Zur Homepage der Dissertation

Plant response to changes in disturbance magnitude

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General introduction

Background

Disturbances and management

Disturbances are present in all ecosystems, occur over a wide range of spatial and temporal scales and are continuous across all levels of ecological organisation (White & Pickett 1985). To understand the influence of disturbances on vegetation, their spatial and temporal dimension, frequency of occurrence and magnitude have to be considered (White & Jentsch 2001). The study of disturbance – sensu White & Pickett (1985)[1] – has attracted much attention since it is known that these processes play a crucial role in maintaining biotic diversity (White & Jentsch 2001, see also literature cited within). Evidence suggests that, for the majority of grasslands in temperate regions, disturbance is required to maintain the typical species composition; otherwise such areas would be covered by forest and shrublands (Leps 1990, Briemle et al. 1991, Ellenberg 1996). In recent decades traditional forms of land use such as intensive grazing and reaping have been replaced by less costly and more practical alternative disturbance systems (Poschlod & Schumacher 1998). Systems such as burning, mulching, variation in dates and frequencies per year of mowing, extensive grazing, and combinations thereof have all been tested with a view to the preservation of open grasslands (Schiefer 1981, Briemle et al. 1991, Plachter 1995, Schreiber 1997). Nevertheless, there still is a need for management experiments which are more flexible and less expensive. Conservation managers should be open to controversial or unusual management (Poschlod & WallisDeVries 2002).

Disturbance systems under study

The present study incorporates two cyclic disturbance systems, namely: mowing (the current conservation management system, applied for at least 20 years) and rototilling (the alternative under consideration). Even though both disturbances are man-made, large-scale, and applied after seed shedding in late summer, there are big differences between both systems. Important dissimilarities, with respect to population survival, are the differences in terms of biomass removal, disturbance intensity and return interval, all of which strongly affect survival and recruitment of plant species.

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[1] 'Disturbance is a relatively discrete event in time that disrupts the ecosystem, community or population structure and changes the resources, substrate availability or physical environment'

Mowing removes annual aboveground biomass, prevents litter accumulation over years, and enhances the availability of resources by the annual creation of new gaps, but widely preserves vegetation cover and plant composition (Rydgren et al. 2001, Box 3) and leaves overall site potential unchanged. Plant species abundances fluctuate from year to year within defined boundaries which depend on weather conditions, but over a long time period populations are (more or less) at equilibrium, owing to functional adaptations to this kind of disturbance system (Klapp 1971, DeAngelis & Waterhouse 1987, Leps 1990, Briemle et al. 1991, White & Jentsch 2001). According to concepts of stability this property is called 'resistance'[2] (review in Grimm & Wissel (1997)).

Rototilling, on the other hand, has a massive impact on both above-ground and below-ground components. This sort of management is similar to ploughing and the subsequent effects can impact at depths of up to 20 cm, depending on soil conditions. In general, rototilling is applied via a track-laying tractor that is especially constructed to cultivate steep slopes such as vineyards. Such management can have direct and indirect effects on plant population. Direct effects of rototilling are the destruction of vegetation cover, disturbance of plant modules, and even death of individuals and changes in population structure. Indirect effects are observed through succession due to increasing biomass and through competition until the treatment is repeated. Should rotoilling be considered as an alternative management regime, if the impact on the plant community is allegedly so severe? The idea of using mechanical cultivation for the maintenance of grasslands originates from neolithic agriculture, where cultivation was followed by an indefinite time of succession (Abel 1978, Briemle et al. 1991, Bonn & Poschlod 1998). There is evidence that many grasslands would be able to tolerate rototilling, but only if applied at low frequencies (every 3–5 years), due to the regeneration time of the hypocotyl buds (Kleyer 1998). Eriksson (1989), Crawley (1990) and Amiaud & Touzard (2004) showed that most plant species on cultivated grassland soils regenerate from vegetative fragments rather than by germination of seed. Furthermore, many studies have shown that intervention down to the root horizon and destruction and breakdown of biomass activate germination from the soil seed bank (Leck et al. 1989, Bakker et al. 1991, Bazzaz 1996, Kalamees & Zobel 2002, Jentsch 2004) and provide new germination sites by creating gaps (Aguilera & Lauenroth 1995, Krenova & Leps 1996, Jutila & Grace 2002). These facts have led to the hypothesis that mechanical cultivation by rototilling could be an alternative to annual mowing (Kleyer 1998).

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[2] 'Resistance' - sensu Leps (1990) - characterizes the ability of an ecosystem to remain in equilibrium when stressed.

Regeneration strategies of plant species

Changing management – i.e. changing disturbance severity – influences plant population dynamics with respect to both life history and biological traits. Plants have different degrees of exposure to any form of disturbance. White & Pickett (1985) demonstrate that severity is a measure of the plant's perception of a disturbance event. Thus, different plants exposed to one disturbance event of particular intensity, perceive it at different levels of severity (Bellingham 2000). This is often the reason for an increase or even the invasion of some species, while other species decrease in population size in reaction to a disturbance (White & Jentsch 2001). Only if plant species have the possibility to recruit new reproductive individuals into the population, to compensate individual mortality, will the population be able to persist in the face of a certain disturbance system. Each species has physiological, morphological, and life history characteristics that are unique to itself and which determine population survival (Tilman 1988). Nevertheless, most species occur at intermediate disturbance frequencies (Connell 1978), i.e. they occupy a niche in which their regeneration ability (to deal with disturbance) and their competitive ability (to deal with increasing competition with subsequent succession) allow survival.

Species are successful either due to disturbance resistance adaptation or, in cases of extinction, through an ability to recolonise the disturbed patches before disturbance happens again (Eriksson 1996). The event of local extinction of populations and the subsequent recolonisation are the basis of the metapopulation concept of Levins (1969) extended by Hanski & Gilpin (1997). The functional significance of corridors, and the related conception of connectivity, have been investigated, but mostly for animal species (Hanski 2001). Very few plant studies have as yet adopted the spatial concept of a landscape as a patch-corridor-matrix mosaic (see de Blois et al. 2002). Poschlod (1996) reviewed the applicability of the metapopulation concept to plant species. His opinion was that, although we lack knowledge about the existence of metapopulations[3], the concept is practical for probably only a few plant species (for examples see Cipollini et al. 1994, Reich & Grimm 1996; Valverde & Silvertown 1997, Löfgren et al. 2000). Freckleton & Watkinson (2002, 2003) showed that the metapopulation theory is not applicable for all plant species. Eriksson (1996) therefore suggested, based on a review of literature, that three types of dynamics are common in plant species depending on the longevity

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[3] A metapopulation is a spatial pattern of distribution and thus, a collective of populations. Populations are connected by pollen or/and seeds interchanges. Seed dispersal is responsible for colonisation and recolonisation processes of suitable habitats and sites. Factors determining the number of seeds (thus, the extinction of populations), are beside the population dynamic highly responsible for the survival of a species or a metapopulation, respectively (sensu Levins (1970) and Reich & Grimm (1996) extended by Schemske et al. (1994)).

of their life cycle stages and dispersal ability. The short-lived or highly habitat specialised plant species, with good dispersal possibilities, tend to build up metapopulations. On the other hand, long-lived plants with clonal propagation, or plants with extensive seed banks, tend to build up remnant population systems, in which many local populations persist over time to bridge unfavourable phases of succession. Evidence suggests that on the patch level, the probability of recolonisation via long-distance dispersal after extinction decreases with increasing distance from a source population (Menges 1990, Fahrig & Merriam 1994). Recolonisation is even less likely in highly fragmented landscapes, as are commonly found in central Europe (Settele et al. 1996). Several investigations show that relevant grassland species are poor colonisers by long-distance dispersal (Primack & Miao 1992, Poschlod et al. 1996, Kollmann 1997, Poschlod et al. 1997). Thus, immigration by long-distance dispersal is suggested to be a rare event; an observation which is supported by field observations by e.g. Poschlod & Jordan (1992) and Kollmann & Staub (1995). These facts emphasise the importance of studies on persistence and regeneration strategies in many plants on the local and/or patch levels. At the landscape level, the limited evidence available from rare long-distance dispersal events is crucial, as these processes are key factors in understanding rapid plant emigration (Higgins & Richardson 1999) in such cases as, for example, the prediction of postglacial tree and herb migration rates (Cain et al. 1987, Clark 1998) or the rate of spread of invasive plant species (Shigesada et al. 1995, Higgins et al. 2001).

Disturbance resistance adaptation can take several forms, such as resprouting from buds or basal meristems, or vegetative propagation via stolons or rhizomes (Doust & Doust 1988). Resprouting has been shown to be an efficient mechanism for perennial plant species to regain biomass immediately after disturbance, and clonal regeneration is the main regeneration strategy in temperate perennial grasslands and forests (Eriksson 1989, 1993). For annual plants, who do not have the ability to regenerate vegetatively, the existence of an extensive seed bank makes it possible to persist over periods long enough to bridge unfavourable phases in succession (see above). This ability to buffer environmentally unfavourable phases with the aid of seed banks has been demonstrated for e.g. desert annuals (Pake & Venable 1996).

Frequency of occurrence is, together with disturbance magnitude, the most influential factor in plant persistence (see above). Plant species with a short life cycle and transient or a short-term persistent seed bank are expected to be more vulnerable to less frequent cyclic disturbances, especially when compared to species with a storage ability, e.g. perennials, clonal plants or species with a long-term persistent seed bank (Harper 1977, Warner & Chesson 1985, Stöcklin & Fischer 1999, Higgins et al. 2000). This is in accordance with the C-S-R strategy theory of Grime (1977) and other theories regarding about disturbance level and plant persistence, in that only high disturbance levels select for short-lived species with a high population growth rate e.g. McArthur (1962) and McArthur & Wilson (1967) extended by Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987). Schippers et al. (2001) found a clear segregation of perennial and annual species due to disturbance. At low disturbance levels annuals were replaced by competitive, long-lived plant species. However, it has to be taken into account that small-scale natural disturbances (e.g. summer drought), allow the coexistence of species with contrasting life histories within closed grassland communities that are more or less free from a major human impact (Grubb 1986). Summer drought reduces biomass of perennial matrix species, and annuals may germinate within these gaps. However, only below-ground disturbances stimulate the germination of seeds from the soil seed bank and thus ensure the survival of annual species in such cases when the above-ground populations are extinct.

Methods and stage of research

To understand the underlying reasons for and mechanisms leading to vegetation change after a change in management[4], studies on the community level are not sufficient; investigations on the population level are needed (Harper 1977, Fiedler & Kareiva 1997, Henle et al. 1999, Laska 2001). A popular method is the division of the life cycle of a plant species into discrete stages. This can be done by following development of individuals over time, and additionally collecting data on e.g. fecundity and biological traits, allowing calculation of demographic parameters (Tamm 1972, Hutchings 1987, Oostermeijer et al. 1996). Kery & Gregg (2003) point out that plant demographers must bear in mind the possible problems that can occur due to difficulty of detection of certain plant species, especially in case of small, inconspicuous species in larger investigation plots.

In this context, target plant species can serve as an indicator in monitoring programmes if population changes reflect changes in species composition within the wider plant community (Bühler & Schmid 2001). According to the theory of functional types (Gitay & Noble 1997), species with similar biological traits should respond in similar ways to a specified disturbance. Bühler & Schmid (2001) therefore strongly suggest that characteristic and abundant species (e.g. *Plantago media*, Eriksson & Eriksson 2000) should be studied in addition to rare and endangered plant species.

Since long-term demographical studies are often expensive and too time consuming to be used in conservation management, many recent studies work at the changes in population structure of plants, mostly considering only one target plant species (Oostermeijer et al. 1994, Bühler & Schmid 2001, Hegland et al. 2001, Colling

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[4] Since many landscapes were created by human-induced disturbance regimes land-management practices were nessessary to maintain typical and endangered species. In sense of White & Pickett (1985) every management is a disturbance event for an ecosystem.

et al. 2002). Another alternative for the prediction of long-term consequences of management actions relies increasingly on population and community dynamics modelling (Kalisz 1992, Beissinger & Westphal 1998, Menges 2000, Buckley et al. 2003, Emlen et al. 2003). Population models often form the basis of population management decisions regarding threatened or endangered species in nature conservation ('population viability analysis', PVA; Beissinger & Westphal 1998, Lindenmayer et al. 1993, Menges 2000, Schwartz & Brigham 2003). Many authors have stressed the need for plant population models to be able to reflect the biology of the species in question and to provide an insight into the environmental perturbations that cause much of variability observed in nature (Cousens 1995, Buckley et al. 2003). PVAs have a long history of use for management of endangered animals, but have only recently also been applied to plant species (reviewed in Menges 2000, Schwartz & Brigham 2003). At first, PVA modelling approaches (Miller & Botkin 1974) comprised simple, equation-based deterministic matrix-based models, but subsequent development led to complex, spatial explicit individual-based population- and metapopulation models (Gonzalez-Andujar & Perry 1995, Valverde & Silvertown 1997, Brigham & Thomson 2003). Presently, stage- or size-classified matrix-models are the main used method in plant PVAs (Menges 2000).

Simulation models, based on empirical demographic parameters, have been used to:

- determine the effect(s) of natural disturbances on plant population dynamics such as the effect of hurricanes (Pascarella & Horvitz 1998), fire (Bradstock et al. 1998, Manders 1987, Marsula & Ratz 1994, Menges & Dolan 1998, Pfab & Witkowski 2000), forest dynamics (Cipollini et al. 1994, Busing 1995, Lett & Walter 1999, Palik et al. 2002) and herbivory (Ehrlen 1995, Pfab & Witkowski 2000). Effects of fine-scale disturbances on bryophyte population dynamics are highlighted by Rydgren et al. (2001) and Kimmerer (1993).
- determine the effect(s) of man-made disturbances such as harvesting (Busing & Spies 1995, Nantel et al. 1996), fire (Gross et al. 1998, Menges & Dolan 1998, Garnier & Dajoz 2001), grazing (Waite & Hutchings 1991, Bullock et al. 1994, Löfgren et al. 2000, Hunt 2001, Adler et al. 2001, Lennartsson & Oostermeijer 2001), trampling (Maschinski et al. 1996, Gross 1998, Löfgren et al. 2000) or mowing (Menges & Dolan 1998, Lennartsson & Oostermeijer 2001), in order to identify promising disturbance systems or combinations of multiple management strategies that allow species maintenance without time-consuming field tests (Beissinger & Westphal 1998, Menges 2000, Buckley et al. 2003).
- test suitable disturbance return intervals. Attention in this area has focused on effects of e.g. fire (Manders 1987, Canales et al. 1994, Gross 1998, Drechsler

et al. 1999) and trampling (Gross 1998). Oostermeier (1996) suggests an optimal return interval for sod-cutting in order to maintain the rare *Gentiana pneumonanthe* on heath land. Kimmerer (1993) predicts effects of variation of disturbance frequencies on the population dynamic of a moss.

- predict the most effective management strategies for the control of invasive weeds and herbs (Wadsworth et al. 2000, Buckley et al. 2001, Witkowski & Wilson 2001, Buckley et al. 2003).

Hypotheses and objectives

Although rototilling is a destructive management method, the most characteristic species of the disturbed patches can return immediately straightaway after rototilling thanks to their good regeneration potential (see above). According to concepts of stability, this ability to return to a reference state after a temporary disturbance (resilience; Grimm & Wissel 1997, Jentsch 2004) means that rototilling does not result in higher extinction rates of typical semi-natural grassland species on the patch level in the short-term. Over a longer time period, species survival depends on life history characteristics and disturbance frequency. It is assumed that:

- Annual plant species react positively to disturbance. Such species are initially supported by rototilling, but become endangered with increasing competition during succession. To maintain annual plant species, a frequent rototilling return interval has to be applied.
- Rototilling may be advantageous for perennials with a high vegetative regrowth potential and species with multiple regeneration strategies, but only if rototilling frequency is low.
- The regeneration vigour of shrub species (e.g. *Prunus spinosa*) after rototilling is reduced, as resprouting capability depends on not only both above- and below-ground reserves but also the possibility of making or maintaining the necessary storage organs between disturbances. However, only a frequent rototilling return interval will prevent overgrowth of vegetation by shrubs.

Nevertheless, a suitable rototilling return interval by which all focal species can survive can be found. To verify this hypothesis, the impact of disturbance on plant species and community at the patch level in experimental fields was analysed at both the community and the population level.

The monitoring of above- and below-ground vegetation on the community level will provide information about vegetation structure, species diversity and changes in species abundance due to a change in management (Box 2 & 3). Analysis at the population level attempts to explain which parameters decide on population response.

The plant species on which the study is focused can serve as indicators for changes in population dynamics after changing management (see above). Three characteristic plant species (*Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia pratensis*) were chosen for detailed investigation into biological traits and demography on both mown and rototilled plots. For detailed species description see Chapter 2 & Table A3 (Appendix). On the population level, two approaches can be distinguished: (1) demographic studies, which are often used to parameterise simulation models, and (2) changes in plant population structure (see above). To understand more of the mechanisms of plant species' responses to disturbance, the two approaches have been combined (Chapter 4).

Since conversion of management could be problematic, given that reduced management implies colonisation of shrub vegetation with negative consequences especially for Mesobromion and Brometalia species, intensive studies on the regeneration vigour of *Prunus spinosa* after rototilling were carried out (Box 1). The present study aims to verify the hypothesis that the resprouting vigour of *Prunus spinosa* is reduced after rototilling. Secondly, the study seeks to answer the question: Is cyclic disturbance by rototilling a suitable tool for prevention of shrub development on semi-natural grasslands?

The consequences of cyclic disturbances for population dynamics in time are explored through the application of simulation models (Chapter 3 & 5).

Outline of the thesis

This thesis is part of the MOSAIK-project funded by the German Federal Ministry of Education and Research under FKZ 01 LN 0007. The aim of the project is to test alternative management techniques (grazing & rototilling versus mowing) and to evaluate their efficiency for nature conservation to preserve open grasslands, which are threatened by land use change, e.g. intensification and abondonment.

This thesis considers vegetation and population dynamics under a rototilling and a mowing system. In the third chapter I conduct analyses of the population dynamics of an annual plant species under the two different disturbance regimes. A simulation model extrapolates my three year field data to calculate the probability of extinction and time to extinction over a period of 30 years. Chapter 4 focuses on the regeneration and recolonisation potential (incl. the effects on population structure) of the two perennial plant species *Sanguisorba minor* and *Salvia pratensis* after changes in management (mowing versus rototilling). Chapter 5 investigates the effects of different rototilling frequencies on population dynamics over time, aiming to identify a disturbance frequency by which the focal species can survive. Box 1 focuses on the regeneration vigour of *Prunus spinosa* after rototilling. The plant community regeneration potential and the response after rototilling are discussed in Box 2 & 3, respectively.

In the articles (Chapters) and short communications (Boxes) the design and all parts of the fieldwork were carried out by myself (but to some extent with the help of many dedicated students!). I had the major responsibility for the data analyses and writing of the manuscript drafts, whereas Chapters 3 - 5 were carried out together with the co-authors. The construction of the simulation models in Chapters 3 & 5 were conducted in close collaboration with Dr. Robert Biedermann.

Chapter 2

Introduction to study site, experimental design and species

Chapter 2

Introduction to study site, experimental design and species

Study site

The study was performed on semi-natural grassland communities in 'Hohe Wann' (10°35’ N, 50°3’ E), a nature reserve situated in the Haßberge in southern Germany. This region is in the most northern part of the 'Keuperbergland' between the break-through-valley of the river Main in the south and the 'Grabfeld' around Königshofen in the north (Kühne 1971).

The Haßberge are the northernmost part of the 'Fränkisches Schichtstufenland'. Having originated for the most part from the Trias period, the region consists mainly of the sedimentary rock Keuper (Kühne 1971), frequent changes in sediment conditions (marine to terrestrial) at the time of 'Keuper' means that gypsum, clay stone and sandstone can also be found. The region is characterised by a high range of soil types based on these underlying rocks. A high clay content is responsible for swelling and shrinkage processes with consequences for the holding and transmission of water especially on slopes, which impact significantly upon plant growth. During dry periods, cracks are generated and the water transmission is fast, resulting in dry conditions, whereas under wet conditions the water transmission is restricted (Elsner 1994).

The region is situated within a transition zone between an oceanic and a continental macroclimate. The mean precipitation is in summer ranges between 650 and 700 mm/year (Bayerische Landesanstalt tür Bodenkultur & Pflanzenbau 2001). The mean temperature per year is 7.5 - 8.5°C. The average variation of temperature is 17 - 17.5°C (Kühne 1971).

Extensive forests border the eastern part of the area, whereas the western part is bordered by farmlands. Land in this region, and especially the slopes, is split up into narrowly mosaics of semi-natural grasslands, orchard meadows, vine-yards and thermophile bushes (Fig. 2.1, Elsner 1994). This is due not only to geo-morphological heterogeneity and climate, but also to microclimatic differences brought about by exposition, inclination and land use.

Fig. 2.1 Impression of the landscape in the nature reserve 'Hohe Wann'. Land in this region, and especially the slopes, is split up into narrowly mosaics of semi-natural grasslands, open orchard meadows, vineyards and thermophile bushes.

Fig. 2.2 To maintain the typical grassland vegetation and to prevent shrub encroachment, the slopes are nowadays managed mainly by annually mowing in late summer. Most of the grasslands on the steep slopes must be mown by hand.

The semi-natural grasslands are the most obvious characteristics of the nature reserve and are of high conservation value, since many rare and protected plants and animals can be found there. The conservation of these grasslands is a major goal of conservation efforts for this region (Elsner 1994). To maintain the typical grassland vegetation and to prevent shrub encroachment, the slopes are nowadays managed mainly by annually mowing in late summer, as agreed in a written covenant between farmers and the conservation authority (contract of nature conservation). Unfortunately, the management strategy of mowing is time-consuming and thus expensive, since most of the grasslands on the steep slopes must be mown by hand (Fig. 2.2). Furthermore, hay must be taken away to avoid re-fertilisation.

Four sampling points showing different degrees of spontaneous colonisation by shrub were choosen for investigations. The dominant shrub species on all sampling points is the blackthorn (*Prunus spinosa*). The most important characteristics of the four investigation points are shown in Table 2.1.

Table 2.1 Characteristics of the four sampling points.

No.	name	height above sea level	geology	exposition	inclination (°)
1	Lichtlein	250	Gyps Keuper	250 ° WSW	20-30
2	Molkengrund	280	s.a.	180 ° S	15-35
3	Rappberg	320	s.a.	180 ° S	20-30
4	Regelberg	290	s.a.	185 ° S	15-30

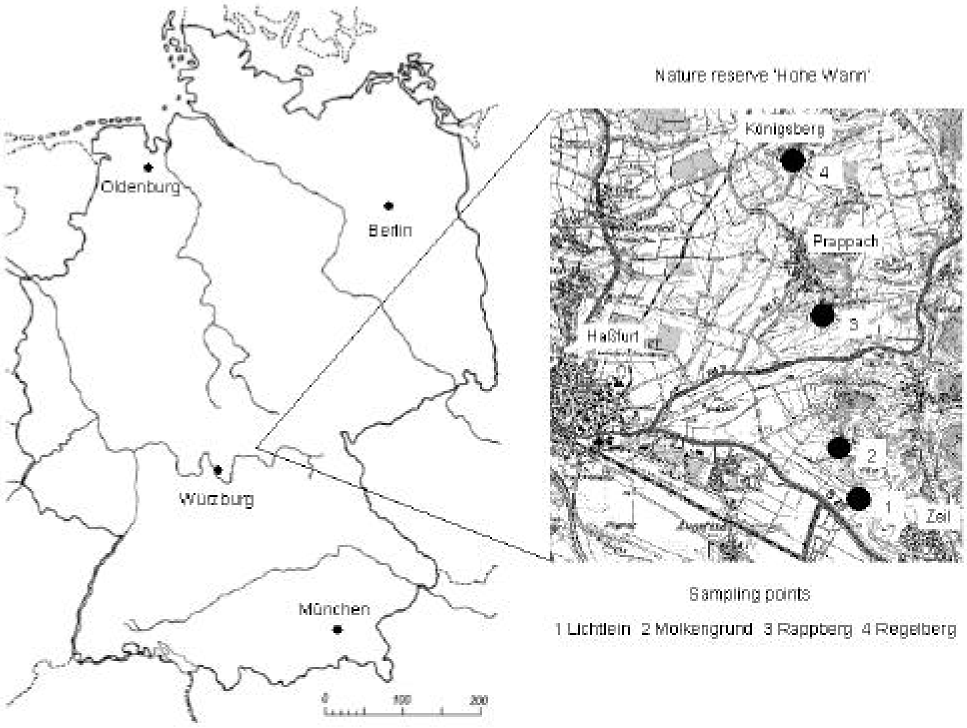

Fig. 2.3 Study site with the four sampling points Lichtlein, Molkengrund, Rappberg and Regelberg (modified section of TK 5929 Haßfurt, Bayerisches Landesvermessungsamt München).

The first sampling point (Lichtlein) is situated northwestern of the village Zeil (Fig. 2.3). The slope is southwest exposed (Table 2.1). It is considered a Mesobromion consisting of the matrix species *Bromus erectus*, *Festuca rupicola, Fragaria viridis* and *Coronilla varia*. The degree of spontaneous colonisation by *Prunus spinosa* is high ranking between 50 % and 60 % on all experimental fields. Shrubberies, mainly consisting of *Prunus spinosa*, *Cornus sanguinea*, *Ligustrum vulgare* and *Rosa canina* agg., border the north, south and east of the slope (Fig. 2.4).

The second sampling point (Molkengrund, Fig. 2.3) is dominated by the tussock grass species *Festuca rupicola*. Patches of bare soil were covered by a dense layer of mosses. Other dominant species are *Brachypodium pinnatum* (locally), *Potentilla tabernaemontana, Fragaria viridis, Euphorbia cyparissias*, and *Sanguisorba minor.* The degree of spontaneous colonization by shrub is low (about 10%). Westwards there is a vineyard still in use.

The third sampling point (Rappberg) is situated southeast of the village Prappach (Fig. 2.3). The vegetation is a dry sub-community of the Arrhenatheretum elatioris. The coarse-leaved tussock grass *Arrhenatherum elatius* and the Lamiaceae *Salvia pratensis* are conspicuous and dominant. Beneath this taller species there is a layer of fine-leaved grasses, with e.g. *Poa angustifolia*, *Festuca rupicola* and *Elymus* *repens* and small dicotyledones e.g. *Achillea millefolium*, *Onobrychis viciaefolia, Sanguisorba minor*, *Lotus corniculatus* and *Leucanthemum vulgare*. Bryophytes are confined to thin wefts of pleurocarpous mosses. Occasionally there are old fruit trees (e.g. *Pyrus communis*, *Malus domestica*) and *Rosa* shoots within the meadow. In the north, east and south the meadow is bordered by shrubberies consisting of *Prunus spinosa* and *Rosa canina* agg. (Fig. 2.4).

