat die ungestörte Sekundärsukzession zu einem grundlegenden Wandel des Vegetationsbildes geführt: ein ehemals hochgradig durch die landwirtschaftliche Nutzung beeinflusstes System entwickelte sich in Richtung eines durch Naturnähe gekennzeichneten Waldökosystems. Anstelle der zu Beginn vorherrschenden Ackerunkrautgesellschaften, dominiert durch einjährige Pflanzenarten, findet man heute eine artenreiche Pionierwaldsituation vor, unabhängig davon ob zu Beginn die Bodensamenbank vorhanden war oder nicht (*Fig. 2.1*). Die dominanten Arten der Baumschicht sind *Salix caprea*, *Fraxinus excelsior* und *Betula pendula* (*Fig. 2.2*), sie bilden ein geschlossenes Kronendach und erreichen Höhen von bis zu 22 m. Die Pionierarten *S. caprea* und *B. pendula* sind aus der Verjüngung verschwunden, *F. excelsior* ist in der Kraut- und Strauchschicht die dominierende Baumart. Die Gesamtartenzahl zeigt eine deutliche Abnahme im Verlauf des Untersuchungszeitraums (*Fig. 2.3*). Typische Offenlandarten sind weitestgehend von den Flächen verschwunden, typische Arten der Krautschicht geschlossener Wälder wanderten dagegen nur sehr langsam ein (*Fig. 2.4*).

Die beschriebenen Flächen haben sich innerhalb eines relativ kurzen Zeitraumes zu artenreichen Pionierwaldsituationen entwickelt. Daher ist eine aktive Aufforstung auf vergleichbaren Flächen nicht zwingend notwendig. Wenn wesentliche Ziele der Waldvermehrung der Natur- und Landschaftsschutz sind, dann ist ungestörte Sekundärsukzession die einzig sinnvolle Alternative. Sukzession ist kostengünstig und

naturnah, ihr sollte mehr Aufmerksamkeit in der Praxis der Waldbegründung auf ehemaligen Ackerflächen geschenkt werden.

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CHAPTER 3

Changes in life history trait composition during undisturbed old-field succession

Dölle, M., Bernhardt-Römermann, M.,

Parth, A. & Schmidt, W. (2008)

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Pictures of plot L₄. Top left (1): Annual stage (1969), bottom left (2): Perennial-grassland stage (1977), top right (3): Late shrub thicket stage (1990), bottom right (4): Pioneer forest stage (2005). Photos 1-3 taken by W. Schmidt, photo 4 by M. Dölle.

3.1 Abstract

This paper describes the patterns of vegetation change by spontaneous succession on former agricultural land. In 1968, initiated by Heinz Ellenberg, an experimental study site was set up on an arable field in the new botanical garden of Göttingen University (Germany). The undisturbed successions on four plots of a long sere (since 1968/69) and on four additional plots of a shorter sere (since 1982) were evaluated. The seres were classified into stages by cluster analysis, which yielded to four subsequent stages for the long sere and to three subsequent stages for the short sere. The early succession is characterized by a high proportion of species invasion, whereas with developing time species extinction increased. On all study plots undisturbed succession directed to the development of pioneer forests. Altogether 247 vascular plant species were recorded. The total species richness shows a fluctuating course during the successional seres, with a significantly increased numbers shortly after succession has started and a decline in the pioneer-forest stage, when stands age and close down. The primary aim was to compare the characteristics (particular traits) of species occurring at different stages of succession. The majority of the traits concerned exhibited some clear trends in the course of succession. Exclusive reproduction by seeds decreased and the ability for additional vegetative reproduction increased. Anemochorus dispersal significantly decreased, whereas the importance of dispersal by animals, especially endochorus, dominates in the pioneer-forest stage. The mean seed weight significantly increased. During early succession, plant species staying green over winter dominated, but are of none relevance in the pioneer-forest stage, where summergreen plant species dominates. The change in strategy type features a significant increase of competitive species. The mean indicator value for light in the herb layer decreased significantly in the pioneer-forest stage.

Key words: abandoned field, life history traits, long-term study, permanent plots

3.2 Introduction

During the last decades, much attention has been paid to changes in vegetation composition, including the development of general concepts of succession (e.g. Clements, 1928; Gleason, 1939; Egler, 1954; Connell and Slayter, 1977; Tilman, 1985). Vegetation development following agricultural abandonment has been studied primarily by comparing fields in various successional stages (Bard, 1952; Pickett, 1982; Vankat and Carson, 1991). Nevertheless, a confirmation of these results by using data from long-term permanent plot studies is strongly recommended (e.g. Bakker et al., 1996; Prach, 1990; Rosenthal and Müller, 2005; Bornkamm, 2007). The overall goal should be to provide a basis for a more comprehensive understanding of the basic patterns of successional processes (McCook, 1994). Various investigations showed that the complexity of undisturbed succession following agricultural abandonment makes a general prediction on how succession proceeds difficult (Pickett, 1982; Schreiber, 1995; Fike and Niering, 1999). In case of the undisturbed vegetation development after abandonment only a few permanent plot studies are available that offer continuous datasets over more than 15 years (e.g. Pickett, 1982; Schreiber and Schiefer, 1985; Bornkamm, 2006; Dierschke, 2006).

In theory, a succession on former arable land starts with the dominance of annuals and perennial ruderals rapidly replaced by common perennial grasses and forb species (Brown and Southwood, 1987; Schmidt, 1993). In temperate zones, succession is strongly dependent on various local factors, like seed rain (distance effects) or soil seed bank (soil disturbance effects), and usually culminates in forest vegetation as climax state (Ellenberg, 1996). One main objective of the present permanent plot study is to analyse the dynamics of the vegetation change during the successional seres of up to 36 years. This is, up to our knowledge, the longest direct report on undisturbed old-field succession in Germany. Europe-wide only very few studies (e.g. Osbornová et al., 1990; Debussche et al., 1996; Harmer et al., 2001) analyse comparable long-term observations on old-field succession. From the north-eastern states of the USA, some additional studies on old-field succession are known (Buell et al., 1971; Pickett, 1982; Myster, 1993). A common goal of all these studies is to enlarge our knowledge on patterns and processes of successional vegetation dynamics (Glenn-Lewin et al., 1992). Considering that individual successional processes appear to be unique and strongly dependent on initial conditions, like starting time or the surrounding vegetation, any generalisation should be deduced from numerous studies (Sousa, 1984; Glenn-Lewin et al., 1992; McCook, 1994). Furthermore, the identification of the life histories of the plant species involved may be useful to understand the processes of succession (Drury and Nisbet, 1973; Pickett, 1976; Walker and Chapin, 1987). Species can invade the system and become dominant in dependence of their specific trait composition. During succession, the life history trait

composition of the whole community may change (Noble and Slatyer, 1980; Huston and Smith, 1987; Walker and Chapin, 1987; Brown, 1992; Glenn-Lewin and van der Maarel, 1992; Prach et al., 1997). Going along with changes in the resident community, the requirements of potential invaders concerning for example establishment, colonisation and persistence patterns, must be seen as being dynamic during the processes (van der Valk, 1992).

With focus on a descriptive approach, the main objectives of the current study on dynamics of plant species composition during undisturbed old-field succession are: (1) The identification of a successional pathway characterised by a sequence of different stages and (2) the estimation of different aspects of life history trait composition during ecosystem development. Winners and loser of the successional process should be identified to find main attributes of the different stages.

3.3 Material and methods

3.3.1 Study site

All plots of the current study are part of an experiment located in the New Botanical Garden of Göttingen University, Lower Saxony, Germany (180 m a.s.l., 51°34'0"N, 9°56'60"E; mean annual temperature: 8.5°C; average annual rainfall: 635 mm). Initiated by Heinz Ellenberg, the experiment was set up on a former arable field cultivated until 1968 on deep, calcareous and fertile soil (alluvial loamy brown earth). Regional forest vegetation is dominated by *Fagus sylvatica* (Fagion sylvaticae) which is the natural vegetation type (Bohn and Neuhausl, 2003). The surrounding landscape may be characterised by a mixture of arable fields, grasslands, ruderal communities, and forests with a high diversity in mature trees as potential seed dispenser in close vicinity. A more detailed description of the study site and methods is given in Schmidt (1981, 1983, 1993).

Altogether 175 relevées from eight permanent plots were evaluated: Four plots of undisturbed succession since 1968/69 (L_1 , L_2 , L_3 , L_4) and four plots of undisturbed succession since 1982 (S_1 , S_2 , S_3 , S_4), herein after referred to as short (S_{1-4}) and long term sere (L_{1-4}). For vegetation sampling the plots are each subdivided into subplots. The entire study site was farmed as crop field up to and including 1967, so that the long term sere meets accurately the particular conditions of an abandoned agricultural field. The history of the short term sere differed by experimental treatment with one-time soil disturbance per year up to and including 1982. Despite from the comparable site conditions the plots differ in their treatment in the beginning of the experiment (1968): ploughing (L_4 , S_3 , S_4), herbicide treatment (L_3 , S_1 , S_2) or sterilised by heating (L_1 , L_2) (Schmidt, 1981). Considering the species composition of the plots only, an influence of different treatments at the beginning of the experiment is clearly noticeable (Schmidt, 1981, 1983, 1993). Nevertheless, as the evaluation of the

ecosystem function is described by traits only, not by species, it shall be possible to discuss general comparisons between the different treatments.

3.3.2 Data evaluation

Vegetation relevés, including records of the percentage cover of all vascular plant species were conducted twice per year in the beginning (1969-1987) and once per year since trees have started to dominate. From 1968 until 1993 vegetation was recorded annually, afterwards vegetation relevés were conducted in 1995, 1999, 2004 and 2005. Species names for vascular plants follow Wisskirchen and Haeupler (1998). The continuous change of the successional seres was classified into stages based on a cluster analysis separately for the long (L_{1-4}) and the short term (S_{1-4}) seres. To describe the dynamics of the vegetation changes for each single species, the turnover from stage to stage has been characterised by the following classification:

- (-2) extinction of species: present in <1% of the relevés of the subsequent stage;
- (-1) decreasing species: decrease of >40% in presence;
- (0) stable species: decrease or increase in presence of the relevés <40%;
- (+1) increasing species: increase of >40% in presence;
- (+2) invasion of species, newcomer: present in >1% of the relevés of the subsequent stage, no occurrence in the preceding stage. For each species a mean value for frequency and coverage per stage was estimated. The calculation of the change in species composition from one to the following stage was calculated using the mean frequency per stage.

For further evaluation of the vegetation development, the successional seres of the eight permanent plots were estimated together by using the yearly means for each single species. Species richness and evenness of the herb layer were calculated as parameters for diversity. For the functional characterisation of vegetation changes, selected plant traits regarding morphology (leaf anatomy, leaf persistence; Klotz et al. (2002)), as well as propagation characteristics (type of reproduction; Klotz et al. (2002), seed weight, seed dispersal; Flynn et al. (2006) were evaluated for all vegetation layers. Furthermore, life strategy (Klotz et al., 2002) and Ellenberg's indicator value for light were considered (Ellenberg et al., 2001). If ecosystem functioning was of main interest, analyses were done with weighted data (weighted by coverage) for leaf persistence, leaf anatomy, strategy type and indicator value for light. If priority was set on species diversity aspects, only presence-absence of the species was used; this approach was applied for type of reproduction, dispersal type and seed weight. For diversity aspects, an unweighted evaluation seems to be more reasonable because it stresses the recruitment success of the species and not of the composition of the plant community.

The classification of the vegetation data into stages results in a cluster analysis (Distance Measure: Bray-Curtis, Group linkage: Group Average). Based on the cover values, the response of all plots was estimated by an ordination (DCA- Detrended Correspondence Analysis) using the program PC Ord 5.02 (McCune and Mefford, 1999). Since the coverage of a species is not only dependent on the site conditions but might be a specific characteristic of a certain species, the data were transformed by $y = x^{0.25}$ to minimise differences in coverage.

3.3.3 Statistical analysis

All plant traits were tested for significant differences between the different successional stages. For all normally distributed data with homogeneous variances, parameters were tested for differences by one factorial ANOVA with subsequent post-hoc Tukey-test. If the criteria of homogenous variances were not met, the Dunnett T3-test was used as post-hoc-test. Data showing neither normal distribution nor homogeneous variances were compared by Kruskal-Wallis-H-test with subsequent Mann-Whitney-U-test. For all statistical tests, SPSS 12.5 (SPSS Inc.) was used. For all statistics the following significance levels were used: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = not significant ($p \geq 0.05$).

Table 3.1. Pathway of the development of abandoned old-fields on permanent plots in the Experimental Botanical Garden, University of Göttingen.

	I	II	III	IV
Stage	Annual	Perennial-Grassland	Shrub	Pioneer-Forest
Characteristics	Dominated by therophytes	Dominated by perennial herbs and grasses	Increasing dominance of shrub layer	Dominated by Trees
Duration, long series	1 to 2 yrs	3 to 8 yrs	10 to 14 yrs	after about 20 yrs of succession up to now
Duration, short series	Missing	2 to 3 yrs	9 to 11 yrs	after about 17 yrs of succession up to now

3.4 Results

3.4.1 Vegetation development during succession

The classification of the relevés into stages by cluster analysis leads to a pathway divided into three and four consecutive stages respectively (Fig. 3.1, Tab. 3.1). For the short term sere (S_{1-4}) the pathway consists of three, for the long term sere (L_{1-4}) of four subsequent stages. The difference between the two sere types is the lack of the annual stage (Tab. 3.1) on the plots of the short term sere. The plots of the long term sere stayed in the perennial-grassland stage for at least four years. In contrast, the

plots of the short term sere reach the third stage (shrub) within two or at most three years. The ordination in Fig. 3.1 shows a clear arrow-shaped arrangement of the vegetation relevés. The first axis is positively correlated with the time since abandonment (time: $r^2 = 0.81^{***}$), the cover of shrub ($r^2 = 0.63^{***}$) and tree layer ($r^2 = 0.71^{***}$) as well as the number of shrub ($r^2 = 0.93^{***}$) and tree species ($r^2 = 0.69^{***}$). The cover of therophytes ($r^2 = 0.67^{***}$) shows a negative correlation. The starting points of undisturbed succession of the eight different plots show a wide scattered distribution along the second axis. With progress in time, all plots converged to the more homogeneous structured pioneer forest stage.

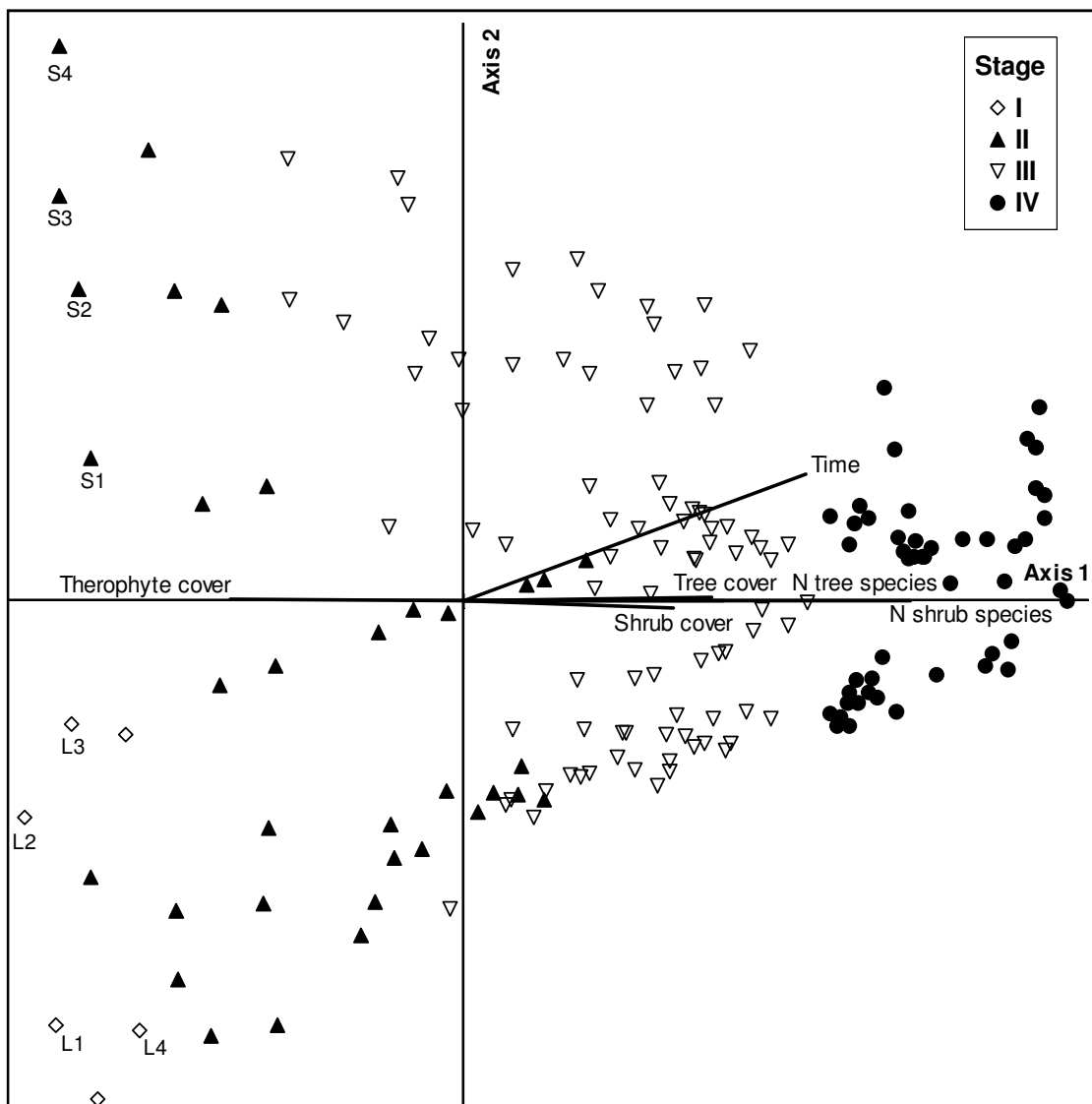


Fig. 3.1. DCA of the relevés of the eight permanent plots of undisturbed old field succession. The ordination was done with 294 species (all layers) and 175 relevés (axis 1 $r^2 = 0.77$, axis 2 $r^2 = 0.07$). To present a bi-plot, different environmental parameters were correlated with the axes of the ordination (correlation threshold: $r > 0.6$). The classification into the four groups results from a cluster analysis of the vegetation data (distance measure: Bray-Curtis, group linkage: group average). Initial situation is indicated by plot labels.

3.4.2 Vegetation dynamics and diversity

In total 247 vascular plant species were recorded on the eight study plots (stage I: 90 species, stage II: 174 species, stage III: 184 species, stage IV: 139 species). The amount of species that invaded the plots (newcomers) is highest in the transition from the annual stage to the perennial-grassland stage (Fig. 3.2). Species extinction is highest in the transition from the shrub stage to the pioneer forest stage. Species which show an increasing rate were less abundant in the first transition than in the transition from perennial-grassland to shrub stage and to pioneer-forest stage. A similar trend was given for the decreasing species.

Diversity fluctuates during succession. There was a significant increase in total plant species richness from the first to the second stage (Fig. 3.3), followed by a phase of stability until it decreased significantly from the third to the fourth stage to the initial level. The evenness of the herb layer shows almost the opposite trend (Fig. 3.3). Plots show highest evenness of the herb layer species in the first stage and lowest in the third.

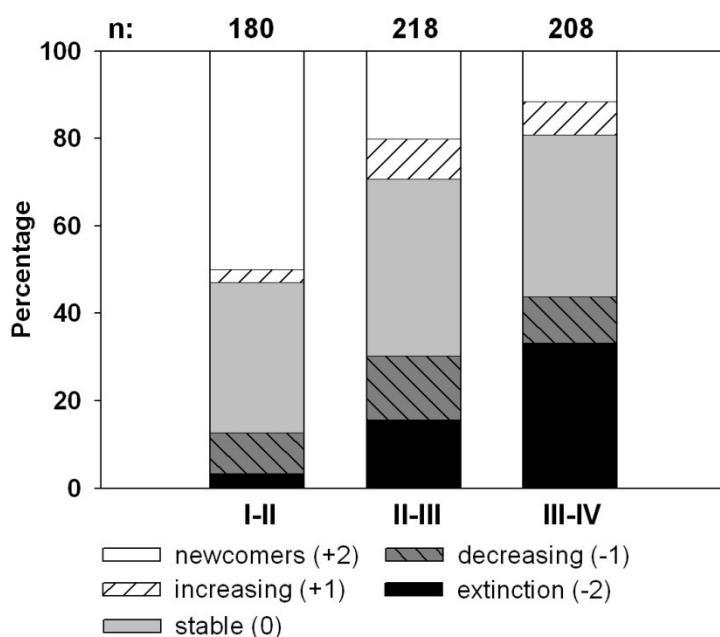


Fig. 3.2. Dynamic of the vegetation change at the transition of the four successional stages (n= cumulative number of species of the two consecutive stages).

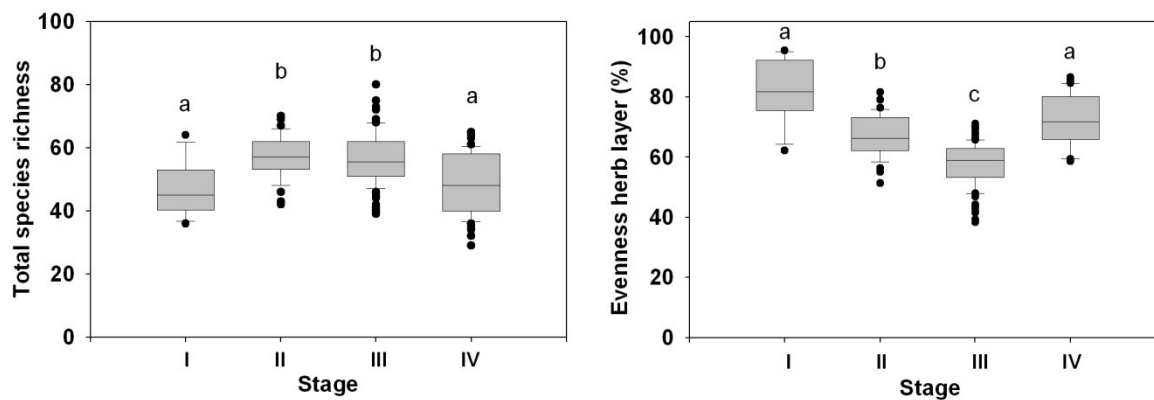


Fig. 3.3. Box-Whisker-Plots of total species richness and herb layer evenness in the four stages during old-field succession. Bars which do not share the same letters differ significantly between stages.

3.4.3 Functional and ecological description of the vegetation change

The annual stage was dominated by species that reproduce exclusively or mostly by seeds (65 % of all occurring species). This percentage decreased significantly during time to a level of 40 % in the pioneer forest stage (Fig. 3.4). Species, which reproduce by seeds and vegetative to the same part showed a slight increase, as well as species which reproduce rarely vegetative and mainly by seeds. Mainly vegetative reproduction was of none importance to any time of the successional seres.