Fig. 2.4 View on two out of four sampling points showing different degrees of spontaneous colonisation by shrub (above: Lichtlein, below: Rappberg)

The northernmost slope (Regelberg) is situated south of the village Königsberg (Fig. 2.3). More than half of the slope (about 60%) is colonised by shrubs. The meadow is dominated by the grasses *Bromus erectus*, *Arrhenatherum elatius*, *Festuca rupicola*. *Brachypodium pinnatum* is locally prominent. The most frequent herbs are *Achillea millefolium*, *Sanguisorba minor*, *Salvia pratensis*, *Potentilla tabernaemontana* and *Fragaria viridis*. Shrubberies, mainly consisting of *Prunus spinosa*, *Cornus sanguinea*, *Ligustrum vulgare*, border the west, south and east of the slope. Northwards there are remnants of dry grasslands.

Experimental design

In 2000 four experimental fields were set up on each of the four slopes at the study site. One plot, the reference plot (M), was mown once a year. The remaining three plots were rototilled (R) once, each in a different year beginning in 2000 (R 2000, R 2001, R 2002, Fig. 2.5). After rototilling they were left to succession. Thus, experimental fields lay beside each other in a successional gradient.

Within each experimental field 20 sub-plots (2 x 2 m) were established. Of these subplots, 10 (numbered 1 to 10) were used to analyse the established surrounding vegetation and vegetation structure. Five permanent plots of 1 m^2 (Fig. 2.5) were set up within each management plot to determine demographic response to disturbance and succession of selected species. Data on morphological traits of the studied species were collected from randomly chosen individuals within 10 plots (numbered I to X). On eight 1 m x 1 m subplots frequency analysis were conducted (Fig. 2.5). For analysis of the seed bank soil samples were taken from five subplots (Fig. 2.5)

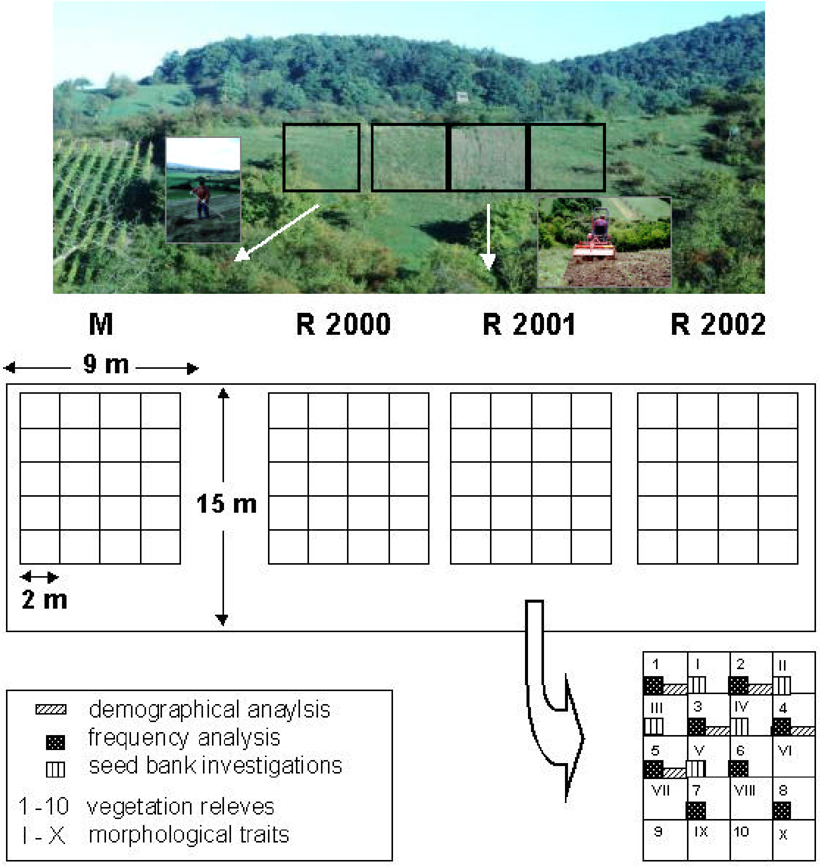

Fig. 2.5 Experimental design. On each investigation site, four different 9 by 15 m experimental plots were set up. On the reference plot (M) mowing was continued once each year. The other three plots were rototilled only once, each in a different year beginning in 2000. R 2000 = rototilling was performed in the year 2000, R 2001 = rototilling was performed in the year 2001, R 2002 = rototilling was performed in the year 2002. Within each experimental plot 20 sub-plots of 2 x 2 m were established for investigations (see text).

The focal species

Four species were studied on the population level. The species had to meet several criteria. First of all they had to be typical representatives for semi-natural grasslands. Furthermore, the species have to be present on all sampling points and need to occur in high abundances as for investigations on the life cycle a sufficient number of individuals for all life stages has to be present. Finally, they were chosen according to certain life histories and biological traits (i.e. life span and seed bank longevity) since a change in management influences plant population dynamics regarding these attributes (see Chapter 1). The attributes of the focal species are listed in Table A3 (Appendix).

Thlaspi perfoliatum was chosen as representative for annual species, which are thought to be sensitive to a change in management. As week competitors annuals suffer by increasing competition and litter accumulation during successional stages. Populations may go extinct on the patch level in the case when disturbance frequency is too low. ***Sanguisorba minor*** and ***Salvia pratensis*** were chosen as representative species for perennials with the ability for both vegetative and generative regeneration after disturbance. Perennials with multiple regeneration strategies may take advantage after rototilling, but will suffer under a frequent disturbance regime. Finally, shrub development after treatment is of special interest since overgrowing by bushes and shrubs is one of the most factors endangering grassland species (Bazzaz 1983). Thus, ***Prunus spinosa*** was chosen for detailed investigations on the resprouting vigour after rototilling.

Chapter 3

Effects of cyclic disturbance on the persistence of an annual plant in semi-natural grasslands

Chapter 3

Effects of cyclic disturbance on the persistence of an annual plant in semi-natural grasslands

with Robert Biedermann, Boris Schröder & Michael Kleyer

Abstract Plant species are differentially affected by disturbance, depending on their life histories and biological traits. The long-term survival of plants confronted with changing habitat quality during disturbance-induced succession may be covered by different strategies for persistence, regeneration or recolonisation. We present an empirical and modelling approach to investigate the population dynamics of annual plant species and in order to learn more about persistence strategies under cyclic disturbance. The study was carried out on semi-natural grasslands in the Hassberge area in Lower Franconia (Southern Germany). Nowadays, semi-natural grasslands, as part of cultural landscapes, only persist thanks to human-induced disturbance regimes. We tested whether the traditional, less intense disturbance regime 'mowing' may be replaced by the infrequent but massive disturbance regime 'rototilling' without evoking negative impacts on plant species' persistence. For that purpose, we set up a system of experimentally managed plots. Referential 'mowing' plots were mown once a year. In the 'rototilling' plots, the rototilling regime was applied only once, in each plot in a different year throughout the three years of study. After rototilling the plots were left to succession. Annual species are thought to be especially sensitive to a change in management. As a representative we selected the annual plant *Thlaspi perfoliatum.* Mortality rates as well as biological traits such as seed production and dispersal were measured within the plots. Based on these field data, we applied a spatially explicit model to study the dynamics of *Thlaspi perfoliatum* populations under the two disturbance regimes. The empirical data highlight that *Thlaspi perfoliatum* initially profits from reduced competition and increased resource availability caused by rototilling, but as weak competitor the species suffers under ongoing succession. The most strongly affected parameters under secondary succession after rototilling are fecundity, germination and establishment (seedling survival). The simulation model predicts population extinction of *Thlaspi perfoliatum* after an average of 24 years for a rototilling return interval of eight years. Sensitivity analyses highlight the importance of seed bank depletion and germination to predict population viability for this species. In summary, a disturbance return interval of less than 8 years has to be applied to maintain *Thlaspi perfoliatum* populations in a rototilling system.

Introduction

Disturbance (sensu White & Pickett 1985) is necessary to maintain the majority of grasslands in temperate regions. Without regular disturbance most grasslands would undergo succession to forests and shrublands (Leps 1990, Briemle et al. 1991, Ellenberg 1996). In recent decades traditional forms of land use such as regular grazing and mowing have been replaced by alternative management systems that are probably less costly (Poschlod & Schumacher 1998). Burning, mulching, variation in dates and frequencies per year of mowing, extensive grazing, and combinations thereof have been tested (Schiefer 1981, Briemle et al. 1991, Plachter 1995, Schreiber 1997). However, there is still a demand for management experiments which are more flexible and less expensive (Poschlod & WallisDeVries 2002). We tested the usefulness of rototilling, a new and unusual cyclic disturbance system for maintaining plant diversity of semi-natural grasslands (Kleyer et al. 2002). The present study thus incorporates two cyclic disturbance systems, namely: mowing and rototilling. Mowing once a year means a frequent, but comparatively light impact on plant populations. Mowing removes annual aboveground biomass, prevents litter accumulation over years, and enhances the availability of resources by the annual creation of new gaps. However, vegetation cover and plant composition are widely preserved (Box 3, Rydgren et al. 2001). Rototilling, on the other hand, has a massive impact on both above-ground and below-ground components. Direct effects of rototilling are the destruction of vegetation cover, the disturbance of plant moduls and even the death of individuals. Rototilling thus may cause changes in population structure of plant species. Indirect effects are observed through subsequent succession due to increasing biomass and through competition until the treatment is repeated.

A change in management strategy may influence the population dynamics of plants with respect to both life history and biological traits. Plants response in different ways to different forms of disturbance. This explains that some plant populations will profit and expand, while others will suffer and decrease (Box 3, White & Jentsch 2001). Species are successful either due to disturbance resistance adaptation or, in case of extinction, due to the ability to recolonise the disturbed sites before disturbance happens again (Eriksson 1996). However, after extinction on the patch level recolonization by long-distance dispersal is less likely with increasing distance from a source population (Menges 1990, Fahrig & Merriam 1994). For species without the ability to disperse over long distances it is therefore essential to persist on the local level. Species which have no apparent mechanism for storing reproductive potential between generations, as an extreme example annual plants without a persistent seed bank, would not be able to persist over periods long enough to bridge unfavourable phases of recruitment (Higgins et al. 2000).

We hypothesise that in the mowing system populations fluctuate stochastically depending on weather conditions ('good' years, 'bad' years for the species), but in the long run, populations are more or less at equilibrium. In contrast to the mowing system, populations might become extinct in the rototilling system because of a change in demographical parameters during succession.

Winter annuals are typical colonisers of gaps in semi-natural grasslands and apparently profit from a regeneration niche at small-scale open microsites (Grubb 1977), conforming to the short-lived interstitial-strategy in the matrix-interstitial model of Grubb (1986). Their seedlings colonise the gaps in autumn when plant biomass has decreased as a result of season and treatment (e.g. mowing in late summer). Winter annuals complete their life cycles after setting seeds in late spring, before small-scale microsites are closed by increasing cover of perennials (Grubb 1976 & 1986, Geißelbrecht-Taferner et al. 1997). They are thus thought to be sensitive to a change in management regime, especially in cases of successional phases, in which increasing biomass closes gaps and thus germination sites. We hypothesise that in the beginning, rototilling has positive effects on annual species due to the removal of vegetation cover since annuals profit from small-scale microsites. However, usually annual species are weak competitors that will suffer by increasing competition during succession. Evidence suggests that high levels of disturbance generally facilitate annuals, whereas low disturbance levels would select for competitive, long-lived species (McArthur 1962, McArthur & Wilson 1967, Grime 1977, Venable & Lawlor 1980, Levin et al. 1984, Klinkhamer et al. 1987, Schippers et al. 2001). Since we still lack knowledge about the effects of cyclic disturbance on the survival of plants, we analysed *Thlaspi perfoliatum* as an exemplary species, to quantify the impact of different temporal scales of disturbance on the performance of annuals. A change in land use, i.e. abandonment and fertilisation, is assumed to be responsible for the decline of *Thlaspi perfoliatum* populations in England (Rich et al. 1998).

In this paper we report the results of an empirical study on a semi-natural grassland community, using permanent plots over a period of three years. Our field study provides information about the demography of an annual plant species in the two different disturbance systems. We adressed the following question: (1) How strongly does a change of disturbance magnitude and frequency influence biological traits and demographic parameters of an annual plant species? By applying a simulation model we seek to answer the following questions: (2) How strongly does a change in management influence population dynamics in future? (3) What is the relationship between temporal scale of disturbance and the survival of this annual species? (4) Is a less frequent applied rototilling return interval (e.g. 8 years) able to maintain populations of *Thlaspi perfoliatum*? (5) How does seed bank longevity influence population survival in a rototilling system?

Methods

Study sites

Management experiments were carried out on semi-natural grasslands in the nature reserve 'Hohe Wann' in the Hassberge area located in Lower Franconia (Southern Germany, 10°35’ E, 50°3’ N). The experimental fields were established on slopes which have been mown at more or less regular intervals supposedly for at least 20 years. We set up experimental plots of 9 x 15 m^2 to compare population parameters and population dynamics of *Thlaspi perfoliatum* on the two treatments mowing and rototilling. The reference plots were mown each year in late summer (August-October), and the hay has been taken away to avoid re-fertilisation. Three other plots were rototilled (R) only once in early August, each in a different year beginning in 2000. We used a track-laying tractor that is especially constructed to cultivate steep slopes such as vineyards. Depending on soil conditions a depth down to 20 cm was affected. After rototilling these plots were left to succession (Fig. 3.1). These experiments were replicated on four different slopes within the study area Hassberge. On each experimental plot five subplots of 1 x 1 m^2 were established. Then, each subplot was divided into 100 cells of 10 x 10 cm^2 in order to study the demography of *Thlaspi perfoliatum*.

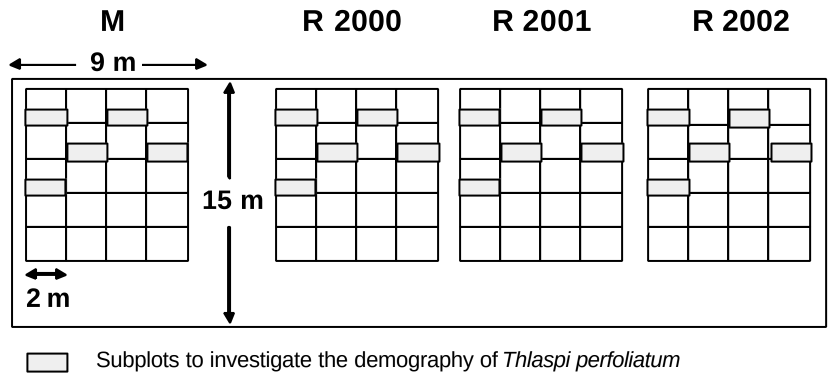

Fig. 3.1 Experimental design. Four different experimental plots of 9 x 15 m^2 were set up on each investigation site in the Hassberge area. The referential plot (M) was mown once a year. Three other plots (R) were rototilled only once, each in a different year from 2000 to 2002. Within each experimental plot five subplots of 1 x 1 m^2 were established in order to study the demography of *Thlaspi perfoliatum*.

Life cycle of Thlaspi perfoliatum L.

Thlaspi perfoliatum (Brassicaceae) is an annual reproducing by seed; it does not resprout vegetatively. Plants are self-compatible, and are assumed to be self-pollinated. *Thlaspi perfoliatum* is a typical winter annual and a regular member of the community species pool of managed dry grasslands and rocky outcrops in Central Europe (Oberdorfer 1978). It is rarely seen in fields or ruderal habitats. Seeds germinate exclusively in autumn in conditions of both light and darkness (Rich et al. 1998). Seedlings develope into a small vegetative rosette before winter. *Thlaspi perfoliatum* flowers in spring and sheds seeds from May onwards. The adult individuals die at the end of July, that is, before any treatment is applied. The species survives the summer as seed. It is reported to be phenotypically plastic with regard to height, branching, and seed production according to habitat quality (Rich et al. 1998). The species has no accessories for long-distance dispersal and dispersal distances are usually short (Baskin & Baskin 1979, Rich et al. 1998). Terminal velocity of seeds is measured to be 2.93 $m*s^{-1}$ (Tackenberg 2001). According to Rich et al. (1998) *Thlaspi perfoliatum* develops a seed bank, whereby most of the seeds germinate within the first year, with increasingly smaller proportions in the second and third year. For *Thlaspi perfoliatum* no explicit information on seed bank depletion is available. However, Kalisz (1991) found for an annual species with similar life cycle (*Collinsia verna*) that 16 % of the seeds remained viable for one year, 12 % persisted for two years, and 6 % for three years.

Field investigations and statistical analyses

Within the life cycle of *Thlaspi perfoliatum* we distinguished four well-defined developmental stages: seeds (0), seedlings (1), vegetative adults (2), and generative adults (3) (Fig. 3.2). From March to October, every single individual in each developmental stage was counted, marked and their position within the plot was recorded to observe survival rates on mown plots and rototilled plots in different successional stages (R1 = first year, R2 = second year, R3 = third successive year). For each management system we calculated mean values of demographic parameters from four replicates, i.e. four different slopes within a vicinity of 6 km.

Biological traits, such as seed production, were analysed by sampling 40 (year 2001) and 25 individuals (2002), respectively. Individuals were randomly selected within each experimental plot. We tested for differences in these biological traits between the experimental plots using non-parametric tests (H-test for overall comparisons and U-test for pairwise comparisons). For all experimental plots dispersal distances were quantified by measuring the distance between seedling and mother individual. We fitted Weibull functions on the empirical data for two consecutive years to parameterise the dispersal function (Higgins & Richardson 1999).

As all experimental plots were mown before the start of the experiment (see above), we assumed that the seed bank was consistent within both treatments. Hence, soil samples were taken from the mown plots in order to determine seed bank longevity and seed bank density, and to calculate the percentage recruitment of seeds from the soil seed bank after rototilling (see Box 2). Vertical distribution of seeds was used as an indicator of seed bank longevity (Thompson et al. 1997, Bekker et al. 1998, Jackel 1999, Bakker et al. 2000).

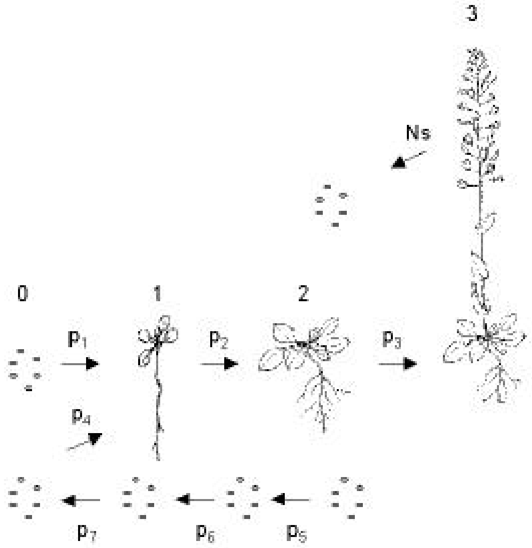

Fig. 3.2 Life cycle graph of *Thlaspi perfoliatum* showing the four stages seed (0), seedling (1) vegetative adult (2), and generative adult (3). Demographic parameter as used in the model: Ns = seed production, p_1 = germination, p_2 = seedlings mortality, p_3 = mortality of vegetative adults, p_4 = seedbank germination, p_{5-7} = within-year soil seed bank depletion. From Rothmaler (1991), modified.

Generel model description

We used the spatially explicit individual-based model INPLAMOSE (Biedermann, unpubl.) to study the spatial dynamics of *Thlaspi perfoliatum* populations in a grid of 25 x 25 cells (each 10 x 10 cm). The cell size of all simulations was identical to the cell size in the field experiment. The life-cycle was modelled with time steps of three months, according to the four stages within a year. The model takes into account senescence of individuals, mortality, reproduction, germination, and dispersal within the plot (Fig. 3.3). Population parameters were mainly based on empirical data. Parameters for seed bank depletion were based on Kalisz (1991).

Assumptions

Since the field work was limited to three years, model parameters referring to later successional stages in the rototilling treatment were unknown. They were taken from field data either from the mown plots – if the field values were approximately the same – or – in case of great deviations – from the third successional year. For a seed bank longevity of more than three years, seed mortality in the soil remained 50 %.

Models regarding mowing and rototilling were parameterised with the original field data. We assumed that populations of *Thlaspi perfoliatum* are more or less at equilibrium in the mowing system. Unfortunately, field data showed a decline of populations on mown plots, perhaps due to high precipitation during the study period, subsequent expansion of perennial species and closing regeneration gaps for *Thlaspi perfoliatum*. In this case of non-equilibrium, the mowing model was adjusted by shifting the germination rate till equilibrium, since we assumed germination to be the most sensitive demographic process. In order to account for the same conditions on all experimental plots the germination rate in the rototilling model was changed by the same percentage.

Initialisation

Habitat quality is assumed to be equal in all cells. According to densities measured in the field, 47 adults are randomly distributed within the grid for initialisation.

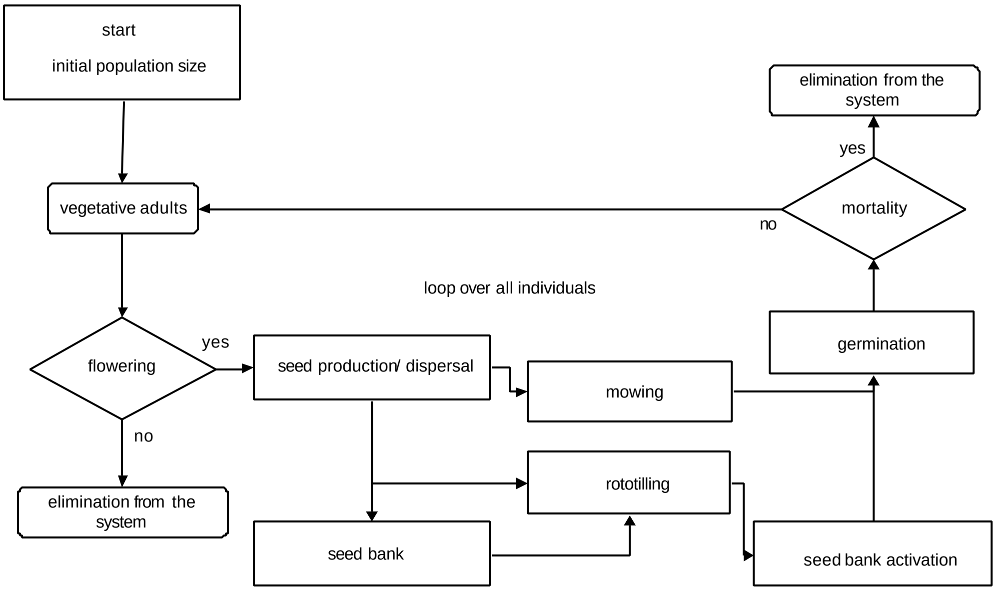

Fig. 3.3 Flow chart of the individual-based model of *Thlaspi perfoliatum*. During each simulation year the model simulates the life-cycle of *Thlaspi perfoliatum* including senescence of individuals, mortality, reproduction, germination, and dispersal within the plot.

Simluation

At each time-step all individuals enter the next stage. Reproductive adults (stage three) die after reproduction and are deleted from the system. We estimated mortality rates specific to both management regimes and, in case of rototilling, specific to each successional stage. Only generative individuals reproduce (stage 3). Seed production was calculated for each individual following the distribution found in the field. Lognormal (3.1) or normal distribution (3.2) were fitted on field data.

$$y = y_0 + ae^{\frac{-(\ln(\frac{x}{\mu}))^2}{2s^2}} \tag{3.1}$$

$$y = ae^{-\frac{1}{2}*(\frac{x-\mu}{s})^2} \tag{3.2}$$

with $a = \frac{1}{\sqrt{2x^2 s^2}}$

In the mowing system seeds germinate without entering into the soil seed bank. Recruitment from the soil seed bank happens exclusively after recent disturbance by rototilling. The percentage stimulation of seeds to germinate from the soil seed bank (S_r) was calculated using following term:

$$S_r = \frac{N_1 - N_2}{N_{Soil}} \tag{3.3}$$

with N_1 = number of seedlings per m² on recently rototilled plots.

N_2 = number of seedlings per m² on mown plots

N_{soil} = seed density per m² on mown plots

Seeds remain viable in the soil seed bank to germinate after rototilling for three years. The within-year seed bank depletion was estimated according to Kalisz (1991). According to field data, the seeds dispersed randomly with regard to direction. Consequently, we applied a random angle for each seed and calculated the amount of seeds reaching a certain distance (see Fig. 3.4). Dispersal was determined by measuring the distance between seedling and mother individual within all experimental fields. Weibull functions fitted on the empirical data for two consecutive years gave the dispersal function:

$$y = ae^{-bx^c} \tag{3.4}$$

We use a 'torus simulation' to avoid edge effects due to seed loss at the edges. If seeds were dispersed over the edges of our simulation grid they re-entered the grid on the opposite side (Haase 1995, Ruxton 1996, Hovestadt et al. 2000). Using a logarithmic function we incorporated density dependence by mortality of seedlings through self-thinning (Maron & Gardner 2000, Silvertown & Lovett Doust 2001). The maximum number of seedlings that can survive in one cell was set to 55, which is close to the maximum number of seedlings found in the field.

Sets of simulation runs

To predict the time to extinction and the probability of population extinction, we applied Monte Carlo simulations (Vose 1996) representing stochastic variations of single simulation runs. We performed at least 1000 runs to obtain stable results as recommended by Beissinger & Westphal (1998) and Menges (2000). Time to extinction, as well as the probability of population extinction, takes both above-ground and below-ground (seed bank) subpopulations into consideration. Application of the rototilling regime and reporting of the model results started after an initialisation period of five years, in order to reach a stable population structure.

Analysis of model results

The population size of *Thlaspi perfoliatum* was calculated once per simulation year by counting generative individuals only. The proportion of extinct populations was obtained from the fifteenth year (for a given parameter combination). Extinction probability was used as response variable in sensitivity analysis of the rototilling model (see below). The time to extinction was calculated for every single simulation. A population was considered to be extinct if both the number of seeds in the soil and the number of generative adults had decreased down to 0.

Sensitivity analysis

Sensitivity analysis determined model parameters exhibiting strong effects on extinction probability (Rushton et al. 2000, Buckley et al. 2003). Apart from seed bank longevity which varied from two to five years we systematically varied all model parameters by ± 5 % and 10 % of their mean value, respectively. We analysed the relationship between each parameter value and the simulated extinction events by logistic regression analysis (McCarthy et al. 1995, Hosmer & Lemeshow 2000, Cross & Beissinger 2001). A parameter’s sensitivity is its regression slope (cf. Table 3.3).

Management scenario

A rototilling frequency of eight years was chosen to analyse sensitivity and time to extinction in the rototilling system, since there was only a low extinction probability for *Thlaspi perfoliatum* populations up to a disturbance return interval of seven years.