Wind was the most important dispersal factor in the annual stage and decreased continuously during time. Endochore dispersal was initially very low (3 %), but showed a continuously increasing rate up to 30 % in the pioneer forest stage. The mean seed weight of the occurring plant species shows a continuously increasing rate throughout all stages (Fig. 3.5).

The leaf persistence as a plant trait to characterise changes in plant morphology indicates that summergreen species increase significantly with time (Fig. 3.4). From about 40 % in the annual stage their percentage increased to more than 90 % of the total vegetation cover in the pioneer forest stage. In contrast, plant species with leaves staying green over the cold season showed a significant decrease during time, and were in the annual stage of major importance. Persistent green plant species were only typical for the perennial-grassland stage with about 25 %, and decreased afterwards to an amount of 5 % in the pioneer forest stage.

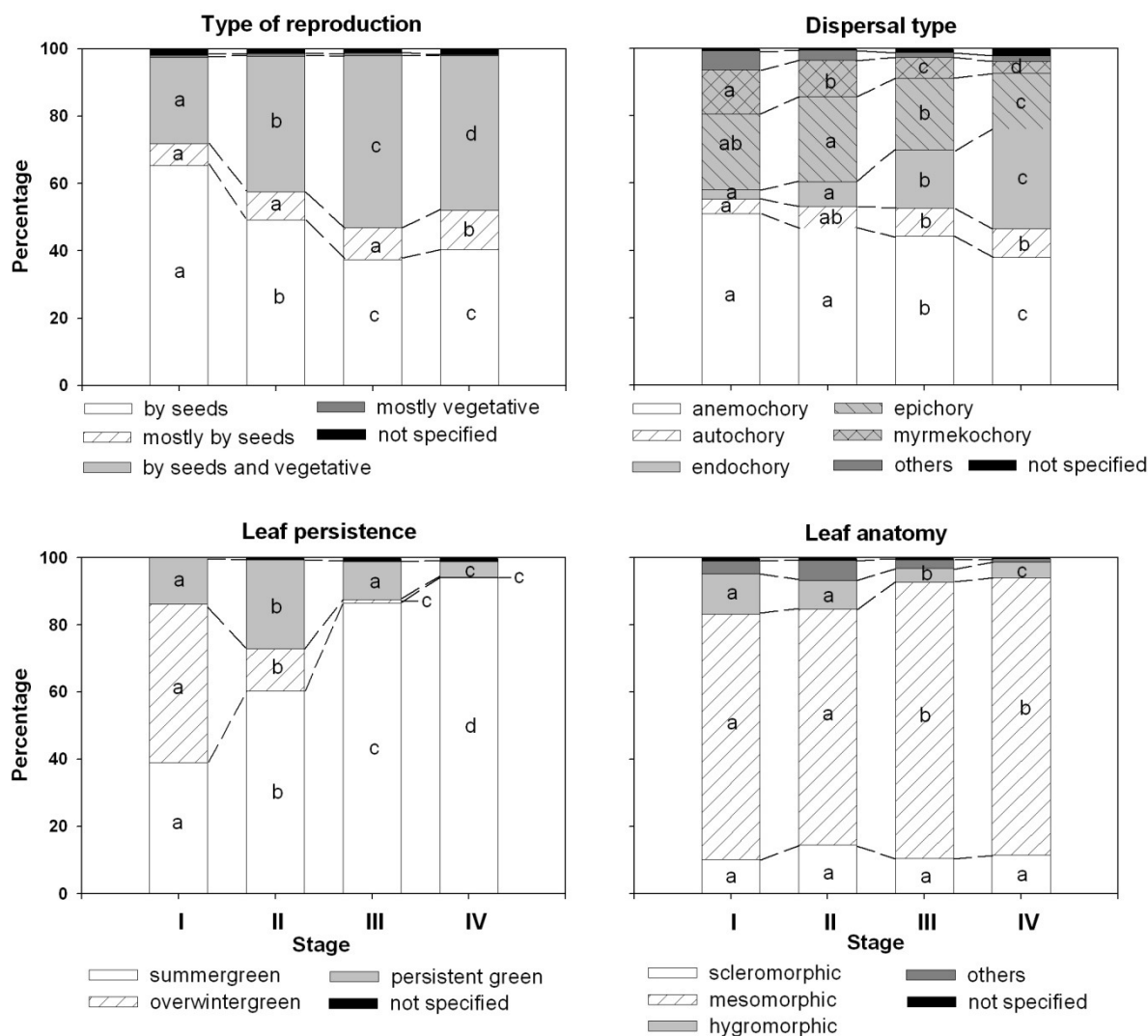


Fig. 3.4. Changes in type of reproduction, type of seed dispersal, leaf persistence and leaf anatomy of all plant species occurring during the four stages of old-field succession. Letters indicate significant differences among the stages for a given category.

The proportion of hygromorphic species (plants of shade and semi-shade) showed a decreasing rate over time. Mesomorphic plants (between scleromorphic and hygromorphic) held with more than 70 % always the highest proportion of the total coverage and showed a slightly increasing rate during time. Scleromorphic plant species (plants with firm and stiff leaves with thickened epidermis and cuticulae and mechanisms to promote water transport under bad conditions) were with about 10 % at all stages of lower importance; except in the perennial-grassland stage when they increased to almost 15 % of the total coverage.

Looking at Grimes strategies, the annual stage was dominated by ruderals and competitive species (Fig. 3.6). The ruderals showed a significant decrease during succession and have no relevance anymore in the pioneer forest stage. Competitive species showed the opposite trend with a clear increasing rate from almost 45 % in

the annual stage to 95 % in the pioneer forest stage. Stress tolerators reached in the perennial-grassland stage their highest proportion, but all in all they were of minor importance.

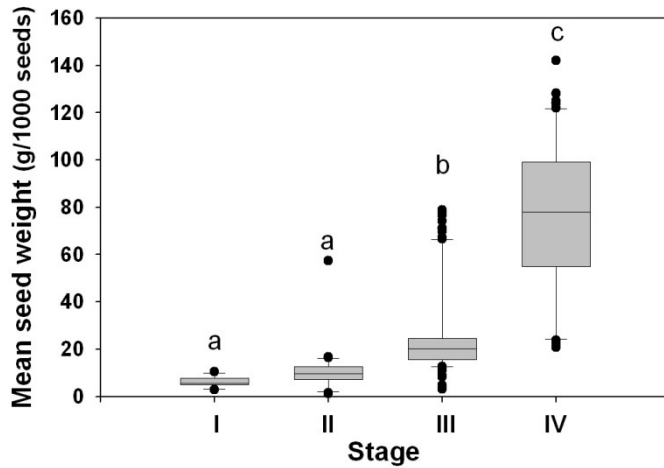


Fig. 3.5. Box-Whisker-Plots of the changes in mean seed weight of occurring plant species during the four stages of old-field succession. Letters indicate significant differences among the stages.

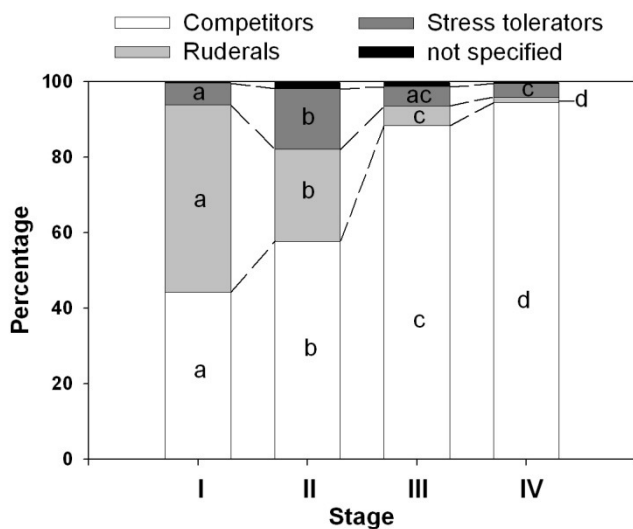


Fig. 3.6. Change in strategy type according to Grime (1979) of all plant species occurring during the four stages of old-field succession, letters indicate significant differences among the stages for a given category.

The mean Ellenberg indicator value for light for the herb layer showed a significant decrease from the shrub to the pioneer forest stage. But with a mean of 6.3 in the pioneer forest stage the values were still in the range of “half-light” to “half-shade” plants (Fig. 3.7). Light demanding species of early successional stages were still present as scattered individuals on the plots. However, the closed canopy of the pioneer forest, together with dense shrub layers reduce the light availability on the ground to a minimum, so that light demanding species of open landscapes start to vanish (time-delayed reaction).

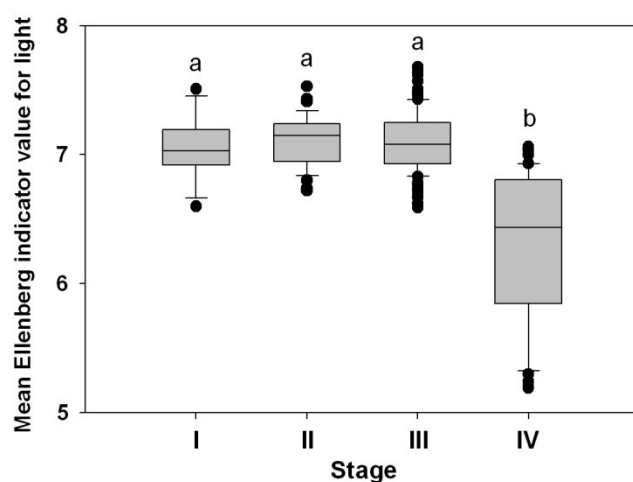


Fig. 3.7. Box-Whisker-Plots of the change in mean Ellenberg's indicator values for light for the herb layer during the four stages of old-field succession, letters indicate significant differences among the four stages.

3.5 Discussion

The arrow-shaped arrangement of the relevées in the ordination diagram shows that the floristic composition of the plant community becomes more similar with time. Our findings support Peet's (1992) restatement of the Clementsian model (Clements, 1928), that the differentiation between climax types in a region should be less than that among earlier successional stages. Therefore complete convergence is unlikely. Similar patterns of high variability in early succession and a decline with successional development in old-field succession are to be found at Inouye et al. (1987) and Myster and Pickett (1990). However, this great variability of early successional situations as obvious in our case highlights the individualistic nature of vegetation change (Gleason, 1927; Glenn-Lewin, 1980; Pickett, 1983). It points out as well that succession is fundamentally a stochastic process, highly dependent upon local conditions and chance (Botkin, 1981).

Our findings indicate that the plant community of the annual stage is a highly unstable situation which survival is strongly dependent on a periodical disturbance. In this case it is given by a yearly agricultural treatment with intensive soil perturbation as disturbance measure. The short term sere did not meet the conditions of the defined annual stage at the time of abandonment; the annual stage exist only for a very short time after abandonment and already passed when the first vegetation sampling was applied. Additionally the applied experimental treatment before succession initiated, with soil disturbance only once a year, was less intensive than arable farming. Furthermore, the short term sere passed more rapidly through the perennial-grassland stage and thus arrived much quicker at the shrub stage as well as at the pioneer forest stage. Possibly seed rain and vegetative invasion from the adjacent plots of the long term sere accelerated the process. Bringing together, the development of the two seres seems comparable in case of floristic composition and functional characterisation, even if the duration of the stages is different. A high variability of similar successional stages is discussed in Dierschke (2006). Similar to our findings, the first stages were described as very temporary, whereas later stages can continue for several decades.

The strongly increased extinction rate in the transition from shrub to pioneer-forest stage and the relatively high percentage of early successional species in the pioneer-forest, indicate a still high dynamical situation. The preponderance of species invasion from the annual to the perennial-grassland stage seems to be not in agreement with Huston and Smith (1987). They mention species replacement as of high importance and more rapidly in early than in late succession. Only if the above presented successional seres are altogether considered as an early successional situation, or at maximum in a change over to mid-succession, than a rough balance between invasion and extinction can be found. However, species extinction and invasion are at no time

really balanced. There is rather a paradigm shift from a prevail in immigration at the beginning toward extinction today. Numerous early successional species were able to survive, probably as feeble and sterile individuals until the shrub stage (e.g. *Arenaria serpyllifolia*, *Myosotis arvensis*). They are even present through the pioneer forest stage as the stands have aged and closed (e.g. *Cirsium arvense*, *Equisetum arvense*). The percentage of newcomers decreased to about 10 % from shrub to pioneer-forest stage. Immigration processes during the early stages of succession and an increase in extinction processes later on are of high importance (Bonet and Pausas, 2004; Harmer et al., 2001). Furthermore, in theory typical late successional species show low immigration rates throughout limited dispersal vectors (Bonn and Poschlod, 1998; Verheyen and Hermy, 2001). Thus an increasing proportion of species immigration in the future is unlikely. If the remnants of typical open landscape species will disappear, a further decrease in total species richness with progress in time can be expected.

Similar patterns of fluctuating species diversity as observed were found in a number of successional studies (Habeck, 1968; Peet, 1978; Bonet and Pausas, 2004). The early peak in species richness can be explained by the coexistence of annual and biennial species, perennial forbs, grasses and woody species in the perennial-grassland and later stages. The property of prolonged coexistence in mid-succession is a widely observed feature of natural succession (Huston and Smith, 1987). With developing time the initially dominating species groups start to vanish. The concept of initial floristic composition of Egler (1954) suggests the colonisation of early and late successional species in initial stages. The today on our plots dominating tree species, above all *Betula pendula*, *Salix caprea* and *Fraxinus excelsior* already germinated in the first year of abandonment and thus affirm this theory. Lower evenness values in the perennial-grassland and shrub stage indicate that at this point some species could attain dominance. Several studies on abandoned agricultural fields confirm this observation, especially in productive environments (Hard, 1976; Krumbiegel et al., 1995; Prach and Pyšek, 2001; Grabow and Manthey, 2002; Bornkamm, 2007). Above all *Calamagrostis epigejos*, *Elymus repens*, *Solidago canadensis* and *Urtica dioica* are referred to as species which quickly form dominant stands. They may remain stable for many years and are able to inhibit the further development of woody species. These highly competitive species, the so-called "superspecies" (Huston and Smith, 1987), do not follow the usual terms of being early- or late successional (Prach and Pyšek, 2001). They often produce large numbers of easily dispersed seeds and have the ability for rapid vegetative spread. In this study only temporary dominance of *S. canadensis* and *C. epigejos* occurred (see similarly to Bornkamm, 2007), but they could not pose a threat to the establishment and successful competition of woody species.

To get a closer view on the processes of vegetation development during succession, a functional trait approach was applied. However, many of the estimated traits show clear response to successional stages. Looking at the dispersal type, an increase in the rate of animal dispersal was observed, whereas anemochory became less important (Bard, 1952; Hodgson and Grime, 1990; Rydin and Borgegård, 1991). The increase in endochory dispersal (which is mainly ornithochory) with increasing successional age as observed, can be seen as a function of the physical structure of the vegetation. As plants get older and taller, bird use increases because plants provide fleshy fruits and perching sites (McDonnell and Stiles, 1983; Dzwonko and Loster, 1992; Bazzaz, 1996; Debussche et al., 2001). Regarding phanerophytes the first colonising species (*B. pendula*, *S. caprea*) were light seeded and wind dispersed, followed by species like *Acer platanoides*, *A. pseudoplatanus* and *F. excelsior* as wind-dispersed species with heavier seeds. Most animal dispersed species are heavy seeded (*Daphne mezereum*, *Fagus sylvatica*, *Sorbus aria*, *Viburnum lantana*, *V. opulus*) and arrived late in succession, so that seed weight increases during succession. All of the observed phanerophyte species were common part of the surrounding vegetation (Schmidt, 1981; 1983). Thus, the availability of seed dispenser in the close vicinity of the study site probably accelerated the process of tree and shrub invasion.

The leaf persistence mainly determines primary production (photosynthetic rate) and thus the competitive ability of a plant species. It is strongly correlated with the life cycle and potential age of a certain plant species (Schulze et al., 2002). Summergreen species become dominant at the pioneer forest stage, being mainly perennial herbs, deciduous shrubs and tree species. As annual species dominating in early succession, they are to a high amount staying green over winter (winter annuals: e.g. *A. serpyllifolia*, *M. arvensis*, *Poa annua*, *Sinapis arvensis*, *Veronica spec.* and *Viola arvensis*). With short life cycle and low competitive ability (e.g. no clonal growth) they very quickly decrease in dominance with ongoing succession (Fenner, 1987; Huston and Smith, 1987), underline the increase of c- and decrease of r-strategists (Horn, 1981; Burrows, 1990; Prach et al., 1997; Prach and Pyšek, 1999). In case of the leaf anatomy as parameter reflecting general adaptation on particular ecological conditions, mainly of water and gas flow of a certain plant species, there is only a weak trend distinguishable. Hygromorphic plants show a slight decrease in dominance during time, in theory an increase has to be expected since it is a characteristic of "shade" to "half-shade" plants (Schulze et al., 2002). Hence, it is not surprising that under the given beneficial conditions on the study site (e.g. balanced water supply) mesomorphic plant species are dominating. The mean Ellenberg indicator value for light reflects an increase in shade tolerance during succession as an effect of the closing canopy. The lower availability of light with increasing shrub and tree growth

might be the main driving force for the change in species composition (Pykälä et al., 2005).

3.6 Conclusion

A fundamental vegetation change took place within the study plots within relatively short time periods. On all plots, undisturbed succession has lead to a change from open annual or perennial vegetation into mixed pioneer forest stands; or in other words, from a profoundly affected agricultural land-use system towards an ecosystem much more close to nature. The study shows that on the same site, on plots with different initial conditions different pathways may occur, but that they obviously converge with progress in time. Our conclusion supports that species colonisation on a certain site is dependent of plant life history traits and there are some features contributing to the chance of a species to become a dominant (Prach and Pyšek, 1999). The results indicate that the characteristics of early successional and late successional species can be reasonably explained by their life history and physiological characteristics (Bazzaz, 1975; Huston and Smith, 1987). Most of the plant traits considered in this study are clearly associated with life form as well as life strategy as schemes summarizing biological and ecological traits (Prach and Pyšek, 1999).

Table 3.2. Mean coverage (means < 0.1% = +), frequency and transition status of all species with > 5 % frequency during the four stages of old-field succession.

	Mean cover (%)				Frequency (%)				Transition		
	I	II	III	IV	I	II	III	IV	I to II	II to III	III to IV
<i>Solidago canadensis</i>	0.8	8.6	26.2	3.3	100	100	100	94	0	0	0
<i>Tussilago farfara</i>	2.1	5.3	1.7	+	100	100	100	63	0	0	0
<i>Cirsium arvense</i>	1.4	2.5	0.7	+	100	100	97	31	0	0	-1
<i>Taraxacum officinale</i>	1.1	4.9	1.3	0.1	100	100	91	58	0	0	0
<i>Epilobium tetragonum</i>	0.6	1.6	0.6	+	100	91	88	6	0	0	-1
<i>Myosotis arvensis</i>	0.6	0.5	+		100	89	37		0	0	-2
<i>Viola arvensis</i>	1.1	0.5	+		100	74	6		0	-1	-2
<i>Plantago major</i>	0.5	0.2	+		100	71	19		0	-1	-2
<i>Arenaria serpyllifolia</i>	1.2	1.7	+		100	71	7		0	-1	-2
<i>Sonchus asper</i>	1.0	1.5	+		100	60	7		0	-1	-2
<i>Papaver rhoeas</i>	4.7	0.9	+	+	100	57	2	2	0	-1	0
<i>Conyza canadensis</i>	2.9	0.9	+		100	54	5		0	-1	-2
<i>Poa annua</i>	0.5	0.2			100	49			0	-2	
<i>Fallopia convolvulus</i>	0.4	0.1	+	+	100	34	2	2	-1	-1	0
<i>Senecio vulgaris</i>	1.5	0.2	+		100	29	6		-1	-1	-2
<i>Atriplex patula</i>	0.7	+			100	29			-1	-2	
<i>Capsella bursa-pastoris</i>	1.4	0.1			100	23			-1	-2	
<i>Chenopodium album</i>	0.8	+			100	23			-1	-2	
<i>Sonchus oleraceus</i>	0.3	+			100	20			-1	-2	
<i>Fraxinus excelsior</i>	0.4	1.3	11.8	31.9	86	89	100	100	0	0	0
<i>Epilobium ciliatum</i>	0.5	1.2	+		86	83	56		0	0	-2
<i>Epilobium parviflorum</i>	0.3	1.2	+		86	71	41		0	0	-2
<i>Tripleurosp. perforatum</i>	0.5	0.2	+		86	71	3		0	-1	-2
<i>Galium aparine</i>	1.3	0.2	+	+	86	60	29	65	0	0	0
<i>Chaenorhinum minus</i>	0.6	+	+		86	26	1		-1	-1	-2
<i>Veronica polita</i>	0.2	+			86	26			-1	-2	
<i>Stellaria media</i>	0.8	+			86	17			-1	-2	
<i>Poa trivialis</i>	0.5	5.7	4.1	+	71	100	100	63	0	0	0
<i>Picris hieracioides</i>	0.1	5.2	1.1	+	71	97	78	2	0	0	-1
<i>Equisetum arvense</i>	0.3	0.3	1.3	0.3	71	91	100	94	0	0	0
<i>Epilobium angustifolium</i>	0.7	1.5	1.1	1.2	71	86	74	67	0	0	0
<i>Salix caprea</i>	0.1	2.1	14.1	26.8	71	80	86	100	0	0	0
<i>Alchemilla vulgaris</i>	0.3	+	+	+	71	51	12	2	0	-1	-1
<i>Matricaria discoidea</i>	0.2	+			71	11			-1	-2	
<i>Cirsium vulgare</i>	0.1	0.3	+	+	57	89	34	2	0	-1	-1
<i>Acer platanoides</i>	+	+	0.8	4.8	57	69	91	100	0	0	0
<i>Betula pendula</i>	0.1	1.1	9.8	22.3	57	51	74	75	0	0	0
<i>Sambucus nigra</i>	+	+	+	0.2	57	37	13	23	0	-1	0
<i>Sinapis arvensis</i>	0.5	1.3	+		57	31	9		0	-1	-2
<i>Polygonum aviculare</i>	0.2	+			57	14			-1	-2	
<i>Persicaria minor</i>	0.1	+			57	9			-1	-2	
<i>Dactylis glomerata</i>	+	0.6	3.4	1.2	43	89	100	100	0	0	0
<i>Clematis vitalba</i>	+	0.5	4.0	5.5	43	80	100	100	0	0	0
<i>Epilobium hirsutum</i>	0.3	0.3	+		43	63	30		0	0	-2
<i>Stachys palustris</i>	0.2	0.2	0.1	+	43	51	47	6	0	0	-1
<i>Aethusa cynapium</i>	0.3	0.1	+		43	43	2		0	-1	-2
<i>Elymus repens</i>	0.1	1.4	0.6	+	43	34	21	8	0	0	-1
<i>Veronica persica</i>	+	1.5	+		43	34	15		0	0	-2
<i>Sherardia arvensis</i>	+	+	+		43	34	1		0	-1	-2
<i>Lactuca serriola</i>	0.5	0.2			43	34			0	-2	
<i>Thlaspi arvense</i>	+	+			43	11			-1	-2	
<i>Crepis biennis</i>	+	0.2	+	+	29	69	69	6	0	0	-1
<i>Agrostis stolonifera</i>	+	0.6	1.3	+	29	69	49	4	0	0	-1
<i>Phleum pratense</i>	+	0.1	+	+	29	66	27	13	0	0	0
<i>Calamagrostis epigejos</i>	+	1.6	10.3	4.4	29	63	95	96	0	0	0
<i>Senecio jacobaea</i>	+	0.1	+	+	29	57	67	23	0	0	-1
<i>Ranunculus repens</i>	0.1	3.8	1.0	+	29	51	62	2	0	0	-1
<i>Urtica dioica</i>	+	+	0.1	+	29	46	45	50	0	0	0
<i>Rumex crispus</i>	0.4	0.2	+		29	31	19		0	0	-2
<i>Veronica hederifolia</i>	0.1	+	+		29	31	1		0	-1	-2
<i>Acer pseudoplatanus</i>	+	+	0.2	1.5	29	29	80	83	0	+1	0
<i>Achillea millefolium</i>	+	0.1	+	+	29	29	37	17	0	0	0