Results

Effects of management on biological traits and demographic parameters in the field

There were significant differences in mean releasing height, number of branches, number of fruit, number of seeds per fruit, and total seed production between individuals of *Thlaspi perfoliatum* between mown and rototilled plots in the first year of succession (Table 3.1). Individuals on the rototilled plots were twice as tall, built up new branches with fruits, produced more seeds per fruit and spread about 20 times more seeds than individuals on the mown plots. In the second year of succession however, the mean height, number of branches, and number of seeds per fruit dropped down again to the average value of the mown plots. Seed production was nonetheless still significantly higher than on the mown plots. In the third year of succession all values (excluding number of branches) were lower than in the mowing system. Individuals were significantly smaller than on mown plots. Seed production went down to an average value of 20 seeds per individual. This parameter followed a lognormal distribution on both kind of plots in the first and second successive year after disturbance, whilst a normal distribution was found for seed production data in the third year of succession (Table A1, Appendix).

Table 3.1 Comparison of biological traits between mown (M) and rototilled plots in different successional stages, R1: first, R2 = second, R3 = third year of succession. Mean of replicates ± SD. (Mann-Whitney U-test, ** p < 0.01, *** p < 0.001, ns p > 0.05), °seed production per individual

	M	R1	R2	R3
mean releasing height [cm]	8.15±3.16	19.25±4.69***	8.45±2.44**	3.79±1.12***
number of branches	1±0	6±3***	1 ±0^{NS}	1±0 ^{NS}
number of fruits	7±4	90±72***	8±4 ^{NS}	6±2 ^{NS}
number of seeds/fruit	4±1	7±1***	4± 1^{NS}	3±1 ^{NS}
fecundity°	24±20	537±462***	32±29**	20±8^{NS}

The treatment had negligible effects on dispersal (Fig. 3.4). We fitted Weibull functions to empirical data for two consecutive years (Table A2, Appendix). Seedling density decreased in both systems with increasing distance from a reproductive individual. A high percentage of seeds germinated in the immediate vicinity of the mother individual (about 10 cm). The maximum dispersal distance was nearly equal for both management systems with 20 cm for M, 21 cm for R1, and 19 cm for R2. Figure 3.4 shows that there was no relationship between the mean releasing height of seeds of the mother individuals and the mean dispersal distance.

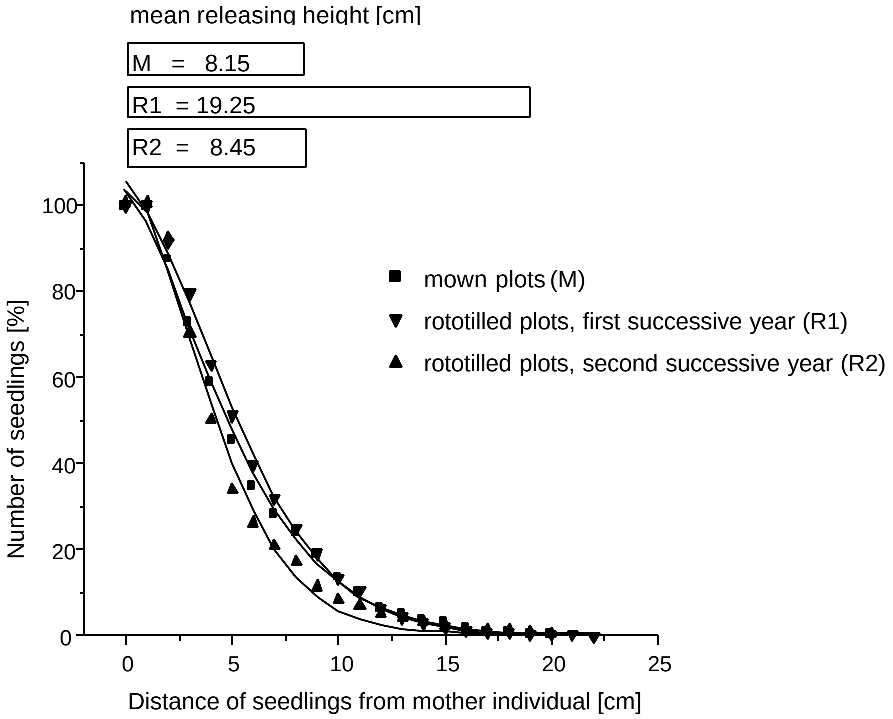

Fig. 3.4 Dispersal curves of *Thlaspi perfoliatum* on mown (M) and rototilled plots in the first (R1) and second (R2) year of succession as well as the mean releasing height of seeds. We fitted Weibull functions (curves) on empirical data (symbols) for two consecutive years. (M) n = 603, (R1) n = 2612, (R2) n = 222.

The mortality rate of vegetative individuals (p_3, Table 3.2) did not differ between both management systems and successional stages, indicating that this demographic parameter was not affected by disturbance. On the other hand, the germination rates (p_1) and seedling mortality (p_2) were greatly affected by disturbance. The germination rate on recently rototilled plots was twice as high as on mown plots, due to the activation of seeds to germinate from the soil seed bank. However, there is a dramatically decline of the germination probability in the second and third years of succession. Seedling mortality on rototilled plots was significantly lower in the first year of succession than on the mown plots, but increased during succession.

Table 3.2 Comparison of demographic parameters between mown (M) and rototilled plots in different successional stages, R1: first, R2: second, R3: third year of succession. p1 = germination, p_2 = seedling mortality; p_3 = mortality rate of vegetative individuals. Each value (in %) represents the mean of the four replications (Mann-Whitney U-test, p-values * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns $p > 0.05$).

	M	R1	R2	R3
p_1	9.975	24.98**	0.709***	1.282*
p_2	66.66	55.49*	94.19**	95.04*
p_3	4.672	2.506^{NS}	1.375^{NS}	8.333^{NS}

The number of seedlings increased in the second successional year following rototilling. In the field, up to 48 seedlings were observed in one 10 x 10 cm cell. We found a relation between seedling density and seedling mortality. Seedling survival was negatively influenced by seedling density (see Fig. 3.5). Field data are fitted with a logarithmic function that puts a ceiling of 55 on the maximum number of seedlings that can survive in one cell. Densitiy-dependent seedling mortality was found neither in mown plots nor in rototilled plots of other successional stages.

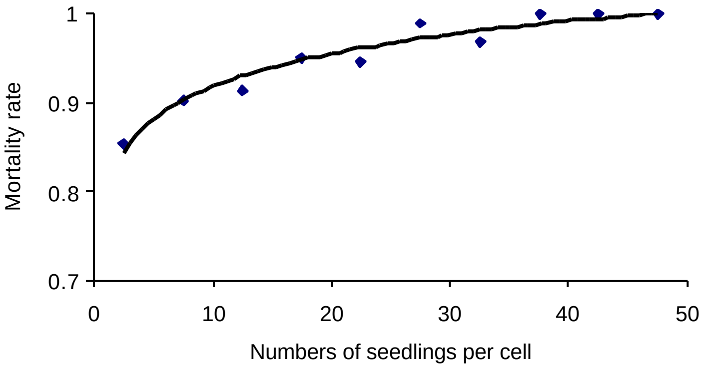

Fig. 3.5 Example for a self-thinning process in *Thlaspi perfoliatum* populations. Relationship between seedling density per cell and seedling mortality in the second year of succession on rototilled plots. Field data are fitted with a logarithmic function (mortality = 0.0531 ln(density) + 0.7957) that puts a ceiling of 55 on the maximum number of seedlings that can survive in one cell.

Investigating the seed bank reveals that seeds were found more frequently in the upper than in the lower soil layer (Box 1). According to the vertical distribution of seeds, we classified the seed bank as short-term persistent on three sites and as transient on one site. That is, the classification of the seed bank type for *Thlaspi perfoliatum* did not differ much between the four study sites. Mean seed density on mown plots was 80 per m². Since on average additional 37 seedlings appeared on recently rototilled plots, the activation of seeds from the seed bank was estimated to be 46.25 %.

Modelling results

The model was used to simulate the population dynamics of *Thlaspi perfoliatum* (Fig. 3.6), applying rototilling every 8th year.

Mowing model with field data set and adjusted mowing model

Using the field data set for simulation, the overall *Thlaspi perfoliatum* population slowly decreases and goes extinct after an average of 9 years (Fig. 3.6). Above- and below-ground subpopulations showed similar dynamics, but the above-ground subpopulation became extinct earlier than the below-ground subpopulation. In order to achieve an equilibrium, i.e. comparatively stable populations over longer time scales, the germination rate was adjusted from 9.975 to 12.95, which is an increase of 29.82 %. Then, the number of above-ground individuals fluctuated between 45 and 47 (Fig. 3.6).

Adjusted rototilling model (return interval 8 years)

Germination rates in the rototilling model were increased according to the mowing model (+ 29.82 %), i.e. from 9.975 to 12.95 in the first year of succession, from 0.709 to 0.92 in the second year and from 1.287 to 1.664 in the third successional year. In case of a rototilling frequency of 8 years (Fig. 3.6) the above-ground population of *Thlaspi perfoliatum* at first increased up to more than 1700 individuals after rototilling, but decreased quickly to an average of less than 10 individuals. The below-ground subpopulation followed above-ground population dynamics with a time lag. The number of seeds in the soil seed bank increased due to a higher seed production after rototilling, but decreased already in the second year. This effect is continuously repeated: recurring rototilling increased both above- and below-ground populations temporarily, but the number of individuals decreased during the following successional years. *Thlaspi perfoliatum* populations became extinct after an average of 24 years.

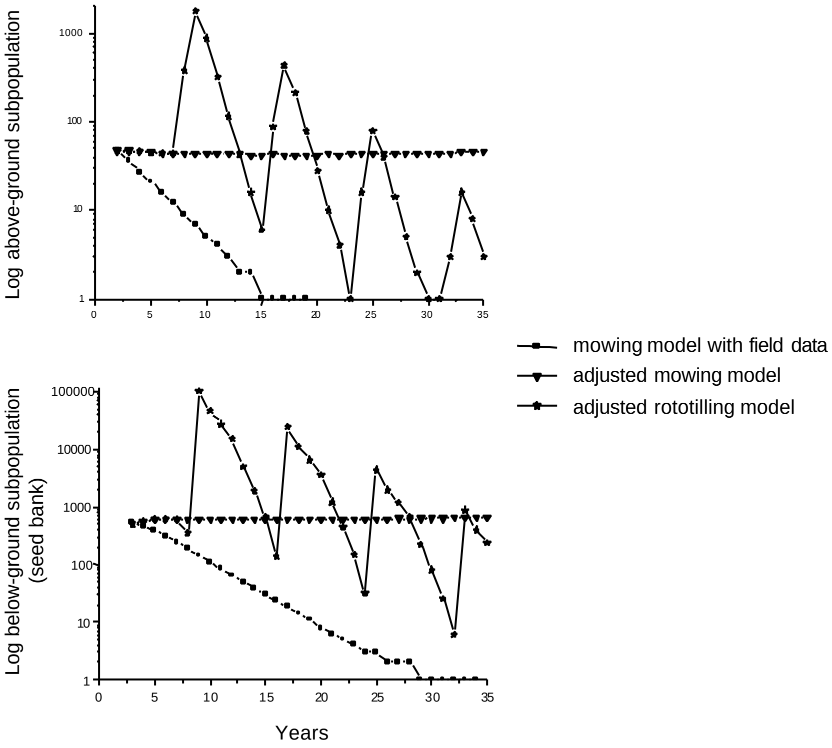

Fig. 3.6 Below-ground and above-ground population dynamics of *Thlaspi perfoliatum* over 30 years on mown and rototilled plots (rototilling every 8th year, beginning in the fifth year). Each curve represents the mean of 1000 model runs.

Sensitivity analysis

Sensitivity was calculated as the ratio of the relative change of the probability of extinction to the relative decrease of parameters by 5 % and 10 %. Extinction probability was most sensitive to seed bank depletion (p_5, p_7, Table 3.3). Reducing the first year mortality of seeds in the soil (p_5) by 10 % decreased the probability of extinction by 41 % (Fig. 3.7a, Table 3.3). On the other hand, decreasing the germination rate in the third year of succession, increased extinction probability of *Thlaspi perfoliatum* populations (Fig. 3.7b). Generally, increasing the input values of seed production, seed bank germination and germination resulted in a decrease of the probability of population extinction (Table 3.3).

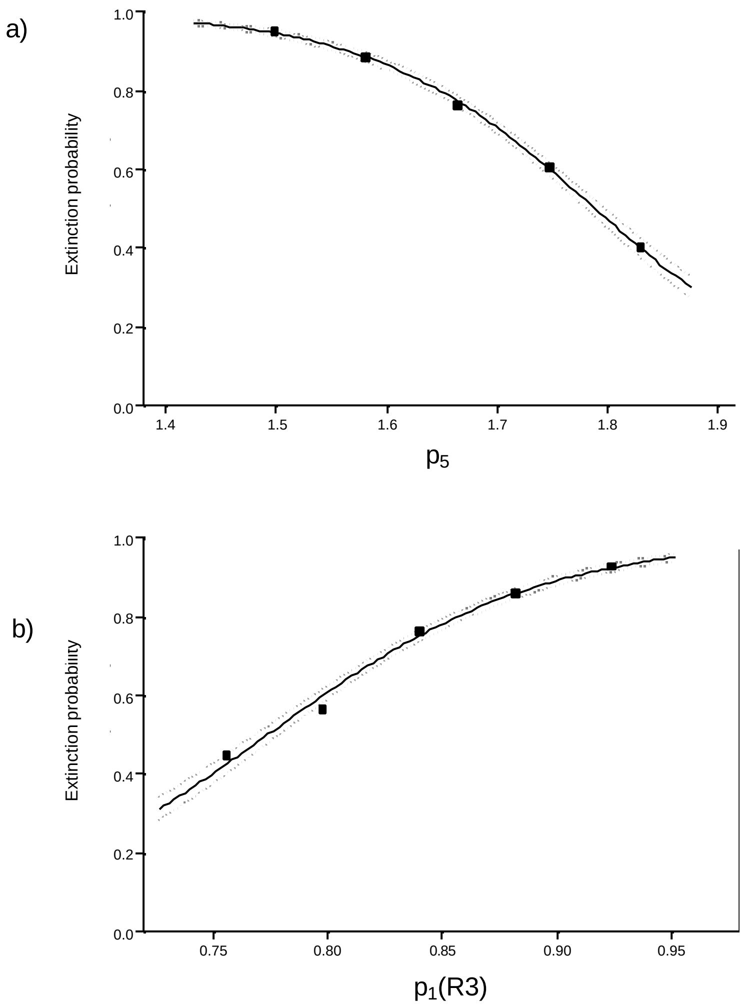

Fig. 3.7 The probability of population extinction with a) varying the soil seed bank depletion rate in the first year (p_5) and b) varying the germination rate in the third successional year (p_1(R3)) following rototilling using log. regression (for a: $y = 1/(1+\exp(-9.851 * x - 17.620))$, for b: $y = 1/(1+\exp(16.742 *x + 12.953))$. 95 % confidence intervals are given by the dotted lines. The values ranged from 5 % and 10 % on either side of the average parameter value. Each point represents the mean of 1000 model runs.

Changing the mean values for seedling mortality (p_2) and mortality of vegetative adults (p_3) by 10 % has a comparatively low impact on the probability of population extinction (Table 3.3). Nevertheless, an increase of 10 % resulted in higher extinction probabilities.

Table 3.3 Sensitivity of the model to variation in parameter values. Logistic regression was applied to analyse the relationship between each parameter value and the simulated extinction events. Further are given the extinction probabilities for a decrease of each parameter value of 10 % and the percentual deviation of the extinction probability from the mean probability (0.76). The most sensitive parameters are indicated by bold letters. ° we ran the simulation with a longevity of 2 years (that means a change of 33.33 % of the mean longevity value of 3 years). In order to compare the sensitivity of seed bank longevity with the sensitivity of the other tested parameters the result was translated to a divergency of 10 %.

parameter (treatment year R1-R3) (for explication see Fig. 3.2)	Sensitivity		regression slope	significance of regression slope ≠ 0	Extinction prob. for mean parameter value - 10 %	deviation (%) from the mean extinc. prob. (0.76)
	10 %	5 %				
germination						
p_1(R1)	0.0050	0.0010	-0.070	ns	0.76	0.65
p_1(R2)	0.0500	0.0350	-3.599	< 0.001	0.81	6.5
p_1(R3)	**0.1890**	**0.1230**	-9.851	< 0.001	0.95	25
seedling mortality						
p_2(R1)	0.0040	0.0001	0.543	ns	0.76	0.52
p_2(R2)	0.0050	0.0045	0.974	ns	0.76	0.66
p_2(R3)	0.0010	0.0065	0.477	ns	0.76	0.13
mortality of vegetative adults						
p_3(R1)	0.0310	0.0010	0.459	0.015	0.73	4.1
p_3(R2)	0.0010	0.0055	0.218	ns	0.76	0.13
p_3(R3)	0.0300	0.0280	0.247	< 0.001	0.73	3.9
seedbank germination						
p_4_R1	0.0180	0.0150	-25.88	< 0.001	0.78	2.4
fecundity						
Ns(R1)	0.0520	0.0370	-0.005	< 0.001	0.81	6.8
Ns(R2)	0.0390	0.0370	-0.079	< 0.001	0.80	5.1
Ns(R3)	0.0070	0.0010	-0.053	0.022	0.77	0.92
seed bank depletion						
p_5	**0.3160**	**0.1970**	16.74	< 0.001	0.45	41
p_6	0.0110	0.0140	17.16	< 0.001	0.75	1.4
p_7	**0.1860**	**0.1600**	11.86	< 0.001	0.58	24
seedbank longevity	0.0345°	-	-	-	0.88°	15

We also tested the effects of variation in seed bank longevity on above-ground population dynamics and time to extinction (Fig. 3.8 and Fig. 3.9). Decreasing seed bank longevity from 3 to 2 years reduced population survival and time to extinction from 24 to 22 years (Fig. 3.9). Increasing seed bank longevity enhanced survival and prolonged time to extinction. With a seed bank longevity of 5 years, time to extinction exceeded 30 years (Fig. 3.9). Nevertheless, on larger time scales populations will go extinct in all scenarios.

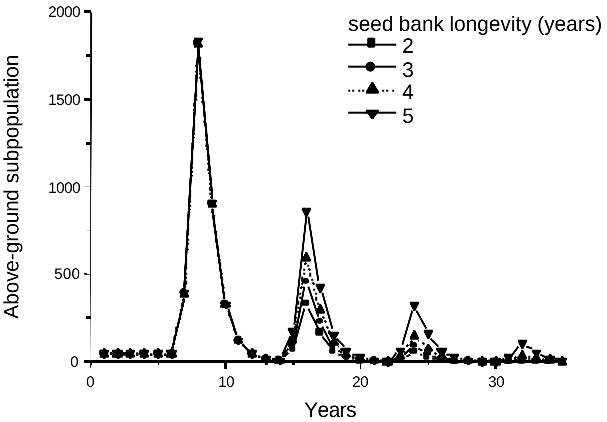

Fig. 3.8 The effects of variations in seed bank longevity on above-ground population dynamics of *Thlaspi perfoliatum* if plots are rototilled every 8th year. Seed bank longevity varied from 2 to 5 years. Each curve represents the mean of 1000 model runs.

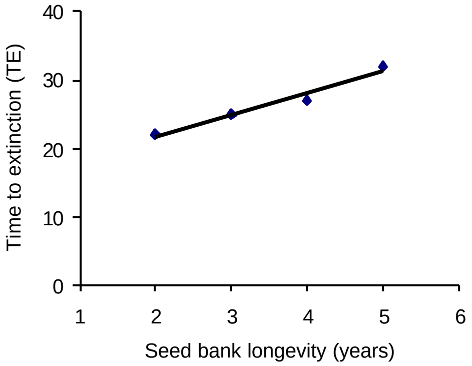

Fig. 3.9 The effects of variations in seed bank longevity on the time to extinction of *Thlaspi perfoliatum* populations under the management system rototilling every 8th year. Seed bank longevity varied from 2 to 5 years. Each point represents the mean of 1000 model runs.

Discussion

Annuals are reported to be especially sensitive to changes of abiotic and biotic conditions (Harper 1977, Doust & Doust 1988). A change in management and thus a change in the degree of disturbance influences competition and the availability of resources, both having a great impact on plant fitness and plant demography (Salisbury 1942, Harper 1977). Even though both management regimes are man-made large-scale disturbances and are both applied in late summer, there are considerable differences in terms of biomass removal. Mowing resets succession at any mowing event, i.e. every year. Rototilling creates bare soils open for recolonisation, but detailed investigations show that they were quickly recovered by semi-natural grassland species and gaps disappeared during early successional stages (Box 3). Our results confirm that *Thlaspi perfoliatum* is phenotypically highly plastic with regard to height, branching and seed production depending on habitat quality (Rich et al. 1998). *Thlaspi perfoliatum* responded to rototilling by vigorous branching and thereby enhanced production of seeds in the first year after rototilling, probably due to reduced competition and an increase of resources availability. As a winter-annual *Thlaspi perfoliatum* profited from available space by germinating in autumn when most perennial plant species had not yet recovered. Although species differ in their ability to colonise gaps (Schütz 2000), seed sowing experiments with *Thlaspi perfoliatum* (Fritzsch, unpubl.) support the importance of extant regeneration niches for plant species as largely emphazised by many studies (Grubb 1977, Silvertown & Smith 1988, Hutchings & Booth 1996, Stöcklin & Bäumler 1996, Eriksson & Eriksson 1997, Lindig-Cisneros & Zedler 2002). As hypothesised, fecundity, seedling survival, and germination rate increased due to rototilling, but declined already during the second successional year after the treatment. (Canales et al. 1994) also reported reductions in both fecundity and germination for an annual grass during succession through disturbance exclusion. Lennartsson & Oostermeijer (2001) stated that different management systems affect population viability mainly through their impact on fecundity and establishment.

As *Thlaspi perfoliatum* grew higher on rototilled plots and due to the fact that habitats were more open especially in the first year after rototilling, we hypothesised that a change in management may influence dispersal 'behaviour'. But contrary to Abs (1999), we found no relationship between mean releasing height of seeds and dispersal distance. *Thlaspi perfoliatum* has no ability for long-distance dispersal of seeds. The majority of seedlings appeared in the immediate vicinity of the mother individuals. Therefore, *Thlaspi perfoliatum* is a poor coloniser by long-distance dispersal such as many other grassland species (Primack & Miao 1992, Poschlod et al. 1996, Kollmann 1997, Poschlod et al. 1997) which highlights the importance of population persistence on the patch level.

For annual plant species density-dependent fecundity and mortality through self-thinning have been observed frequently in a range of habitats (Symonides 1988, Watkinson et al. 1989, Buckley et al. 2001, Silvertown & Lovett Doust 2001). The high number of seedlings appearing in the second successional year after rototilling was the result of increased fecundity. We observed an increased mortality of seedlings as a result of crowding of *Thlaspi perfoliatum* as has been reported for other annual species as well e.g. by Maxwell et al. (1986) and Symonides (1983). Density-dependent seedling mortality through self-thinning is mainly caused by intraspecific competition for limited resources, whilst the level of herbivorous and pathogenic activities can also be expected to be affected by the level of crowding (Symonides 1988). Even though densitiy-dependent seedling mortality was not detected for the mown plots and rototilled plots in other successional stages due to the fact that the overall seedling density was too low (maximum 8 seedlings/cell), we suggest that the same process takes place. Detailed investigations revealed no density-dependent fecundity (Grein, unpubl. data).

Contrary to Rich et al. (1998) we found the seed bank to be only short-term persistent. The classification of the seed bank type for *Thlaspi perfoliatum* did not differ much between the four study sites. It is known that the depth distribution of individual species shows a wide range of variation. Poschlod (1993) and Bekker et al. (1998) found depth distributions for many species to be very different on different grassland sites. Reasons for this deviation may be both abiotic conditions of the investigation sites and the origin (genetics) of seeds (Thompson et al. 1997). More data on seed persistence of *Thlaspi perfoliatum* on semi-natural grasslands would be required to enhance the reliability of the modelling results.

In order to evaluate the usefulness of a rototilling regime to maintain populations of semi-natural grassland species compared to the reference mowing regime, populations in the latter regime are assumed to be at equilibrium, i.e. exhibiting comparatively stable populations over longer time scales. Our field data showed a decrease in population size of *Thlaspi perfoliatum* on mown plots. This is extrapolated in the model revealing a population extinction after an average of nine years (Fig. 3.6a). However, as the mowing system is maintained since many years and *Thlaspi perfoliatum* is still present, our three year field data may rather represent the negative slope of a stochastic fluctuation in the regeneration niche of *Thlaspi perfoliatum*, stimulated by abundant precipitation during the study period, subsequent expansion of perennial species and closing regeneration gaps for *Thlaspi perfoliatum.* It has been shown that fitness and demography of annual species may fluctuate strongly from year to year depending, for instance, on weather conditions (Grubb 1986). Beissinger & Westphal (1998), Maschinski et al. (1996) and Menges (2000) point out that extrapolating population dynamics using short-term investigations may be problematic since short periods of study can not genuinely represent a species' population dynamic. However, several studies have shown that it is possible to get useful information and knowledge from snap-short demographic studies (Löfgren et al. 2000, Magda & Jarry 2000, Wiegand et al. 2000). We conclude that our short-term investigations cannot sufficiently include the stochastic fluctuations. Since germination is one of the processes most affected by weather conditions (Grubb 1976), we adjusted the models to achieve equilibrium conditions by increasing germination rate.

The simulations demonstrate that if rototilling is applied in a cyclic regime with a return interval of 8 years *Thlaspi perfoliatum* populations do not persist for longer periods. This result is in accordance with theories regarding about disturbance level and plant persistance e.g. the C-S-R strategy theory of Grime (1977), McArthur (1962), McArthur & Wilson (1967) extended by Venable & Lawlor (1980), Levin et al. (1984)

and Klinkhamer et al. (1987): High levels of disturbance generally facilitates annuals. Populations increased after disturbance due to increased seed production and stimulation of the soil seed bank, but decrease quickly due to reduced vital rates during succession. We assumed that the seed pool exists for three years only. Longevity of seed bank enables populations to survive even if the above-ground population has gone extinct. Increasing seed bank longevity by one year prolongs population survival by 8 % (see Fig. 3.9, Dutoit & Alard (1995), Kalisz & McPeek (1993)).

Sensitivity analysis provide practical information for model builders and conservation biologists by highlighting the parameters that have the greatest influence on the results of the model (McCarthy et al. 1995). High sensitivity means that uncertainties of the corresponding parameters are highly relevant and the research resources available should be focused on measuring these sensitive parameters. In contrast, low sensitivity indicate that the model results show minor variation in response to changes in the parameters. Therefore uncertainty in parameter values may be ignored in this case (Frank et al. 2003). Our sensitivity analysis shows that the model results are robust to changes in the most parameters. The most sensitive parameters for the model outcome are seed bank depletion and germination. We gathered a reliable set of field data regarding germination, but not for seed bank depletion. Thus, yearly depletion rates had to be taken from the literature (Kalisz 1991). This kind of quantitative data are very scarce, as most seed bank studies provide longevity in three categories (transient, short-term, long-term persistent) only. Given the sensitivity of yearly seed bank depletion rates in the model, we advocate for more detailed studies in this field of research.