Table 3.2. (continued)

	Mean cover (%)				Frequency (%)				Transition		
	I	II	III	IV	I	II	III	IV	I to II	II to III	III to IV
<i>Valerianella dentata</i>	+	+	+		29	23	3		0	-1	-2
<i>Silene noctiflora</i>	0.2	+			29	23			0	-2	
<i>Lolium perenne</i>	+	+	+		29	17	1		0	-1	-2
<i>Impatiens parviflora</i>	+	+			29	14			0	-2	
<i>Agrostis gigantea</i>	+	+	+		29	11	7		0	0	-2
<i>Apera spica-venti</i>	0.3	+			29	6			-1	-2	
<i>Lamium amplexicaule</i>	+	+			29	6			-1	-2	
<i>Senecio vernalis</i>	+				29				-2		
<i>Cerastium holosteoides</i>	+	0.2	+		14	83	52		+1	0	-2
<i>Poa pratensis</i>	+	0.8	2.2	0.5	14	71	84	71	+1	0	0
<i>Rosa canina</i>	+	0.3	2.0	2.0	14	69	97	100	+1	0	0
<i>Trifolium dubium</i>	+	0.8	+		14	63	50		+1	0	-2
<i>Geum urbanum</i>	+	+	0.5	0.2	14	54	76	94	+1	0	0
<i>Inula conyzae</i>	+	+	+		14	34	20		0	0	-2
<i>Trifolium pratense</i>	+	+	+		14	26	5		0	-1	-2
<i>Aster novi-belgii</i>	+	+	0.3	0.2	14	23	65	58	0	+1	0
<i>Euphorbia helioscopia</i>	+	0.2	+		14	23	3		0	-1	-2
<i>Bromus arvensis</i>	+	+	+		14	14	1		0	-1	-2
<i>Eupatorium rugosum</i>	+	+	+		14	11	3		0	-1	-2
<i>Trifolium hybridum</i>	+	+	+		14	11	3		0	-1	-2
<i>Buddleia davidii</i>	+	+	+	+	14	9	16	10	0	0	0
<i>Senecio ovatus</i>	+	+	+	+	14	3	16	17	-1	+1	0
<i>Carduus nutans</i>	+	+			14	3			-1	-2	
<i>Galeopsis tetrahit</i>	+			+	14			2	-2		+2
<i>Erechtithes hieraciifolius</i>	+				14				-2		
<i>Euphorbia exigua</i>	+				14				-2		
<i>Matricaria recutita</i>	+				14				-2		
<i>Persicaria lapathifolia</i>	+				14				-2		
<i>Daucus carota</i>		0.2	0.1			71	37		+2	0	-2
<i>Epilobium montanum</i>		0.2	0.3	+		66	99	79	+2	0	0
<i>Crepis capillaris</i>		4.9	0.4	+		66	31	2	+2	0	-1
<i>Cornus sanguinea</i>		0.1	3.6	19.4		63	99	100	+2	0	0
<i>Arrhenatherum elatius</i>		0.8	11.2	0.5		60	91	90	+2	0	0
<i>Solidago gigantea</i>		0.2	0.9	0.7		60	59	46	+2	0	0
<i>Poa palustris</i>		+	0.7	0.4		57	90	73	+2	0	0
<i>Fragaria vesca</i>		0.2	2.0	2.1		54	91	100	+2	0	0
<i>Sorbus aucuparia</i>		+	0.4	1.2		46	78	98	+2	0	0
<i>Deschampsia cespitosa</i>		+	0.1	0.1		37	50	60	+2	0	0
<i>Rubus fruticosus</i>		0.4	1.0	0.4		37	45	56	+2	0	0
<i>Hieracium murorum</i>		+	+	+		37	38	40	+2	0	0
<i>Hypericum perforatum</i>		+	0.3	+		34	78	60	+2	0	0
<i>Artemisia vulgaris</i>		+	+			34	24		+2	0	-2
<i>Sonchus arvensis</i>		0.5	+			34	6		+2	-1	-2
<i>Valeriana officinalis</i>		+	0.8	0.3		31	86	90	+2	+1	0
<i>Clinopodium vulgare</i>		0.1	0.4	+		31	80	48	+2	+1	0
<i>Pastinaca sativa</i>		0.1	+	+		29	49	15	+2	0	-1
<i>Prunus avium</i>		+	0.4	1.1		26	56	90	+2	0	0
<i>Medicago lupulina</i>		+	+	+		26	40	15	+2	0	-1
<i>Luzula luzuloides</i>		+	+	+		26	28	35	+2	0	0
<i>Holcus lanatus</i>		+	+			26	24		+2	0	-2
<i>Euphrasia officinalis</i>		0.1	+			26	22		+2	0	-2
<i>Bromus sterilis</i>		6.6	0.7			26	8		+2	-1	-2
<i>Crataegus monogyna</i>		+	0.5	2.5		23	88	100	+2	+1	0
<i>Senecio erucifolius</i>		+	+	+		23	50	13	+2	0	-1
<i>Scrophularia nodosa</i>		+	+	+		23	42	33	+2	0	0
<i>Prunus spinosa</i>		+	+	+		23	41	27	+2	0	0
<i>Prunella vulgaris</i>		+	+	+		23	36	4	+2	0	-1
<i>Bromus hordeaceus</i>		+	+			23	3		+2	-1	-2
<i>Brachypodium sylvaticum</i>		0.2	0.6	1.8		20	48	98	+2	0	0
<i>Agrimonia eupatoria</i>		+	+	+		20	48	33	+2	0	0
<i>Bellis perennis</i>		+	+			20	12		+2	0	-2
<i>Campan. rapunculoides</i>		+	+	+		20	2	6	+2	-1	+1
<i>Trifolium repens</i>		+	+	+		17	37	2	+2	0	-1
<i>Leucanth. ircutianum</i>		+	+			17	12		+2	0	-2
<i>Crepis pulchra</i>		+	+			17	3		+2	-1	-2

Table 3.2. (continued)

	Mean cover (%)				Frequency (%)				Transition		
	I	II	III	IV	I	II	III	IV	I to II	II to III	III to IV
<i>Erigeron acris</i>		+			17				+2	-2	
<i>Hordeum murinum</i>		+			17				+2	-2	
<i>Trifolium campestre</i>		+	+		14	21			+2	0	-2
<i>Festuca rubra</i>		+	+	+	14	13	19		+2	0	0
<i>Veronica arvensis</i>		+	+		14	13			+2	0	-2
<i>Poa compressa</i>		+	+	+	14	8	2		+2	0	-1
<i>Torilis japonica</i>		+	+		14	1			+2	-1	-2
<i>Acer campestre</i>		+	+	0.7	11	60	92		+2	+1	0
<i>Populus tremula</i>		+	2.2	5.7	11	42	50		+2	+1	0
<i>Galium sylvaticum</i>		+	+	+	11	21	23		+2	0	0
<i>Salix alba</i>		+	0.2	0.6	11	14	25		+2	0	0
<i>Tanacetum corymbosum</i>		+	+	+	11	10	6		+2	0	0
<i>Lapsana communis</i>		0.1	+	+	11	7	2		+2	0	-1
<i>Persicaria maculosa</i>		+			11				+2	-2	
<i>Hieracium aurantiacum</i>		+	+	+	9	40	21		+2	+1	0
<i>Vicia sativa</i>		0.2	+	+	9	34	38		+2	+1	0
<i>Hypericum hirsutum</i>		+	+	0.1	9	24	33		+2	+1	0
<i>Convolvulus arvensis</i>		+	+	+	9	21	2		+2	0	-1
<i>Campanula trachelium</i>		+	+	+	9	20	31		+2	0	0
<i>Lathyrus sylvestris</i>		+	+	+	9	16	23		+2	0	0
<i>Angelica sylvestris</i>		+	+	+	9	8	13		+2	0	0
<i>Melilotus albus</i>		+	+		9	5			+2	0	-2
<i>Cirsium oleraceum</i>		+			9				+2	-2	
<i>Rhamnus cathartica</i>		+	0.1	0.4	6	53	85		+2	+1	0
<i>Ligustrum vulgare</i>		+	+	0.5	6	23	90		+2	+1	+1
<i>Geranium robertianum</i>		+	+	+	6	14	31		+2	0	0
<i>Luzula multiflora</i>		+	+		6	5			+2	0	-2
<i>Aphanes arvensis</i>		+	+		6	1			+2	-1	-2
<i>Hypochoeris radicata</i>		+	+		6	1			+2	-1	-2
<i>Fumaria officinalis</i>		+			6				+2	-2	
<i>Hieracium umbellatum</i>		+			6				+2	-2	
<i>Mycelis muralis</i>		+			6				+2	-2	
<i>Verbena officinalis</i>		+			6				+2	-2	
<i>Rubus caesius</i>		+	1.2	1.5	3	55	92		+2	+1	0
<i>Cotoneaster divaricatus</i>		+	+	0.1	3	43	69		+2	+1	0
<i>Heracleum sphondylium</i>		+	+	+	3	29	31		+2	+1	0
<i>Rhinanthus angustifolius</i>		+	0.1	+	3	29	8		+2	+1	-1
<i>Quercus robur</i>		+	+	+	3	21	75		+2	+1	+1
<i>Picea abies</i>		+	+	+	3	19	21		+2	+1	0
<i>Hypericum tetrapterum</i>		+	+		3	14			+2	+1	-2
<i>Anthriscus sylvestris</i>		+	+		3	6			+2	0	-2
<i>Viburnum opulus</i>			0.2	1.1			77	100		+2	0
<i>Viburnum lantana</i>			0.1	0.5			51	88		+2	0
<i>Lonicera xylosteum</i>			+	0.3			29	52		+2	0
<i>Carpinus betulus</i>			+	0.1			21	65		+2	+1
<i>Poa nemoralis</i>			+	0.1			21	65		+2	+1
<i>Galium odoratum</i>			+	0.2			21	42		+2	0
<i>Euonymus europaea</i>			+	0.2			20	75		+2	+1
<i>Origanum vulgare</i>			0.3	+			16	4		+2	-1
<i>Plantago lanceolata</i>			+				13			+2	-2
<i>Veronica chamaedrys</i>			+	+			12	40		+2	+1
<i>Lathyrus pratensis</i>			+	+			12	8		+2	0
<i>Filipendula ulmaria</i>			+	+			10	13		+2	0
<i>Hieracium schultesii</i>			+				9			+2	-2
<i>Pimpinella saxifraga</i>			+				8			+2	-2
<i>Crataegus laevigata</i>			+				7			+2	-2
<i>Cephalanth. damasonium</i>			+	0.1			5	38		+2	+1
<i>Cornus sericea</i>			+	0.1			5	33		+2	+1
<i>Hieracium sabaudum</i>			+	+			3	8		+2	0
<i>Viola hirta</i>			+	+			3	8		+2	0
<i>Fagus sylvatica</i>			+	+			2	19		+2	+1
<i>Carex sylvatica</i>			+	+			1	15		+2	+1
<i>Digitalis lutea</i>			+	+			1	13		+2	+1
<i>Paeonia daurica</i>			+	+			1	13		+2	+1
<i>Cornus mas</i>			+	0.7			1	8		+2	+1

Table 3.2. (continued)

	Mean cover (%)				Frequency (%)				Transition		
	I	II	III	IV	I	II	III	IV	I to II	II to III	III to IV
<i>Listera ovata</i>			+	+			1	6		+2	+1
<i>Daphne mezereum</i>				+				25			+2
<i>Viola reichenbachiana</i>				+				25			+2
<i>Melica uniflora</i>				+				23			+2
<i>Dryopteris filix-mas</i>				+				19			+2
<i>Milium effusum</i>				+				13			+2
<i>Prunus padus</i>				+				10			+2
<i>Sorbus aria</i>				+				10			+2
<i>Pinus sylvestris</i>				+				6			+2

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CHAPTER 4

Impact of tree species on nutrient and light availability: Evidence from a permanent plot study of old-field succession

Dölle, M. & Schmidt, W. (accepted: November 2008)

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Pictures: Top left: Fisheye view of the *Betula pendula* dominated overstory of plot L_{S1}, top right: view in L_{S1}, bottom left: Fisheye view of the *Fraxinus excelsior* dominated overstory of plot L_{C1}, bottom right: view in L_{C1}. (photos taken by M. Dölle)

4.1 Abstract

This paper compares vegetation composition, light availability, carbon and nutrient pools and Ellenberg indicator values among four old-field successional permanent plots that have received an initial treatment (ploughing, herbicide, or sterilisation) prior to being left undisturbed in 1969, a second set of six plots received additional treatments (continued ploughing or mulching until 1982). On all plots species rich pioneer forests developed. Vegetation still varies among plots with different initial treatments: Sterilised plots can be distinguished from the others by dominance of *Betula pendula*, ploughed plots by *Fraxinus excelsior*, whereas herbicide-treated plots are intermediate with proportions of both species. By affecting light availability at the ground, tree species in turn influences ground vegetation and soil properties. Light availability turned out to be the dominant factor determining the composition of the vegetation in old-field succession.

Keywords: *Betula pendula*, *Fraxinus excelsior*, Initial floristic composition, Photosynthetic active radiation, Resource-Ratio-Hypothesis, Soil organic carbon

4.2 Introduction

Regular soil disturbance by ploughing and biomass removal are main characteristics of arable land use and hinder the accumulation of organic matter and nutrients in the soil (Tiessen et al. 1982). When land is no longer used for cultivation and allowed to revert to natural vegetation, ecosystem properties such as soil chemical parameters and light conditions may change significantly. Vegetation and environmental factors of abandoned old-fields in particular often change radically within relatively short time periods (Schmidt 1981; Pickett 1982).

On most sites in temperate Europe succession leads to the development of forest ecosystems. With changing structure of the vegetation, light availability to the ground flora decreases and since plant biomass is no longer removed, nutrients and carbon tend to accumulate. Later on, regrowing temperate forests develop surface organic horizons which modify the microclimate at the soil surface and the physical, chemical, and biological features of the soil. The pool of nutrients contained in plant biomass increases during succession as plant biomass accumulates. Accumulation of nitrogen in the ecosystem is probably one of the main driving variables that determine the rate of succession (Tilman 1987). Since the input of nitrogen by atmospheric deposition can be at some places extremely high, its effect on natural plant communities may be crucial (Berendse 1990; Bobbink et al. 1998).

Determining the factors that drive successional changes in ecosystems is difficult, since various interacting factors influence the course of succession. It is also difficult to predict the direction of the development of a successional sere. In order to predict long-term changes in vegetation composition and structure during secondary succession, knowledge on the changes of nitrogen, other nutrients and carbon, as well as light availability and water supply in the soil are necessary. In general, successional changes in abandoned fields have been interpreted in terms of competitive ability mediated by resource availability, particularly light and nutrients (Tilman 1985; Gleeson and Tilman 1990; Tilman 1994). Tilman's (1985) formulation of the resource ratio hypothesis focuses on two plant resources: light availability at the soil surface and nutrient concentrations in the soil. Tilman (1985; 1988) viewed successional changes as a gradient from high availability of light and resource-poor soils in the beginning, to nutrient-rich soils and low availability of light later in succession.

Plants and resources interact in dynamic ways. Vegetation structure can exert large influences on the light transmittance (Binkley and Giardina 1998; Richter et al. 1994; Knops et al. 2002), as well as on water and nutrients in ecosystems (Leuschner 2002). Several authors showed that dominating tree species in forests can greatly impact soil properties (Binkley and Giardina 1998; Knops et al. 2002; Zhong and Makeshin 2004) or that different dominating plant species may have significant effects on environmental conditions, e.g. understory light supply (Bazzaz 1990; Barkman 1992; Jennings et al. 1999; Porté et al. 2004; Barbier et al. 2008), rate of nitrogen supply (Berendse 1990), or C/N ratio and N-mineralisation rate (Miles and Young 1980; Hagen-Thorn et al. 2004). Moreover that single plant species can act as ecosystem engineers who have significant effects on species diversity and ecosystem function (Wedin and Tilman 1990; Mitchell et al. 2007; Schmidt 2007).

Additionally, cultural and tillage practices before abandonment have marked consequences on overall vegetation development (Bonet 2004) and agricultural land use intensity and site history may have irreversible effects on subsequent biodiversity (Bossuyt et al. 1999; Dupouey et al. 2002). Successions may also differ due to varying climate conditions or diaspore supply in the initial stage (Schmidt 1981; 1983; Peet 1992). The initial floristic composition is a significant factor in old-field succession, since dominants of later stages usually arrive soon after abandonment and early dominants substantially influence the further vegetation development (Egler 1954).

In the present study we investigated long-term experimental plots of undisturbed old-field succession for 36 and 22 years. The study site in the Experimental Botanical Garden of Göttingen University was started in 1968 on a former arable field. Since that time four plots were left undisturbed to revert to natural vegetation through succession and six additional plots were left abandoned in 1982 undergoing either

experimental ploughing or mulching once per year up to this time (Schmidt 1993). The plots are located close together; hence site-specific influences on the process of secondary succession such as soil type, climatic conditions, and surrounding vegetation are basically the same. Such long-term permanent plot studies can offer, in contrast to short-term investigations or chronosequence studies, valuable insights into changes in ecosystem properties during succession.

We addressed the following questions: (1) Do our findings support the resource ratio hypothesis of Tilman (1985) and if so (2) how quickly do resources change over time? (3) Do our findings confirm the initial floristic composition model by Egler (1954) and thus (4) does the initial treatment of the plots, through differences in plant species composition, have lasting effects on nutrient supply, soil organic matter or light availability?

4.3 Materials and methods

4.3.1 Study site

All plots of the current study are part of an experiment located in the Experimental Botanical Garden of Göttingen University, Lower Saxony, Germany (180 m a.s.l., 51°34'N, 9°57'E; mean annual temperature: 8.5°C; average annual rainfall: 635 mm). Initiated by Heinz Ellenberg, the experiment was set up on a former arable field cultivated until 1968 on deep, calcareous and fertile soil (alluvial loamy brown earth). Regional forest vegetation is dominated by *Fagus sylvatica* (*Fagion sylvaticae*) which is the natural vegetation type (Bohn et al. 2003). The surrounding landscape may be characterised by a mixture of arable fields, grasslands, ruderal communities, and forests with a high diversity in mature trees as potential seed dispenser in close vicinity. A more detailed description of the study site and methods is given in Schmidt (1981; 1983; 1993).

Vegetation development and associated successional changes of 10 permanent plots were evaluated: four plots of undisturbed succession since 1969 (L_{S1} , L_{S2} , L_{H1} , L_{C1}) and six plots of undisturbed succession since 1983 (S_{H1-3} , S_{C1-3}), herein after referred to as short and long sere (Table 4.1). For vegetation sampling the plots are each subdivided into three subplots. The entire study site was farmed as crop field (wheat and sugar beet, intensive conventionally farmed) up to and including 1967, so that the long sere meets the conditions of an abandoned agricultural field. The history of the short sere differed by experimental treatment with soil disturbance once per year up to and including 1982 for the plots S_{H1-2} and S_{C1-2} , and mulching once per year for the plots S_{H3} and S_{C3} (Table 4.1). The plots differ in their treatment in the beginning of the experiment (1968): ploughing (L_{C1} , S_{C1-2}), herbicide treatment (L_{H1} , S_{H1-2}) or sterilised by heating (L_{S1} , L_{S2}) (Schmidt 1981).

Table 4.1 Summary of the 10 permanent plots of undisturbed old-field succession, their plot size, their assignment to the time since abandonment and resultant sere category, their initial treatment and treatment until 1982 and group membership based on indicating tree species (plot letter codes: sere: L = long, S = short, initial treatment: S = sterilized, H = herbicide, C = control (ploughing)), numbers: 1+2 = only ploughing, 3 = mulching between 1969 and 1982).

Plot	Plot size (m ²)	Abandoned since	Sere	Initial treatment in 1968	Treatment until 1982	Group
L _{S1} , L _{S2}	200	1969	Long- term	Sterilisation by heating	-	Betula
L _{H1}	200			Herbicide treatment	-	Intermediate
L _{C1}	150			Ploughing (Control)	-	Fraxinus
S _{H1} , S _{H2}	200	1982	Short- term	Herbicide treatment	Ploughing	Intermediate
S _{H3}	200			Herbicide treatment	Mulching	Intermediate
S _{C1} , S _{C2}	150			Ploughing (Control)	Ploughing	Fraxinus
S _{C3}	150			Ploughing (Control)	Mulching	Fraxinus

4.3.2 Vegetation sampling

Percentage cover of all vascular plant species on the whole subplot area (25-100 m²) was surveyed twice per year in the beginning (1969-1987) and once per year thereafter (since trees began to dominate). From 1968 until 1993 vegetation was recorded annually, afterwards vegetation relevés were conducted in 1995, 1999, 2003, 2004 and 2005. Species names for vascular plants follow Wisskirchen and Haeupler (1998).

4.3.3 Light measurement

In summer 2005 on overcast days with homogeneous diffuse light conditions, relative irradiance was measured directly in 0.5, 2 and 5-m height of the stands with PAR-sensors, type LI-190 (Licor, Nebraska, USA) fixed on a telescope bar. Nine spatial evenly distributed recordings of the absolute light intensity were done in each subplot and simultaneously on a nearby field the open field situation. From each measurement the ratio of the absolute light intensity in the stands and in the open field was computed. For further evaluation mean values of photosynthetically active radiation (PAR) and standard error (\pm SE) per subplot were calculated.