Conclusions

Our results showed that a change in the management regime, i.e. a change in disturbance magnitude and frequency, has a strong effect on population dynamics and population viability of an annual plant. Lennartsson & Oostermeijer (2001) stated that different management systems affect population viability mainly through their impact on fecundity and establishment. The present study confirms these findings. Seed production, seedling survival and germination are the most strongly influenced demographical parameters under secondary succession after rototilling. *Thlaspi perfoliatum* populations suffer under increasing competition till succession will be reset by repeated treatment. The simulation model predicts population extinction of *Thlaspi perfoliatum* after an average of 24 years for a rototilling return interval of eight years. To maintain annuals with biological traits and demography similar to those of *Thlaspi perfoliatum* by rototilling a more frequent disturbance return interval is required.

Chapter 4

Effects of contrasting disturbance regimes (rototilling versus mowing) on the population dynamics of two perennial plant species (*Sanguisorba minor* Scop., *Salvia pratensis* L.)

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Effects of contrasting disturbance regimes (rototilling versus mowing) on the population dynamics of two perennial plant species (*Sanguisorba minor* Scop., *Salvia pratensis* L.)

with Michael Kleyer

Abstract Experimental fields were established on a semi-natural grassland community in the southern part of Germany to observe population dynamics in mown and rototilled systems. We selected the perennial species *Sanguisorba minor* and *Salvia pratensis* to investigate effects on fecundity, establishment and survival due to a change from mowing to rototilling as two options for conservation management. Mowing was applied yearly, rototilling once in the three year study period and these plots were then left to succession. Rototilling affected population parameters of *Sanguisorba minor* in the first successional year only. All parameters were significantly higher than on mown plots. Fecundity, measured as number of seeds per inflorescence, was twice as high as on mown plots, but decreased already in the second year of succession down to the average value of mown plots. Vegetation structure, e.g. the cover of herb layer was found to be correlated with fecundity. No influence of a change in management on any biological trait was observed in *Salvia pratensis*. Demographic data were mainly influenced by a change in adult and juvenile mortality and in the flowering rate of adults. Both species exhibited low adult mortality on mown plots. Resprouting ability after rototilling differed strongly between both species. Most of the above-ground population (70 – 80 %) of *Salvia pratensis* survived rototilling and was able to regrow. The proportion of flowering to vegetative rosettes did not changed. Contrary to the findings for *Salvia pratensis,* a high percentage of the above-ground population of *Sanguisorba minor* was destroyed. The flowering rate decreased strongly in the first successional year after rototilling. Although both species exhibit similar persistence and regeneration trait attributes as compared to other species of the community, the shift from mowing to rototilling had very different effects on demography and population structure. Both species are able to persist rototilling by compensating the loss of individuals. A comparison of the regeneration strategy in response to rototilling showed that *Salvia pratensis* survived mainly owing to resprouting from a bud bank, while *Sanguisorba minor* survived due to generative regeneration by seedlings and seed bank activation.

Introduction

Biodiversity of marginal grasslands in temperate regions is threatened by land use intensification or abandonment (Poschlod et al. 1998, WallisDeVries et al. 2002). In order to conserve biodiversity, many marginal grassland sites became reserves, with the need to prevent shrub encroachment and to remove standing biomass. Grassland management by annual mowing requires large state subsidies and there is a constant need to find alternative management systems that are less costly (Poschlod & WallisDeVries 2002). In the framework of disturbance ecology the magnitude of a disturbance impact such as mowing is measured in the amount of biomass destroyed (White & Pickett 1985, White & Jentsch 2001). Annual mowing could be seen as relatively frequent but light disturbance as it removes only the above-ground biomass. Disturbance magnitude with ploughing or rototilling is higher because plants are destroyed down to the roots. Replacing a light and frequent disturbance impact with a more severe but less frequent impact would perhaps be less costly and result in similar conservation effects. Little is known on survival of hemicryptophyte perennial plants under infrequent below-ground disturbance regimes as such impacts are almost exclusively applied annually in arable landscapes and favour either a seeding strategy with an annual life cycle or vegetative regeneration from a deep bud bank as in geophyte perennials (Bellingham 2000, Klimešová & Klimeš 2003).

Studies on the population level can be used to understand the mechanisms of vegetation development following such modifications in management (Harper 1977, Fiedler & Kareiva 1997, Henle et al. 1999, Laska 2001). Demographic studies point out species responses to changes in habitat quality due to changes in the disturbance regime. This response is species-specific and depends on the traits of the species (White & Pickett 1985, Bellingham, 2000). This is the reason for the increase or invasion of some species, while others decrease or retreat (White & Jentsch 2001). Plants can only persist if they recruit new reproductive individuals into the population to compensate individual mortality following disturbance impacts.

In this context, target plant species can serve as an indicator in monitoring programmes, if the change of the target species population reflects a change in the composition of the whole plant community (Bühler & Schmid 2001). Species with similar trait attributes should respond similarly to disturbances (Gitay & Noble 1997). Hence, target species should be representatives of relevant functional groups in the community under study. As a consequence, there is a need to study not only rare and endangered plant species, as has been done in most demographic studies, but also characteristic and abundant species (Eriksson & Eriksson 2000, Bühler & Schmid 2001). Since long-term demographic studies are are often too time consuming to be used in conservation management, many recent studies concentrate on the changes in the population structure of target plants (Oostermeijer et al. 1994, Bühler & Schmid

2001, Hegland et al. 2001, Colling et al. 2002). Studying population structure often yields faster yet less precise results than complex long-term demographic studies.

This chapter aims at understanding the regeneration potential of *Sanguisorba minor* and *Salvia pratensis*. Both are perennial polycarpic herbaceous plant species abundant in semi-natural grasslands of Central Europe, with an ability for vegetative and generative regeneration after disturbance. We compare the response of these species to annual mowing and infrequent rototilling as two alternative management regimes of grasslands. Contrary to mowing, rototilling causes destruction of biomass below the hypocotyl. However, many species of grasslands have regenerative buds below the hypocotyl and may regenerate from these buds if the return interval of rototilling is not too small (Grime et al. 1988, Klimeš & Klimešová 1999). Also, rototilling leads a more effective decomposition of biomass by chopping up and burying plant material. Hence, expensive biomass removal from the area may not be necessary. Because roots become destroyed, mineralised nutrients are not taken up by remaining plants which may lead to nutrient losses desired in conservation management of semi-natural grasslands. Also, seed banks may become activated and establishment of seedlings is possible. These assumed effects led us to consider infrequent rototilling as an alternative management regime to annual mowing. However, if rototilling is applied each third or fifth year, secondary succession is initiated in the meantime and an assortment in dominance of species populations takes place over time (Bazzaz 1983). Plots undergo succession till rototilling is being repeated. Although there is some knowledge about regeneration strategies of grassland species by means of regenerative buds or activation of seed bank (Crawley 1990, Thompson & Baster 1992, Bakker et al. 1996, Poschlod et al. 1998, Wagner et al. 2003, Amiaud & Touzard 2004) effects on population dynamics by strong disturbance impacts with long return interval are hardly known.

By studying the demography and the population structure of *Sanguisorba minor* and *Salvia pratensis* we address the following questions: (1) How strongly does a change of disturbance system influence the demographic parameters and population structure; (2) How do the species differ in terms of their reaction to disturbance; (3) Does lateral and vertical vegetation structure of surrounding plants influence fecundity of the two species? (4) Is there a trade-off between vegetative and generative regeneration?

Methods

Field experiment

The experiment was carried out on four regularly mown semi-natural grasslands in Southern Germany (Lower Franconia, Bavaria, 10°35’ E, 50°3’ N). On each site, four experimental fields have been established with treatments (i) mowing continued, (ii) rototilling in 2000 (iii) rototilling in 2001, and (iv) rototilling in 2002. Five permanent plots within each of the experimental fields were established and observed over a period of three years.

Field sampling

Each plot was divided into 100 subplots of 10 x 10 cm. The plots were visited during the entire vegetation period from March to October. Within each plot all seedlings, juveniles and adults of the two species were counted, marked and their plot position was recorded with a square grid of wires to observe survival rates and fecundity in the following years. To account for vegetative reproduction new rosettes resulting from vegetative resprouting were distinguished from rosettes originating from seeds. Dispersal was determined by measuring the distance between seedling and mother individual within all experimental fields. Weibull functions fitted on the empirical data for two consecutive years gave the dispersal function (Higgins & Richardson 1999).

As single genets are difficult to distinguish in the field we counted single rosettes and distinguished between seedlings, juveniles, vegetative adults, and generative adults (see Fig. 4.1). Seedlings were discriminated from juveniles by the existence of cotyledons. Our classification of vegetative adults of *Salvia pratensis* conforms with (Hegland et al. 2001). Vegetative adult rosettes of both species are larger than 10 cm and leaves of *Savia pratensis* are considerable thicker than those of juveniles. In case of *Sanguisorba minor* adult rosettes have a thicker stem diameter and are often lignificated.

Traits concerning fecundity, such as individual releasing height, branching, and number of seeds per head were measured in 2002 from 20 randomly chosen individuals or rosettes per experimental field from four sites. Seed production was calculated by collecting ripe inflorescences and by counting numbers of seeds per inflorescence (Menges & Dolan 1998, Menges 2000, Maschinski et al. 1996).

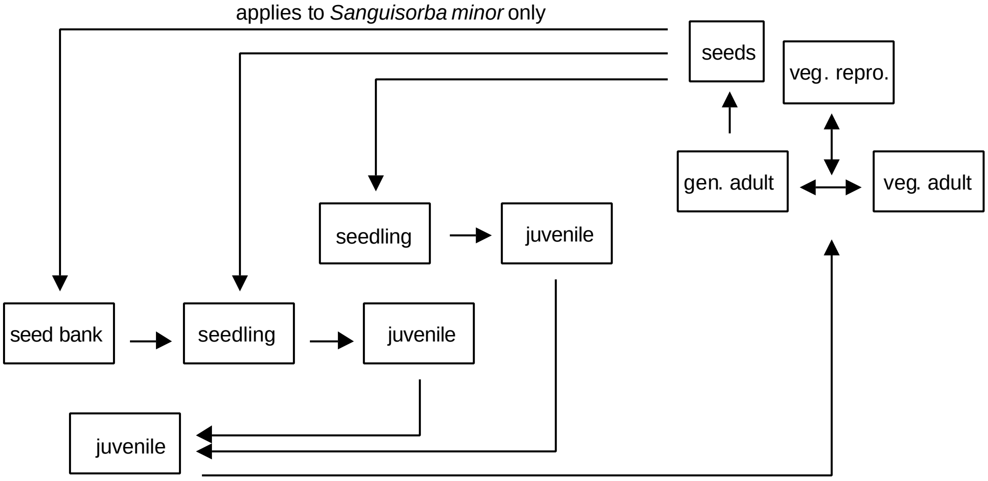


Fig. 4.1 Schematic life cycle for both species *Sanguisorba minor* and *Salvia pratensis* including fecundity, germination twice a year, senescence of seedlings, vegetative reproduction, adult mortality, and - in the case of *Sanguisorba minor* - a soil seed bank. The life cycle scheme of *Salvia pratensis* is abbreviated as juveniles need at least 3 years to reach critical flowering size in the field (see results).

Horizontal and vertical vegetation density was recorded in order to determine the influence of vegetation structure on fecundity of the target species. This was done by estimating (i) the total percentage vegetation cover, (ii) the cover of herbs and bryophytes, and (iii) the height [cm] of the herb layer at various levels in the surrounding (20 x 20 cm) of 20 randomly chosen individuals or rosettes. From the latter data, the weighted average vegetation height (GMV) was calculated (Gibson et al. 1987, Barkman 1988, Sundermeier 1999).

The seed bank was assumed to be consistent within both treatments since all plots were mown in the same way before the start of the experiment. Thus, a direct comparison between traditional and new management was possible as mown plots represent the initial stage prior rototilling. For seed bank analysis the seedling emergence method was used (Fischer 1987, Bakker et al. 1996, Ter Heerdt et al. 1996, Thompson et al. 1997). Vertical distribution of seeds was used as an indicator for longevity (Thompson et al. 1997, Bekker et al. 1998, Bakker et al. 2000) following the classification scheme by Thompson et al. (1997) modified by Jackel (1999). However, this indicator does not work when below-ground disturbances such as rototilling are applied. Therefore, soil seed bank samples from the mown plots served to calculate the percentage recruitment of seeds from the soil seed bank. The following assumptions were made: (1) recruitment from the soil seed bank is only possible for recently rototilled plots as mowing does not affect or activate seeds buried in the soil; (2) there is no import of seeds from surrounding sites since both species spread their seeds in the immediate vicinity of the mother individual. Recruitment from the seed bank (S_r) on recently rototilled plots was calculated by the following term:

$$S_r = \frac{N_1 - N_2}{N_{Soil}} \tag{4.1}$$

with N_1 = number of seedlings per m² on recently rototilled plots.

N_2 = number of seedlings per m² on mown plots

N_{soil} = seed density per m² on mown plots

Vegetative regeneration after rototilling was determined by two approaches. Firstly, the stems of adult individuals were marked with metal rings near the soil surface. Secondly, the number of individuals was counted on five permanent 2 x 2 m plots before and after disturbance. In order to avoid mistakes we repeated the sampling three times with time steps of 8 weeks beginning in the spring following the disturbance event. If a rosette did not reappear during this period, it was considered extinct.

Species

Sanguisorba minor Scop. (Salad burnet) and *Salvia pratensis* L. (Meadow sage) are long-lived herbaceous species which propagate mostly through seeds. Biological attributes for both focal species are listed in Table A3 (Appendix). Inflorescences of *Salvia pratensis* are arranged in whorls. Usually the species has six flowers per whorl and each flower contains four ovules. Flowers of *Sanguisorba minor* are arranged in heads. Seeds of both species were released from mid-July onwards. Autumn is the main season for seeds to germinate, although germination of seeds also occurs in spring (Fig. 4.1). If moisture is sufficient, seeds of *Salvia pratensis* germinate soon after being released in August (Ouborg & Treuren 1995). Laboratory experiments by Rich et al. (1999) showed that 72 % of the released seeds germinate directly after wetting in daylight or darkness. Seed masses for both species are similar with 2.56 mg for *Salvia pratensis* (Kühner, unpubl. data) and 2.84 mg for *Sanguisorba minor* (Grime et al. 1996, Cerabolini et al. 2003). Seeds of both species are assumed to disperse only over short distances (Ouborg & Treuren 1995). Individuals of *Sangiusorba minor* need 1-2 years (Krebs 1992) and *Salvia pratensis* needs 4-5 years to reach flowering size (Hegland et al. 2001). Both species produce more than one flower stalk per rosette and are able to produce new shoots ('daughter rosettes') from the rootstock. Both species have similar compressed rhizomes with regenerative buds and belong to the same clonal growth type according to Klimeš et al. (1997). They may resprout if aboveground organs are damaged (Grime et al. 1988). Poschlod (personal communication) investigated the life span of *Sanguisorba minor* by colouring and counting annual rings (see also Dietz & Ullmann 1997). He found that the maximum age is about 15/16 years on fallow land and only 10-15 years on managed sites. No reliable records of the life span of *Salvia pratensis* are available, but demographic data suggest that the average life span of an adult may range to a few decades (Marti 1994, Ouborg & Treuren 1995). The seed bank longevity index (SLI) for *Sanguisorba minor* according to records listed in Thompson et al. (1997) was calculated to be 0.375. Thus, the species tends to be rather short-term persistent. Data in Thompson et al. (1998) indicate that the seed bank type of *Salvia pratensis* is transient.

Results

1. Effect of rototilling on the life cycle

a) Fecundity

There were significant differences in all parameters between mown and rototilled plots in the first year of succession concerning fecundity of *Sanguisorba minor* (Table 4.1). Releasing height was significantly higher in the first year and the species produced significantly more heads per inflorescence as well as seeds per heads. Thus, the overall average number of seeds per inflorescence was around twice as high as on the mown plots. In the second year of succession following rototilling, no more significant differences were found in mown plots.

Table 4.1 Difference in fecundity parameters of *Sanguisorba minor* between the mown (M) and rototilled plots (R) at two different successional stages using Mann-Whitney U-test: Releasing height [cm], seed heads per inflorescence, seeds per head, and total seed production. Ns = not significant, * p = 0.05; ** p = 0.01; *** p = 0.001. R1 = first year of succession, R2 = second year of succession.

management	M	R1	p	R2	p
releasing height [cm]	42.38±7.65	47.27±9.3	**	44.58±10.92	ns
heads per inflorescence	3±2	5±2	***	4±2	ns
seeds per head	19±5	21±4	***	19±6	ns
total seed production	54±33	105±52	***	69±51	ns

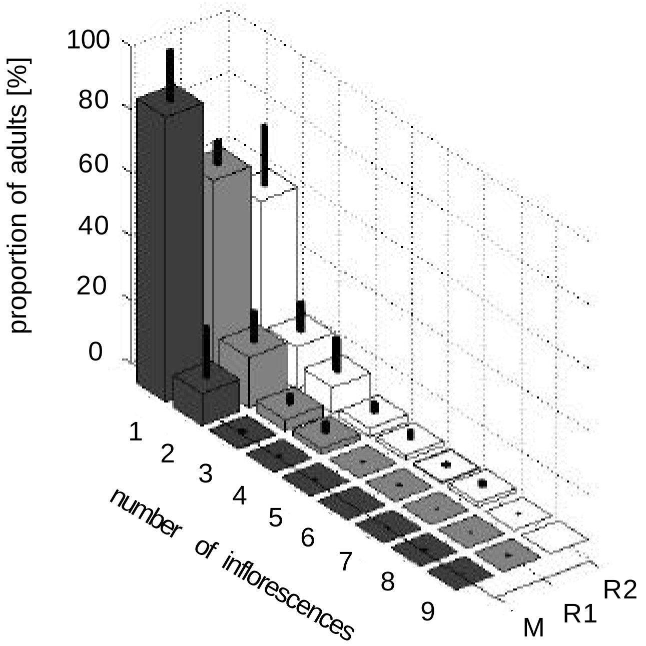
For *Salvia pratensis*, a change of the disturbance system has no significant impact on most fecundity parameters (Table 4.2). Only releasing height was significantly higher on rototilled plots in the first successional year than on mown plots, but decreased down to 61 cm in the second successional year after rototilling.

Table 4.2 Difference in fecundity parameters of *Salvia pratensis* between mown plots (M) and rototilled plots (R) at two different successional stages using Mann-Whitney U-test: Releasing height [cm], seed heads per inflorescence, seeds per head, and total seed production. Ns= non significant, * p = 0.05; ** p = 0.01; *** p = 0.001. R1 = first year of succession, R2 = second year of succession.

management	M	R1	p	R2	p
releasing height [cm]	62±10.9	56.5±13.7	**	61.1±9.65	ns
numbers of whorls	27±11	28±14	ns	25±10	ns
numbers of flowers	164±66	167±83	ns	153±63	ns
branches per infloresc.	3±1	3±1	ns	3±1	ns
total seed production	656±264	669±331	ns	612±250	ns

Since both species are able to produce more than one flowering stalk per rosette we counted the number of inflorescences per rosette on mown and rototilled plots (Fig. 4.2). A change in management led to small changes in the proportion of flowering stalks produced per rosette, even though on rototilled plots most individuals continued producing one flowering stalk. In the case of *Sanguisorba minor* the number of rosettes producing only one stalk decreased from 89 % on mown plots to 52 % on rototilled plots in the second successional year. Consequently, the percentage proportion of individuals producing more than one (two up to seven) flowering stalks increased on rototilled plots. Contrary to *Sanguisorba minor,* production of one stalk per rosette in *Salvia pratensis* increased from 44 % on mown plots to 62 % on rototilled plots in the second successional year, whereas on recently rototilled plots one stalk rosettes occurred for 87 % of the individuals. For *Salvia pratensis* up to 9 flowering stalks per rosette were observed, but less than 1 % of the rosettes built more than 5 stalks.

a) *Sanguisorba minor*



b) *Salvia pratensis*

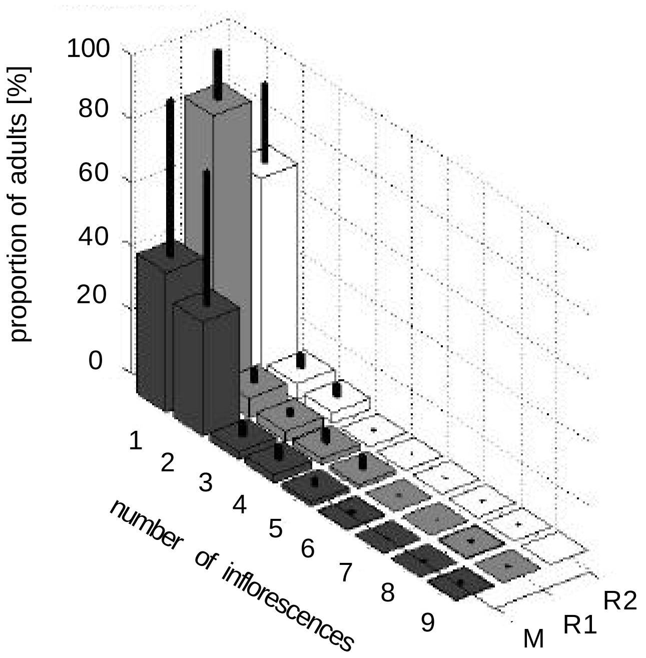


Fig. 4.2 Mean number of inflorescences of adult rosettes for mown (M) and rototilled plots in the first two successional years (R1,R2) for a) *Sanguisorba minor* and b) *Salvia pratensis*. Data were pooled for four investigation sites and two consecutive years in the case of mown and recently rototilled plots. a) mown plots n = 483; rototilled plots first year of succession n = 61; rototilled plots second year of succession n = 121. b) mown plots n = 166; rototilled plots first year of succession n = 246; rototilled plots second year of succession n = 128.

While ca. 60 % of all adults of *Sanguisorba minor* flowered on mown plots, only 24 % flowered on rototilled plots in the first year of succession (Table 4.3). During succession the proportion of flowering to nonflowering adults increased and approximated mowing value. No differences between both management systems concerning flowering rate were found for *Salvia pratensis*.

Table 4.3 Demographic parameters (± SD) of a) *Sanguisorba minor* and b) *Salvia pratensis* on mown plots (M) compared to rototilled plots in different successional stages, (R1) = first year of succession, (R2) = second year of succession, (R3) = third year of succession. Each value [%] is the mean of the four study sites and for time replications. Significant differences between mowing and rototilling are indicated by bold letters. (Mann-Whitney U-test, < 0.05 = significant). Seedling mortality_autumn = mortality of seedlings germinated in autumn; juvenile mortality_autumn = mortality of juveniles germinated in autumn; Seedling mortality_spring = mortality of seedlings germinated in spring; juvenile mortality_spring = mortality of juveniles germinated in spring; nd = data not available.

	M	R1	R2	R3
a) *Sanguisorba minor*				
germination rate	1.76±2.35	2.39±1.74	2.54±2.49	1.76±1.11
seedling mortality_autumn	51.11±24.29	45.92±35	70.21±11.76	nd
seedling mortality_spring	69.71±13.14	52.55±12.18	61.70±37.63	nd
juvenile mortality_autumn	**48.95±16.33**	**81.94±6.26°**	39.28±14.51	nd
juvenile mortality_spring	**45.45±4.93**	**81.94±6.26°**	37.5±11.13	nd
adult mortality	**6.87±5.68**	**81.94±6.26°**	1.10±4.88	3.91±4.08
proportion of flowering	**60.22±9**	**29.11±10.12**	66.29±17.79	58.72±17.83
vegetative reproduction	0.89±4.89	6.49±3.23	0±0	0±0
b) *Salvia pratensis*				
germination rate	0.08±0.001	0.01±0.001	0.07±0.002	0.08±0.002
seedling mortality_autumn	61.44±26	69.81±22.21	86.11±7.96	nd
seedling mortality_spring	50.0±37.5	20.0±40.82	nd	nd
juvenile mortality_autumn	**12.5±0**	21.32±7.18°	**100±0**	nd
juvenile mortality_spring	66.67±35.35	21.32±7.18°	25.0±47.14	nd
adult mortality	**2.62±4.67**	**21.32±7.18°**	3.82±4.11	0.73±1.61
proportion of flowering	50.68±27.72	56.34±19.10	56.68±20.53	37.27±30.07
vegetative reproduction	4.08±7.34	2.90±3.99	0±0	0±0

° The survival rates for juveniles and adults were calculated from the second approach only. This table gives the mean value for two years (cp. Tab. 4.6).

b) Dispersal

Figure 4.3 shows within-plot dispersal curves of *Sangiusorba minor* and *Salvia pratensis* for both disturbance regimes. The coefficients for the Weibull function fitted on dispersal field data for *Sanguisorba minor* and *Salvia pratensis* are listed in Table A2

(Appendix). The dispersal curves of *Sangiusorba minor* on mown and rototilled plots in the second year of succession are nearly identical. Half of the seeds germinated in the immediate vicinity (< 15 cm) of the potential mother individual. The maximum distances were 57 cm and 46 cm, respectively. However, in the first year following rototilling, the slope of the dispersal curve of *Sanguisorba minor* was lower indicating a larger number of seeds reaching a greater distance from the mother individual. Half of the seeds germinated at a distance of more than 20 cm from the mother individual.

The dispersal curves of *Salvia pratensis* for mown and rototilled plots in the first successional year are highly similar (Fig. 4.3). Half of the seeds germinated at a distance of around 20 cm from the mother individual. Maximum distance of seedlings from the mother individual was lower on mown plots (42 cm) than on rototilled plots in the first year of succession (48 cm). However, in the second successional year after rototilling, it decreased down to 33 cm. A higher proportion of seeds germinated in the immediate vicinity of the mother individual. Half of the seeds did not reach more than 15 cm. Compared to *Sanguisorba minor* all seedlings of *Salvia pratensis* germinated in a smaller distance from the mother individual.