4.3.4 Soil chemical properties

In 1969, 1973, 1977, 1989 and 2004 three randomly selected soil samples per subplot were removed to a mineral soil depth of 30 cm using an 8-cm-diameter soil auger. The soil cores were divided into 0-10 cm, 10-20 cm and 20-30 cm sections. For the year 1969 only values for the depth 0-10 cm are available. Since humus

accumulation proceeded with the successional change from open vegetation to pioneer forests, samples of the litter layer (O_L) were taken by a 25 x 25 cm frame in the year 2004. Soil samples of each depth per subplot were pooled. The soil was sieved with a 2-mm riddle and stones and any living plant material were removed. Samples were dried at 65°C (organic layer) and 105°C (mineral soil) respectively and finely ground with a grinder. All other measurements were determined using fresh samples. Samples were analysed for $pH_{(H_2O)}$, total carbon (C), organic C (SOC), nitrogen (N), and phosphorus (P) content. The pH values were measured with a glass electrode; concentrations of total C and N in the soil were determined by combustion (C/N analyzer, Carlo Erba Elemental Analyser). The total P was determined colorimetrically and the $CaCO_3$ content according to Scheibler (Schlichting et al. 1995).

4.3.5 Data analysis

To select the most influencing parameters, the correlation structure of the analysed soil chemical parameters, the vegetation structure and diversity, and the selected Ellenberg indicator values (weighted and unweighted) were analysed through detrended correspondence analysis (DCA) and bivariate Pearson correlations based on the cover values of the plant species (271 species) in the years where the soil properties were analysed. Since the coverage of a species is not only dependent on the site conditions but might be a specific characteristic of a certain species, the data were transformed by $y = x^{0.25}$ to minimise differences. Axis 2 of the DCA was highly significant ($P \leq 0.001$) correlated with the initial treatment of the plots ($r = 0.717$). Therefore the effect of the initial treatment on current species composition was evaluated by a second DCA of all subplot data (at this point log-transformed cover values) 36 years after abandonment for the long sere and 22 years after abandonment for the short sere. All species in all layers (128) and different environmental parameters were correlated with the ordination axes. In order to identify differences in plant species composition between the different treated plots, significant indicator species were detected by indicator species analysis (ISA). For evaluation of the current vegetation composition on the plots, according to the results of the second DCA and ISA, the initially different treated plots (ploughing, herbicide, or sterilisation) were pooled together (Table 4.1).

Mean Ellenberg indicator values for light, nitrogen and soil reaction (Ellenberg et al. 2001) were evaluated on the basis of cover values and presence-absence data. The variability of the time since abandonment for the selected variables and of the different initial treatments was, if the data met the assumptions, assessed through one-way ANOVA with post-hoc Scheffé-test. If the assumption of normal distribution and homogeneous variances were not fulfilled, even after log-transformation, data were tested by Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test. All

statistical analyses were performed using STATISTICA 6.0 (Anonymous 1998); the ordination and correlation analyses, as well as indicator species analyses with PC Ord 5.12 (McCune and Mefford 1999). The following significance levels were used for all statistics: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; n.s. = not significant ($P \geq 0.05$).

4.4 Results

4.4.1 Successional change

The DCA of the successional change grouped the plots along the first axis explaining 83 % of the total variance and being highly significant ($P \leq 0.001$) and positively correlated with the time since abandonment ($r = 0.928$). A close relationship revealed between the floristic gradient of the successional change and the changes in soil chemical properties (Fig. 4.1, Table 4.2). There was a highly significant positive correlation with the first axis of the DCA for the total amount of soil organic carbon (SOC) which increased significantly with successional age. The total nitrogen content remained almost stable in the first ten years of abandonment, then increased in the top 10 cm of the soil but decreased in the 10-30 cm soil. Major changes occurred between the ninth and 21st year of abandonment with an average increase over all plots of $2.60 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the top 10 cm and an average decrease of $2.55 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the lower soil (10-30 cm). The changes slowed down within the 22nd and 36th year of abandonment with an increase of $1.96 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the top 10 cm and a decrease of $1.88 \text{ g N m}^{-2} \text{ yr}^{-1}$. The total nitrogen pool remained stable during succession. The C/N ratio at all soil depths increased significantly with succession. The supply of phosphorus showed no significant trend in the top 10 cm of the soil, but decreased drastically in 10-30 cm soil depth, resulting in a significant decrease in the total phosphorus supply. There were no clear changes in the pH values during succession.

The Ellenberg indicator values for light, nitrogen and soil reaction of the herb layers showed significant negative correlations with the time since abandonment (Fig. 4.1). Both weighted and unweighted indicator values for light and nitrogen significantly decreased during succession, whereas for soil reaction only the weighted evaluation showed a weak decreasing trend (Fig. 4.2). The weighted and unweighted values of the Ellenberg indicator values for light, nitrogen, and soil reaction became more similar with increasing time since abandonment.

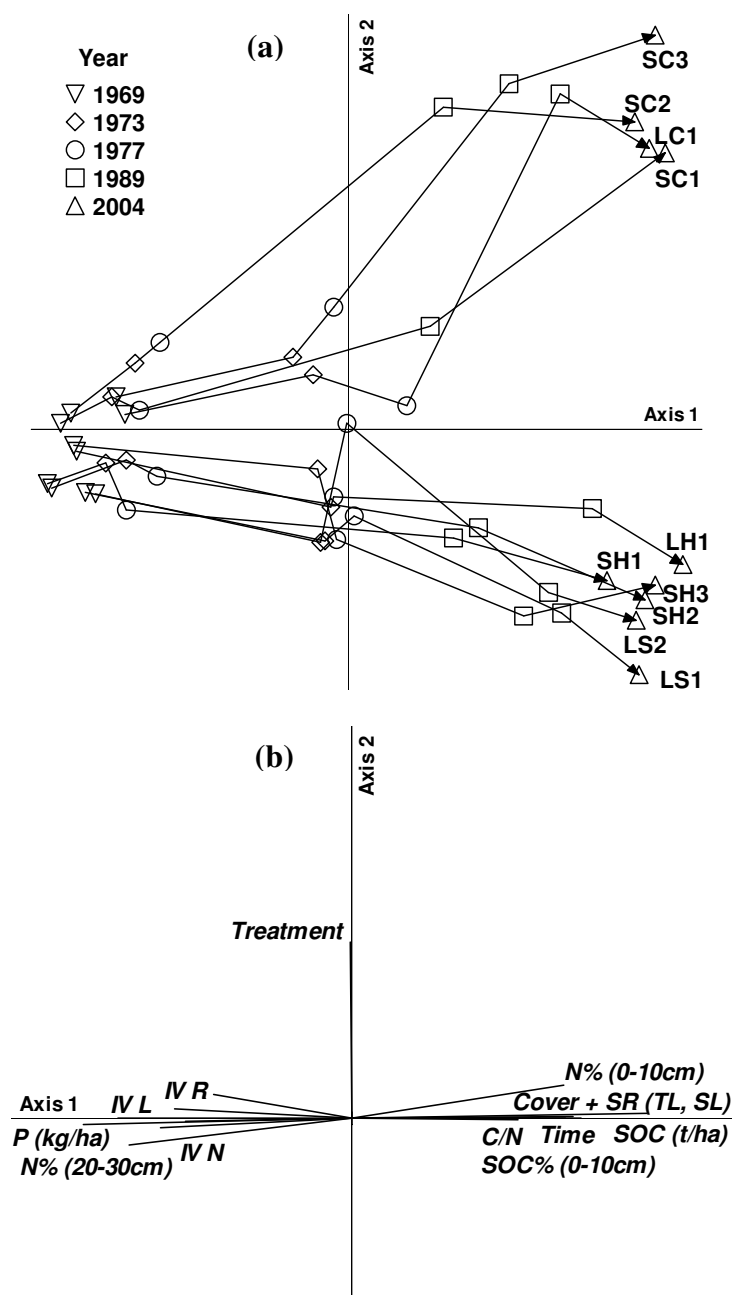


Fig. 4.1 (a) DCA of the vegetation relevés (all layers) in 1969, 1973, 1977, 1989 and 2004 of the 10 permanent plots of undisturbed old-field succession (length of gradient Axis 1: 4.87, Axis 2: 2.00; r^2 Axis 1: 0.830, Axis 2: 0.026). Label points of the same plot are connected by successional vectors; sere end points are indicated by plot labels. **(b)** Correlation matrix of different environmental parameters with the ordination axes. Pearson r of all highly significant ($P \leq 0.001$) correlated parameters ($r \geq 0.6$) with Axis 1: Time (since abandonment) = 0.928, cover = 0.804 and richness (SR) = 0.782 of tree layer (TL), cover = 0.790 and richness = 0.913 of shrub layer (SL), soil organic carbon (SOC) (t/ha) = 0.819, SOC% (0-10 cm) = 0.742, nitrogen concentration (N%): in 0-10 cm = 0.787, in 20-30 cm = -0.752, C/N = 0.700, P (kg/ha) = -0.808; weighted Ellenberg indicator values: nitrogen (IV N) = -0.697, light (IV L) = -0.607, soil reaction (IV R) = -0.718, and with Axis 2: initial treatment = 0.717.

Table 4.2 Mean soil chemical parameter in 0-10, 10-20 and 20-30 cm soil depth in the years 1969 (only for 0-10 cm soil depth), 1973, 1977, 1989 and 2004 for the 10 plots (both series estimated together) of undisturbed old-field succession. Total pool of SOC, N and P in 0-30 cm soil depth was calculated for the years 1973, 1977, 1989 and 2004, in 2004 sum includes the organic layer (O_L). Significant changes within one parameter and soil depth are indicated by differing letters ($P \leq 0.05$) according to Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test.

Parameter	Depth (cm)	<i>H</i>	1969	1973	1977	1989	2004
pH (H_2O)	O_L	-	-	-	-	-	8.0
	0-10	56.1 ***	7.8 a	7.8 a	7.6 b	7.8 a	7.6 b
	10-20	42.3 ***	-	7.8 a	7.6 b	7.9 a	7.6 b
	20-30	47.0 ***	-	7.8 a	7.6 b	7.9 a	7.7 b
SOC (t/ha)	O_L	-	-	-	-	-	2.6
	0-10	85.5 ***	13.8 a	11.7 b	14.9 a	20.2 c	28.0 d
	10-20	81.1 ***	-	12.9 a	11.5 b	15.9 c	18.7 d
	20-30	56.1 ***	-	15.3 a	10.1 b	16.1 a	17.4 c
N (kg/ha)	O_L -30	86.2 ***	-	39.9 a	36.7 b	52.2 c	66.7 d
	O_L	-	-	-	-	-	99.2
	0-10	84.0 ***	1343 a	1387 b	1375 ab	1650 c	1943 d
	10-20	46.5 ***	-	1661 a	1618 a	1512 b	1428 c
C/N	20-30	63.7 ***	-	1792 a	1773 a	1568 b	1370 c
	O_L -30	0.78 n.s.	-	4840	4766	4730	4837
	O_L	-	-	-	-	-	26.5
	0-10	78.7 ***	10.2 a	8.5 b	10.9 a	12.2 c	14.5 d
P (kg/ha)	10-20	86.6 ***	-	7.9 a	7.2 b	10.3 c	13.1 d
	20-30	81.0 ***	-	8.7 a	5.7 b	10.2 c	12.8 d
	O_L	-	-	-	-	-	8.3
	0-10	24.6 ***	662 a	728 b	707 c	688 c	666 ac
	10-20	75.9 ***	-	970 a	803 b	758 c	701 d
	20-30	53.3 ***	-	926 a	897 a	842 b	743 c
	O_L -30	64.8 ***	-	2624 a	2387 b	2288 c	2118 d

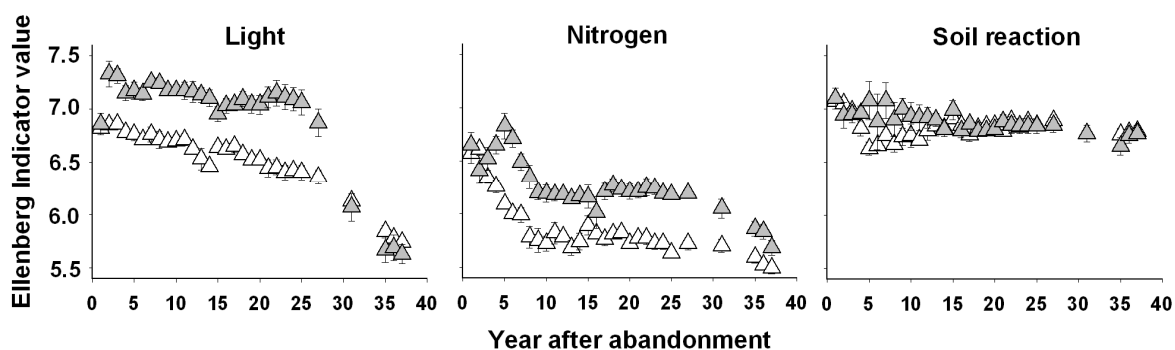


Fig. 4.2 Changes in mean Ellenberg's indicator values for light, nitrogen and soil reaction in the herb layers summarised for the plots of undisturbed succession since 36 and 22 years. Analyses were done with both data, weighted by coverage (\blacktriangle) and presence-absence of the species (\triangle).

4.4.2 Influence of the initial treatment on current species composition

The second DCA of the current species composition grouped the plots along the first axis explaining 60 % of the total variance, separating the plots according to their initial treatment in the beginning of the experiment. The axis 1 of the DCA of the current vegetation composition was highly significant ($P \leq 0.001$) correlated with the coverage of *Fraxinus excelsior* ($r = 0.789$) and *Betula pendula* ($r = -0.868$), PAR-irradiance ($r = -0.831$), and the C/N ratio of the humus layer ($r = -0.791$) and of the mineral soil ($r = -0.729$). The most intensively treated plots (L_{S1} , L_{S2} : sterilized by heating) are now dominated by *B. pendula* in tree layer and have the highest PAR transmittance to the ground (Fig. 4.3, Table 4.5). In contrast the control plots (S_{C1-3} , L_{C1} : ploughing) are to distinguish from the other plots by a high frequency of *F. excelsior* in the tree layer as indicating tree species for this group and significant lowest PAR-transmittance to the ground (Table 4.3, Fig. 4.3). The herbicide-treated plots (S_{H1-3} , L_{H1}) form an intermediate group with no certain tree species indicating this group (Table 4.3).

This gradient is also evident in the indicator species analyses (ISA) of the current vegetation composition (Table 4.3). In the *Betula* group initially sterilized by heating there is a high amount of nanophanerophytes with an Ellenberg indicator value for light of 6 (between semi-shade and partial-shade plants) or 7 (plants generally in well-lit place, but also occurring in partial shade). *Quercus robur* as late successional tree species in the herb layer is characteristic of the *Betula* group. The *Fraxinus* group, with lowest intensity of the initial treatment, had a high amount of indicator species with light indicator value of 4 (between shade and semi-shade plants).

4.4.3 PAR-irradiance

The relative irradiance in the stands significantly differed between the three groups of differing initial treatment (Fig. 4.3). On average extreme low relative irradiance was measured for the *Fraxinus*-dominated plots with values ranging from 3.7% (± 0.34) in 5 m height to 0.9% (± 0.04) in 0.5 m height of the stands. The *Betula*-dominated group showed with a mean of 11.0% (± 3.3) in 5 m height to 2.7% (± 0.11) in 0.5 m height of the stands significant higher relative irradiance intensity.

Table 4.3 Result of the Indicator species analysis (ISA) of all species with significant indicator value (IV) ≥ 40 for all layers, their Ellenberg indicator value for light (L-value) and their correlation with the first and second axis of the DCA of the vegetation composition 36 or 22 years after abandonment (Monte Carlo test of significance of observed max IV; (1,000 permutations)).

Species	Layer	L-value	IV	P-value	1. Axis		2. Axis	
					r	P-value	r	P-value
Betula group								
Betula pendula	tree	(7)	55.7	0.0002	-0.87	0.000	-0.02	n.s.
Viburnum lantana	shrub	7	59.5	0.0004	-0.65	0.000	0.08	n.s.
Sorbus aucuparia	shrub	(6)	49.1	0.0078	-0.35	0.042	-0.18	n.s.
Lonicera xylosteum	shrub	5	39.7	0.0140	-0.34	0.045	-0.09	n.s.
Betula pendula	shrub	(7)	45.3	0.0190	-0.36	0.044	-0.33	n.s.
Cornus sanguinea	herb	7	40.5	0.0002	-0.41	0.014	0.11	n.s.
Viburnum opulus	herb	6	47.6	0.0002	-0.76	0.000	0.30	n.s.
Sorbus aucuparia	herb	(6)	56.8	0.0006	-0.75	0.000	-0.22	n.s.
Viburnum lantana	herb	7	58.3	0.0008	-0.66	0.000	0.18	n.s.
Euonymus europaea	herb	6	56.6	0.0032	-0.38	0.024	-0.11	n.s.
Rhamnus cathartica	herb	7	57.6	0.0056	-0.56	0.000	-0.14	n.s.
Cotoneaster divaricatus	herb	-	47.5	0.0110	-0.51	0.002	-0.03	n.s.
Quercus robur	herb	(7)	50.0	0.0174	-0.47	0.004	-0.16	n.s.
Intermediate group								
Rubus caesius	shrub	6	45.2	0.0154	-0.05	n.s.	0.64	0.001
Rubus caesius	herb	6	54.8	0.0032	-0.12	n.s.	0.41	0.015
Fraxinus group								
Fraxinus excelsior	tree	(4)	50.4	0.0030	0.79	0.000	-0.14	n.s.
Prunus avium	shrub	(4)	49.1	0.0072	0.24	n.s.	-0.42	0.011
Fraxinus excelsior	shrub	(4)	41.6	0.0210	0.66	0.004	-0.02	n.s.
Daphne mezereum	herb	4	48.2	0.0032	0.41	0.016	-0.14	n.s.
Hypericum hirsutum	herb	7	41.7	0.0048	0.47	0.004	-0.02	n.s.

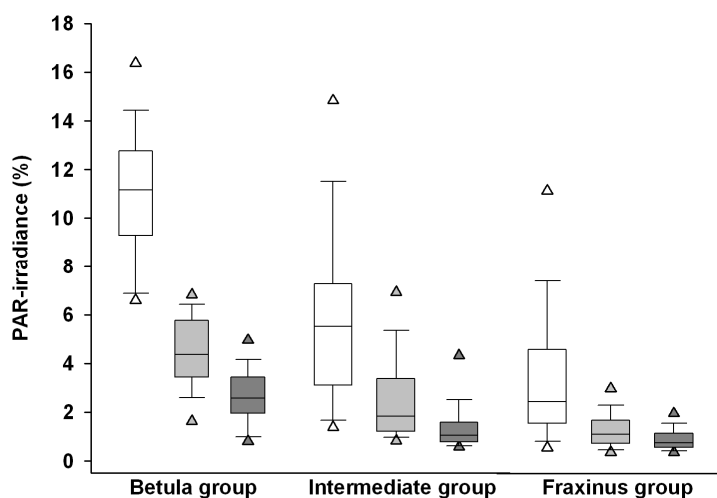


Fig. 4.3 Distribution of PAR-irradiance as percentage of open field irradiance in the three groups of differing initial treatment in 5 m (\square), 2 m (\square) and 0.5 m (\square) height of the stands 36 and 22 years after abandonment, respectively. For all groups and canopy height PAR values differing significantly according to Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test ($P < 0.05$), 0.5 m height: $H = 158.9^{*}$, 2 m height: $H = 212.0^{***}$, 5 m height: $H = 124.2^{***}$.**

4.4.4 Litter pool and soil chemical parameters

After about 20 years of abandonment, stand structure had changed to pioneer forest vegetation and typical L-mull humus had developed. Noticeable differences in the amount of litter pool and its nutrient composition occurred between the three groups of plots of differing tree species composition (Table 4.4). The *Betula*-dominated plots had significantly lower amounts of accumulated humus than the *Fraxinus*-dominated plots. Accordingly nitrogen, SOC and phosphorus (kg/ha) were lowest in the *Betula*-dominated plots. Nitrogen concentration (%) was lowest in the *Betula*-dominated plots, whereas SOC concentration (%) was significantly higher. The C/N-ratio was widest for the *Betula*-group.

Table 4.4 Litter pool and pH, C/N and amount of N, C and P of the litter layer (O_L) and the mineral soil per 0-10, 10-20 and 20-30 cm soil depth of the plots of undisturbed succession 36 or 22 years after abandonment, respectively, for the three groups of differing initial treatment. Means \pm standard error, significant differences are indicated by differing letters ($P < 0.05$) according to Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test, except for the total amount (O_L -30 cm) of SOC, N and P here after one-way ANOVA with post-hoc Scheffé-test.

Parameter	Depth (cm)	H (F)-value		Betula group	Intermediate group	Fraxinus group
Litter pool (kg/ha)	OL	16.1	**	4318 \pm 322 a	7875 \pm 625 b	6450 \pm 842 b
pH	OL	14.0	**	7.8 \pm 0.1 a	8.0 \pm 0.1 ab	8.2 \pm 0.1 b
	0-10	6.3	*	7.5 \pm 0.1 a	7.6 \pm 0.1 b	7.6 \pm 0.1 b
	10-20	3.2	n.s.	7.5 \pm 0.1	7.7 \pm 0.1	7.7 \pm 0.1
	20-30	1.7	n.s.	7.6 \pm 0.1	7.7 \pm 0.1	7.7 \pm 0.1
SOC %	OL	5.8	n.s.	42.3 \pm 1.2	40.3 \pm 1.0	38.8 \pm 0.7
SOC (t/ha)	OL	14.9	**	1.8 \pm 0.1 a	3.1 \pm 0.2 b	2.5 \pm 0.4 a
	0-10	9.1	*	31.8 \pm 15 a	26.9 \pm 13 b	25.6 \pm 14 b
	10-20	2.5	n.s.	19.9 \pm 10	18.4 \pm 8.2	17.8 \pm 7.6
	20-30	1.7	n.s.	18.0 \pm 12	16.5 \pm 6.4	17.7 \pm 12
	Σ (OL-30)	(4.03)	*	71.5 \pm 2.5 a	65.4 \pm 2.2 a	63.6 \pm 1.3 b
N %	OL	11.9	**	1.4 \pm 0.1 a	1.5 \pm 0.1 a	1.7 \pm 0.1 b
N (kg/ha)	OL	17.2	***	61.2 \pm 5.2 a	116 \pm 10 b	108 \pm 16 b
	0-10	0.1	n.s.	1918 \pm 56	1925 \pm 66	1985 \pm 102
	10-20	4.6	n.s.	1359 \pm 32	1467 \pm 37	1453 \pm 30
	20-30	7.6	*	1261 \pm 48 a	1426 \pm 40 b	1414 \pm 29 b
	Σ (OL-30)	(4.77)	*	4598 \pm 66 a	4934 \pm 104 b	4960 \pm 95 b
C/N	OL	20.9	***	30.0 \pm 0.6 a	27.7 \pm 0.7 b	23.6 \pm 0.5 c
	0-10	21.2	***	16.5 \pm 0.4 a	14.2 \pm 0.4 b	13.0 \pm 0.4 c
	10-20	7.0	*	14.6 \pm 0.6 a	12.6 \pm 0.5 b	12.3 \pm 0.6 b
	20-30	8.0	*	14.3 \pm 0.8 a	11.7 \pm 0.6 b	12.5 \pm 0.8 b
P ppm	OL	6.9	*	1085 \pm 78 a	1328 \pm 119 ab	1314 \pm 59 b
P (kg/ha)	OL	14.2	**	4.7 \pm 0.5 a	11.1 \pm 1.8 b	8.2 \pm 0.8 b
	0-10	1.5	n.s.	682 \pm 16	678 \pm 16	641 \pm 28
	10-20	2.2	n.s.	707 \pm 17	711 \pm 14	686 \pm 11
	20-30	4.0	n.s.	714 \pm 26	754 \pm 19	758 \pm 20
	Σ (OL-30)	(0.51)	n.s.	2101 \pm 53	2154 \pm 41	2093 \pm 43

Chemical properties of mineral soil also differed significantly between the three groups (Table 4.4). Plots dominated by *Betula* had a higher amount of SOC, higher C/N-ratio but lower total nitrogen, and a slightly lower pH-value than the plots dominated by *Fraxinus* at all soil depths. The amount of phosphorus was higher in 0-10 cm but lower in 10-20 cm for the *Betula*-dominated plots.