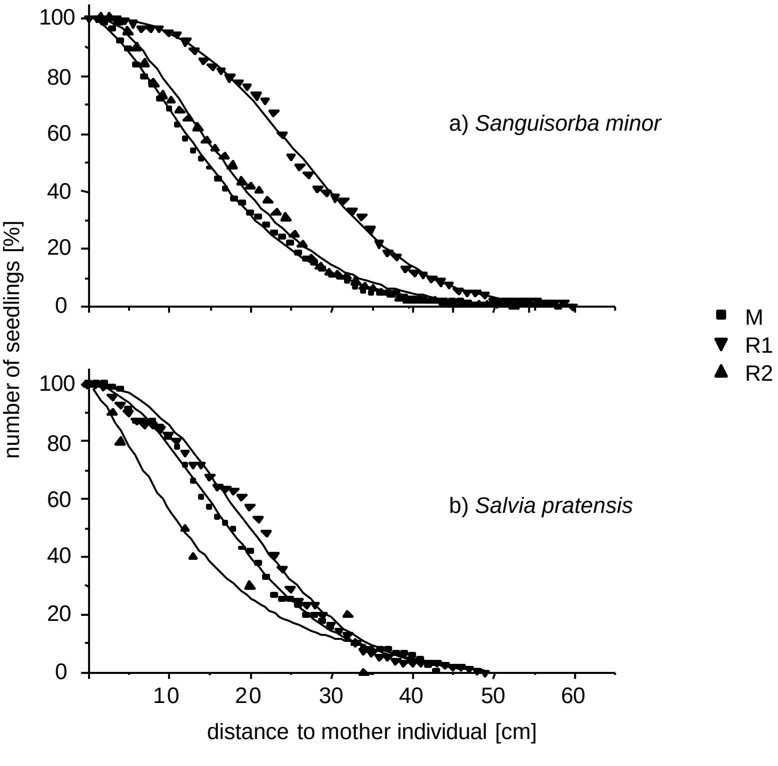


Fig. 4.3 Within-plot dispersal curves for a) *Sanguisorba minor* and b) *Salvia pratensis*. The figures show the distance of seedlings to the mother individual on mown (M) and rototilled plots in the first two successional years (R1, R2). We fitted Weibull functions (curves) on empirical data (symbols) for two consecutive years. a) mown plots n= 390; rototilled plots, first year of succession n= 161; rototilled plots second year of succession n= 234. b) mown plots n= 91; rototilled plots, first year of succession n= 144; rototilled plots, second year of succession n= 10.

c) Germination (incl. seed bank activation)

Germination rates did not differ significantly, neither for *Sanguisorba minor* nor for *Salvia pratensis* between the two disturbance regimes (Table 4.3). Germination rates of *Salvia pratensis* were generally lower than for *Sanguisorba minor*. Germination occurred in autumn and spring, with a higher proportion in autumn. For *Sanguisorba minor* the proportion of autumn to spring emergence of seedlings was 3:1 (Table 4.4). *Salvia pratensis* germinated directly after seed shed in summer. We found no *Salvia pratensis* seedlings in spring on rototilled plots (Table 4.4).

Table 4.4 Proportion [%] of seedling emergence in autumn for cumulative germination rate. Data were pooled from four sites in the year 2002. In case of *Salvia pratensis* germination occurred directly after seed set in summer since abiotic conditions were appropriate.

	Proportion [%] of seedling emergence in autumn			
	M	R1	R2	mean
Sanguisorba minor	75.49	77.65	71.13	71.34
Salvia pratensis	82.76	100	100	94.25

The vertical distribution of seeds in the soil indicated that *Salvia pratensis* was not able to build up a persistent seed bank as seeds were present in the upper layer only (Box 2). Thus, no seed bank activation after rototilling was calculated for this species. Seeds of *Sanguisorba minor* were more frequent in the upper soil layer, but also present in the lower soil layer. This indicates that seeds were persistent and activation for germination after rototilling was possible. The mean seed density in the seed bank on mown plots for *Sanguisorba minor* was 32 per m². The mean seedling density on mown plots was found to be 13 per m². Since an additional seedling per m² appeared from the seed bank on recently rototilled fields, approximately 3 % of the seeds in the seed bank were activated by rototilling.

d) Seedling and juvenile mortality

We found no significant differences in the two management systems in seedling mortality for the two species neither for seedlings emerged in autumn nor in spring (Table 4.3). *Sanguisorba minor* juvenile mortality differed significantly in the first year of succession after rototilling. The mortality of juveniles which germinated in autumn was increased during later successional years for *Salvia pratensis* (Table 4.3). Observation of seedling development indicates that *Sanguisorba minor* needs at least 2 years to reach flowering size. No seedling of *Salvia pratensis* reached flowering size during our study period. Apparently, seedlings of this species need at least 3 years to reach critical rosette size for reproduction, regardless of treatment. Time until first seed production of both species did not differ between the two disturbance systems.

e) Adult mortality and regrowth ability

Adult mortality was low on mown plots and on rototilled plots in later successional years for both species (< 7 %, Table 4.3). In the first year after rototilling, adult mortality was influenced by regrowth ability which differed strongly between both species. We tested two methods to investigate regenerative vigour on rototilled plots (Tables 4.5 and 4.6). For both methods we found a higher survival rate of *Salvia pratensis* after rototilling (70 - 80 %) compared to *Sanguisorba minor* (14 – 24 %), even though only half of the marked individuals were found after rototilling.

Table 4.5 Comparison of data on recovery rate and regeneration vigour of *Salvia pratensis* and *Sanguisorba minor* after rototilling. 80 individuals were marked and sampled before and after rototilling. Field data were summed up for four study sites in the year 2002.

	# above-ground ind.		Recovery rate [%]	# above-ground ind.	Survival rate [%]
species	before rototilling	after rototilling		after rototilling	
Salvia pratensis	80	37	46,25	26	**70,27**
Sanguisorba minor	80	46	57,50	6	**24,92**

Table 4.6 Comparison of the survival of *Salvia pratensis* and *Sanguisorba minor* individuals after rototilling for two consecutive years. The number of above-ground individuals was counted before and after rototilling. Field data were summed for four study sites.

	year 2001			year 2002		
	# above-ground ind.		Survival rate [%]	# above-ground ind.		Survival rate [%]
species	before rototilling	after rototilling		before rototilling	after rototilling	
Salvia pratensis	482	385	**79.87**	564	437	**77.48**
Sanguisorba minor	529	75	**14.18**	424	93	**21.93**

f) Vegetative reproduction

Vegetative reproduction was found to be highest on recently rototilled plots for *Sanguisorba minor* (Table 4.3). A very low amount of new rosettes (< 1 %) originated from vegetative reproduction on mown plots. Contrary to these findings, *Salvia pratensis* showed decreased ability of vegetative reproduction on rototilled plots. For later successional stages on rototilled plots no vegetative reproduction could be detected for either species. All differences concerning vegetative reproduction between the management systems were not significant.

2. Effects of rototilling on the population structure

Sanguisorba minor seedlings increased after rototilling from about 40 % (on mown plots) up to more than 60 % (Fig. 4.4). At the same time juveniles and adults decreased. Furthermore, rototilling caused a change of the proportion of vegetative and generative adults. We found a higher percentage of flowering adults on mown (38 %) than on rototilled plots (< 10 %). The ratio of seedlings and juveniles to generative adults increased from 1.05 on mown to 9.28 on recently rototilled plots. In both disturbance regimes, less than 10 % of all individuals of *Salvia pratensis* were seedlings while adults were the most dominant life stage (Fig. 4.4). In contrast to *Sanguisorba minor*, management did not change the ratio of vegetative to generative adults of *Salvia pratensis* populations. In both systems we found more non-flowering plants than flowering rossettes. The ratio of seedlings plus juveniles to generative adults decreased from 1.28 on mown to 0.46 on rototilled plots.

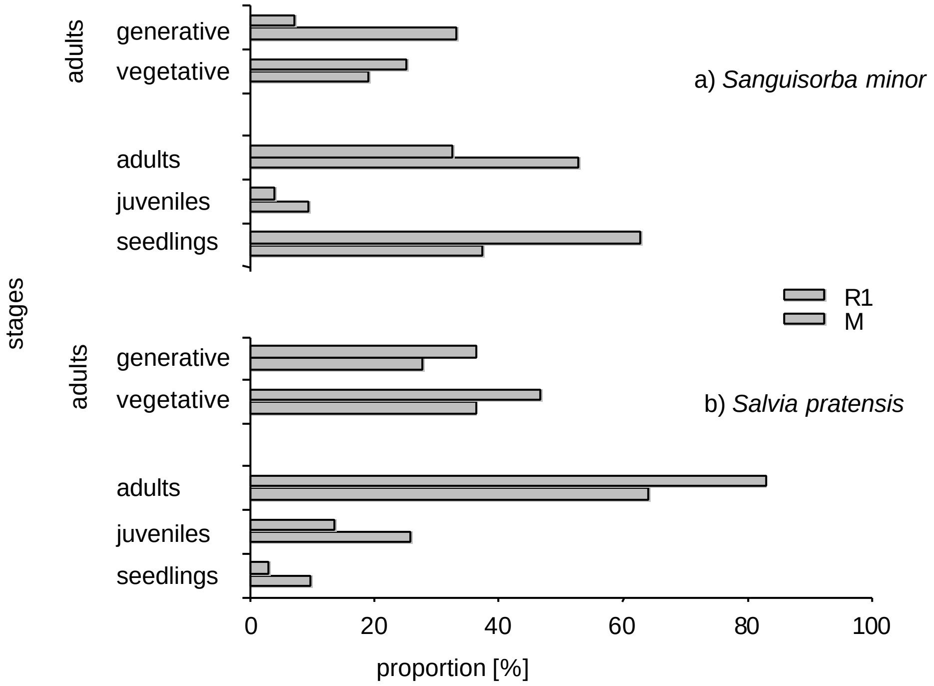


Fig. 4.4 Effects on the population structure of a) *Sanguisorba minor* and b) *Salvia pratensis* through shifting disturbance system according to field data of the year 2001. The diagram shows the proportion of life stages in mown and rototilled plots in the first successional year. Juveniles were pooled from different ages.

3. Effects of vegetation structure on fecundity

There was a weak but significant negative correlation between vegetation density and fecundity (number of seeds per inflorescence) for *Sanguisorba minor* (Table 4.7). Correlation was strongest for density of herb layer and lowest for the weighted average vegetation height. For *Salvia pratensis* no correlations were found between any parameter of vegetation structure and fecundity (Table 4.7).

Table 4.7 Spearman correlations between number of seeds per inflorescence (infl.) and vegetation structure parameter such as vegetation cover, herb layer, bryophytes layer, and weighted average vegetation height (GMV) for a) *Sanguisorba minor* and b) *Salvia pratensis*. Significance level: * p = 0.05; ** p = 0.01; n.s. = not significant.

		Vegetation cover [%]	Herb layer [%]	bryophytes layer [%]	GMV [cm]
Seeds/infl.	a) *Sanguisorba minor*	- 0.42**	- 0.47**	- 0.34**	- 0.34**
	b) *Salvia pratensis*	- 0.04n.s.	- 0.01n.s.	- 0.05n.s.	0.11n.s.

Discussion

Replacing a light and frequent disturbance with a severe but infrequent disturbance in terms of biomass removal led to differential response of both species. Generally speaking, *Sanguisorba minor* displays strong fluctuations in life stages while *Salvia pratensis* showed a more buffered response. Rototilling involves disturbance down to the roots and an unshaded habitat open for recolonisation afterwards. However, while regular mowing resets succession at any mowing event, secondary succession then carries on for several years until rototilling is again applied. This means, after complete removal of established competitive hierarchies following the disturbance impact, increasing competition is far more likely in the following years than on mown plots.

Effects on life cycle parameters

Varying habitat conditions may strongly influence attribute performance of populations (Bazzaz 1983). If the summer is wet and warm, the bulk of *Salvia pratensis* seeds germinates directly after seed shed. This was also found by Rich et al. (1999) through laboratory experiments and by Ouborg & Treuren (1995) through field observations. Germination rate was low on both mown and rototilled plots. Large standard deviation indicates site-specific differences. Due to the fact that seed production of *Salvia pratensis* (mean value of seeds per inflorescence was more than 600) is very high, but germination rate very low (< 1 %) and a seed bank does not exist, the predation and decomposition rates of *Salvia pratensis* seeds have to be very high. Furthermore, our observations indicated that many seeds were infested by insects and would probably be unable to germinate. In contrast to *Salvia pratensis*, the change from mowing to rototilling has a positive effect on the germination of *Sanguisorba minor*. In accordance with studies compiled by Thompson et al. (1997) *Sanguisorba minor* was able to build up a short-term persistent seed bank. Rototilling increased seedling appearance due to activation of seeds germinating from the soil seed bank. The relative activation of the seed bank was calculated to be 3 %.

Hegland et al. (2001) hypothesise an effect of vegetation structure and open ground on the proportion of adults flowering in grasslands for *Salvia pratensis*. Their results indicate that a higher proportion of adults flower in open habitats. Our results do not support these findings. The number of inflorescences produced per rosette did not differ between treatments for neither species and there were no differences in the proportion of vegetative to generative rosettes for *Salvia pratensis* on mown or rototilled pots. On the contrary - although vegetation cover is especially reduced in the first successional year, we found a lower proportion of *Sanguisorba minor* rosettes flowering on recently rototilled plots.

Resprouting after rototilling differed significantly between both species even though shoots and roots should have been destroyed in similar magnitude. *Salvia pratensis* recovered very well after disturbance, *Sanguisorba minor* did not. Clonal spread and vegetative regeneration can be an effective method for survival on disturbed patches (Fahrig et al. 1994). Under a mowing or trampling regime, species having a protected bud bank either below or near the soil surface responded less than plants with upright growth form and exposed buds (Maschinski et al. 1996). However, both species have similar compressed rhizomes with regenerative buds and belong to the same clonal growth type according to Klimeš et al. (1997). Apparently, clonal growth is not responsible for differential response to rototilling. *Salvia pratensis* has a continuously renewed cork layer which makes the species highly drought resistant (Kutschera 1982). Thickened clonal growth organs of *Salvia pratensis* may store accumulated resources better than those of *Sanguisorba minor*. This indicates that it may be not the bud bank distribution but storage efficiency, which makes *Salvia pratensis* a superior resprouter.

In general, *Salvia pratensis* and *Sanguisorba minor* follow different initial pathways to cope with a destructive disturbance. *Sanguisorba minor* takes a seeding strategy which relies almost exclusively on increased seed production and germination in the first year when competition with established plants is still low. In contrast, *Salvia* *pratensis* resprouts from the bud bank. Seed number per plant is also high. *Salvia pratensis* can therefore be seen as a counterexample to a trade-off between vegetative performance and generative reproduction in perennial plants (Doust & Doust 1988, Chaloupecka & Leps 2004). However, due to seed predation and low germination the generative pathway plays only a minor role in recruitment. Recruitment from a bud bank may be of competitive advantage because relative growth rate of a shoot emerging from regenerative buds differ from that of a seedling (Klimešová & Klimeš 2003) and may be usually higher. Likewise, *Sanguisorba minor* displays no such trade-off. Although there is an increase of vegetative reproduction in the first year after rototilling and a decrease of the probability to flower for adults at the same time for *Sanguisorba minor,* these differences were not significantly proved. High standard errors indicate that these differences were more likely to be explained by site conditions than by management.

During secondary succession in the years following rototilling, seed production of *Sanguisorba minor* decreased and was negatively correlated to vegetation height and density. Similarly, Hegland et al. (2001) and Sundermeier (1999) showed a negative relationship of vegetation height and density with reproduction parameters, such as seed production, number of inflorescences, and the proportion of flowering to nonflowering individuals for some species of semi-natural grasslands. For *Salvia pratensis* no correlations were found between fecundtiy and any of the tested parameters of vegetation height and density. Seed production did not differ on mown plots nor on rototilled plots.

We could not find differences in seedling mortality between both management systems, although studies on *Salvia pratensis* seedlings indicated that establishment is generally unsuccessful in tall undisturbed grasslands due to litter accumulation (Rich et al. 1999). There is evidence that seedlings became reproductive more quickly in disturbed systems (Bazzaz 1983, Maschinski et al. 1996, Hautekeete et al. 2002). Studies concerning seedling development have shown that (i) plants subjected to disturbance flower early in their life-cycle and (ii) plants that suffer from resource limitation favour vegetative growth and biomass accumulation rather than flowering (reviewed in Kobayashi 2001). Since rototilling has a more severe impact on biomass than mowing, one may expect that changing the disturbance regime would influence this life-cycle parameter, but no differences were found for either of both focal species. Age at first flowering does not differ between mown and rototilled plots. Thus, seed production and seed germination can be identified as the most responsive traits triggering the population dynamics of *Sanguisorba minor* on rototilled sites.

Our results indicate that both species are able to disperse only for short distances (< 1 m). Although there is evidence for long-distance zoochorous dispersal in *Salvia pratensis* and *Sanguisorba minor* (e.g. Jackel 1999), we assume the likelihood of this kind of dispersal as small. The probability to be dispersed by the rototilling machine is low (Talmon, personal communication). Long-distance dispersal is often found to be a rather rare event in grasslands (Primack & Miao 1992, Poschlod et al. 1996, Kollmann 1997, Poschlod et al. 1997).

Effects on the population structure

Effects of a change in management on demographic data are reflected in the population structure. Since a large number of rosettes of *Salvia pratensis* were able to persist rototilling via vegetative regeneration, fecundity did not differ between both treatments and germination was a rare event in both mown and rototilled populations. Compared to *Sanguisorba minor*, the change in management has lower effects on the structure of *Salvia pratensis* populations. The dominating stage in both disturbance systems was adults, but the proportion of seedlings and juveniles to generative adults ((S + J)/G ratio see Hegland et al. 2001) decreased from 1.28 to an average ratio of 0.46 on recently rototilled plots. According to the classification of Hegland et al. (2001) who clustered *Salvia pratensis* populations into three groups (dynamic, normal and regressive) based on the relative proportions of the different life stages, populations on mown plots can be described as 'dynamic' and populations on rototilled plots as 'normal'. The results for mown plots support the findings of Hegland et al. (2001) who also observed higher proportions of young stages at a late mowing regime. They conclude that conservation of the remaining populations of *Salvia pratensis* in Dutch semi-natural floodplain grasslands will be best achieved by late mowing with hay removal. Contrary to the findings for *Salvia pratensis* the population structure of *Sanguisorba minor* was highly affected. Since most of the juvenile and adult rosettes were lost after rototilling, populations were dominated by seedlings. The (S + J)/G ratio shifted from 1.05 on mown to 9.28 on recently rototilled plots. One may suggest that rototilling is a better management regime than mowing to maintain *Sangiusorba minor* populations, but this suggestion only holds if the return intervall is not too small. In frequently rototilled sites *Sanguisorba minor* will not be able to recruit new reproductive individuals into the population to exceed mortality by disturbance and to ensure population survival over a long time period. Only a sufficient number of adults can provide enough juveniles (Warner & Chesson 1985). The extrapolation of the demographic data of *Sanguisorba minor* and *Salvia pratensis* in time by using individual-based models will show population dynamics under different rototilling frequencies (Chapter 5).

Conclusions

We showed that both perennial plant species perceive rototilling at a different levels of severity. Although their regeneration ability was hypothesised to be similar, effects on biological traits, demographic data and population structure through shifts in management differed strongly between both perennial species. Both species are able to persist rototilling by compensating the loss of individuals from population, but a general comparison of the regeneration strategy after rototilling showed that *Salvia pratensis* survived mainly owing to resprouting from a bud bank, while *Sanguisorba minor* survived due to generative regeneration by seedlings and seed bank activation. These different pathways to survival demonstrate very clearly that communities are often composed of a multitude of plant strategies (Semenova & van der Maarel 2000, Westoby et al. 2002) which cannot be lumped per site as it often happens in plant functional trait studies. Moreover, *Sanguisorba minor* and *Salvia pratensis* would probably be assigned to the same plant functional type in such studies, given their overall similarity in readily recordable traits such as canopy height, seed mass, SLA, clonal growth organ, etc. (Kühner & Kleyer, in prep). The only trait perceivable on the level of trait – environment studies that discriminates both species is seed bank longevity. Thus, our study shows the added value of a population based approach to plant functional trait studies in understanding plant – environment relations.

Chapter 5

Prediction of the population dynamics of three plants with contrasting life histories under different disturbance frequencies

Chapter 5

Prediction of the population dynamics of three plants with contrasting life histories under different disturbance frequencies

with Robert Biedermann & Michael Kleyer

Abstract Disturbance frequency plays a major rule in conservation biology. The aim of this study was to demonstrate how disturbance frequency affects population dynamics with respect to plant life history attributes. Using individual-based models for three plant species, we compared the model parameters having the greatest influence on each model outcome, and tested the impact of different rototilling frequencies on population dynamics and time to extinction. This approach allowed us to give recommendations for the conservation of semi-natural grassland plant species. The influence of disturbance frequencies on the population dynamics and time to extinction of populations depended on plant life history attributes. A shorter disturbance return interval ensured population survival and prolonged the time to extinction of dormant (i.e. existence of a seed bank) annual plant species (represented by *Thlaspi perfoliatum*), while populations of perennial plant species (e.g. *Sanguisorba minor* and *Salvia pratensis*) declined and the time to extinction increased. We found a sequence of population survival under increasing disturbance frequencies of non-dormant perennials, followed by dormant perennials and dormant annuals. There was no disturbance return interval allowing collective survival of three species with contrasting life histories. The results show that demographic parameters of the three species display great differences in sensitivity, and thus strengthen the importance of achieving accurate field data for these parameters for the predictive power of the models. The most sensitive parameters of the dormant annual species are seed bank depletion and germination. The response of the *Sanguisorba minor* model is highest for a change in the mortality rates of juveniles and adults, whereas the probability of extinction of *Salvia pratensis* populations is most affected through a shift in the germination rate in the first year after rototilling. Furthermore, the sensitivity analysis reveals that the *Salvia pratensis* model is more robust to variations in parameter values than the models for the other focal species. According to the results of this study we emphasise that rototilling cannot be used as an alternative management method to preserve Mesobromion communities and dry sub-communities of the Arrhenatheretum elatioris without accepting the loss of plant species.

Introduction

Disturbances are present in all ecosystems, occur at a wide range of spatial and temporal scales and are continuous across all levels of ecological organisation (White & Pickett 1985). Magnitude in terms of biomass removal, frequency and return interval are the disturbance factors which affect plant persistence the most (White & Jentsch 2001). Small seeded plant species with a short life cycle and transient or short-term persistent seed bank are expected to be more vulnerable to increasing return intervals, compared to species with storage effects and competitive abilities in their major life stages, e.g. clonal perennial plants or large-seeded species with a long-term persistent seed bank (Harper 1977, Warner & Chesson 1985 Stöcklin & Fischer 1999). This is particularly important for recommendations in conservation management when it comes to considering the return interval of disturbances.

Simulation models, based on empirical demographic values, are a suitable tool for identifying disturbance regimes in order to maintain focal species without having to set up long-term field tests (Beissinger & Westphal 1998, Menges 2000, Buckley et al. 2003). So far, this approach is mainly used to make decisions for population management of threatened or endangered species ('population viability analysis', PVA, Lindenmayer et al. 1993, Beissinger & Westphal 1998, Menges 2000). PVAs have mainly been used for the conservation of endangered animals and have only recently been applied to predict the viability of plant species. Hence, many authors have stressed the need for plant population models to be able to reflect the biology of the species in question, and to provide an insight into the environmental perturbations which cause much of the variability observed in nature (Cousens 1995, Buckley et al. 2003, Schwartz & Brigham 2003). Attention has focused on effects of e.g. fire (Gross et al. 1998, Menges & Dolan 1998, Pfab & Witkowski 2000, Garnier & Dajoz 2001), trampling (Maschinski et al. 1996, Gross et al. 1998), mowing (Menges & Dolan 1998, Lennartsson & Oostermeijer 2001), grazing (Waite & Hutchings 1991, Bullock et al. 1994, Hunt 2001; Lennartsson & Oostermeijer 2001), and periodic sod-cutting (Oostermeijer 1996). Effects of different disturbance frequencies on the dynamics of plant population have been tested for e.g. fire (Manders 1987, Silva et al. 1991, Canales et al. 1994, Gross et al. 1998, Drechsler 1999) and trampling (Gross et al. 1998). Oostermeier (1996) suggested an optimal return interval for sod-cutting to maintain the rare *Gentiana pneumonanthe* on heath land. Kimmerer (1993) predicted effects of varying disturbance frequencies on the population dynamics of a moss. There are very few studies modelling the dynamics for a number of plant species in relation to disturbance frequencies using only abundance data (Rego et al. 1993, Lloret et al. 2003). However, most studies are single species analyses. To our knowledge, the effects of disturbance frequencies on a number of species using empirical life tables to initialise simulation models have not yet been studied.

For the conservation of semi-natural grasslands, management is needed to prevent shrub encroachment. If management is required, conservationists need to compromise between ecological (i.e. the maintenance of the plant community) and economical aspects (i.e. low costs for the treatment). Infrequent rototilling has been suggested as a less expensive management for the conservation of semi-natural grasslands as compared to frequent (i.e. annual) mowing (Kleyer 1998, Kleyer & Mosaik-Projekt, in press). The idea of using mechanical cultivation for the maintenance of semi-natural grasslands has its origin in the neolithic agriculture, where cultivation was followed by a fallow period (Abel 1978, Briemle et al. 1991, Bonn & Poschlod 1998). Rototilling is similar to ploughing, depending on soil conditions, a depth of up to 20 cm can be reached. Following rototilling, the sites undergo secondary succession until rototilling is repeated. Under an infrequent rototilling regime, small grassland species first experience a destructive impact, followed by an open environment offering growth with almost no competition. As secondary succession carries on, habitat quality decreases due to increasing competition. Nevertheless, there is evidence that many grasslands would be able to survive rototilling – if applied less frequently (every 3 - 5 years) – because of regeneration buds below the hypocotyl (Kleyer 1998). Eriksson (1989), Crawley (1990) and Amiaud & Touzard (2004) showed that most plant species on cultivated grassland soils regenerate from vegetative fragments rather than by germination of seed. Furthermore, many studies have shown that intervention down to the root horizon, and destruction and breakdown of biomass activate germination from the soil seed bank (Leck et al. 1989, Bazzaz 1996, Jentsch 2004, Kalamees & Zobel 2002) and provide new germination sites by creating gaps (Aguilera & Lauenroth 1995, Krenova & Leps 1996, Jutila & Grace 2002).

The spatially explicit individual-based models presented in this chapter, assess the sensitivity of life history parameters of three species with contrasting life histories to various disturbance frequencies. Specifically, we address the following questions: (1) Which rototilling frequencies provide extinction risks for focal plant species? (2) Is sensitivity of life history parameters consistent across all three plant species? (3) Is there any interval between rototilling impacts allowing collective survival of three species with contrasting life histories?

Methods

Study system

The data obtained from a three-year field experiment on semi-natural grasslands showing the temporal dynamics of three plant species on mown and on rototilled plots (Chapter 3 & 4). They include mortality rates for each life stage (seedlings, juvenile, adults) as well as seed production and dispersal within a plot. The experimental plots were established on slopes which have been mown at more or less regular intervals for at least the last 20 years. Sites are either considered to be a Mesobromion with different degrees of shrub encroachment, or a dry sub-community of the Arrhenatheretum elatioris (Chapter 2).

Species

Thlaspi perfoliatum is a winter annual plant: seeds germinate in autumn, develop to a small rosette, flower in the following spring, and die after seed set in summer (Chapter 3). Both *Sanguisorba minor* and *Salvia pratensis* are polycarpic herbaceous perennial plants with a life cycle including two main germination periods in spring and autumn (seedlings appearing in summer were added to the autumn cohorts), seed set in summer, and the ability to resprout from a bud bank (Chapter 4). Germination from a soil seed bank after rototilling is possible for *Thlaspi perfoliatum* and *Sanguisorba minor* only (Chapter 3 & 4, Box 2). Table 5.1 summarises life history differences between the three species.