4.4.5 Vegetation structure and diversity

Light supply on the ground had no significant effect on herb layer richness (Fig. 4.4b). Likewise no influence of the tree layer canopy and thus the light supply on the ground was detected on the richness of tree species in the herb layers. In contrast the species richness in the shrub layers was significantly influenced by light supply (Fig. 4.4a).

The shrub and herb layers of all plots are dominated by *F. excelsior* (Table 4.5). No seedlings or saplings of *B. pendula*, *Salix caprea* or *Populus tremula* were recorded in the current herb layers.

4.4.6 Ellenberg indicator values

The mean Ellenberg indicator values for light in the herb and shrub layers and for the total stands were significantly higher in plots dominated by *Betula pendula* (Table 4.6). Indicator values for nitrogen and soil reaction were slightly lower in the *Betula* group. The differences were more pronounced in the weighted evaluation, but the differences between the three groups were in both cases rather small.

Table 4.5 List of all tree species, their mean coverage in the tree, shrub and herb layer and the number of stems per ha and basal area ($\text{m}^2 \text{ha}^{-1}$) for the tree layers for the three groups of differing initial treatment 36 and 22 years after abandonment, respectively. (^aestimated only for the plots of undisturbed succession since 36 years).

Species	Group (mean coverage)		
	Betula	Intermediate	Fraxinus
Tree layer			
n ha^{-1} (dbh > 4 cm) ^a	4650	4530	5600
Basal area ($\text{m}^2 \text{ha}^{-1}$) ^a	75	95	80
<i>Betula pendula</i>	50.5	20.8	1.3
<i>Fraxinus excelsior</i>	1.4	7.1	27.9
<i>Salix caprea</i>	6.2	20.4	28.3
<i>Acer platanoides</i>	2.7	14.6	6.3
<i>Acer pseudoplatanus</i>	1.8	0.8	2.1
<i>Populus tremula</i>	-	4.2	8.3
<i>Prunus avium</i>	0.5	-	1.5
<i>Sorbus aucuparia</i>	0.5	-	0.4
<i>Salix alba</i>	-	0.8	1.7
Shrub layer			
<i>Fraxinus excelsior</i>	6.5	27.8	29.2
<i>Betula pendula</i>	3.4	1.9	1.6
<i>Acer platanoides</i>	1.8	1.4	1.5
<i>Sorbus aucuparia</i>	1.8	1.0	0.9
<i>Acer pseudoplatanus</i>	0.7	1.5	0.7
<i>Prunus avium</i>	0.5	0.3	1.9
<i>Acer campestre</i>	0.3	0.9	0.6
<i>Populus tremula</i>	-	0.6	0.5
<i>Salix caprea</i>	0.8	0.3	0.4
<i>Carpinus betulus</i>	-	0.2	0.2
<i>Sorbus aria</i>	0.1	-	<0.1
<i>Picea abies</i>	0.4	-	-
<i>Pinus sylvestris</i>	-	0.1	-
<i>Quercus robur</i>	-	0.1	-
<i>Juglans cinerea</i>	-	0.1	-
Herb layer			
<i>Fraxinus excelsior</i>	1.7	2.0	1.3
<i>Sorbus aucuparia</i>	1.6	0.7	0.3
<i>Acer campestre</i>	0.6	0.6	0.2
<i>Acer platanoides</i>	0.3	0.6	0.2
<i>Prunus avium</i>	0.5	<0.1	0.4
<i>Quercus robur</i>	0.3	0.1	<0.1
<i>Acer pseudoplatanus</i>	0.1	0.1	0.1
<i>Carpinus betulus</i>	0.1	<0.1	0.1
<i>Sorbus aria</i>	<0.1	<0.1	0.1
<i>Fagus sylvatica</i>	<0.1	<0.1	<0.1
<i>Prunus padus</i>	-	-	0.1
<i>Tilia platyphyllos</i>	<0.1	-	-

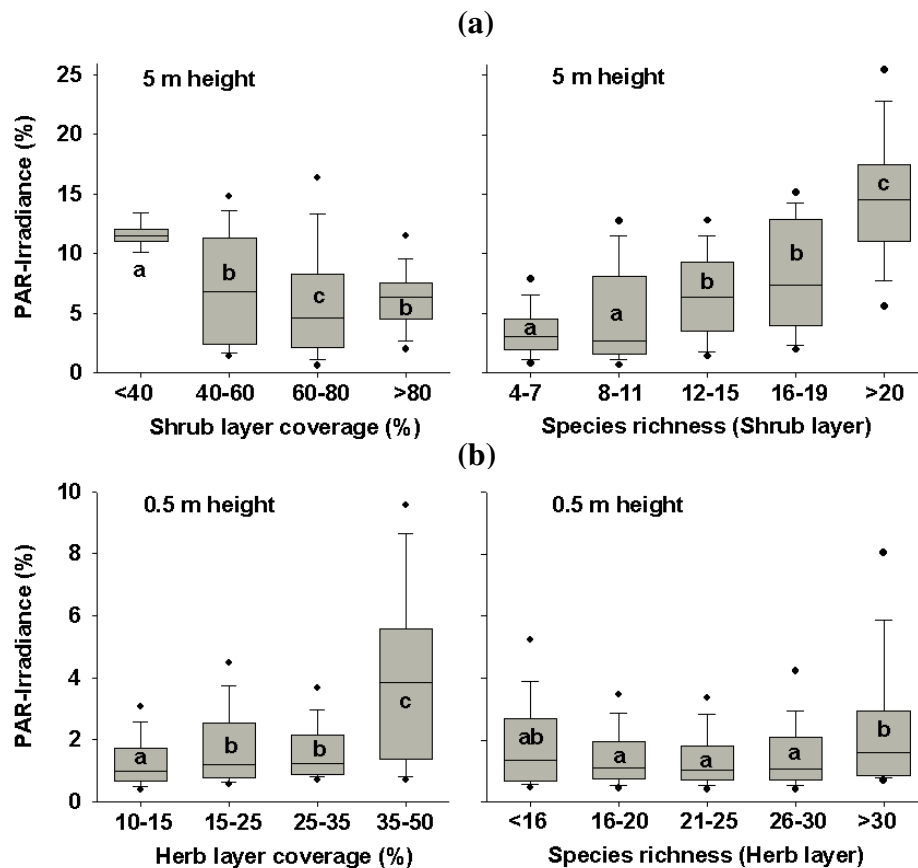


Fig. 4.4 Distribution of PAR-irradiance 36 and 22 years after abandonment respectively (a) as a function of shrub layer coverage and species richness in 5 m height and (b) as function of herb layer coverage and species richness in 0.5 m height of the stands. Significant differences are indicated by differing letters (Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test $P < 0.05$). For herb layer and PAR in 0.5 m height: coverage $H = 32.3^{***}$, species richness $H = 12.4^*$; for shrub layer and PAR in 5 m height: coverage $H = 14.0^{**}$, species richness $H = 58.4^{***}$.

Table 4.6 Weighted mean Ellenberg indicator values (IV) for light, nitrogen and soil reaction in the herb and shrub layers and the total stands (all layers) of the three groups of differing initial treatment 36 or 22 years after abandonment (1 = *Betula* group, 2 = Intermediate group, 3 = *Fraxinus* group). Significant differences within one group are indicated by differing letters ($P < 0.05$) after Kruskal-Wallis ANOVA with post-hoc Mann-Whitney-U-test.

Mean IV for:	Herb layer			Shrub layer			Total stand		
	Group			Group			Group		
	1	2	3	1	2	3	1	2	3
Light	5.9	5.6	5.5	6.3	5.8	5.7	6.4 a	5.9 b	5.7 b
	$(H=4.57, n.s.)$			$(H=5.63, n.s.)$			$(H=14.1, p=0.001)$		
Nitrogen	5.5	5.7	5.6	5.7 a	6.5 b	6.3 b	5.9 a	6.6 b	6.5 b
	$(H=2.53, n.s.)$			$(H=9.2, p=0.01)$			$(H=15.5, p=0.001)$		
Soil reaction	6.7	6.8	6.8	7.0	7.0	7.1	6.9	7.0	7.0
	$(H=1.71, n.s.)$			$(H=0.50, n.s.)$			$(H=5.74, n.s.)$		

4.5 Discussion

4.5.1 Effects of successional changes on soil chemical properties and vegetation attributes

Impact of past land use on the patterns of changes in vegetation and soil characteristics has received considerable attention over the last decades, particularly in temperate forest ecosystems in Europe and North America (review in Flinn and Vellend 2005). On abandoned old-fields it is to be expected that nutrient and carbon levels change significantly over time as with the agricultural abandonment no fertilisation is applied anymore and the cessation of harvesting results in biomass accumulation.

In this study soil organic carbon (SOC) increased linearly with time since abandonment ($r^2 = 0.951$) with an average annual increase of $39.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the top 10 cm during the 36 years of abandonment. Similar rates of SOC accumulation have been reported for northern ecosystems (Bormann and Siddle 1990; Bormann et al. 1995; Hooker and Compton 2003); in many cases the forest floor turned out to be a major sink for carbon after agricultural abandonment (Hooker and Compton 2003). In our study the decrease in SOC in the top 10 cm within the first five years of abandonment and the initial decrease in the lower soil were not sustained. From the tenth year onwards the total amount (0-30 cm) of SOC showed a steady increasing rate of on average $94.7 \text{ g C m}^{-2} \text{ yr}^{-1}$. However, SOC showed a distinct vertical gradient with an increasing difference between upper and lower soil during time. This increasing differentiation is obvious by the consequence of the perturbation by ploughing ceasing. Subsoil SOC also accumulated, presumably through mechanisms such as root turnover and exudation, sorption of dissolved organic carbon, and pedoturbation. Approximately 10% of the total SOC accumulation occurred in the subsoil (20-30 cm). Hooker and Compton (2003) also found significant accumulation of carbon in the subsoil (20-70 cm), other studies show no significant changes (Hamburg 1984) or decreasing rates (Richter et al. 1999) or assume based on large-scale assessments or soil C models, no carbon accumulation in the subsoil (Turner et al. 1995; Gaudinski et al. 2000). The extend to which deeper soil layers store carbon appears to depend on several factors such as soil texture, management history, recovery time scale, and vegetation development. Furthermore, in our study as in many others, the stocks were evaluated by assuming constant bulk density. Further research is required to identify the most important factors influencing patterns of carbon storage in the soil.

In accordance with other studies (Knops and Tilman 2000) the C/N ratio increased in all depths with successional age, as a result of increasing input of partly recalcitrant organic matter with high C/N ratio due to high lignin concentrations, e.g. dead woody debris in the pioneer forest stage (Berendse 1990).

The total nitrogen pool did not significantly change over time. But there was a clear redistribution of N within the soil profile. Nitrogen supply significantly decreased in the deeper soil, and significantly increased in the upper soil. Hooker and Compton (2003) estimated a significant decline of nitrogen over a 115-year chronosequence after agricultural abandonment of $1.24 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the mineral soil (0-70 cm), and an accumulation of nitrogen in the plant biomass and organic layer that exceeded the losses from mineral soil. Other sources than plant uptake from the mineral soil, like inputs from atmospheric deposition, and bacterial N_2 fixation must contribute to nitrogen accumulation in regrowing ecosystems. Nitrogen inputs by atmospheric deposition for most parts of Western Europe averages at least $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Ellenberg et al. 2001). Since pioneer forests established on our study site within a relative short time period, a high amount of accumulated nitrogen in the above- and belowground biomass is to be expected. Schmidt (2001) reported for beech (*Fagus sylvatica*) forest ecosystem in the same region after disturbance ten years ago, aboveground pools of up to 15 kg N ha^{-1} for the herb layer and up to 200 kg N ha^{-1} for the tree species saplings (up to 9 m in height), and rates of nitrogen accumulation in above- and belowground biomass of tree species regeneration of about $2 \text{ to } 3 \text{ g N m}^{-2} \text{ yr}^{-1}$.

In contrast to Hooker and Compton (2003) and our findings, numerous studies report an increase of total nitrogen in the soil during succession (Woodmansee 1978; Bornkamm 1984; Stöcklin and Gisi 1989; Knops and Tilman 2000; Du et al. 2007). Possible reason for this discrepancy might be a failure of samples in the deeper soil layers, thus it is not possible to follow the profile changes over time. In their study on abandoned agricultural fields Knops and Tilman (2000) exclude pronounced profile changes due to mining of deeper soil nitrogen, since grasses are dominating on the fallows which have the highest amount of root biomass in the upper soil horizon. In our study on abandoned arable fields, vegetation structure changed rapidly from initial dominance of annuals (1-2 years) to a dominance of perennial herbs and grasses to shrub and tree colonisation five years after abandonment, and after about 20 years of succession plots exhibited pioneer forest stands (Dölle et al. 2008). Hence early incipient and intensive root penetration to the lower soil layers is apparent (Crocker and Major 1955; Olson 1958; Tilman 1988; Berendse 1990).

Although the total amount of nitrogen in 0-10 cm soil depth increased (most important for herb layer), the Ellenberg indicator value for nitrogen for the herb layers, both weighted and unweighted decreased over time. It suggests a decline in nitrogen availability since probably more nitrogen tied up in organic material. More in accordance with the changes in Ellenberg indicator value for nitrogen is the broader C/N ratio in the later stages, which suggests a lower mineralisation activity. At this

point data on N mineralisation rate would be more informative to describe nitrogen availability.

The mean Ellenberg indicator value for light in the herb layers showed the most distinctive decreasing rate over time. This emphasises light as being a main driving force for changes in plant species composition during succession (Tilman 1985; Pykälä et al. 2005). In forest ecosystems relative irradiance is commonly considered to be a main factor influencing the composition and diversity of the ground flora (Bazzaz 1990; Jennings et al. 1999; review Barbier et al. 2008).

The increasing convergence of the weighted and unweighted Ellenberg indicator values with increasing successional age is mainly caused by the more even distribution of the herb layer species in the pioneer forest stage (Dölle and Schmidt 2007). The herb layer coverage showed a sharp decline during time, and herb layer species in current pioneer forests ground vegetation showed a scattered composition. In contrast, throughout the early stages of succession, the herb layers were often dominated by one or a few species with high coverages (Schmidt 1981).

Soil reaction showed a slight but not continuous decrease by 0.2 pH units in 0-20 cm soil depth during succession, and a marginal decrease in the weighted Ellenberg indicator value for soil reaction emerged. Decreasing pH during succession is caused by the increasing biomass accumulation, caused by continuous extraction of base cations from the soil and a release of protons into the soil (van Bremen et al. 1984). Acidification by acid deposition may play a role, in our study there was no perceptible indication of ongoing acidification of the soil with progressive succession. It has been shown that changes in soil reaction during succession depend on initial pH. Thus, acidification during succession varies accordingly to soil type and initial buffering capacity (Blake et al. 1999; García et al. 2007) and only a slow decline in soil reaction on soils with high buffering capacity (like our study site) is expected (Leuschner and Gerlach 2000).

The decreasing amount of phosphorus in the soil indicates accumulation of phosphorus in the living plant biomass. Since in contrast to other main nutrients, phosphorus scarcely undergoes leaching processes and its pool in the soil is primary dependent on organic matter decomposition (Scheffer and Schachtschabel 2002), an increase especially in the lower soil is not expected. This was confirmed in our study by the more pronounced decline in the lower soil (10-30 cm), indicating relocation of phosphorus due to uptake by plant roots and storage in the plant biomass. Decreasing phosphorus supply in the soil with increasing time since abandonment of old-fields seems to be a common phenomenon (Warning 1996; Glemnitz and Wurbs 1999; Due et al. 2007).

4.5.2 Long-term effect of the initial plot treatment on soil chemical properties, light transmittance and vegetation attributes

The obvious divergent development of the study plots regarding the initial treatment in the beginning of the experiment was already described in Schmidt (1981). The observed gradient strongly supports the initial floristic composition model by Egler (1954) and the strong and persistent influence of the land use history on the plant community and the pathway of succession, respectively (Koerner et al. 1997; Dupouey et al. 2002; Bonet 2004; Dölle and Schmidt 2007). Which species dominate during succession can be determined by numerous factors like differences in seed dispersal, interannual differences in seed production (mast years), soil seed bank, germination requirements, relative growth rate, competition with other plant species, as well as various environmental parameters (Hard 1975; Schmidt 1981; Tilman 1988; Zeiter et al. 2006; Standish et al. 2007).

A main question therefore is, whether or not the plant community itself can induce the changes in environmental conditions which may in turn affect these processes, and with that influencing competitive interaction between the species during succession. Two main processes of competitive interaction between plant species induced by the modification of environmental conditions are facilitation and inhibition (Connell and Slayter 1977). Both processes can intensively interact during succession (Bornkamm 1988). On the one hand, the occurrence of *Quercus robur* as significant indicator for the herb layers of the *Betula* group explains facilitation, since *Q. robur* has a high demand on relative irradiance intensity in the recruitment and young-growth stage (Ellenberg et al. 2001). On the other hand there is a lack of pioneer tree species saplings, like *B. pendula* and *Salix caprea* in all current herb layers indicating inhibition of their germination and successful establishment.

There were significant correlations between the differences in current vegetation composition and the amount of SOC and nitrogen. Effects of canopy species on soil carbon content are well in accordance with other studies (e.g. Raulund-Rasmussen and Vejre 1995; Alriksson and Eriksson 1998; Hagen-Thorn et al. 2004). The differences between the three groups were more pronounced for nitrogen. The significantly higher amount of nitrogen in the forest floor (O_L) of the *Fraxinus* group can partly be explained by the significantly larger litter pool on the *F. excelsior* dominated plots. The lower amount of nitrogen in the deeper soil (20-30 cm) for the *Betula* group indicates a stronger nitrogen uptake of the *B. pendula* roots.

Mean Ellenberg indicator values for light showed a slight gradient with being highest in the *Betula* group. For the herb layers, values are comparable high in the range of half-light to semi-shade plants, although the relative PAR transmittance to the ground is at very low levels in all groups. Values for mature forest ecosystem in the same region with comparable relative irradiance intensity for the herb layer

exhibited clearly lower light indicator values, about 2-4 (Schmidt 2001; Ebrecht 2005; Schmidt 2005). The missing reflection of the low PAR transmittance to the ground by the herb layer is caused by scattered individuals of early successional species (Dölle et al. 2008). But since the closed canopy of the tree layers, together with the dense shrub layers permanently reduces the light availability on the ground, such light demanding species of open landscapes get repressed and a further decline is most likely. This is in accordance with Thomas et al. (1999) who pointed out that the light-vegetation relationship might be better explained by the past light regimes rather than by current light conditions because of the slowness of plant community changes. Therewith it might be an explanation for the lack of relationship between herb layer richness and PAR transmittance to the ground, in accordance with other studies (e.g. Weisberg et al. 2003).

4.6 Conclusion

Our study plots changed from open herbaceous to closed pioneer forest within relatively short time periods. Therewith light supply on the ground dramatically decreased over time. Nitrogen showed a clear accumulation in the upper soil but not in total, the C/N ratio significantly increased over time, and phosphorus showed a slight decreasing rate. Thus our results do not completely fit the resource ratio hypothesis proposed by Tilman (1985), but rather emphasise light as being a main influencing factor for vegetation development during succession.

Our findings clearly confirm the initial floristic composition model by Egler (1954). Differences caused by the initial treatments at the beginning of the experiment, fundamentally determined the initial floristic composition and the subsequent development of vegetation on the plots. The differences in plant species composition, in particular current tree species dominants in turn influenced light availability on the ground, as well as litter pools and nutrient supply in the soil.

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CHAPTER 5

The relationship between soil seed bank, above-ground vegetation and disturbance intensity on old-field successional permanent plots

Dölle, M. & Schmidt, W.
submitted



Picture: Plant trays with emerged seedlings; in front 0-10 cm, middle 10-20 cm and back 20-30 cm soil depth (photo taken by M. Dölle).

5.1 Abstract

Questions: How does disturbance and successional age influence richness, size and composition of the soil seed bank? What is the potential contribution of the soil seed bank to the plant community composition on sites differing in their successional age or disturbance intensity?

Location: Experimental Botanical Garden of Göttingen University, central Germany.

Methods: Above-ground vegetation and soil seed bank were studied on formerly arable fields in a 36-year-old permanent plot study with five groups of different disturbance intensity from yearly ploughing over mowing treatment to long-term undisturbed succession. The main focus was set on the comparison of species composition, seed densities and functional features of the soil seed bank and above-ground vegetation.

Results: The soil seed bank was mainly composed of early successional species of high disturbance habitats. The difference between seed bank composition and above-ground vegetation decreased with increasing disturbance intensity. The species of greatest quantitative importance in the seed bank was the non-native forb *Solidago canadensis*.

Conclusions: The regeneration ability of an existing plant community dramatically decreases with increasing successional age and decreasing disturbance intensity. For many grassland and woodland species the present study underlines the importance of dispersal capacity, due to low seed accumulation capacity and the fact that most of them do not build up persistent seed banks. Since rare and target species were almost absent from the soil seed bank, after local elimination their reappearance or the colonisation of a new site would be dependent on invasion from elsewhere.

Keywords: C-S-R strategy; Grassland; Old-field succession; Recruitment limitation; *Solidago canadensis*; Ploughing.

Nomenclature: Wisskirchen & Haeupler (1998).

5.2 Introduction

During the last century farming practices throughout Europe have drastically changed due to intensification, characterised by the use of high-yielding crop varieties, fertilisation and pesticides. In addition, the abandonment of less productive marginal sites has caused considerable decline in agricultural ecosystems with a traditional small-scale mosaic of different habitats of high species richness. Both processes are considered to have detrimental effects on the biodiversity of agricultural landscapes as well as being main causes for the decrease in vascular plant species richness (Korneck et al. 1998; Waldhardt 2003).

The aim of most restoration projects is to enhance the presence and abundance of species that are characteristic of reference or target communities. In this study, the potential role of the soil seed bank in various old-field communities was investigated. Such insight into seed bank composition and dynamics in successional habitats may contribute to a more accurate prediction of the restoration success of degraded plant communities in general. Moreover, the knowledge of the soil seed bank is of vital importance for the estimation of the resilience of a plant community.

The role of the soil seed bank for initiating the re-colonisation of disturbed sites is well studied (e.g. Bakker et al. 1996b; Bakker et al. 2005; Luzuriaga et al. 2005). In many cases it has been shown that the potential of the soil seed bank as resource for recovery after disturbance is limited depending on plant community, seed densities or germination requirements (Brown & Oosterhuis 1981; Milberg 1995; Davies & Waite 1998; Bekker et al. 2000; Jalili et al. 2003). Several studies suggest a correlation between land use disturbance history and seed bank composition, indicating an increased abundance of early successional species in high disturbance sites (Bekker et al. 1997; Honnay et al. 2002; Matus et al. 2003). Some studies offer a comparison of soil seed bank composition with previous and present above-ground vegetation (e.g. Grandin & Rydin 1998; Matus et al. 2003) or the relationship between disturbance levels of historical land use and soil seed bank composition (e.g. Thompson 1978; Korb et al. 2005; Wellstein et al. 2007). Little information exists on how the composition of seed banks changes during succession (Thompson 1978; Donelan & Thompson 1980; Kalamees & Zobel 1998; Bekker et al. 2000). Therefore, we investigated the soil seed banks on five groups of long-term permanent plots of different disturbance intensity, simulating different management regimes, on a former arable field. They provide a gradient from highly disturbed habitats by ploughing, featuring open herbaceous vegetation dominated by annual plants, to plots with different mowing regimes, featuring various closed ruderal herbaceous or grassland vegetation, to long-term undisturbed plots (for 36 years) featuring closed pioneer forest stands. Continuous data on the vegetation development during succession make it possible, to determine its influence on current seed bank composition. In view of

this, the primary aim of our study was to assess and quantify the seed bank diversity and its relation to above-ground vegetation and disturbance intensity on old-field successional plots. In order to find general explanations to plant community patterns and processes, the identification of functional traits were implicated.

We address the following research questions: (i) How does disturbance regime and successional age influence richness, size and composition of the soil seed bank? (ii) What is the potential contribution of the soil seed bank to the plant community composition on sites differing in their successional age or disturbance intensity?

This study on long-term permanent plots integrates a descriptive approach with the opportunity to draw conclusions for the use of the gained knowledge to estimate the potential of the soil seed bank on different disturbed habitats. The information will be particularly useful for the management or restoration of various grassland or successional ecosystems.

5.3 Materials and methods

5.3.1 Study site and experimental design

All plots of the present study are part of a long-term experiment located in the Experimental Botanical Garden of Göttingen University, Lower Saxony, Germany (180 m a.s.l., 51°34'0"N, 9°56'60"E; mean annual temperature: 8.5 °C; average annual rainfall: 635 mm). Initiated by Heinz Ellenberg, the experiment was set up on a former arable field cultivated until 1968 on deep, calcareous and fertile soil (alluvial loamy brown earth). Regional forest vegetation is dominated by *Fagus sylvatica* (Fagion sylvaticae) which is the natural vegetation type (Bohn et al. 2003). The surrounding suburban landscape may be characterised by a mixture of arable fields, grasslands, ruderal communities and forests. A detailed description of the study site and experimental design is given in Schmidt (1981, 1993). The total size of the plots varies between 125 and 200 m². The plots are each subdivided into three subplots (total number of subplots: 69). For a concise presentation of the results, the study plots were arranged into five groups of different disturbance intensity given by a particular annual treatment (number of subplots in parentheses):

- Group P1: Soil disturbance once per year, ploughing in spring (3) or summer (3),
- Group M2-8: Intensive mowing treatment during summer; twice (6), four (6) or eight times (6) per year,
- Group M1: Extensive mowing treatment, each once per year in spring (6) or fall (9),
- Group S23: Short-term undisturbed succession for 23 years (18),
- Group S36: Long-term undisturbed succession for 36 years (12).

5.3.2 Seed bank sampling

Soil cores were collected in early march 2004, after winter stratification but before emergence of early spring annuals. Using an 8 cm diameter soil corer, three soil samples per subplot were removed to a depth of 30 cm. After removing the litter layer the soil cores were divided into 0-10 cm, 10-20 cm and 20-30 cm sections. For further analysing soil samples of the respective depths per subplot were mixed. The soil samples represent 150.9 cm² of the soil surface in each subplot. The indirect seedling emergence method was used for analysing (Thompson et al. 1997). After sieving of the soil samples to remove stones, roots and rhizomes they were spread in 25 x 45 cm plant trays on a sterilized sandy subsoil of ca. 2 cm depth. The flats were put into an unheated greenhouse and regularly watered from above. The trays were covered with gauze to prevent contamination by external seeds. Over a period of one year (March 2004 to February 2005) all emerging seedlings were identified as soon as possible, counted and removed. Species that were not easy identifiable as seedlings were removed and grown on until identification was possible. To ensure maximum seed germination, at two times over a period of one week the soil was dried out, mixed, and then watered again, so that seeds on the ground would be brought to the surface and with that to possibly better conditions for germination.

5.3.3 Above-ground sampling

Above-ground vegetation was recorded on species level including record of coverage of all vascular plant species in the same year in which the seed bank was sampled. The vegetation sampling was performed on the whole subplot area. In order to assess the period of extinction of a certain species, vegetation relevées from 1969 onwards are available for all study plots. From 1969 until 1993 vegetation was recorded annually, afterwards vegetation relevées were conducted in 1995, 1999 and 2004. For the undisturbed succession plots vegetation relevées were conducted twice per year in the beginning (1969-1987) and once per year since trees have started to dominate. For the treatment plots vegetation relevées were conducted twice per year throughout, during spring and in the vegetation period (prior the treatment) when the development of plants was in its optimum.

5.3.4 Data analysis

For quantitative analysis, the seed bank data were recalculated into numbers of seeds per m². The seed bank type of each species was determined according to the classification scheme by Thompson et al. (1997), using abundance of seeds in upper and lower layers of soil and presence-absence of species in the vegetation. For species present in the above-ground vegetation only, the seed bank database by Thompson et al. (1997) was consulted. Three main types of seed longevity are defined therein –

transient (seed surviving less than 1 year), short-term persistent (seed surviving 1-5 years), long-term persistent (seed surviving for > 5 years).

To compare the composition and abundance of species in the above-ground vegetation and the soil seed bank we applied a Detrended Correspondence Analysis (DCA) using the program PC Ord 5.12 (McCune & Mefford 1999). DCA was used to identify differences in plant species composition and was applied to the species frequency data. Simultaneous ordination of above-ground vegetation and seed bank samples was performed. Since the abundance or coverage of a species is not only dependent on the site conditions but might be a specific characteristic of a certain species, the data were transformed by $y = x^{0.25}$ to minimise differences. The floristic overlap between the seed bank and the above-ground vegetation was calculated by using the SØRENSEN similarity index. Additionally, the seed accumulation index (SAI) as a continuous value of seed persistence was calculated to express the relationship between the presence of a certain species in the above-ground vegetation and the soil seed bank (Hölzel & Otte 2004). The index ranges between zero (only present in above-ground vegetation) and 100 (only present in the soil seed bank).

For analysing characteristics of the plant community, a coarse habitat classification following Ellenberg et al. (2001), data on seed mass of the species (Flynn et al. 2006), and the established strategy (Grime et al. 1988; in case of missing values Klotz et al. 2002) were considered. Abundance-weighted evaluation for all species found was done, i.e. in case of the soil seed bank, weighted for the number of seeds germinated from all soil samples or in above-ground vegetation percentage coverage of a species.

For all normally distributed data with homogeneous variances, differences between the five disturbance types were tested by one-way ANOVA with subsequent post-hoc Scheffé-test. The data were log-transformed to fulfil the assumption of normally distributed data required for ANOVA. Data showing neither normal distribution nor homogeneous variances were compared by Kruskal-Wallis-H-test with subsequent Mann-Whitney-U-test. All tests were carried out using STATISTICA 6.0 (Anon. 1998).

5.4 Results

5.4.1 Seed bank richness and size

A total of 10 042 seeds from 105 species of vascular plants germinated. The total seed bank species richness per plot ranged between 20 under pioneer forest community (short-term succession) and 39 under species rich grassland community dominated by *Solidago canadensis*, *Arrhenaterum elatius* and *Filipendula ulmaria* (mowing once per year). The soil seed bank richness per subplot was significantly lower for the long-term succession (Fig. 5.1A).

Seed density showed a high variability between the study plots. Highest mean

seed density was recorded for the plots of yearly tillage (Fig. 5.2). It was markedly lower for the long-term succession plots. Highest absolute seed density was found in *S. canadensis* dominated vegetation on a plot with mowing treatment once per year (49 560 seeds per m² in 0-10 cm). On average 66 % of all counted seeds were found in the top 10 cm of the soil, 25 % in 10-20 cm depth and 9 % in 20-30 cm depth. For all types seed density and the number of species in the soil seed bank decreased with depth. The plots with yearly tillage and the short-term succession plots showed highest seed density in lower soil layers.

The most widely distributed and dominant species in the soil seed bank was the non-native forb *Solidago canadensis* which was frequent on all plots (App. 5.1). It was contained in 71 % of all samples and accounted for 34 % of all emerged seedlings. *Arenaria serpyllifolia*, *Betula pendula* and *Chaenorhinum minus* were also widely distributed with comparatively high seed densities.

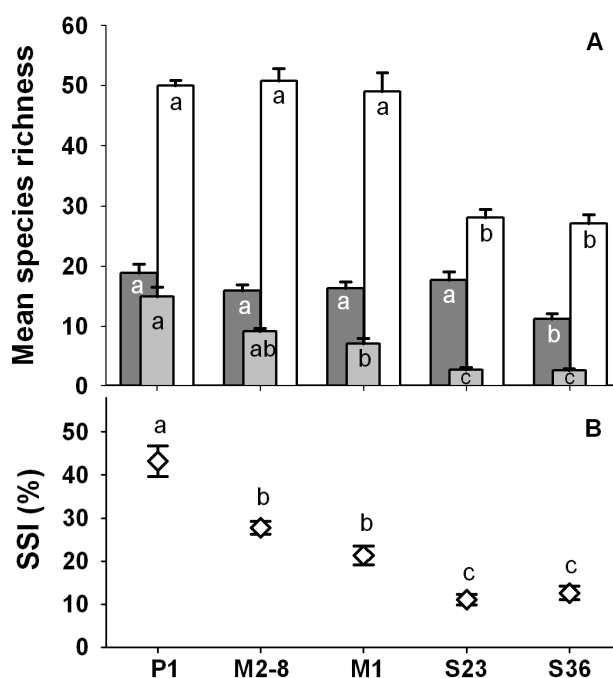


Fig. 5.1A. Mean species richness per subplot in the seed bank (■), the above-ground vegetation (□), and the species overlap (◻) between both and B. mean Sørensen Similarity Index (SSI %) for the five disturbance groups (\pm SE). Different letters indicate significant differences ($p < 0.05$) within one group between the five disturbance groups according to Scheffé-test after one-way ANOVA. Soil seed bank: $F=6.61$, $p=0.000$; above-ground vegetation: $F=39.02$, $p=0.000$; species overlap: $F=34.73$, $p=0.000$; SSI: $F=37.4$, $p=0.000$. (P1=ploughing once per year, M2-8=mowing two to eight times per year, M1=mowing once per year, S23=old-field succession for 23 years, S36=old-field succession for 36 years).

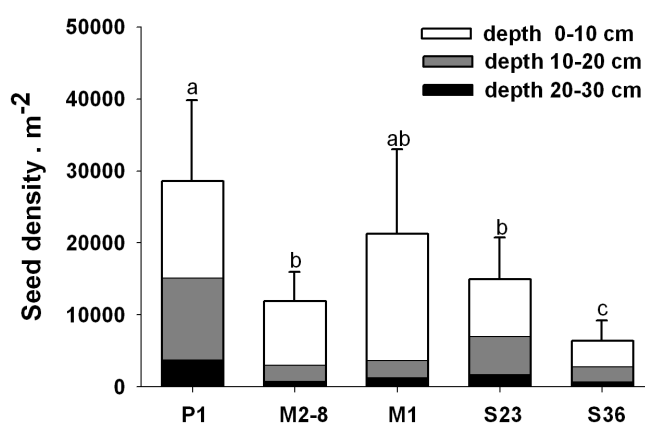


Fig. 5.2. Density distribution of mean seeds. m^{-2} (\pm SE for 0-30 cm) as a function of soil depth within the five disturbance groups (abbreviations as in Fig. 5.1). Significant differences for mean seed density in 0-30 cm are indicated by differing letters (Kruskal-Wallis-H-test: $H=24.88$, $p=0.000$ with post-hoc Mann-Whitney-U-test $p < 0.05$).

5.4.2 Above-ground vegetation and its relationship to seed bank composition

Mean species richness in the current above-ground vegetation was significantly higher on the plots with yearly disturbance measure (tillage or mowing) than on the plots of undisturbed succession (Fig. 5.1A). In the combined DCA of above-ground and soil seed bank composition the above-ground plots show a distinct gradient along the first axis, whereas the seed bank plots are clustered in the first quadrant (Fig. 5.3). It emphasises a high dissimilarity in the above-ground vegetation but a high similarity in soil seed bank composition. The distance between above-ground and seed bank species composition increased with decreasing disturbance intensity indicating an increasing floristic dissimilarity (Fig. 5.3). According to this, the SØRENSEN Similarity Index (SSI %) was significantly highest on the plots with annual soil disturbance and both groups of undisturbed succession showed significantly lowest similarity between soil seed bank and above-ground vegetation (Fig. 5.1B).

Several species showed a close correlation in time between above-ground and seed bank population and were widely distributed (e.g. *Betula pendula*, *Clematis vitalba*, *Hypericum perforatum*, *Poa trivialis*, *Solidago canadensis*, *Taraxacum officinale*). A few species were restricted to a specific disturbance group (e.g. *Cardamine hirsuta* in both mowing groups). Another group of species had restricted above-ground populations to the intensively disturbed plots, but were frequent in the seed bank population of almost all disturbance types (e.g. *Aethusa cynapium*, *Anagallis arvensis*, *Arenaria serpyllifolia*, *Chenopodium album*, *Euphorbia helioscopia*, *Papaver rhoeas*, *Picris hieracioides*, *Sonchus oleraceus*, *Viola arvensis*). Several species found only as seeds in the soil although did not contribute to the above-ground vegetation of the respective plots (e.g. *Chaenorhinum minus*).

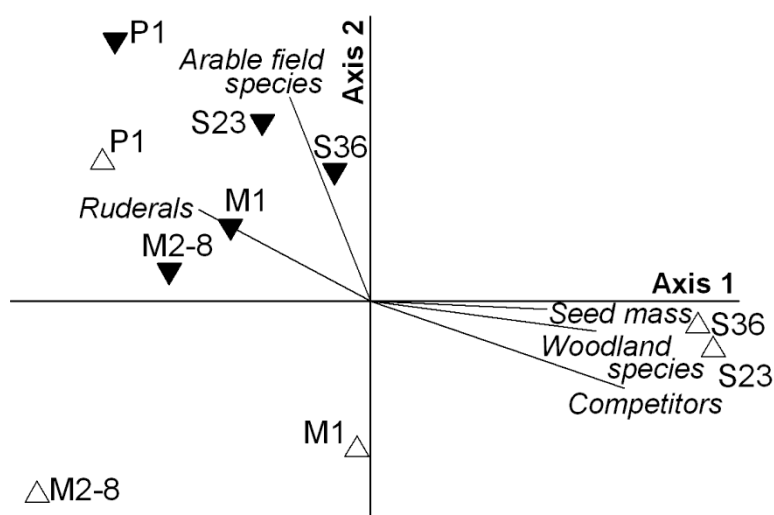


Fig. 5.3. DCA of the above-ground (\triangle) and "below-ground" (∇) vegetation of the five disturbance groups (abbreviations as in Fig. 5.1) (r^2 : axis 1=0.42, axis 2=0.29). Centroides are plotted, but ordination was done with all subplot data (Dist. Measure: Bray-Curtis, length of gradient: axis 1=3.11, axis 2=3.35). To present a bi-plot, different parameters were correlated with the axes of the ordination (correlation threshold: $r \geq 0.65$). Pearson r of all highly significant ($p \leq 0.001$) correlated parameters ($r \geq 0.65$) with the two first ordination axis: Seed mass axis 1: $r=0.814$, Woodland species axis 1: $r=0.847$, Arable field species axis 2: $r=0.675$, Competitiveness axis 1: $r=0.734$, Ruderals axis 1: $r=-0.684$. In case of the above-ground vegetation quantities of species were measured as cover and in case of the seed bank composition as frequency. Data were transformed by $y=x^{0.25}$.

5.4.3 Seed bank type and functional aspects

Referring to the classification scheme by Thompson et al. (1997) 31 % of the seed bank species were classified as transient, 41 % as short-term persistent, and 28 % as long-term persistent (App. 5.1). Species occurring in the above-ground vegetation only were mainly of the short-term persistent type (85 %). For the classification of the above-ground species into the four principal habitat types a clear gradient from high seed accumulation of arable field species (56 % with $SAI \geq 50$) to distinctly low or no seed accumulation of woodland species (85 % with $SAI = 0$) revealed (Fig. 5.6, App. 5.1).

The plots of undisturbed succession showed the highest dissimilarity between soil seed bank and above-ground vegetation referring to habitat classification and C-S-R strategy type. The proportion of ruderal strategy was in general higher in the soil seed bank than in the above-ground vegetation (Fig. 5.5). Except for the mowed plots it occurred inversely to competitiveness. The highest amount of competitive strategy in the soil seed bank was calculated for the plots mowed once per year, which showed in case of strategy type the highest similarity between soil seed bank and above-ground vegetation. In spite of no significance of arable field species and ruderal strategists in the above-ground vegetation of the undisturbed succession plots, in their soil seed

banks they contributed to a higher amount than in the soil seed banks of the mowed plots. Whereas above-ground compositions of the different disturbance groups were highly dissimilar in case of the habitat classification, for the seed bank composition of all groups more than 50 % of the distribution were assigned to highly disturbed habitats, i.e. arable fields and ruderal sites (Fig. 5.4).

Mean seed mass differed significantly between above-ground and soil seed bank composition for all disturbance groups (Fig. 5.7). The above-ground vegetation of the undisturbed succession plots showed higher seed mass than the disturbed plots despite being significantly different only for the plots of repeated mowing. No significant difference in mean seed mass was found for the soil seed bank composition of the five groups.

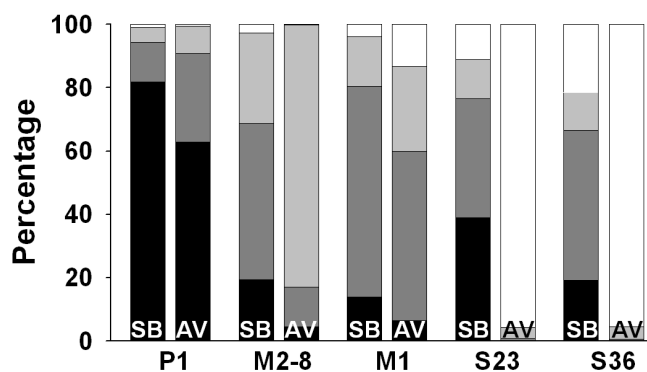


Fig. 5.4. Percentage contribution of species associated with four principal habitat types; arable fields (■), ruderal sites (■), grasslands (■) and woodlands (□) according to Ellenberg et al. (2001) to the soil seed bank (SB) and above-ground vegetation (AV) in the five disturbance groups (abbreviations as in Fig. 5.1).

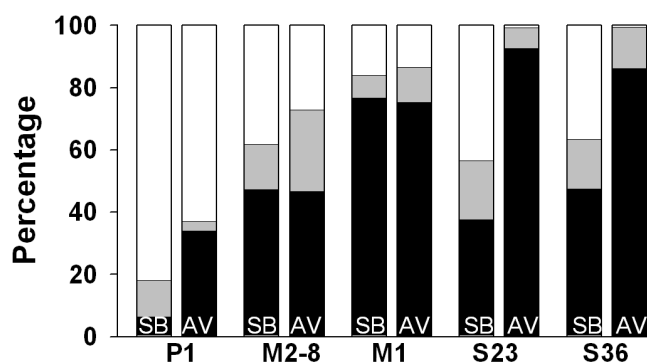


Fig. 5.5. Percentage contribution of C-S-R strategy type according to Grime et al. (1988) divided into competitors (■), stress tolerators (■) and ruderals (□) of soil seed bank (SB) and above-ground vegetation (AV) of the five disturbance groups (abbreviations as in Fig. 5.1).

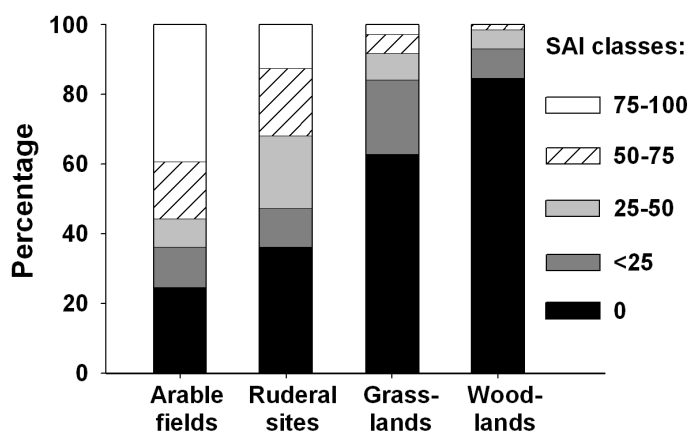


Fig. 5.6. Percentage contribution of different seed accumulation index (SAI) classes (Hölzel & Otte 2004) in the four principal habitat types according to Ellenberg et al. (2001) for all species in the above-ground vegetation.