Table 5.1 Biological attributes for the three focal plant species *Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia pratensis.* Abbreviations used: a = autumn, s = spring; data source: [1] = Grime et al. (1996), [2] = Rothmaler (1990), [3] = Rich et al. (1998), [4] = Rich et al. (1999) [5] = Krebs (1992), [6] = Hegland et al. (2001), [7] = Kleyer (1995), [8] = Thompson et al. (1997), [9] = Thompson et al. (1998), [10] = Ouborg & Treuren (1995), [11] = Cerabolini et al. (2003), [12] = Müller-Schneider (1986), [13] = empirical data according to the present study (Chapter 3), [14] = empirical data according to the present study (Chapter 4), [15] Kühner = (unpubl.data), [16] = Tackenberg (2001), [17] = Maurer & Stöcklin (unpubl. data), n.a. = not applicable.

	species		
	Thlaspi perfoliatum	*Sanguisorba minor*	*Salvia pratensis*
life span	[2]winter annual	[1]polycarpic perennial	[1]polycarpic perennial
canopy structure	[2]leaves basal	[2]leaves basal	[2]leaves basal
releasing height [cm]	[13]8.15±3.16	[14]42.38±7.65	[14]62±10.9
SLA	[15]22.69	[15]21.23	[15]18.85
germination saison	[3]a	[1]a/s, main a	[4]a/s, main a
age at first flowering	n.a.	[5]1-2 years	[6]4-5 years
seed mass [mg]	[1] 0.27	[1,12]2.84	[17]2.56
seed number	[15]24±20	[16]54±33	[16]656±264
terminal velocity [m*s^{-1}]	[16,17]2.93	[16]3.14	[16]2.96
dispersal range	[3,12,13]short	[6,12,14] short	[10,12,14]short
lateral spread [mm]	n.a.	[7]< 100	[7] < 100
type of veg. regen.	n.a.	[1]regrowth by buds	[1]regrowth by buds
seed bank longevity	[3]persistent, [13]long-term	[8]persistent, [14]short-term	[9,14]transient n.a.

General model features

We developed spatially explicit individual-based models with lattices of 25 by 25 square cells (each 10 x 10 cm). Therefore, the cell size in the models was the same as the sub-plot size in the field experiment (Chapter 3 & 4). Habitat quality is assumed to be equal in all cells. We use a 'torus simulation' to avoid seed loss and edge effects. One time step is three months, which allows the simulation of the four seasons spring, summer, autumn, and winter. Four time steps add up to one simulation year. The models were parameterised with demographic data sets from experimental studies on semi-natural grasslands in Southern Germany (Chapter 3 & 4, Table A4, Appendix). Disturbance occurs in summer, after seed set. Different disturbance frequencies were tested. The rototilling return interval ranged from one to ten years for all species.

Seed production and dispersal

Seed production was calculated for each individual following the distribution found in the field. Lognormal (5.1) or normal distribution (5.2) were fitted on field data for each species.

$$y = y_0 + ae^{\frac{-(\ln(\frac{x}{\mu}))^2}{2s^2}} \tag{5.1}$$

$$y = ae^{-\frac{1}{2}*(\frac{x-\mu}{s})^2} \tag{5.2}$$

with $a = \frac{1}{\sqrt{2x^2 s^2}}$

Table A1 (Appendix) gives the coefficients for lognormal or normal distribution fitted on field data for the focal species.

Dispersal was determined by measuring the distance between seedling and mother individual within all experimental fields. A random angle was applied as empirical data did not indicate a specific dispersal direction. Weibull functions fitted on the empirical data for two consecutive years gave the dispersal function in the model:

$$y = ae^{-bx^c} \tag{5.3}$$

Table A2 (Appendix) gives the coefficients for the Weibull functions fitted on field data for the focal species.

Model descrition for Thlaspi perfoliatum

For the annual species, the model reflects a typical winter annual life cycle in which procedures such as germination, aging, mortality, seed set, and dispersal within a plot were integrated. The features of this model are described in (Chapter 3).

Model description for Sanguisorba minor and Salvia pratensis

The models of the two perennials are more complex due to the fact that perennials build up an extensive population structure by germinating twice a year, having several juvenile stages, and being perennial (Chapter 4). Since single genets are often difficult to delimit in the field, we simulated single rosettes. The term individuals in the following always refers to rosettes. At the start of the simulations, a specified number of seedlings, juveniles, and adult individuals according to population structures found in the field are randomly distributed within the grid (Fig. 5.1). Mature individuals reproduce in summer. They are able to build up more than one flowering stalk. According to the distribution measured in the field, the number of flowering stalks was randomly distributed across individuals. Seedlings of *Sanguisorba minor* need two years to reach maturity, while those of *Salvia pratensis* need three years. About two-thirds of *Sanguisorba minor* (74.85 %) and 90.25 % of *Salvia pratensis* seeds germinate directly in autumn after seed set, the remainings in the following spring. Stimulation of seed germination from the soil seed bank occurs on recently rototilled sites and for *Sanguisorba minor* only. We estimated that 3 % of the seeds in the soil were activated to germinate from the seed bank (Chapter 4). Seeds are dispersed according to the distribution measured in the field. Vegetative resprouting occurs once after disturbance. Adults reaching the maximum age (*Sangiusorba minor* ten years (Poschlod, personal communication), *Salvia pratensis* 15 years (Marti 1994, Ouborg & Treuren 1995, Chapter 4)) are deleted from the system. Mortality of adults occurs once per simulation year. Vegetative multiplication during later years after rototilling is not explicitly modelled, but included by decreasing adult mortality. To incorporate density dependence, the number of juveniles and adult individuals per cell is restricted to a maximum of eight for *Sanguisorba minor* and seven for *Salvia pratensis*, according to field data. Every simulation year, the cycle is repeated. In order to estimate the time to extinction for the focal species, simulation models run over a time period of 200 years.

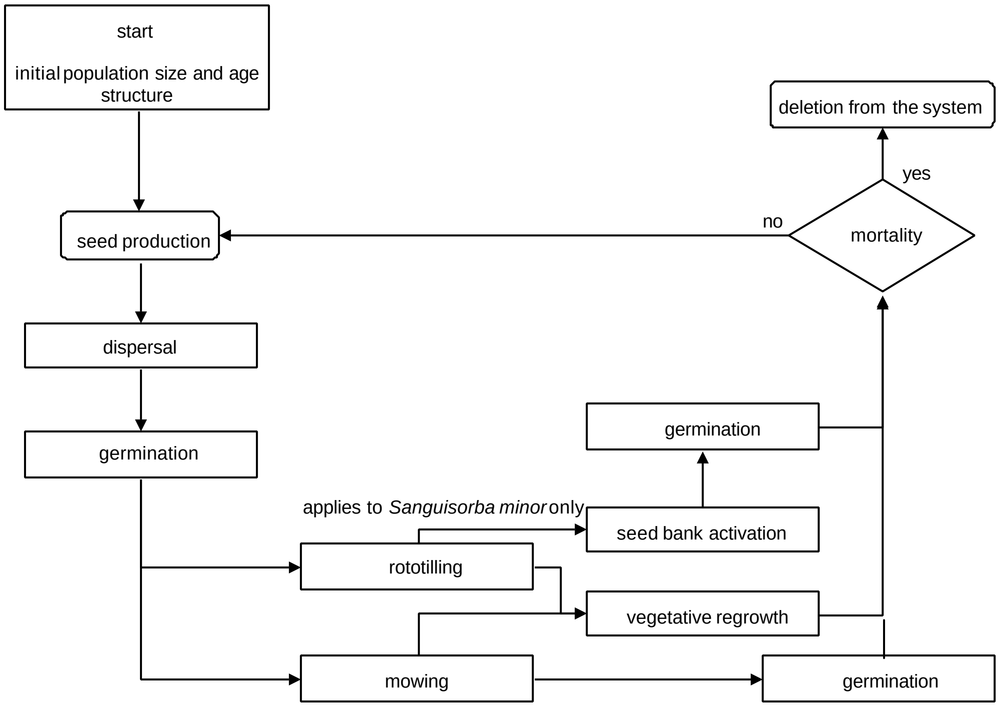


Fig. 5.1 Schematic structure of the models of *Sanguisorba minor* and *Salvia pratensis*.

Model assumptions

The mowing and rototilling models were parameterised with the original field data set. We assumed that in the mowing system, the populations are more or less at equilibrium. In case of non-equilibrium of populations, the mowing models were adjusted by shifting the germination rate till equilibrium, since germination is assumed to be the demographic process which is most sensitive. In order to account for the same conditions on all experimental plots, the germination rate in the rototilling models were also changed by the same percentage (for further model features see Chapter 3). For later successional stages (> 3 years *for Thlaspi perfoliatum*, in case of *Sanguisorba minor* and *Salvia pratensis* > 2 years) after rototilling, the parameter values were either taken from the mown plots – if the field values are approximately the same – or, in case of great deviation from the mown values, the field values from the last successional year were used.

Sensitivity analysis

Sensitivity analyses were performed to test the effects of changes in life history parameter values on the model outcome (Rushton et al. 2000, Buckley et al. 2003). Sensitivity was calculated as the ratio of the relative change of the probability of extinction for populations of the focal species to the relative decrease of parameters by 10 %. In order to calculate the probability of extinction for the focal species, different rototilling frequencies were used (8 ys for the annual, 1 y for the perennials). For each parameter value 5000 model runs were done.

Model analysis

Analysis was done by comparing population dynamics and time to extinction across various disturbance return interval scenarios, with 5000 replicates for each disturbance scenario. Disturbance was applied from that year on, in which the models reached a stable population structure. This was a period of 5 years for the *Thlaspi perfoliatum* model, a period of 10 for the *Sanguisorba minor* model and a period of 15 years for the *Salvia* pratensis model, respectively. For the analysis of the probability of extinction and time to extinction these time periods were ignored.

Results

Population dynamics at different rototilling return intervals

The population dynamics of the species depended on the disturbance frequency (Fig. 5.2). The annual plant species *Thlaspi perfoliatum* showed a decline in the population size over time, if rototilling was applied every nine years. At disturbance frequencies of three and six years, the population size increased after every single disturbance event and the population survived infinitely. The maximum population size of *Thlaspi perfoliatum* was lower (about 6000 individuals) at a disturbance frequency of three years than for a disturbance return interval of six years (more than 10,000 individuals). On the other hand, a change in the disturbance return interval towards lower frequencies ensured population survival of *Sanguisorba minor.* At return intervals of one year or two years, the population size showed a decline. For *Salvia pratensis* none of the simulated disturbance return intervals prevented a decrease in population size.

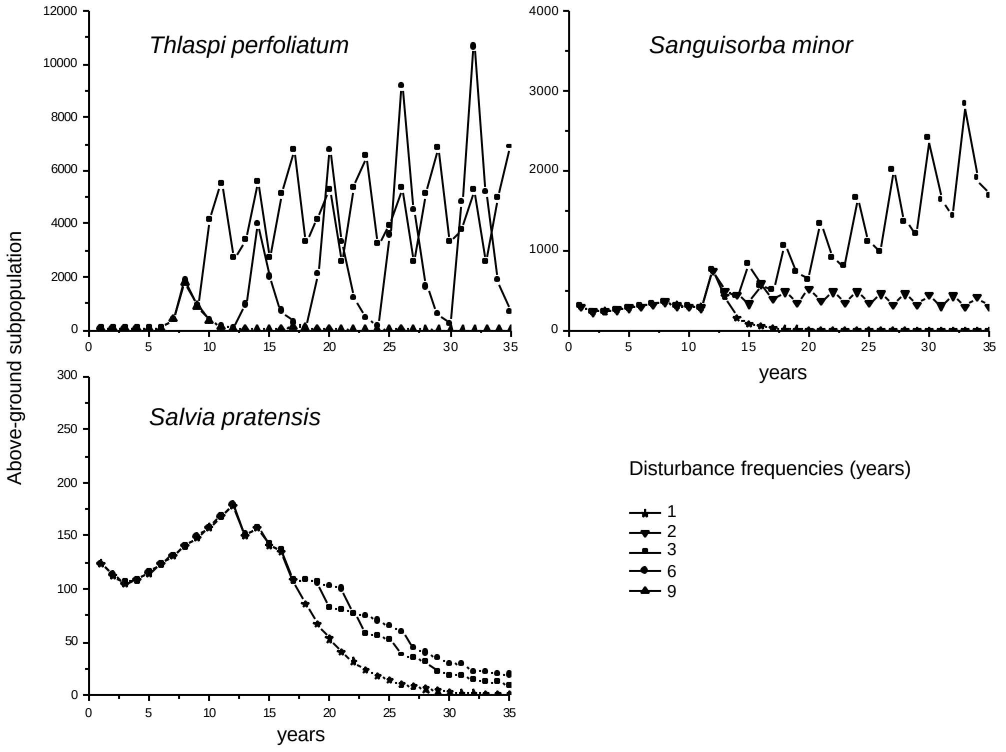


Fig. 5.2 Dynamics of above-ground subpopulations, i.e. the number of adult individuals of *Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia pratensis* over a time period of 35 years. Each dot represents the mean of 5000 simulations. Disturbance was applied from that year on, in which the models reached a stable population structure. This was a period of 5 years for the *Thlaspi perfoliatum* model, a period of 10 for the *Sanguisorba minor* model and a period of 15 years for the *Salvia* pratensis model, respectively.

Time to extinction

Time to extinction was affected by disturbance frequencies (Table 5.2). For *Thlaspi perfoliatum* high levels of extinction probabilities were found at low disturbance frequencies of more than six years. For instance, the average time to extinction (TE) decreased from 81 years at a rototilling return interval of seven years to TE = 24 years at a return interval of eight years. Contrary results were found for the perennial plant species *Sanguisorba minor.* Being infinite at return intervals of more than two years, TE decreased to eleven years at a return interval of one year. Likewise, for *Salvia pratensis*, time to extinction increased with increasing disturbance return interval, however the population would become extinct even at low disturbance frequencies. A return interval of ten years resulted in 53 years until extinction.

Table 5.2 Average time to extinction (TE in years) for populations of *Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia pratensis* for different disturbance frequencies. Given are median values (± SD) for 1000 model runs.

disturbance frequencies (years)	***Thlaspi perfoliatum***	***Sanguisorba minor***	***Salvia pratensis***
1	>200	11±2	19±4
2	>200	158±5	29±7
3	>200	>200	34±8
4	>200	>200	38±9
5	>200	>200	43±11
6	>200	>200	46±11
7	81±8	>200	48±12
8	24±5	>200	50±12
9	19±4	>200	51±13
10	16±5	>200	53±15

Model sensitivities

The model analyses showed that the demographic parameters of the three species display great differences in sensitivity. Seed bank depletion and germination rate in the third successional year following rototilling were the most sensitive parameters in the *Thlaspi perfoliatum* model (Table 5.3). The analyses further showed that changing adult mortality in the first year of succession had the greatest impact on the model outcome for *Sanguisorba minor*, considerable larger than alterations in e.g. juvenile mortality. On the other hand for the *Salvia pratensis* model germination rate in the first successional year after rototilling was more sensitive than juvenile and adult mortality.

Table 5.3 Ranking of sensitivity to model parameters of *Thlaspi perfoliatum*, *Sanguisorba minor*, and *Salvia pratensis*. Sensitivity was calculated as the ratio of the relative change of the probability of extinction and the relative decrease of parameters by 10 %. Bold numbers indicate the three most sensitive parameters. Abbreviations used: Juvenile1...4: age of the juvenile plant; autumn, spring: season of germination; R1,2,3: first, second or third successional year following rototilling; n.t. = not tested, n.a. = not applicable.

	Thlaspi perfoliatum	***Sanguisorba minor***	***Salvia pratensis***
parameter		sensitivity	
germination			
germination_R1	0.005	0.003	**0.048**
germination_R2	0.050	0.002	0.032
germination_R3	**0.189**	0.002	0.031
seedling mortality			
seedling mortality_autumn_R1	0.004	0.002	0.005
seedling mortality_autumn_R2	0.005	0.005	0.022
seedling mortality_autumn_R3	0.001	n.t.	n.t.
seedling mortality_spring_R1	n.a.	0.017	0.034
seedling mortality_spring_R2	n.a.	0.001	0.030
juvenile mortality			
juvenile2 mortality_autumn_R1	n.a.	**0.085**	0.034
juvenile2 mortality_spring_R1	n.a.	0.001	0.025
juvenile2 mortality_autumn_R2	n.a.	0.001	0.034
juvenile2 mortality_spring_R1	n.a.	0.005	0.033
juvenile3 mortality_autumn_R1	n.a.	**0.088**	**0.039**
juvenile3 mortality_spring_R1	n.a.	0.006	0.035
juvenile3 mortality_autumn_R2	n.a.	0.005	0.033
juvenile3 mortality_spring_R2	n.a.	0.004	0.030
juvenile4 mortality_autumn_R1	n.a.	n.a.	0.037
juvenile4 mortality_autumn_R1	n.a.	n.a.	0.035
juvenile4 mortality_autumn_R2	n.a.	n.a.	0.025
juvenile4 mortality_spring_R2	n.a.	n.a.	0.025
adult mortality			
adult mortality_R1	0.031	**0.112**	0.024
adult mortality_R2	0.001	0.004	**0.038**
adult mortality_R3	0.030	< 0.001	0.033
seed bank germination	0.018	0.021	n.a.
seed bank depletion			
first year	**0.316**	0.034	n.a.
second year	0.011	< 0.001	n.a.
third year	**0.186**	n.a.	n.a.
seed bank longevity	0.035	n.t.	n.a.
proportion of flowering			
proportion of flowering _R1	n.a.	0.020	0.035
proportion of flowering _R2	n.a.	< 0.001	0.034
proportion of flowering _R3	n.a.	0.004	0.032
seed production			
seed_production_R1	0.052	0.017	0.038
seed_production_R2	0.039	0.007	0.033
seed_production_R3	0.007	n.t	n.t.

Discussion

Rototilling semi-natural grasslands of temperate regions is a considerably different way of conservation management than the traditional mowing twice a year. In temperate grasslands, the latter stands for intermediate disturbance intensity, where phytodiversity should be maximised (Connell 1978, Huston 1979). In interaction with intermediate soil resources, mowing periodically sets back competitive interactions and provides unshaded microsites for recruitment through removal of nutrients and biomass, which would otherwise cover the soil as litter. Mowing conserves the spatial configuration of competitive interactions among perennials because the rooted position of the shoot remains unaffected. In contrast, rototilling redistributes spatial competitive interactions by destroying above-ground and below-ground plant biomass. An empty space is generated which is open for recolonisation from seed rain and regeneration from the seed and bud bank. Secondary succession then proceeds towards a canopy with higher vertical density than in mown plots (Box 3), resulting in exclusion risks for subordinate species with high competitive response.

The annual *Thlaspi perfoliatum* is a regular member of the community species pool of managed dry grasslands and rocky outcrops in Central Europe (Oberdorfer 1978). It is rarely seen in fields or ruderal habitats. In mown semi-natural grasslands, it apparently profits from a regeneration niche in small-scale open microsites (Grubb 1977), conforming to the short-lived interstitial – strategy in the matrix-interstitial model of Grubb (1986). After rototilling, the matrix of perennials is erased and small-scale microsites become large-scale open space. Our results show that *Thlaspi perfoliatum* populations dramatically increase after rototilling in an almost weedy habit. However, high recruitment lasts only for one year. Reasons for a decline in the following years are decreases in fecundity, germination and establishment under ongoing succession, with values falling far below those in mown plots (Chapter 3). In terms of Grubb (1986), restoration of the matrix slowly closes the regeneration niche of *Thlaspi perfoliatum*, in contrast to yearly mowing. Storage effects (Warner & Chesson 1985) in form of a seed bank allow the storing of some reproductive capacity until the next rototilling event. However, as the seed bank depletes over time, no recruitment is possible at larger rototilling return intervals (> 6 years). The sensitivity analysis identified seed bank depletion as the most important trait (Table 5.3). This is in accordance with simulations of the dynamics of annual grass species by Canales et al. (1994) and Silva et al. (1991). Both emphasise changes towards lower disturbance frequencies as the major reason for the decline of populations of annual plant species.

Our simulations reveal that the maximum number of adult individuals of *Thlaspi perfoliatum* increases with decreasing disturbance frequency (Fig. 5.2). This pattern can be explained by density-dependent seedling mortality. There is evidence that for annual plant species density-dependent fecundity and mortality through self-thinning is frequent in a range of habitats (Symonides 1988, Watkinson et al. 1989, Buckley et al. 2001, Silvertown & Lovett Doust 2001). We incorporated an increased mortality of *Thlaspi perfoliatum* seedlings in the model as a result of crowding. This was done by putting a ceiling of 55 on the maximum number of seedlings that can survive in one cell using logarithmic functions based on field observations (Chapter 3). At low disturbance frequencies (e.g. every third year) a higher amount of cells are occupied by seedlings than at lower frequencies (e.g. every sixth year), since both seed dispersal over short distances and seed bank stimulation following each disturbance resulted in higher seedling appearance. Higher seedling densities per cell resulted in higher seedling mortalities, and consequently in lower population sizes of adults.

With respect to its life cycle, *Sanguisorba minor* takes an intermediate position between the annual *Thlaspi perfoliatum* and the perennial *Salvia pratensis.* It flowers in its second year and dies at the age of ten. Age of first flowering is therefore responsible for extinction, if the rototilling return interval is lower than three years, as offspring can no longer be produced. Enlarging the disturbance return interval prolonged population survival of *Sanguisorba minor* and *Salvia pratensis. Sanguisorba minor* develops larger populations because (1) establishment is not affected as much by higher vertical canopy density as for *Salvia pratensis* (although seed weight is comparable), and (2) activation of the seed bank adds to recruitment following each year with rototilling, what does not occur under mowing. All in all, high recruitment exceeds high adult mortality following rototilling. However, litter production may seriously hamper recruitment in later successional years (Tilman 1988).

In contrast to *Sanguisorba minor*, *Salvia pratensis* populations exhibit a continuous decline under all simulated disturbance return intervals. Although adult mortality is considerably lower than in *Sanguisorba minor* due to effective resprouting following rototilling, an almost complete lack of establishment of new individuals under ongoing succession leads to extinction. Furthermore, germination rates are low in the first year after rototilling because the seed bank is transient. In the long run, *Salvia pratensis* declines due to overaged populations.

Population viability analysis has often shown that decreasing environmental variation increases the likelihood of population extinction (Menges 2000, Menges & Quintana-Ascencio 2003). By replacing a regular and light disturbance such as annual mowing with a more severe and infrequent disturbance (i.e. rototilling), shifts in habitat qualities are increased as species encounter both biomass loss when disturbed, and the risk of competitive exclusion under ongoing succession after disturbance. However, for those species exhibiting storage effects via a persistent seed bank, increasing environmental variation leads to population increase instead of decline

(Higgins et al. 2000). A persistent bud bank as in *Salvia pratensis* obviously is not as effective, if recruitment rates during disturbance intervals are low.

Schippers et al. (2001) made a theoretical evaluation of the role of three important plant life history traits (adult longevity, seed longevity, and seed mass - seed mass as an indicator of dispersal distance and seedling vigour) in relation to different levels of disturbance using a spatially explicit model. Concerning adult mortality, their results showed a clear range within the disturbance gradient in which perennials exclude annuals. The authors explained this segregation by the fact that disturbance affects the adults but not the seeds. Thus, under increasing disturbance levels, the strategy to invest in seeds is more profitable than investment in adult life span. According to Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987), dormancy (i.e. persistent seed banks) and dispersal are alternative ways of coping with disturbance. Schippers et al. (2001) concludes from simulation results that dormancy is a better way of coping with disturbance i.e. that escape in time is better than escape in space. According to dispersability traits such as appendices of the dispersule, none of the species analysed in our study is suspected to be a good disperser. Simulations of Schippers et al. (2001) showed a general sequence of dominance of non-dormant perennials, followed by dormant perennials, non-dormant annuals, and dormant annuals with increasing disturbance level. Our results are in accordance with these findings, showing a sequence of extinction probability of the non-dormant perennial, followed by the dormant perennial and dormant annual with increasing disturbance frequency.

Do population parameters display similar sensitivities across all three species?

Model parameters were taken from three years of field data (Chapter 3 & 4), which is a relatively short period in comparison to time to extinction as modelled in this study. Possibly demographic and other vital parameters are not precisely known over the whole trajectory towards extinction. To take this uncertainty into account, as well as determining the most sensitive parameters and assessing the robustness of the model, a sensitivity analysis was performed. The results show that demographic parameters of the three species display great differences in sensitivity. The most sensitive parameters are seed bank depletion and germination of the dormant annual species, whereas the response of the *Sanguisorba minor* model is highest to changes in mortality rates of juveniles and adults. On the other hand, the probability of extinction of *Salvia pratensis* populations is most affected by a shift in the germination rate in the first year after rototilling. Achieving accurate field data for these parameters is crucial for the predictive power of the *Sanguisorba minor* and *Thlaspi perfoliatum* models, while the *Salvia pratensis* model is more robust to variations in parameter values. The *Salvia pratensis* model highlights the added value of modelling to analysis of field experiments. We concluded (Chapter 4) that resprouting (*Salvia pratensis*) is an alternative strategy to seeding (*Sanguisorba minor*, *Thlaspi perfoliatum*) in coping with infrequent below-ground disturbances. Extrapolating the field study in time through modelling shows that resprouting alone cannot ensure population survival.

Are there suitable disturbance return intervals to maintain populations of focal plant species?

The results show that there is no optimal disturbance return interval at which all species can survive. A rototilling frequency of once every 3-6 years is suitable to maintain populations of dormant annuals (e.g. *Thlaspi perfoliatum*) and dormant perennials (e.g. *Sanguisorba minor*), however there is no rototilling frequency which generates stable growing *Salvia pratensis* populations. We conclude that functional groups of species with similar life histories as *Salvia pratensis* exhibit a high extinction risk, when management is changed from annual mowing to infrequent rototilling.

Conclusions and implications for nature conservation

Our study confirms that simulation models are a useful tool to support management decisions regarding the conservation of plant composition under a change in disturbance frequencies. However, the modelling results for the effects of rototilling frequencies on the population dynamics and extinction probabilities of three plant strategies highlighted a serious dilemma in the conservation of semi-natural grassland communities by rototilling, since obviously, no disturbance return interval exists at which all species can survive. Therefore, mowing can not be satisfactorily replaced by a rototilling system, if the object of the conservation management is to maintain the overall species composition. The ranking of alternative management actions is a central issue in conservation biology (Lindenmayer & Possingham 1996). In this connection decision analysis is used to compare alternative management actions for the protection of single species e.g. Drechsler (2000). For this study, the decisions of conservation managers have to go one step further. The task is to find a solution which provides the best compromise between ecological (i.e. the maintenance of the plant community) and economical (i.e. low costs for the treatment) aspects. This means a benefit-cost ratio has to be arranged. In respect thereof, it has to be taken into account that rototilling with an intermediate frequency may cause the loss of species, but, abandonment would nonetheless cause more species to suffer from succession (Hobbs & Mooney 1986, Kollmann 1997, Poschlod & WallisDeVries 2002, Tasser & Tappeiner 2002, Bouchard et al. 2003). Furthermore, conservation managers may have to make their decision depending on the state and the scarcity value of the species which might be lost.