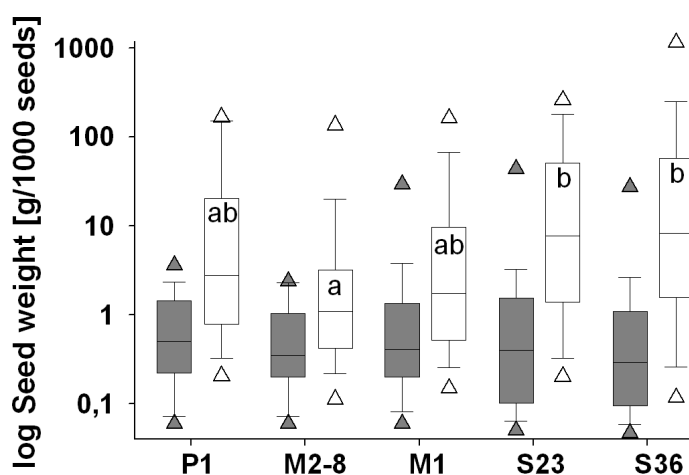


Fig. 5.7. Box-Whisker-plots of seed weight (g/1000 seeds) of all species occurring in the soil seed bank (■) and all species occurring in the above-ground vegetation only (□) for the five disturbance groups (abbreviations as in Fig. 5.1). Significant differences ($p < 0.05$) are indicated by differing letters according to Scheffé-test after one-way ANOVA ($F=5.65$; $p=0.000$). For all types differences between soil seed bank and above-ground vegetation differ significantly ($p < 0.001$) according to Mann-Whitney U-Test after Kruskal-Wallis ANOVA.

5.5 Discussion

5.5.1 Density of buried seeds and seed bank richness

Ignoring for the moment the repeatedly mowed plots, the overall trend clearly shows a declining buried seed density during succession and with decreasing disturbance intensity. The findings correspond well with various other studies indicating an increase in seed density with intensified management (e.g. Bekker et al. 1997; Matus et al. 2005), or a decreasing seed bank density with increasing successional age (Thompson 1978; Donelan & Thompson 1980; Davies & Waite 1998; Bossuyt et al. 2002). The non-conforming results for the repeatedly mowed group, which showed comparatively low seed densities, may be explained by the high mowing frequency, probably preventing the seed setting of many species (Kalamees & Zobel 1998; Mitlacher et al. 2002). However Matus et al. (2005) found increased seed density for intensive grazed sites. Thus it seems less a question of land-use intensity than its nature. For many species the dispersal by pasture livestock (Fischer et al. 1996; Römermann et al. 2005; Martin & Wilsey 2006) is of major importance and can thus enrich the soil seed bank unlike intensively used meadows on which, often before plants can produce flowers, plant biomass is removed.

A clear depletion with increasing soil depth, as typical for undisturbed soil profiles (Blomqvist et al. 2003; Matus et al. 2003) was obvious for the long-term succession and the mowed plots, for which soil disturbance ceased 36 years ago. In case of the undisturbed succession plots the seed bank richness was also significantly affected by the time since last soil disturbance. After 22 years of undisturbed succession comparatively high numbers of arable field species were extant, whereas after 36 years a clear decline has taken place. An exponential depletion over time for arable-land species was identified by Waldhardt et al. (2001) starting around ten years after abandonment; within 20 years the species pool in the soil was almost exhausted. However in our study the time period of seed bank depletion for species typical to arable cultivation clearly exceeds 20 years. The seed banks of the long-term succession plots still contained arable-land species (e.g. *Arenaria serpyllifolia*, *Chenopodium album*, *Euphorbia helioscopia*, *Papaver rhoeas*, *Sinapis arvensis*, *Viola arvensis*). An age of at least 50 to 70 years for ruderal and arable species found as seeds in the soil on scrub-covered old-field successional plots was stated in Davies & Waite (1998). Therefore, the period of exhaustive depletion seems to be highly variable and probably dependent on various factors, like soil characteristics, climate conditions or specific composition of the above-ground vegetation.

5.5.2 Comparison between seed bank and above-ground composition

With increasing successional age the intersection of vascular plant species occurring in both above-ground vegetation and soil seed bank significantly decreased. A low correspondence between soil seed bank and above-ground vegetation seems to be a general pattern (e.g. Donelan & Thompson 1980; Davies & Waite 1998; Blomqvist et al. 2003; Bisteau & Mahy 2005; Vilà & Gimeno 2007). In comparison to the high variability in the above-ground vegetations, the differences in soil seed bank compositions were low. The low occurrence of grassland species in the mowed plots and of woodland as well as grassland species in the succession plots clearly point out that the soil seed bank acts only to a limited extend as a reservoir or memory of the vegetation development of a site. In addition, the soil seed banks were far less diverse than the corresponding above-ground vegetations. This as well seems to be a general phenomenon (e.g. Blomqvist et al. 2003; Wellstein et al. 2007). It implies that seed banks of most species occurring in above-ground vegetation are transient. Only four species (3 %) of the long-term persistent type (*Euphorbia amygdaloides*, *Malva moschata*, *Polygonum persicaria*, *Veronica serpyllifolia*) were found in the above-ground vegetation only. Single exceptions are to be found in literature, for example the much richer seed bank than above-ground vegetation for an arable field described by Donelan & Thompson (1980).

Beside the variation of seed persistency of species (Thompson & Grime 1979; Thompson et al. 1997), spatial variation in size and composition of seed rain (Thompson 1986) may cause a low similarity between seed bank and above-ground vegetation. A high dissimilarity in species composition between each single seed bank sample underlines this assumption. A main reason might be that the majority of seeds remain within a few metres from the parent plants (Bakker et al. 1996b; Donath et al. 2003). Therefore the probability of a species being detected in the soil declines with decreasing population size and degree of coverage in the above-ground vegetation.

Several species were present as seeds in the soil which were not present in the current above-ground vegetation of the respective plots. Their amount increased with decreasing disturbance intensity, which might be caused by the increasing lack of niche availability or the dense vegetation canopy in the less disturbed habitats, preventing seed germination. Altogether 14 species occurred in the seed bank which did not occur in the current above-ground vegetation of any plot. Most of them are light seeded (<1g/1000 seeds) and mainly dispersed by wind over longer distances (these are *Chaenorhinum minus*, *Conyza canadensis*, *Epilobium ciliatum*, *Epilobium hirsutum*, *Epilobium parviflorum*, *Plantago intermedia* and *Sagina procumbens*). For them the presence in the soil seed bank might reflect their dispersal ability more than their ability to persist in the soil. Primary occurrence in the upper soil layer underlines that assumption. However, together with *Parietaria judaica*, *Robinia pseudoacacia* and

Solanum dulcamara, which never occurred in the above-ground vegetation, they might be an indicator of the relevance of recruitment limitation (Tilman 1997; Zobel et al. 2000; Zeiter et al. 2006). However, species found in the soil seed bank only were small components and rare grassland or woodland species were not among. Our results confirm that the chance of finding new target species in the seed bank is small (e.g. Bekker et al. 1997; Blomqvist et al. 2003). They often occur with low population size and coverage. Even if due to insufficient seed bank samples, some species were possibly missed. It might be assumed that they are present in such low numbers, that they would not considerably contribute to the establishment of new plant species (Blomqvist et al. 2003). But either by newly arriving seeds or by temporary storage in the soil seed bank, various target grassland species (e.g. *Alopecurus pratense*, *Bromus erectus*, *Phleum pratense*, *Ranunculus acris*, *Scabiosa columbaria*) in case of the mowed plots, and species typical to closed forests (e.g. *Cephalanthera damasonium*, *Daphne mezereum*, *Lathyrus vernus*) in case of the undisturbed succession plots, could establish themselves to the study site. All of them are components of the vegetation close by (Garve 2007).

5.5.3 Functional aspects

In accordance with other studies carried out in recently disturbed habitats (e.g. Milberg & Hansson 1993; Luzuriaga et al. 2005), the seed banks were dominated by early successional species of arable cultivation or disturbed ruderal sites. The above average occurrence of ruderal strategists in the soil seed banks can be seen as a function of their rapid growth connected with high seed production and the ability to build up long-term persistent seed banks as adaptations to highly disturbed habitats (Thompson et al. 1997; Fenner & Thompson 2005). The significant differences in average seed mass between soil seed bank and above-ground vegetation support the hypotheses of negative correlation between seed size and seed longevity (Bekker et al. 1998). Forest species are typically large seeded, which is necessary for establishment in shaded conditions and for germination under litter (Crawford 1989; Eriksson 1995). In general the reproductive capacity of late successional species is low and thus they are constrained to invade sites mainly by new propagules.

The effect of different disturbance intensity on functional features was less pronounced than the time since last soil disturbance. It is reflected in the higher proportion of ruderal strategists, lower seed weight, and higher amount of arable field species in the soil seed bank of the short-term succession plots in contrast to the long-term succession and mowed plots. Mowed plots showed a higher functional similarity between seed bank and above-ground vegetation than undisturbed succession. A possible reason is suggested by the fact that at least some grassland species tend to accumulate in the soil seed bank, whereas forest species show exceedingly low seed

accumulation capacity. However forest and grassland species were not well represented in the soil seed banks and their occurrence mainly in the upper soil layer suggests a more transient seed bank (Thompson et al. 1997; Bossuyt et al. 2002). Seed bank persistency is largely seen as a key parameter in the regeneration of plant communities (McDonald et al. 1996; Bekker et al. 1997). The risk of local extinction increases in species with short-lived seed banks, particularly in fragmented landscapes where target communities are distant (Stöcklin & Fischer 1999). It is assumed that the restoration of species rich meadows (Milberg & Hansson 1993; Vécrin et al. 2002; Matus et al. 2003; Wellstein et al. 2007) or late successional, less dynamic plant communities (Bekker et al. 2000; Bossuyt et al. 2002) cannot rely on the soil seed bank since most of the target species have transient seed banks and are absent from the soil especially after long-term abandonment (Mitlacher et al. 2002). In many cases only few species dominate the soil seed bank, and rare and threatened species are hardly represented at all (Jentsch & Beyschlag 2003; Matus et al. 2003).

In this study *Solidago canadensis* as perennial species with vegetative spread ability was most frequent in the soil seed bank with outstanding high seed densities. Such highly competitive species, also referred to as “superspecies” (Huston & Smith 1987), often do not fit the general pattern of functional classification. Wind dispersal and high production of light seeds promotes above average propagule pressure, which is assigned as a characteristic attribute of many successful invaders (Williamson 1996). In contrast, many rare and locally excluded species are due to short distance dispersal ability and short-term seed viability in an inferior position and thus often underrepresented in the soil seed bank (Blomqvist et al. 2003).

5.6 Conclusion

The results demonstrate that with increasing disturbance intensity the difference between soil seed bank and above-ground vegetation decreases. The regeneration ability of an existing plant community dramatically decreases with increasing successional age or decreasing disturbance intensity. Since species of disturbed habitats are characterised by high seed accumulation capacity and seed bank persistency, the regeneration potential from the soil seed bank after severe disturbance tends to the establishment of a pioneer community. For many grassland and woodland species the present study underlines the importance of dispersal capacity, due to low seed accumulation capacity and the fact that most of them do not build up persistent seed banks. Since rare and target species were almost absent from the soil seed bank, after local elimination their reappearance or the colonisation of a new site would be dependent on invasion from elsewhere. Therefore, habitat fragmentation plays therefore an important role for population dynamics and

conservation issues. In particular, rare plant species with low dispersal capacity for longer distances are dependent on refuge populations nearby.

5.7 Acknowledgements

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5.9 Appendix

Appendix 5.1. Soil seed bank and above-ground (AV) composition of the five disturbance groups arranged in order of seed bank frequency or in case of species in above-ground vegetation only in order of above-ground frequency (abbreviations as in Fig. 5.1). Abundance lower than 0.1 is noted as <0.1. Habitat type (Ellenberg et al. 2001) is divided into a=arable fields, g=grasslands, r=ruderal sites and w=woodlands. Strategy type (Grime et al. 1988; italics Klotz et al. 2001): c=competitive, s=stress-tolerant, r=ruderal and cr, cs, sr, csr =intermediate strategies. Seed bank persistence is categorized according to the database by Thompson et al. (1997) into three groups: 1=transient, 2=short term persistent, 3=long term persistent and in parentheses the result based on the classification scheme by Thompson et al. (1997). Seed weight (Flynn et al. 2006) is given in g per 1000 seeds (n.s.=not specified). SAI: seed accumulation index (Hölzel & Otte 2004).

Type:	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
Species	Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
In seed bank only															
<i>Chaenorhinum minus</i>	17	67	94	191	263						a/r	r-sr	2 (3)	0.074	100
<i>Plantago major subsp. intermedia</i>		39	5	427	4						r	cr	2 (1)	0.04	100
<i>Sagina procumbens</i>	8			1	1						r	r-csr	2 (2)	0.02	100
<i>Solanum dulcamara</i>	4			1	3						r	cr	2 (1)	0.07	100
<i>Epilobium roseum</i>				13	4						r	cs	n.s. (3)	0.09	100
<i>Conyza canadensis</i>				1	1						g	csr	1 (2)	0.2	100
<i>Paretaria judaeca</i>		6									r	c	2 (1)	0.1	100
<i>Epilobium parviflorum</i>	5										w	c	n.s. (3)	19.8	100
<i>Trifolium campestre</i>			4								g	r	1 (1)	0.25	100
<i>Melilotus albus</i>	2										a	cr	n.s. (3)	2.02	100
<i>Epilobium hirsutum</i>	1										g/r	csr-c	n.s. (2)	44	100
<i>Astragalus glycyphyllos</i>		1									g	c	1 (3)	5.8	100
<i>Epilobium ciliatum</i>					1						g	cs	1 (2)	0.08	100
<i>Robinia pseudoacacia</i>					1						w	csr	n.s. (3)	0.22	100
In seed bank and above-ground vegetation															
<i>Solidago canadensis</i>	8	680	2094	408	211	0.1	0.2	66	0.3	0.1	r	c	1 (2)	0.06	67
<i>Arenaria serpyllifolia agg.</i>	303	40	18	287	14	1.8	<0.1				a	sr	2 (3)	0.07	88
<i>Betula pendula</i>	7	24	32	162	110	<0.1		0.3	16	53	w	c-cs	2 (2)	0.29	42
<i>Papaver rhoeas</i>	48	4	19	159	9	1.2	<0.1	0.1			a	r	2 (3)	0.3	85
<i>Poa trivialis s.l.</i>	4	14	140	39	31	0.4	5.7	3.3	<0.1	<0.1	g	csr-cr	2 (2)	0.2	56
<i>Chenopodium album</i>	27	11	24	82	18	0.8					a	r-cr	2 (3)	0.8	95
<i>Anagallis arvensis</i>	26	14	15	65	10	0.7	<0.1	<0.1			a	r-sr	3 (3)	0.5	89
<i>Clematis vitalba</i>	3	12	6	52	40	<0.1	<0.1	7.2	7.9	4.0	w	c	2 (1)	2.3	36
<i>Sonchus oleraceus</i>	5	21	5	17	22	<0.1	<0.1				a/r	r-cr	2 (2)	0.3	95
<i>Taraxacum sect. Ruderalia</i>	1	42	5	5	3	0.7	1.8	0.5		<0.1	g/r	r-csr	n.s. (2)	0.7	49
<i>Viola arvensis</i>	5	5	11	22	9	0.7	<0.1	<0.1			a	r	2 (3)	0.42	82
<i>Sonchus asper</i>	2	2	6	12	4	0.4	0.1	<0.1			a/r	r-cr	1 (2)	0.28	70
<i>Cerastium holosteoides</i>	8	209	44		1	0.2	1.6	1.2			g	cr	n.s. (2)	0.06	60
<i>Veronica persica</i>	144	53	3	17		2.8	0.1				a/r	r	2 (3)	0.59	78
<i>Hypericum perforatum</i>	21		34	157	4	0.2	0.1	0.8	<0.1	<0.1	g	cr-csr	2 (2)	0.1	72
<i>Fallopia convolvulus</i>	121		4	42	3	2.2	<0.1				a	r	2 (3)	3.42	85
<i>Cerastium glomeratum</i>	4	71	5		1	0.2	0.5	<0.1			a	r	2 (2)	0.23	69
<i>Poa pratensis s.str.</i>		57	14	3	7	0.1	13	0.9		0.4	g	csr	1 (2)	0.2	27
<i>Euphorbia helioscopia</i>	26	1		45	3	2.7					a	r	3 (3)	2.31	79

Appendix 5.1. (continued)

Species	Type	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
		Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
<i>Aethusa cynapium</i>		22	1	2	42		0.5	<0.1				a	c	2 (3)	1.35	88
<i>Valeriana officinalis s.str.</i>		11	18	37	9		<0.1	0.8	0.2	0.1		g	csr	1 (1)	1.04	9
<i>Myosotis arvensis</i>		36	3		16	1	1.5	0.6	0.7			a	r-sr	2 (2)	0.9	47
<i>Picris hieracioides</i>			17	26	3	12	<0.1	1.4	0.2			r	csr	3 (2)	1.44	60
<i>Ranunculus repens</i>		15	5	3	12		3.4	3.0	0.1			g/r	cr	3 (3)	2.3	33
<i>Veronica polita</i>		5	18	1	5		0.2	0.8				a/r	r	3 (2)	n.s.	56
<i>Fragaria vesca</i>			4	6	11	9	0.1	0.6	4.2	1.8	0.7	g	csr	1 (2)	0.3	24
<i>Agrostis stolonifera</i>			7	12	3	5	0.7	2.4	1.2	0.1		g	cr	1 (2)	0.05	34
<i>Trifolium dubium</i>		3	15	6	2		2.2	1.1	0.3			g	r-sr	3 (3)	0.4	37
<i>Aphanes arvensis</i>		1	2	4	3		0.3	0.7	0.2			r	r-sr	1 (2)	0.18	45
<i>Epilobium palustre</i>			2	2	4	2		<0.1				g	csr-s	1 (2)	0.05	93
<i>Fumaria officinalis</i>		4		1	3	2	0.7					a	r	3 (3)	3.28	66
<i>Cirsium arvense</i>		1		2	3	3	1.9	0.3	0.5			a/r	c	1 (2)	1.1	31
<i>Sinapis arvensis</i>		621			49	3	13					a	r	3 (3)	2.4	84
<i>Epilobium tetragonum</i>				4	52	18	<0.1	<0.1				r	cs	2 (2)	0.12	95
<i>Capsella bursa-pastoris</i>			16		30	2		0.1				a/r	r	2 (3)	0.1	75
<i>Medicago lupulina</i>		1	34	11			0.1	1.7	0.1			g	sr-r	1 (2)	1.4	45
<i>Rumex crispus</i>		1	4		36		0.5	0.1				g/r	cr-r	3 (3)	1.6	69
<i>Glechoma hederacea</i>			17	18		1	0.5	0.5	0.4			r	csr	1 (2)	0.69	55
<i>Polygonum aviculare</i>		1	15	1			<0.1					r	r	3 (2)	1.02	78
<i>Sonchus arvensis</i>		8		1	2		6.9	<0.1				a/r	cr	2 (2)	0.43	30
<i>Urtica dioica</i>			1		1	7	0.2	2.6	0.1		<0.1	r	c	2 (2)	0.1	25
<i>Poa annua</i>			2	2	2			0.6				r	r	2 (2)	0.3	39
<i>Veronica hederifolia</i>		1		1	2		1.2	1.2	4.5			a/r	csr	2 (3)	4	8
<i>Epilobium montanum</i>				1	1	1		<0.1	0.1	<0.1		w	csr	2 (1)	0.12	46
<i>Oenothera biennis</i>		1			1	1	0.1					r	cr	n.s. (2)	0.4	70
<i>Cardamine hirsuta</i>			212	130				4.2	4.5			r	sr	2 (2)	0.1	56
<i>Plantago lanceolata</i>			95	43			<0.1	7.8	1.0			g	csr	n.s. (2)	0.2	39
<i>Valerianella dentata</i>			66	59			<0.1					a/g	r	1 (2)	1.09	96
<i>Prunella vulgaris</i>			46	3			0.1	1.3	<0.1			g	csr	1 (2)	0.9	51
<i>Bellis perennis</i>			17	6			<0.1	8.0	<0.1			g	r-csr	1 (2)	0.11	21
<i>Artemisia vulgaris</i>		13		2			1.2					g/r	c-cr	2 (2)	0.17	54
<i>Thlaspi arvense</i>					13	1	<0.1					a/r	r	3 (3)	1.08	91
<i>Veronica arvensis</i>			6	9			0.1	0.7	1.3			g	sr	2 (2)	0.12	24
<i>Stellaria media s.str.</i>		3	4				0.7	0.1				a/r	r	2 (3)	0.3	45
<i>Scrophularia nodosa</i>					1	6				<0.1	<0.1	w	cs	3 (2)	0.11	74
<i>Calamagrostis epigeios</i>					2	2	0.1	0.4	2.9	0.9	2.4	g	c	1 (1)	0.064	6
<i>Silene latifolia subsp. alba</i>			1	3				0.1	<0.1			g/r	c	3 (2)	1	23
<i>Cirsium vulgare</i>					1	3		0.1	0.1			r	cr	1 (1)	2.4	41
<i>Brachypodium pinnatum</i>			1	2				0.3	1.0			g	cs	1 (1)	2.4	21
<i>Sambucus nigra</i>					2	1			0.1		0.6	w	c	1 (1)	77	35
<i>Lamium amplexicaule</i>		1	1				0.2	0.4				a/r	r	1 (3)	0.6	17
<i>Trifolium pratense</i>			1	1				2.0	0.3			g	csr	1 (1)	1.8	8
<i>Achillea millefolium</i>			1	1			0.7	9.6	<0.1			g	csr-cr	1 (1)	0.2	4
<i>Comus sanguinea</i>				1	1		0.1	<0.1	2.1	28	23	w	c	1 (1)	56.5	2
<i>Lathyrus sylvestris</i>				1	1				1.0	<0.1	<0.1	g	c	n.s. (1)	43	17
<i>Valerianella locusta</i>					1	1	0.9	1.1	1.4			a	r	3 (2)	2.6	50
<i>Bromus sterilis</i>		39					12	<0.1				r	r-cr	n.s. (1)	7.1	30

Appendix 5.1. (continued)

Species	Type	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
		Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
<i>Holcus lanatus</i>				21			0.4	1.2				g	csr	3 (1)	0.2	31
<i>Thymus pulegioides</i>		20					20					g	cs	1 (1)	0.18	19
<i>Geranium molle</i>		7					0.1	<0.1				g	r-sr	1 (2)	1.09	77
<i>Poa palustris</i>					5		0.1	1.8	0.1	0.1		g	cs	1 (2)	0.172	11
<i>Tripleurospermum perforatum</i>					4		<0.1					a/r	r	n.s. (2)	0.36	82
<i>Elymus repens</i> s.str.		2					1.2	2.5	2.3			r	c-cr	n.s. (1)	2.5	3
<i>Campanula trachelium</i>				2			<0.1	0.3		<0.1		w	cs	3 (1)	0.21	19
<i>Carex muricata</i> s.str.				2			0.1	0.3		0.1		g	cs	2 (3)	1.84	13
<i>Filipendula ulmaria</i>				2			<0.1	2.2	0.6			g	c-cs	1 (1)	0.8	5
<i>Galium aparine</i>				2			0.2	0.1	1.9	0.1		r	cr	1 (1)	9	5
<i>Geranium sanguineum</i>				2			0.1	0.9				g	csr	1 (3)	8.57	16
<i>Rubus fruticosus</i> agg.					2		<0.1		0.3	0.2	0.3	w	cs	1 (3)	2.23	10
<i>Silene noctiflora</i>					2		<0.1					a	r	3 (3)	1	70
<i>Bromus arvensis</i>	1						33	<0.1				a	cr	1 (1)	1.7	7
<i>Sherardia arvensis</i>	1						0.7	<0.1				a	r	1 (1)	1.6	14
<i>Populus tremula</i>	1							<0.1	8.6	1.2		w	c	1 (1)	0.12	3
<i>Hieracium pilosella</i>		1					3.0	<0.1				g	s-csr	n.s. (1)	0.2	4
<i>Geranium pusillum</i>		1					1.4					a/r	c	3 (1)	1.09	6
<i>Crepis biennis</i>		1					0.4	0.3				g	c	1 (1)	0.23	6
<i>Trifolium repens</i>		1					<0.1	2.4	<0.1			g	csr-cr	1 (1)	0.8	4
<i>Prunus padus</i>		1								0.1	<0.1	w	c	2 (1)	145	20
<i>Hieracium schultesii</i>				1			1.3	0.2		0.1		g	s-csr	n.s. (1)	n.s.	4
<i>Rhinanthus angustifolius</i> s.l.					1			0.4				g	sr	1 (1)	2.54	12
<i>Salix caprea</i>					1		<0.1		1.0	25	20	w	c	1 (1)	0.12	1
In above-ground vegetation only																
<i>Equisetum arvense</i>							9.7	0.7	1.1	0.2	<0.1	a/r	cr	n.s.	n.s.	0
<i>Arrhenatherum elatius</i>							0.1	24	5.2	<0.1	<0.1	g	c	1	2.9	0
<i>Dactylis glomerata</i> s.str.							0.1	5.9	2.8	0.7	0.9	g	csr-c	1	0.8	0
<i>Fraxinus excelsior</i>							0.1	0.1	3.0	46	15	w	c	1	65.07	0
<i>Acer pseudoplatanus</i>							0.1	<0.1	<0.1	2.4	0.9	w	c-cs	1	74.31	0
<i>Rosa canina</i> s.l.							<0.1	<0.1	1.5	1.4	1.8	w	c	1	20.1	0
<i>Crataegus monogyna</i> s.l.							<0.1	<0.1	1.2	3.9	2.8	w	cs	1	184	0
<i>Geum urbanum</i>							<0.1	<0.1	0.8	0.3	0.1	w	csr-s	1	2.9	0
<i>Acer platanoides</i>							<0.1	<0.1	<0.1	7.6	7.2	w	c	1	158.6	0
<i>Tussilago farfara</i>							1.0	<0.1	0.6		<0.1	r	cr	1	0.5	0
<i>Epilobium angustifolium</i>							0.1		4.1	0.1	0.4	a/r	c	n.s.	0.42	0
<i>Viburnum opulus</i>							0.1		0.6	1.1	1.9	w	c	1	36.6	0
<i>Prunus avium</i>							<0.1		0.2	0.8	1.4	w	c	1	159.7	0
<i>Cephalanthera damasonium</i>							<0.1		<0.1	0.3	0.3	w	csr	n.s.	0.002	0
<i>Viola hirta</i>								4.9	0.2	<0.1	<0.1	g	s	1	3.3	0
<i>Veronica chamaedrys</i>								0.4	0.2	<0.1	<0.1	g	csr-s	1	0.21	0
<i>Brachypodium sylvaticum</i>								0.1	2.7	2.2	1.4	w	s-cs	1	2.71	0
<i>Quercus robur</i>								<0.1	0.1	0.1	0.2	w	cs	1	2645	0
<i>Potentilla reptans</i>							0.5	0.2	<0.1			g	csr	1	0.31	0
<i>Vicia angustifolia</i>							0.2	0.1	0.1			r	r	n.s.	n.s.	0
<i>Geranium dissectum</i>							0.1	0.5	0.1			a	cr	1	2.24	0
<i>Senecio jacobaea</i>							<0.1	0.7	0.6			g	r-cr	1	0.23	0
<i>Galium mollugo</i>							<0.1	1.7	<0.1			g	c	1	0.71	0

Appendix 5.1. (continued)

Species	Type	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
		Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
<i>Solidago gigantea</i>							0.2	<0.1		0.1		r	c	1	0.09	0
<i>Clinopodium vulgare</i>							0.5	1.2	<0.1			g	cs	1	0.39	0
<i>Hieracium aurantiacum</i>							0.2	<0.1	0.1			g	csr	n.s.	n.s.	0
<i>Agrimonia eupatoria</i>							<0.1	<0.1	0.1			g	c	1	16	0
<i>Melampyrum arvense</i>							<0.1	2.0		<0.1		a	r	2	14.09	0
<i>Hypericum hirsutum</i>							<0.1		0.2	<0.1		g	csr-s	1	0.08	0
<i>Sorbus aucuparia</i>								0.4	1.0	3.1		w	cs	1	3.2	0
<i>Rubus caesius</i>								0.3	1.9	1.1		w	c	1	3.4	0
<i>Viburnum lantana</i>								0.2	0.2	1.2		w	c	n.s.	47	0
<i>Rhamnus cathartica</i>								0.2	0.3	1.1		w	c	n.s.	19.17	0
<i>Acer campestre</i>								0.1	1.3	0.5		w	c	1	56.8	0
<i>Deschampsia cesp. tosa</i>								0.1	0.2	0.3		g	csr-sc	1	0.25	0
<i>Carex sylvatica</i>								0.1	0.2	0.1		w	csr	1	1.54	0
<i>Melica uniflora</i>								0.1	0.1	0.1		w	s-cs	1	3.9	0
<i>Galium sylvaticum s.str.</i>								0.1	0.1	0.1		w	cs	n.s.	1.3	0
<i>Listera ovata</i>								0.1	<0.1	<0.1		r	csr	n.s.	0.4	0
<i>Carpinus betulus</i>								<0.1	0.2	<0.1		w	c	1	51	0
<i>Galium odoratum</i>								<0.1	0.1	1.0		w	s	1	5.35	0
<i>Euonymus europaea</i>								<0.1	0.1	0.9		w	c	n.s.	34.8	0
<i>Cotoneaster divaricatus</i>								<0.1	0.1	0.2		w	c	n.s.	9.4	0
<i>Prunus spinosa s.str.</i>								<0.1	0.1	0.1		w	c	1	255.1	0
<i>Festuca arundinacea</i>							<0.1	0.1				g	csr	1	2.8	0
<i>Stachys palustris</i>							1.4		0.7			g	c	1	0.775	0
<i>Euphrasia officinalis subsp. rost.</i>								2.7	0.1			g	sr	1	0.31	0
<i>Luzula campestris</i>								2.1	<0.1			g	s-csr	1	0.6	0
<i>Chaerophyllum bulbosum</i>								1.8	1.3			r	c	n.s.	n.s.	0
<i>Carex caryophyllea</i>								1.4	<0.1			g	s	1	1.06	0
<i>Festuca rubra</i>								0.8	0.1			g	csr	1	1	0
<i>Alchemilla vulgaris agg.</i>								0.6	0.1			g	csr	1	0.46	0
<i>Rumex acetosa</i>								0.5	0.1			g	csr	1	0.7	0
<i>Leucanthemum ircutianum</i>								0.5	0.1			g	csr-cr	1	0.44	0
<i>Origanum vulgare</i>								0.5	0.1			g	csr-cs	2	0.1	0
<i>Centaurea jacea</i>								0.2	0.3			g	c	1	1.06	0
<i>Pimpinella saxifraga</i>								0.2	<0.1			g	s	1	1.26	0
<i>Silene dioica</i>								0.1	0.5			g	csr	1	0.66	0
<i>Scabiosa columbaria</i>								0.1	0.1			g	s-sr	1	1.9	0
<i>Daucus carota</i>								0.1	0.1			g	sr-csr	2	1	0
<i>Veronica officinalis</i>								0.1	0.1			g	cr	2	0.13	0
<i>Senecio erucifolius</i>								0.1	<0.1			r	csr	1	0.37	0
<i>Knautia arvensis s.str.</i>								0.1	<0.1			g	c	1	2.91	0
<i>Malva moschata</i>								0.1	<0.1			g	c	3	2.2	0
<i>Crepis capillaris</i>								0.1	<0.1			g	r-sr	1	0.23	0
<i>Festuca pratensis</i>								0.1	<0.1			g	csr	1	2.52	0
<i>Trisetum flavescens</i>								<0.1	0.7			g	csr	1	0.37	0
<i>Vicia tetrasperma</i>								<0.1	0.6			a	r	1	4.203	0
<i>Bromus hordeaceus</i>								<0.1	<0.1			g	r	1	5.26	0
<i>Aster novi-belgii</i>									1.1	0.1		w	c	n.s.	0.4	0
<i>Ophioglossum vulgatum</i>									0.1	<0.1		g	cs	n.s.	n.s.	0

Appendix 5.1. (continued)

Species	Type	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
		Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
<i>Heracleum sphondylium</i>								<0.1	<0.1			g	cr	1	7.6	0
<i>Dryopteris filix-mas</i>								0.1		0.3		w	cs	n.s.	n.s.	0
<i>Comus sericea</i>									0.7	<0.1		w	c	n.s.	28.8	0
<i>Salix alba</i>									0.6	1.2		w	c	1	0.12	0
<i>Ligustrum vulgare</i>									0.5	0.5		w	c	1	23.1	0
<i>Poa nemoralis</i>									0.2	<0.1		w	csr	1	0.3	0
<i>Daphne mezereum</i>									0.1	0.1		w	cs	n.s.	90.7	0
<i>Viola reichenbachiana</i>									0.1	<0.1		w	csr	1	n.s.	0
<i>Luzula luzuloides</i>									0.1	0.3		w	csr	2	n.s.	0
<i>Lonicera xylosteum</i>									<0.1	1.1		w	c	1	5.2	0
<i>Fagus sylvatica</i>									<0.1	<0.1		w	cs	1	260	0
<i>Angelica sylvestris</i>									<0.1	<0.1		w	c-cr	1	1.18	0
<i>Hieracium murorum</i>									<0.1	<0.1		w	csr	n.s.	0.4	0
<i>Polygonum persicaria</i>							1.4					a/r	r	3	2.3	0
<i>Lapsana communis</i>							0.4					r	r-cr	2	1.17	0
<i>Euphorbia amygdaloides</i>							0.2					w	cs	3	2.6	0
<i>Galeopsis tetrahit</i>							0.2					g/r	r-cr	1	4.6	0
<i>Borago officinalis</i>							<0.1					a/r	cr	1	12.18	0
<i>Centaurea cyanus</i>							<0.1					a	cr	1	4.1	0
<i>Dipsacus fullonum</i>							<0.1					r	cr	1	2.26	0
<i>Lamium purpureum s.l.</i>							0.9					a/r	r	2	0.8	0
<i>Galium verum s.str.</i>							0.5					g	csr-cs	1	0.5	0
<i>Pastinaca sativa</i>							0.4					g	c	2	3	0
<i>Veronica teucrium</i>							0.2					g	c	n.s.	0.25	0
<i>Bromus erectus</i>							0.2					g	csr-cs	n.s.	4.37	0
<i>Leontodon autumnalis</i>							0.1					g	csr-r	1	0.7	0
<i>Mentha arvensis</i>							0.1					g	c	1	0.2	0
<i>Alopecurus pratensis</i>							0.1					g	csr-c	1	1.1	0
<i>Chaerophyllum hirsutum</i>							0.1					g	cs	n.s.	n.s.	0
<i>Helictotrichon pubescens</i>							0.1					g	s-csr	1	1.96	0
<i>Lolium perenne</i>							<0.1					g	cr-csr	1	1.6	0
<i>Anthoxanthum odoratum s.str.</i>							<0.1					g	sr-csr	1	0.49	0
<i>Plantago major</i>							<0.1					g	r-csr	2	0.2	0
<i>Plantago media</i>							<0.1					g	csr	1	0.32	0
<i>Tragopogon pratensis</i>							<0.1					g	csr	2	3.5	0
<i>Veronica serpyllifolia</i>							<0.1					g	csr	3	0.054	0
<i>Vincetoxicum hirsutinaria</i>							<0.1					g	cs	1	6.75	0
<i>Ajuga reptans</i>								0.5				g	csr	1	1.47	0
<i>Carex digitata</i>								0.3				w	csr	1	1.09	0
<i>Geranium nodosum</i>								0.3				g	csr	n.s.	5.49	0
<i>Tanacetum vulgare</i>								0.2				r	c	1	0.1	0
<i>Vicia parviflora</i>								0.1				a	r	n.s.	3.61	0
<i>Lathyrus niger</i>								0.1				w	csr	1	15	0
<i>Ranunculus acris</i>								0.1				g	csr	1	1.5	0
<i>Tanacetum corymbosum</i>								0.1				w	cs	n.s.	0.51	0
<i>Phleum pratense s.l.</i>								<0.1				g	csr-cr	1	0.4	0
<i>Crataegus laevigata s.str.</i>								<0.1				w	c	1	52.7	0
<i>Prunus serotina</i>								<0.1				w	c	1	91.5	0

Appendix 5.1. (continued)

Species	Type	P1	M2-8	M1	S23	S36	P1	M2-8	M1	S23	S36	Habitat	Strategy	Seed bank	Seed	SAI
		Total number of seedlings					Mean coverage AV (%)					type	type	Persistence	weight	
<i>Bupleurum longifolium</i>										<0.1		w	c	n.s.	6.19	0
<i>Pulmonaria officinalis</i>										<0.1		w	csr	1	3.64	0
<i>Ranunculus lanuginosus</i>										<0.1		w	cs	1	0.1	0
<i>Rubus idaeus</i>										<0.1		w	c	2	1.4	0
<i>Hieracium umbellatum</i>										<0.1		w	cs	2	0.65	0
<i>Cornus mas</i>											1.1	w	c	n.s.	217	0
<i>Geranium robertianum</i>										0.1		r	r-csr	1	1.08	0
<i>Malus sylvestris</i>										0.1		w	c	n.s.	25.41	0
<i>Pinus sylvestris</i>										0.1		w	c	1	7	0
<i>Senecio ovatus</i>										<0.1		w	c	n.s.	1.17	0
<i>Lysimachia nemorum</i>										<0.1		w	cs	1	n.s.	0
<i>Vicia sepium</i>										<0.1		g	csr-c	1	18.1	0
<i>Dryopteris carthusiana</i>										<0.1		w	cs	n.s.	n.s.	0
<i>Lonicera periclymenum</i>											0.2	w	cs	1	5.24	0
<i>Picea abies</i>											0.1	w	c	1	7	0
<i>Dactylis polygama</i>										<0.1		w	cs	n.s.	0.8	0
<i>Corylus avellana</i>										<0.1		w	c	1	941.7	0
<i>Lathyrus vernus</i>										<0.1		w	csr	1	15	0
<i>Quercus petraea</i>										<0.1		w	cs	1	1873	0

CHAPTER 6

Synthesis



Picture: *Cephalanthera damasonium* in plot IE: undisturbed since 1969 (photo taken by M. Dölle).

6.1 The importance of long-term empirical studies

Every example of vegetation dynamic will be unique, dependent on infinite possible variations in environmental conditions (GLENN-LEWIN et al. 1992). Vegetation dynamics are closely linked to initial site conditions and surrounding landscape (PRACH et al. 2007). Thus the prediction of successional pathways and any generalisation concerning vegetation dynamics should be established on numerous case studies of vegetation changes. But even though the revegetation of disturbed sites through succession is one of the most fundamental processes exceedingly studied by plant ecologists during the last 100 years (MEINERS et al. 2007), there remains an enormous amount of natural variations unstudied (GLENN-LEWIN et al. 1992). This thesis, presenting data from a long-term experimental study of succession can be seen as a considerable contribution to a better understanding of vegetation dynamics. In particular the advantages of long-term permanent plot studies, in contrast to chronosequence studies are often discussed (AUSTIN 1981, LUKEN 1990, BAKKER et al. 1996).

6.2 Main driving variables

A central subject-matter of studying successional processes is whether succession is predictable in space and time (GLENN-LEWIN et al. 1992). Thus understanding the main influencing factors driving successional changes is a major goal to enhance ecological theory. Our results clearly point out that successional process on the same site can vary significantly. Different pathways may occur, but they obviously converge with progress in time. There are various parameters influencing, and hence bearing difficulties in predicting successional outcomes and pathways (PRACH et al. 2007). Beside the dependence on specific geographical and climatical site conditions, succession in abandoned fields is highly variable regarding site history. The character of the surrounding landscape, the nutrient status, and various random events are among others the main driving variables (e.g. WALKER and DEL MORAL 2003, PRACH et al. 2007). When the appropriateness of natural succession for land management options (e.g. natural afforestation) has to be valued, in particular the surrounding landscape and local species pools have to be taken into account (GARDESCU & MARKS 2004, MEINERS et al. 2007).

Factors influencing the establishment and growth of trees may have the most direct impact on the rate of natural succession (MEINERS et al. 2007). The most decisive factor proved to be the propagule bank in the beginning of succession. The initially experimental variations between the plots led to differences in the initial vegetation composition and had lasting effects on current tree species composition. These findings are well in accordance with other studies on variations in initial situations among old-fields, leading to differences in vegetation composition and the rate of

succession (MYSTER & PICKETT 1990). A substantial propagule bank on abandoned arable fields can lead to a fast development of herbaceous vegetation, and thus inhibit the establishment of trees. However, in most cases the tree establishment is only temporally delayed.

Ecosystem parameters significantly change during succession. Light supply revealed as the most decisive factor in the observed secondary succession. It results in dramatical changes in ground flora composition. While open landscape species declined rapidly, typical to closed forest species showed a slow rate of establishment. In addition, most late successional species do not build up persistent seed banks (THOMPSON et al. 1997). Thus, for successful establishment of typical to closed forest species, the availability of a species pool in close vicinity and dispersal vectors are of high importance. And hence, habitat connectivity plays a decisive role for the chance of a species to establish on a site (KOLB & DIEKMANN 2004).

6.3 Implications for nature conservation

The abandonment of agricultural land in most areas in temperate Europe leads to the successional development of forests. Along with that a loss in biodiversity over time occurs, from the perspective of both habitat and species. The decrease in biodiversity with increasing shrub and tree colonisation is an intensively discussed point regarding abandonment of agricultural land and ongoing natural succession (e.g. STAMPFLI & ZEITER 1999, MACDONALD et al. 2000, PYATOS et al. 2003, FISCHER et al. 2008). Further negative impacts of agricultural land abandonment are increasing landscape homogenization and increasing fragmentation of agricultural habitats (BIELSA et al. 2005). To avoid negative impacts of land abandonment and maintain openness of the landscape, natural succession permanently has to be prevented. In particular many types of grassland ecosystems originated from a particular type of land management, like hay meadows or pasture land on marginal sites are threatened by natural succession.

However, the abandonment of agricultural land can be considered as an opportunity for the redevelopment of an ecosystem similar to what was there prior to agricultural operations (HOBBS & CRAMER 2007). It can be a cost-effective option for dealing with agricultural land abandonment (WHISENANTH 2002) and can produce environmental benefits which include contributing to water accumulation and flood control, nutrient recycling and fixation, soil formation, carbon sequestration by trees and soil, wildlife and biodiversity protection, the provision of recreational services and the enhancement of aesthetic value (FAO 2006). Carbon sequestration for example, on abandoned land that subsequently develops to forests, can have a net positive effect on carbon balance (WATSON et al. 2000).

Plant communities emerged from undisturbed succession offer a high nature conversational value due to the fact that natural processes are allowed to proceed. And since today only scattered remnants of Europe's forests can be classified as "undisturbed by humans" (FAO 2000), with natural succession an increase in highly natural ecosystems is to be expected. In agreement with our findings, for biodiversity, natural afforestation is generally more favorable than plantation based afforestation (LÖHMUS & LÖHMUS 2008).

Recently, on the search for a solution to the problem of the world's ever-growing energy demands, scientists see a high potential on abandoned agricultural land for growing biofuels (CAMPBELL et al. 2008). This is, however, questionable, in particular when the land is managed with a high energy input. Further on, it can lead to a competition for land between food and biofuels (FAO 2008).

6.4 Silvicultural potential of natural afforestation

Natural succession on this study site has lead to a tree species rich closed-canopy forest in comparatively short time periods. Thus the relevance of such studies to afforestation projects and the restoration of forested systems are obvious. If the development objective of abandoned agricultural land is forest, the present study clearly points out, that natural succession can be an effective tool for afforestation (HOBBS et al. 2007). Open topsoil, mature trees as potential seed dispenser in the close vicinity as well as the good nutrient and water supply are preconditions which revealed as conducive for the discribed development from arable field to forest.

The need to discuss natural succession as a method for afforestation of abandoned land, increases with increasing amount of land abandonment (HOBBS & CRAMER 2007) and increasing costs for land managing to maintain the openness of the landscape. Further on, afforestation projects should more and more take natural succession as an appropriate instrument to save costs and simultaneously to reach close-to-nature forests. In existing forests natural regeneration after e.g. logging or windstorm events is since the last about 30 years considered as an economical and ecological expedient method for afforestation.

Forest stands developed by natural afforestation are usually composed of native, well site adapted tree species. They are a good starting basis for developing multifunctional forests. Taking advantage of the natural pioneer forests vegetation as a shelter for planted late successional tree species can be an effective tool.

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CURRICULUM VITAE

PERSONAL DATA

Name	Michaela Dölle
Address	Hermann-Hanker-Straße 3 37083 Göttingen
Phone	+49-551-2760003
e-mail	mdoelle@gwdg.de
Date and Place of Birth	04.04.1976, Bleicherode (Germany)
Family Status	1 daughter



EDUCATION

2003 – 2008	Ph.D. student, Department of Silviculture and Forest Ecology, University of Göttingen
1995 – 2001	Studies in Forest Science and Forest Ecology, University of Göttingen
01/2001	Diploma in Forest Science
1991 – 1994	Public Secondary School, Worbis
06/1994	Abitur
1982 – 1991	POS, Kirchworbis

EXPERIENCE

05 – 09/2007	Work experience on a mountain farm, Switzerland
2003 – 2007	Scientific assistant, Department of Silviculture and Forest Ecology, University of Göttingen
03 – 10/2002	Participation in the Postgraduate Program "International and Interdisciplinary Research in Primeval Forests" Stays abroad: Slovakia, Guatemala, Mongolia
2001 – 2002	Work experience in Organic Agriculture, Bischhausen
04 – 08/2001	Internship in Outdoor Education funded by the COMMERZBANK: National Park "Sächsische Schweiz"
1998 – 1999	Graduate Assistant, Institute for Soil Science and Forest Nutrition
06 – 10/1997	Stay abroad, Northern USA and Canada
1994 – 1995	Internship, Thuringian Regional Forestry Office, Leinefelde