Box 1

Can rototilling prevent shrub encroachment on semi-natural grasslands?

Box 1

Can rototilling prevent shrub encroachment on semi-natural grasslands?

Background and aim

The development of shrub vegetation on grasslands without disturbance is a natural process and has been described in detail previously (e.g. Kollmann 1997, Berlow et al. 2002). During succession, shrub canopy increases and correspondingly impacts upon the surrounding microclimate (Lett & Knapp 2003). Shading decreases the microclimate diversity and species composition (Hobbs & Mooney 1986). Growth of shrubs and the resultant cover they provide causes suppression of herbs by competition and interference (Bazzaz 1983). Mesobromion and Brometalia species are particularly sensitive to shading (Kollmann 1997). Thus, management is nessessary to protect grassland character species against overgrowth. Alteration of management strategy – in this case, a change from a frequent (mowing once a year) to a less frequent (but severe) disturbance system (rototilling) – could be problematical, since reduced management implies colonisation of shrub vegetation (Kollmann 1997). Much is known about the mechanisms of succession and invasion of shrubs on grasslands (Berlow et al. 2002) as well as about regeneration strategies of trees after disturbance (Bellingham 2000, Loehle 2000, Kennard et al. 2002, Ickes et al. 2003, Batista & Platt 2003) particularly regarding resprouting of woody plants after snapping or uprooting for forests, as reviewed in (Paciorek et al. 2000). However, the population biology of woody plant species has seldom been studied and hence little is known about generative reproduction (Grubb 1999, Siemann & Rogers 2003), seed bank, and dispersal (Grunicke 1996). Concerning vegetative resprouting of shrubs by underground runners, nearly no empirical data are available.

In this study, I focus on vegetative resprouting, since my own preparatory demographic studies have shown that regeneration by seedlings plays no role in the recolonisation of *Prunus spinosa* on rototilled semi-natural grasslands. This study aims to verify the hypothesis that rototilling diminishes resprouting vigour. A below-ground disturbance may nonetheless stimulate regeneration buds; however, I hypothesise that the perturbance decreases the available plant resources for resprouting. The study also seeks to answer the question: Is cyclic disturbance a suitable tool to prevent shrub encroachment on semi-natural grasslands?

Methods

Species

Prunus spinosa is a thorny shrub which can grow up to a height of about 4 m in undisturbed sites. The species shows a medium to high degree of regeneration potential and a high degree of clonal spreading (Kleyer 1995), spreading massively in semi-natural grasslands by means of root suckers. From initial polycormons it is able to build up thick, monospecies shrubs. At the edge of polycormons *Prunus spinosa* may expand in space with a rate of 25 - 50 cm per year (Wilmanns 1975, Reichhoff & Böhnert 1978, Schiefer 1981). *Prunus spinosa* is responsible for the development of shrubby vegetation on the study sites. According to the seed bank classification of Thompson et al. (1997), *Prunus spinosa* has a transient seed bank. (For further information on biological traits see Chapter 2 & Table A3, Appendix).

Study sites and experimental design

The study was conducted on shrubby semi-natural grassland in the nature reserve 'Hohe Wann' in Lower Franconia. Data collected for each of three study sites comprised measurements of numbers of shoots per m^2, number of basal stems (near the surface) per shoot, shoot height, numbers of first-order branches, length of first-order branches, and percentage cover of *Prunus spinosa*. Four experimental plots (10 m x 15 m) were established. One plot was a referential plot where the current treatment 'mowing once a year in late summer' was continued. Three plots were rototilled once, beginning in the year 2000, thus the last plot was rototilled in the year 2002. Investigations on *Prunus spinosa* began in 2001. The experimental design allows investigation and comparison of traits during different successional stages and permits comparison of the results for two consecutive years. Within each experimental plot, five subplots (1 m x 1 m) were randomly selected from ten regularly arranged permanent plots of two by two meters. (For a more detailed description of the experimental design refer to Chapter 2). The number of shoots and basal stems within the plots were counted prior to the experiment and subsequently once a year in the two years following treatment. All ten plots were used for estimation of the total cover of *Prunus spinosa*. For estimation of shoot height, numbers of first-order branches, and length of branches, 25 shoots were randomly selected from each management plot. Average values were compared between the two treatments (mowing/rototilling) and between successional years. Statistical comparisions between treatments were done using non-parametric H-tests for overall comparisions and U-tests for pairwise comparisions.

Results

Effects of disturbance on the number of shoots/m² and the number of basal stems

According to field data for the year 2001, rototilling decreased the number of shoots per m^2 and the number of basal stems per shoot by an average of 30 % and about 60 %, respectively, in the first year after disturbance (R1 year 2001 in Fig. B1.1). Replicates in the year 2002 confirmed the results from 2001, again showing a decline in the number of shoots per m^2 and the number of basal stems per shoot in the first year after disturbance (R1 year 2002 in Fig. B1.1). Counting of shoots and basal stems after rototilling revealed a higher decrease in comparison to the first year of investigation. Shoots and basal stems were reduced by more than 80 % and 90 %, respectively. Stem density – or rather growth form – did indeed change with respect to treatment: Mowing once a year supported multi-stemmed architecture by stimulating basal meristems to build up basal stems, while rototilling decreased basal stems and supported a more single-stemmed architecture (Fig. B1.1). In the second year after disturbance, the percentage increment of both the number of shoots and the number of basal stems was lower than 1 % (R2 in Fig. B1.1).

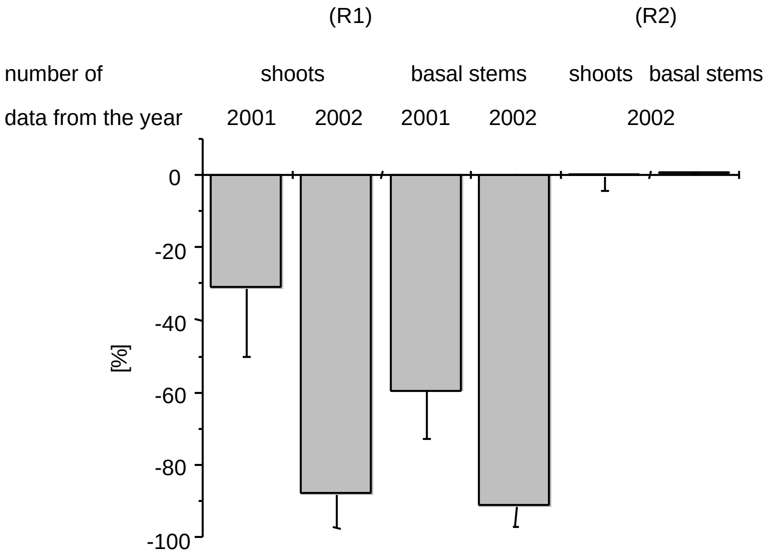


Fig. B1.1 Percentage differences between both the number of shoots and the number of basal stems per shoot after the first year (R1) and the second year (R2) of rototilling, relative to the initial stage before treatment. Data were collected in the years 2001 and 2002. Field data were pooled for three sites. N_{shoots} 2001 = 322, n_{shoots} 2002 = 145, $n_{basalstems}$ 2001 = 1300, $n_{basalstems}$ 2002 = 422. Mean and standard deviation are indicated.

Effects of disturbance on shoot height, number and length of first-order branches

On comparison of shoot height and numbers of first-order branches between mown and rototilled plots at different successional stages (Fig. B1.2), I found no significant differences. A small decrease in height from 32 cm on mown plots to 30 cm on rototilled plots in the first successional year gave way to an increase in height to an average of 34 cm in the second year of sucession. The number of branches initially increased relative to the mown plots, but decreased in the second year of succession. No significant differences were found between branch length for mown plots and rototilled plots in the first year of succession. However, for the second year of succession, branch length was approximately 5 times higher than on mown plots (Mann-Whitney U test, $p < 0.001$).

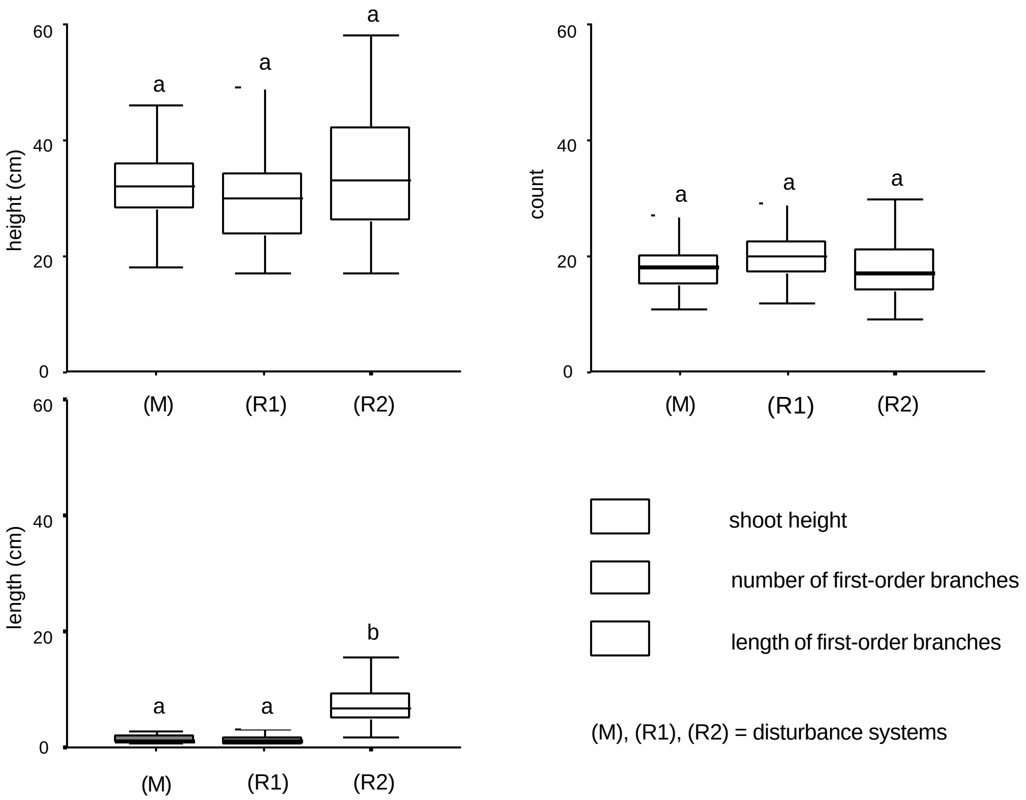


Fig. B1.2 Comparison of average shoot height, average number and average length of first-order branches between mown and rototilled plots at different successional stages, using non-parametric tests (for overall comparisons H-test, for pairwise comparisons U-test). Field data were pooled for three sites. Significant differences between two treatments are indicated by different letters; n = 75. (M) = mown plots, (R1) = rototilled plots, first successional year, (R2) = rototilled plots, second successional year.

Effects of disturbance on total cover

To estimate the lateral expansion of *Prunus spinosa*, the percentage total cover was recorded on mown and rototilled plots over two consecutive years. Contrary to the mown plots, where the total cover of *Prunus spinosa* did not differ much from year to year, total cover of *Prunus spinosa* accumulated dramatically during successional years after rototilling (Fig. B1.3). After two years, total cover was about 5 -10 % higher than the pre-rototilling value.

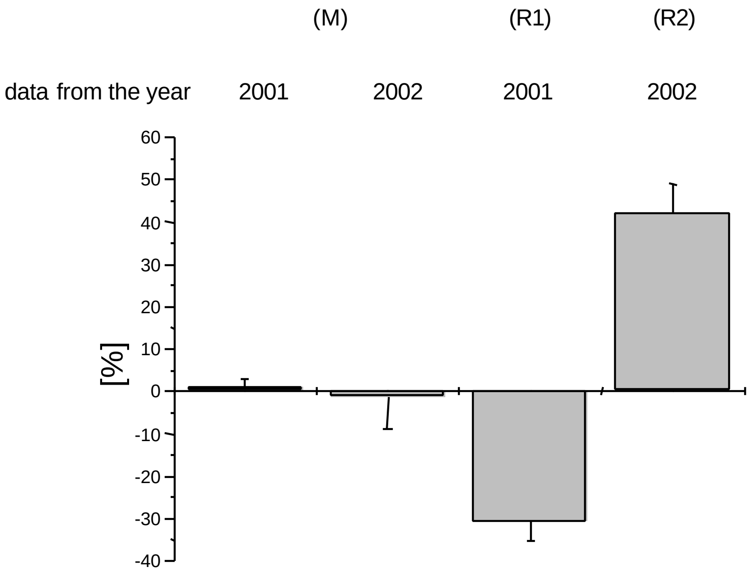


Fig. B1.3 Percentage differences between both the *Prunus spinosa* cover in mown plots in the year 2001 and 2001 and in rototilled plots in the year 2001 and 2002. (M) = mown plots, (R1) = rototilled plots, first year of succession, (R2) = rototilled plots, second year of succession. Field data were pooled for three sites. Mean and standard deviation are given. N for each treatment = 10.

Discussion and conclusions

Resprouting capability of shrubs depends on both above- and below-ground plant reserves, and on the possibility of making or maintaining the necessary storage organs between disturbances (Bellingham 2000). It is known that *Prunus spinosa* spreads primilary by means of root suckers. Since rototilling removes not only above-ground biomass but also disturbs below-ground components, it was feared that regeneration buds may have been stimulated to produce more root suckers via disturbance associated with rototilling than e.g. on mown plots. Resprouting stimulation has been found in some herbaceous weeds such as *Convolvulus arvensis* and *Elymus repens* (Ellenberg 1950) and shrubs (Cirne & Scarano 2001). However, such was not the case in this study, where above-ground shoots were notably reduced. Hodgkinson (1998) also found a reduction of resprouting vigour for some semi-arid woodland species after disturbance through fire. Given that most of the above-ground and below-ground biomass is removed by rototilling, but the mobilisation of below-ground resources will be essential for resprouting (Bellingham 2000), resprouting vigour seems to be reduced because of decreasing plant resource availability.

This study furthermore supports the assumption that there is a relationship between growth form and disturbance. Variation in growth form is often found along with disturbance and productivity gradients resulting from competition (Bellingham 2000). My observation that rototilling decreases basal stems and initially supports a more single-stemmed architecture corresponds with the findings of Halle et al. (1978), who showed that the conifer *Sequoia sempervirens* responds to a servere, but unfrequent disturbance by resprouting to reform a monopodial architecture. On mown plots, on the other hand, the most rapid recovery of canopy area is achieved by multi-stemmed resprouting (Bellingham 2000). By elongation of branches during succession after rototilling, *Prunus spinosa* increases canopy extension and thus competitive advantage.

Although there is no direct evidence for a relationship between soil moisture and management efficiency in reducing shrub shoots, climate data (precipitation and soil moisture) for the two investigation years support this assumption. A decrease in moisture in 2002 was accompanied by an increase in shoot mortality (see Fig. B1.1). Several factors have been found to influence shoot mortality. For some species, sprout mortality correlates with internal factors such as size or age of the original stem and number of sprouts sharing the same root system (Blake 1983, Iwasa & Kubo 1997, Bellingham 2000, Kennard et al. 2002). The season in which disturbance takes place is important in systems in which plant growth is seasonal. Kays & Canham (1991) demonstrate that resprouting vigour coincides with a seasonal maximum in reserve mobility. Moreover, resprouting vigour is of course influenced by the serverity and frequency of disturbance (see above). Vila & Terradas (1995) provide evidence for reduced vigour and survivorship of resprouting shrubs under increasing disturbance frequency.

My results can be summarised as follows: This study verifies the hypothesis that rototilling diminishes resprouting vigour after disturbance, yet weather conditions (moisture) have a great impact on the efficiency of the treatment to control *Prunus spinosa*. The numbers of shoots per m^2 and the number of basal stems per shoot are explicitly reduced. I found no time-lag concerning resprouting, i.e. the percentage increment of both the number of shoots and the number of basal stems was lower than 1 % in the second year following rototilling (R2 in Fig. B1.1). However, as a result of the massive lateral spread of the species in later successional years, only frequent cyclic disturbance by rototilling would be able to push back *Prunus spinosa* cover and to prevent canopy extension. To reduce shading by shrubs during succession, which would reduce the survival of other focal species e.g. *Thlaspi perfoliatum* (see Chapter 3), a combination of the two management strategies of mowing and rototilling may conceivably provide an effective solution. Since woody plants become less competitive with increasing frequency of severe disturbance, a disturbance return interval by rototilling of 3 - 4 years and mowing once in between may be an appropriate management strategy.

Box 2

Regeneration potential of semi-natural grassland species after disturbance by rototilling

Box 2

Regeneration potential of semi-natural grassland species after disturbance by rototilling

Background and aims

Re-establishment and recolonisation of disturbed sites depends on seed availability and vegetative regeneration by resprouting. Seeds either originate from the soil seed bank or arrive via immigration through dispersal. A persistent seed bank ('dispersal in time') is especially important in highly fragmented landscapes, and in cases where long-distance dispersal ability is poor (Bonn & Poschlod 1998). Several studies have shown no long-distance dispersal ability in character species of semi-natural grasslands. (Poschlod et al. 1996, Kollmann 1997). Maas (1994) e.g. found that 70 % of the herbaceous species of calcareous grasslands were dispersed no further than 10 m, 20 % up to 100 m and only the remaining 10 % reached more than 100 m distant. Thus, the seed bank is an important feature for vegetation dynamics, especially after soil disturbance. Knowledge of the seed bank composition is required for management decisions for the conservation of plant communities (Poschlod & Jackel 1993, Poschlod 1996), and for the temporal extrapolation of population dynamics and vegetation development by e.g. simulation models (Chapter 3 & 5). Although much attention has focused on research into grassland seed banks, e.g. Poschlod et al. (1991), Milberg & Hansson (1993), Poschlod (1993); Poschlod & Jackel (1993), Kiefer & Poschlod (1996), Bekker et al. (2000), Kalamees & Zobel (2002), Smith et al. (2002) we still lack knowledge on seed bank longevity of species, which is important for estimation of the role of the soil seed bank in regeneration after disturbance events. This is especially true if depth distribution is used to quantify longevity, as it is known that the depth distribution of individual species shows a wide range of variation depending on soil conditions (Poschlod 1993, Bekker et al. 1998).

There is evidence that regeneration via vegetative fragments is crucial in vegetation development after disturbance. Vegetative regeneration vigour after damage of plant modules could be advantageous for the survival of cyclic disturbances (Harper 1977, Eriksson 1989, Crawley 1990, Fahrig et al. 1994). Crawley (1990) and Amiaud & Touzard (2004) showed that most plant species on cultivate grassland soils regenerate from vegetative fragments rather than by seed germination. Rogers & Hartnett (2001) found that vegetative regrowth is the dominant recolonisation mechanism after soil disturbance in tallgrass prairies. As rototilling destroys and disturbs vegetation cover and below-ground substrates up to a depth of 15 - 20 cm, the vegetation recovers by both individual vegetative regeneration and seed bank activation.

This study aims to determine the regeneration potency and soil seed bank characteristics of semi-natural grassland plant species after rototilling. The following questions are addressed: 1) Are the characteristic plant species of semi-natural grasslands able to regenerate? 2) How fast will the vegetation of the plots recover after rototilling? 2) Are semi-natural grasslands species able to build up a persistent seed bank? 3) How strong is the potential for regeneration from the soil bank and from vegetative resprouting, respectively? 4) How does seed bank density and composition change during the first successive years after rototilling, changes which may themselves affect future vegetation change?

Methods

Data on both seed bank and vegetation composition were collected from four semi-natural grasslands in the nature reserve 'Hohe Wann' in the Hassberge area, Lower Franconia (Southern Germany). On each site (Lichtlein, Molkengrund, Rappberg, Regelberg), different plots with different treatments were established: one referential plot on which mowing was continued once a year, and three plots on which rototilling was conducted once in three consecutive years, so that succession took place in the years following the treatment. Thus, rototilled plots lay beside each other along a successive gradient. (For further information on the experimental design see Chapter 2). The first plot was rototilled in the year 2000. A grid of 20 two by two meter permanent plots was set up within each of the management plots.

Five one by one meter subplots were established within the two by two meter plots to provide soil samples using an auger with a core of r = 2 cm. Each soil sample is a mixture of five cores. After removal of the litter layer, the samples were divided into subsamples of 0 - 5 cm and 5 - 10 cm depth.

As soil samples were taken in early spring 2002 - after winter stratification but before seed shed of spring annuals - data on the soil seed bank were gained for the first two successive years after rototilling. It was assumed that the seed bank is consistent within the plots as all plots were managed in the same way before the start of the experiment. However, vertical distribution of seeds as an indicator for longevity does not work when below-ground disturbances such as rototilling are applied. Therefore, only the mown plots were sampled in order to estimate seed persistence and longevity of the species.

Consequently, three management plots were used for analysis: M = mown plots, R1 = rototilled plots in the first successive year, R2 = rototilled plots in the second successive year.

The seedling emergence method was used to assess the seed bank (Fischer 1987, Bakker et al. 1996, Ter Heerdt et al. 1996, Thompson et al. 1997). Soil samples were firstly concentrated by washing them over sieves of different mesh sizes (2 mm and 0,2 mm) to eliminate fine particles and to reduce soil volume (Ter Heerdt et al. 1996, Bossuyt 2000). Subsequently, seeds were spread on the top of sterilised commercial potting soil in plastic trays. Each tray was covered with a fleece to prevent seed establishment by dispersal from the surrounding vegetation. A second fleece was installed under the potting soil to ensure water delivery. Wicks were used to deliver water from the lower to the upper tray. Four control trays monitored any airborne seed contamination. At first, all trays were cultivated under natural conditions. After a period of 12 weeks the trays were taken into a greenhouse to dry out. The samples were stirred once again to stimulate a second crop of seedlings. In the beginning of November 2002 trays were exposed outside again. All seedlings that appeared were counted, classified, and removed. The experiment ended in December 2002.

Vertical distribution of seeds was used as an indicator for longevity (Bekker et al. 1998, Bakker et al. 2000) (Thompson et al. 1997) following the classification scheme of Thompson et al. (1997) modified by Jackel (1999). Soil samples from the below-ground undisturbed plots (mown plots) were used for classification, using the proportional abundance of the species in upper and lower soil layers. Seeds which were

- present in the upper layer only were defined as transient
- more frequent in the upper, but present in lower soil layer were defined as short-term persistent
- at least as frequent in the lower as in the upper soil layer were defined as long-term persistent.

The longevity index (Thompson et al. 1997) was calculated using following term:

LONGEVITY INDEX (SLI) = $$\frac{\sum \mathbf{(type\,2 + type\,3)}}{\sum \mathbf{(type\,1 + type\,2 + type\,3)}}$$

type1 = transient < 1 year; type2 = short-term persistent > 1 - 5 years; type3 = long-term persistent > 5 years

Values range from 0 to 1. The following classification using SLI range was applied:

- from 0 to 0.33 = transient
- > 0.33 = persistent

Persistent was classified as short-term (0.33 to 0.55) or long-term (> 0.55 to 1).

If no seeds were found but the species was abundant (i.e. present in > 2 out of 5 subplots and cover ? 1%) in the established surrounding vegetation, the species was included in this study and considered to have a transient seed bank (Bekker et al. 1998).

To investigate how fast rototilled plots are recovering, and to estimate the proportion of vegetative and generative regeneration, in 2001 vegetation releves were made twice on ten subplots, once before and once eight weeks after disturbance by rototilling. In order to determine the importance of vegetative reproduction, I used the presence or absence of cotyledons to distinguish between new plant individuals resulting from vegetative resprouting and individuals originating from seeds.

In adjacent plots to those used for seed band analysis, vegetation in 4 by 4 meter squares was analysed using vegetation releves according to a modified system of Londo (1976) see Jackel (1999) in the year 2001 (Table B2.1).

Table B2.1 Scale of percentage cover values according to Londo (1976) modified by Jackel (1999).

percentage cover [%]	< 0.5	= 1	1-2	2-3	3-5	6-10	10-15	15-20	20-30	further steps every 10 %
scale	+	1	2	3	5	10	15	20	30	.....

The relationship between established surrounding vegetation and species in the soil seed bank was investigated using the Sorensen index (Southwood 1978, Pielou 1984).

Sorensen index (SSI) = $$100x \frac{2a}{(2a + b + c)}$$

a = species present in both vegetation and soil seed bank; b = species present only in the seed bank; c = species present only in vegetation

For the analysis, field data were extrapolated into numbers of seeds per m². Since the species of interest were semi-natural grasslands species, data on ruderal species were generally disregarded in the analysis. Since data were not normally distributed, non-parametric tests (H-TEST, U-TEST) were used to test for differences between the treatments.

Results

In total, 3316 seedlings were recorded in the soil seed bank. Seedlings of *Betula pubescens* were recorded in the control trays, indicating that seeds of this species were introduced during cultivation. Thus, seedlings of this species were not taken into analysis. Five seedlings died before identification was possible. Altogether 3291 seedlings belonging to 74 species were classified (Table A5, Appendix).

Effects of a change in management on seed bank density

Seed density in a 10 cm layer ranged between 2023/m² (site Regelberg, M) and 12537/m² (site Lichtlein, R2). Density of seeds in the soil decreased or remained more or less constant in the first year after rototilling compared to mown plots, and then increased in the second successive year (Fig. B2.1a).

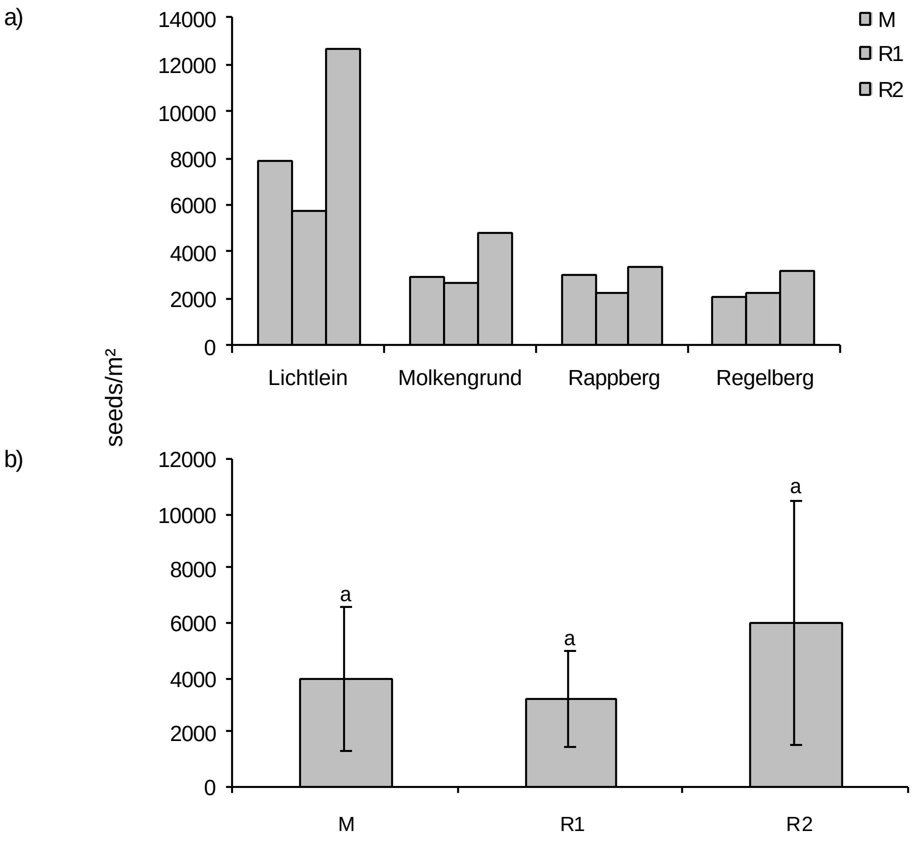


Fig. B2.1 Comparison of seed density (seeds/m²) in a 10 cm layer between a) all sites and treatments and b) pooled for the treatments. N for each treatment = 20. Differences between mown and rototilled plots were tested using non-parametric tests (for overall comparisons H-test). Equality signs indicate that no significant differences were found. M = mown plots, R1 = rototilled plots in the first successive year, R2 = rototilled plots in the second successive year.

For comparison of seed density between treatments, data were pooled for all four sites. However, there were no significant differences between the treatments, which may be due to the large site-specific differences in seed density (H-test, $p > 0.05$, Fig. B2.1b). The following average seed densities/m² were found: on mown plots 3923/m², with a higher amount of seeds in the upper soil layer (2648 seeds/m²), on recently rototilled plots 3206, and on rototilled plots in the second successive year 5978/m².

Changes in seed density due to a change in management strategy during the first two successive years were analysed for 44 characteristic semi-natural grassland species (Table A5, Appendix). Significant differences between the two treatments were found solely for *Thlaspi perfoliatum.* There were no significant differences between mown and recently rototilled plots (on average 80/m² for both), but seed density for *Thlaspi* increased significantly in the second successive year (up to 400/m²). Figure B2.2 shows the number of seeds/m² of 12 selected species. Six groups of species showing different seed bank dynamics could be distinguished. Group 1: Seed density decreased after rototilling (*Achillea millefolium*). Group 2: Seeds were found on specific treatments only e.g. either on mown plots such as *Euphorbia cyparissias* and *Lotus corniculatus* or in later successive years after rototilling such as *Elymus repens*. Group 3: Some species tended towards an increase in seed bank density after a change in management strategy (e.g. *Poa angustifolia*). Group 4: Species did not build up a soil seed bank even though they were present in the above-ground vegetation (e.g. *Festuca rupicola* and *Trisetum flavescens*). Group 5: No influence of a change in management strategy on seed density from mowing to rototilling was ascertained, but evidence was found for an increase in the second successive year (*Arenaria serphyllifolia, Hypericum perforatum*, *Thlaspi perfoliatum.*). Group 6: Seed density decreased immediately after rototilling, but had already increased again by the second successive year (e.g. *Medicago lupulina*).

Table B2.3 Sorensen similarity indices [%] comparing established surrounding vegetation and soil seed bank for the management systems mowing (M) and rototilling (R) on the four investigation sites (Lichtlein, Molkengrund, Rappberg, Regelberg). The numbers following R indicate the successive stage. R1 = first year of succession, R2 = second year of succession, a = species present in both vegetation and soil seed bank, b = species present only in the seed bank, c = species present only in vegetation.

sites	Lichtlein			Molkengrund			Rappberg			Regelberg		
management	M	R1	R2	M	R1	R2	M	R1	R2	M	R1	R2
a	14	13	14	12	8	11	14	12	12	12	9	8
b	19	14	15	7	13	11	9	7	10	6	9	13
c	27	28	27	27	30	28	25	27	27	33	36	37
Sorensen index [%]	**37.8**	**38.2**	**40.0**	**41.4**	**27.1**	**36.1**	**45.2**	**41.4**	**39.3**	**38.1**	**28.6**	**24.2**

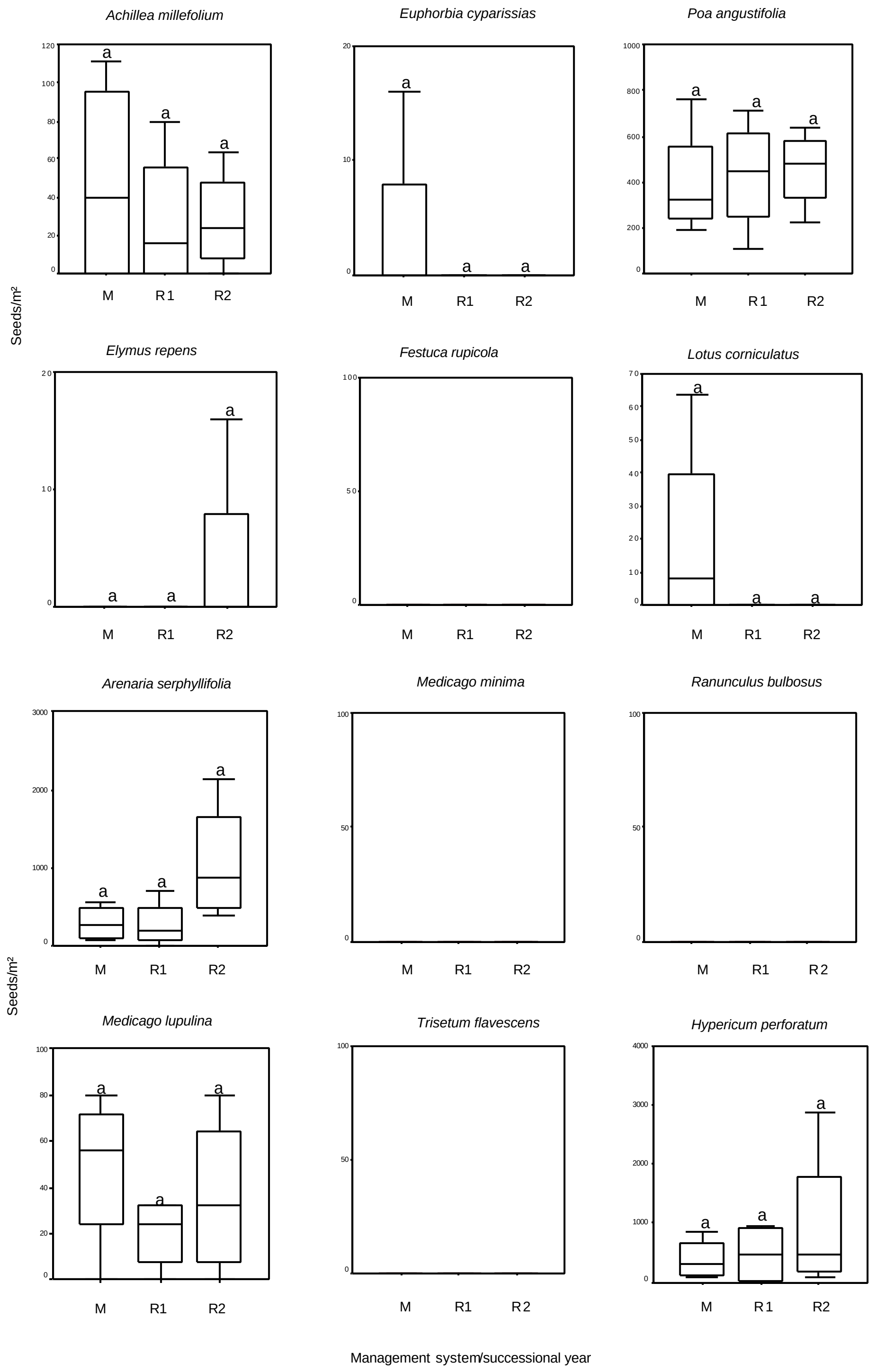


Fig. B2.2 Comparison of seed density of 12 selected species on mown (M) and rototilled plots in different successive stages within a depth of 0 - 10 cm. The same species as for frequency (see Box 3, Fig. B3.6) were selected and appear in both Figures in the same sequence. Mean values and standard deviations are given. Sites were pooled for analysis. N = 25. R1 = rototilled plot in the first year of succession; R2 = rototilled plot in the second year of succession. The scales differ for each species. Differences between treatments were tested using H-test according to Kruskal & Wallis. Equal signs indicate that no significant differences were found.

Seed bank type and longevity of typical semi-natural grassland species

Seed bank type and longevity could be calculated for 44 typical grassland species (Table B2.2). The analysis of type and longevity are based on both my own data and that of Thompson et al. (1997). Half of the typical semi-natural grassland plant species were not able to build up a persistent seed bank – for 22 species seed bank longevity was calculated to be < 0.33. Nearly half of the species with a persistent seed bank tended to be rather short-term (< 0.55) rather than long-term (> 0.55) persistent (classification according to Bakker, R.; personal communication). The comparison of results for seed bank type and longevity from my own investigations with data cited by Thompson et al. (1997) was possible for 35 species; 16 species showed a good or even very good analogy. For seven out of the 35 species, data on seed bank type and longevity differed strongly between the two data sets.

Effects of a change in management strategy on the similarity between seed bank and above-ground vegetation

Similarity was low, ranging from 27.1 % to 45.2 % (Table B2.3). Similarity between above- and below-ground vegetation was highest on mown plots, with the exception of the Lichtlein site. There was no consistent trend concerning similarity. Similarity between mown and rototilled plots increased over successive stages at the Lichtlein site, but for the Rappberg and Regelberg sites, the reverse tendency was found. At the Molkengrund site similarity at first decreased after rototilling, but increased in the second successive year.

Re-occurrence and regeneration strategies after rototilling

Re-occurrence within eight weeks after rototilling was found for a high percentage of species ranging between 66 % and 96 % (Table B2.4). If the influence of stochastic extinction processes was taken into account, i.e. the survival rate of only abundant species (present in > 4 plots) was recorded in order to exclude random extinction and not that which is caused by a change in treatment, even higher survival rates were found. Surprisingly, at the Rappberg site, all species were in fact able to regenerate within short time after rototilling, although most of them are lacking a persistent seed bank.

Table B2.2 Deviance and accordance of longevity indices (SLI) for typical semi-natural grassland species according to Thompson et al. (1997) and my investigations as well as SLI for both data sets.
° deviance was calculated by subtraction of the SLI value cited by Thompson et al. (1997) from the SLI value according to my investigations; ^ analogy was classified by following system: 1 = very good analogy; 2 = good analogy; 3 = low analogy; 4 = great differences.

	SLI		deviance°	accordance^	SLI	seed bank type
species	according to Thompson et al. (1997)	according to my investigations			including Thompson et al. (1997) and my investigation	
Inula conyzae	1.00	1.00	0.00	1	1.00	persistent
Hypericum perforatum	0.81	1.00	0.19	1	0.83	
Silene vulgaris	0.90	0.00	0.90	4	0.82	
Poa angustifolia	0.00	1.00	1.00	4	0.80	
Origanum vulgare	0.73	1.00	0.27	2	0.75	
Fragaria viridis	0.00	1.00	1.00	4	0.75	
Thlaspi perfoliatum	-	0.75	-	-	0.75	
Arenaria serpyllifolia	0.71	0.75	0.04	1	0.72	
Medicago lupulina	0.74	0.00	0.74	4	0.70	
Euphorbia cyparissias	0.80	0.00	0.80	4	0.67	
Silene nutans	0.67	0.50	0.17	1	0.60	
Potentilla neumanniana	0.33	1.00	0.67	4	0.56	
Leucanthemum vulgare	0.52	1.00	0.48	3	0.54	
Plantago lanceolata	0.55	0.00	0.55	3	0.54	
Veronica arvensis	0.48	0.67	0.19	1	0.50	
Campanula rapunculus	0.00	1.00	1.00	4	0.50	
Melampyrum arvense	1.00	0.00	1.00	4	0.50	
Daucus carota	-	0.50	-	-	0.50	
Lotus corniculatus	0.44	0.50	0.06	1	0.44	
Sanguisorba minor	0.38	0.50	0.13	1	0.42	
Plantago media	0.45	0.00	0.45	3	0.42	
Dactylis glomerata	0.43	0.00	0.43	3	0.40	
Convolvulus arvensis	0.35	0.00	0.35	2	0.33	transient
Anthemis tinctoria	1.00	0.00	1.00	4	0.33	
Avenula pubescens	-	0.33	-	-	0.33	
Achillea millefolium	0.23	0.67	0.44	3	0.26	
Viola hirta	0.33	0.00	0.33	2	0.25	
Dianthus carthusianorum	0.00	0.50	0.50	3	0.25	
Trifolium campestre	0.25	0.00	0.25	2	0.20	
Centaurea jacea	0.21	0.00	0.21	2	0.19	
Arrhenatherum elatius	0.21	0.00	0.21	2	0.19	
Brachypodium pinnatum	0.20	0.00	0.20	2	0.18	
Ononis repens	0.00	0.50	0.50	3	0.17	
Galium verum	0.17	0.00	0.17	1	0.16	
Knautia arvensis	0.08	0.00	0.08	1	0.08	
Bupleurum falcatum	0.00	0.00	0.00	1	0.00	
Geranium sanguineum	0.00	0.00	0.00	1	0.00	
Salvia pratensis	0.00	0.00	0.00	1	0.00	
Bromus erectus	-	0.00	-	-	0.00	
Coronilla varia	-	0.00	-	-	0.00	
Elymus repens	-	0.00	-	-	0.00	
Festuca rupicola	-	0.00	-	-	0.00	
Galium album	-	0.00	-	-	0.00	
Trisetum flavescens	-	0.00	-	-	0.00	

Table B2.4 Number of species which had re-occurred by eight weeks after rototilling on the four investigation sites (Lichtlein, Molkengrund, Rappberg, Regelberg). For survival analysis, species were either considered if highly abundant (present > 4 plots) or all species were considered (> 1 plots).

site	species present in	before rototilling	after rototilling	survival [%]
Lichtlein	> 1 plots	49	39	79.6
	> 4 plots	30	27	90.0
Molkengrund	> 1 plots	50	33	66.0
	> 4 plots	20	19	95.0
Rappberg	> 1 plots	42	32	76.2
	> 4 plots	21	21	100.0
Regelberg	> 1 plots	52	50	96.2
	> 4 plots	27	25	92.6

Species re-occurrence may be a result of vegetative and/or generative regeneration. To estimate the relative importance of both strategies in regeneration after rototilling for typical semi-natural grassland species, new plant individuals were classified within eight weeks after disturbance as either having resulted from vegetative resprouting or having originated from seeds. Seedlings of 29 plant species (Table B2.5) were observed. For some species, mainly grasses such as *Brachypodium pinnatum*, the differentiation between individuals resulting from vegetative regrowth or individuals generated by generative regeneration was difficult. For 52 out of 63 plant species vegetative regrowth was observed; for 65 % of the species vegetative regrowth was the only regeneration strategy after disturbance. For 19 species both seedlings and vegetative regrowth were observed. For 15 out of the 19 species (79%) vegetative regrowth was the dominant strategy for re-occurrence.

Table B2.5 Regeneration strategies and seed bank longevity (SLI) of 63 semi-natural grassland plant species after rototilling. Data on SLI includes Thompson et al. (1997) and my investigations (see Table B2.2). Data on the regeneration strategy was recorded in the year 2001 within 8 weeks after rototilling. Abbreviations used: ? uncertainty; ! dominant strategy.

	SLI°	regeneration strategy			SLI°	regeneration strategy	
species		generative seedlings	vegetative regrowth	species		generative seedlings	vegetative regrowth
Achillea millefolium	0.26		X	*Lotus corniculatus*	0.44	X!	X
Agrimonia eupatoria	0.13		X	*Medicago falcata*	0.00	X!	X
Allium oleraceum	0.00		X	*Medicago lupulina*	0.70	X	
Anthemis tinctoria	0.33	X		*Medicago minima*	0.00	X	
Arenaria serphyllifolia	0.72	X		*Melamphyrum arvensis*	0.50	X	
Arrhenatherum elatius	0.19	X	X!	*Melilotus officinalis*	-	X	
Brachypodium pinnatum	0.18	?	X!	*Ononis repens*	0.17	X	X!
Bromus erectus	0.00	X	X!	*Origanum vulgare*	0.75		X
Bupleurum falcatum	0.00	X	X!	*Peucedanum cervaria*	-		X
Centaurea jacea	0.19		X	*Plantago lanceolata*	0.54		X
Centaurea scabiosa	0.25		X	*Plantago media*	0.42		X
Cerastium arvense	0.60		X	*Poa angustifolia*	0.80	X	X!
Convolvulus arvensis	0.33		X	*Potentilla argentea*	0.67	X	
Cornus sanguinea	0.20		X	*Potentilla neumanniana*	0.56	X	X!
Coronilla varia	0.00		X	*Potentilla reptans*	0.50		X
Dactylis glomerata	0.40	X	X!	*Prunus spinosa*	0.00		X
Daucus carota	0.50	X		*Ranunculus bulbosus*	0.50		X
Dianthus carthusianorun	0.25		X	*Rosa canina agg.*	0.00		X
Elymus repens	0.00	X	X!	*Salvia pratensis*	0.00	X	X!
Euphorbia cyparissias	0.67		X	*Sanguisorba minor*	0.42	X!	X
Falcaria vulgaris	0.00	X	X!	*Senecio jacobaea*	0.58	X	
Festuca rupicola	0.00	X	X!	*Silene nutans*	0.67		X
Fragaria viridis	0.75	X	X!	*Sorbus torminalis*	-		X
Galium album	0.19	X!	X	*Tanacetum corymbosum*	-		X
Galium verum	0.16		X	*Thesium barvarum*	-		X
Genista tinctoria	0.00		X	*Thlaspi perfoliatum*	0.75	X	
Geranium sanguineum	0.00		X	*Thymus pulegioides*	0.67		X
Hieracium pilosella	-		X	*Trisetum flavescens*	0.00	X	X!
Inula conyzae	1.00		X	*Veronica arvensis*	0.50	X	
Knautia arvensis	0.08		X	*Vicia cassubica*	-		X
Leucanthemum vulgare	0.54		X	*Viola hirta*	0.25	X	X!
Ligustrum vulgare	0.00		X				

Discussion and conclusions

Seed bank densities and dynamics, similarity in species composition in vegetation and soil seed bank, seed longevity, the ability of vegetative regrowth, and time needed for re-occurrence were analysed as indicators of the regeneration potential of characteristic semi-natural grassland species after disturbance by rototilling. In effect, all species could regenerate following rototilling.

In the study area, the seed density in mown grassland communities was fairly low, ranging between 2023 seeds/m² to 7822 seeds/m² (average 3923 seeds/m²). This is remarkably lower than densities recorded in other grassland communities, such as dry alvar grasslands in Sweden (5600 - 13000 seeds/m², Bakker et al. 1997), chalk grasslands in England (6770 seeds/m², Graham & Hutchings 1988), calcareous pasture and meadows (4000 - 8400 seeds/m², Poschlod 1991) and much lower than in dry acidic grasslands (7620 - 21120 seeds/m², Jentsch 2004) in Germany. The investigation slopes are considered to be Mesobromion communities with different degrees of shrub encroachment, or to be dry sub-communities of the Arrhenatheretum elatioris (Chapter 2). However, for comparable grassland communities Kunzmann

(2000) found densities (1838 - 15837 seeds/m²) which are for the most part higher than the seed densities estimated in this study. There are several reasons for the accumulation of seeds in a permanent soil seed bank. Accumulation depends on the intensity of seed rain, the longevity of seeds, the state of dormancy at the time seeds are shed (Vleeshouwers et al. 1995), and finally on the strength of triggers for germination (Baskin & Baskin 1989). The latter are greatly influenced by both the porosity of the soil and the stability of the habitat. In the case of compact soil conditions, few seeds enter deeper soil layers, where they often fail to germinate (Rees 1996). In this study, soil had a high clay content, which is responsible for swelling and shrinkage processes. During dry periods, cracks are created and the downward movement of seeds may be promoted. However, in Central Europe, a downward movement of seeds is of less importance than in regions where cracks are deeper and more abundant due to climatic and edaphic conditions (Wilding & Puentes 1988, Driessen & Dudal 1991). The low seed densities found on mown plots in this study are more likely the result of short persistence of most species' seeds in the soil (see below) than the other factors mentioned above.

The comparison of seed density between the different management regimes (mowing versus rototilling) demonstrated no significant differences. There was a tendency that seed bank density decreased immediately after rototilling, but then increased in the second year after disturbance. This trajectory may be explained by the fact that rototilling stimulates germination out of the soil seed bank, thus, seed density decreased at first. A higher species number and a higher seed set of single species (e.g. annuals such as *Thlaspi perfoliatum*, Chapter 3) may be responsible for the increase in seed density in the second year after disturbance.

A small number of species, such as *Fragaria viridis*, *Dianthus carthusianorum* and *Inula conyza*, constituted the vast majority of the seed bank. The same was found for dry acidic grasslands (Jentsch 2004). Among these species are many annuals such as *Thlaspi perfoliatum*, *Veronica arvensis* and *Arenaria serphyllifolia*. It is known that, especially for annual plants, the below-ground population is numerically far greater than the above-ground population, and there is evidence that the seed population in the soil may be extremely high for some species (Sarukhan 1974). Most species, however, produce very small numbers of seeds despite being abundant in the above-ground vegetation (e.g. the grass *Arrhenatherum elatius*, see Box 3). Evidence from other studies shows that in grasslands, the grasses themselves form a rather small proportion of the total seed bank of the soil (Sarukhan 1974).

Data on the seed bank abundances and dynamics reveals that a change in management strategy did not result in either significant differences in abundance or consistent abundance patterns during succession after rototilling. Six performance groups were identified, but large standard deviations indicated that some species exhibited irregular abundance patterns at the different sites. Nevertheless, the comparison of above-ground population dynamics (see Box 3) and seed bank dynamics revealed analogies. Increasing abundancy in the established vegetation (e.g. *Arenaria serphyllifolia*, *Thlaspi perfoliatum* and *Elymus repens*) caused a delayed rise in abundance of seeds in the soil. The opposite is observed with decreasing numbers of seeds in the soil due to declining numbers of adult individuals above-ground e.g. for *Euphorbia cyparissias*.

The similarity between seed bank and established vegetation was found to be low (27.1 % to 45.2 %) although the vast majority of seeds of most grassland species settle within a short distance from the mother plant (Milberg & Hansson 1993, see also Chapter 3 & 4). This dissimilarity between seed bank and established vegetation was due to a surplus of certain species such as *Fumaria officinalis* and *Galium aparine* in the seed bank (different for each site) and due to others such as *Festuca rupicola* and *Trisetum flavescens* that were lacking in the seed bank, but abundant in the vegetation. High dissimilarity between seed bank and established vegetation has similarly been found by Looney & Gibson (1995), Bakker et al. (1996), Peco et al. (1998), Bekker et al. (2000), Jentsch (2004), Jutila & Grace (2002) and Smith et al. (2002). High similarity has been found for dune slacks in the Netherlands (60 -70 %, Bekker et al. 1999), for an ancient undisturbed chalk grassland (77 %, Willems 1995) as well as for annual-dominated Mediterranean pastures (80 %, Levassor et al. 1990). There is evidence that similarity between vegetation and seed bank decreases with time after abandonment (Kalamees & Zobel 1998, Thompson 2000, Wagner et al. 2003). In this short-term study, however, no general trend concerning similarity was revealed in the first two successive years after rototilling.

Vertical distribution of seeds as an indicator for longevity – the deeper in the soil the older the seeds, since downward movement of seeds takes time, depending strongly on soil conditions and animals activity in the soil – does not work when below-ground disturbances such as rototilling, which lead to disorder of the layering are applied. Therefore, in order to estimate seed persistence and longevity of species, only the mown plots were sampled. According to the seed bank classification of Thompson et al. (1997), modified by Jackel (1999) most of the semi-natural grassland species observed in this study have a transient or short-term persistent seed bank. Only 12 species could be classified as having a long-term persistent seed bank. This finding is in accordance with observations for other grasslands such as semi-natural meadows in a floodplain (Wagner et al. 2003), for dry acidic (Jentsch 2004) and for calcareous grasslands (Poschlod 1991, Kalamees & Zobel 1998) and for limestone grasslands (Bakker et al. 1997). Since only few species have a long-term persistent seed bank, population persistence after disappearance from the above-ground vegetation (e.g. due to disturbance) is unlikely. This is especially true for low disturbance frequencies if the degradation of the seed bank for most semi-natural grassland species happens faster than the disturbance event re-occurs. It is known that plant populations are able to buffer environmentally unfavourable phases with the aid of seed banks (Pake & Venable 1996). This thesis shows that extinction probability increases if species are not able to regenerate from a persistent seed bank to an extent that exceeds the loss of established individuals by disturbance (Chapter 5) and that seed bank longevity prolongs population survival (Chapter 3). Bossuyt & Hermy (2003) evaluated the potential role of persistent seed banks in restoring grassland and heathland communities in sites that have been afforested or are currently cultivated. They found a low seed longevity index for many grassland species and low densities in the soil, leading them to conclude that restoration of species-rich grasslands cannot rely on the seed bank. Edwards & Crawley (1999) found that the seed bank played a minor role in recruitment into experimentally created gaps in acid grasslands. Jentsch (2004) concluded from her results for acidic grasslands soil seed banks that the regeneration potential of soil seed banks of early successive grassland communities on sandy soils is very limited. Such a conclusion can also been drawn from the present study for semi-natural grassland communities.

There is evidence that soil conditions such as moisture and temperature influence seed persistence (Grime 1981, Cavers & Benoit 1989). Thus, seed persistence of a species varies enormously between habitats. In this study, seed longevity was calculated with the aid of a classification based on depth distribution in the soil (Thompson et al. 1997) extended by Jackel (1999). As the depth distribution for many species was found to be very different on different grassland sites (Poschlod 1993, Bekker et al. 1998), the results were compared to published data (Table B2.2). The comparison reveals that seed persistence did not differ for most species. More than half showed good, or even very good analogy. Nevertheless, the analysis of seed persistence in the region and habitats of study remains important since some species differ in the seed longevity classification.

Regeneration strategies after disturbance by rototilling highlight that re-occurrence by vegetative regeneration is more frequent than re-occurrence by seedlings. The proportion of vegetative to generative reproduction was 64 % to 36 %. 30 % of the species showed the ability to regenerate via multiple regeneration strategies, and for 79 % of these, vegetative regrowth was the main strategy for re-occurrence after disturbance. Similar findings have been observed by e.g. Crawley (1990), Eriksson (1989), Rogers & Hartnett (2001) and Amiaud & Touzard (2004). Their results have shown that regrowth strategies were the dominant recolonisation mechanisms after disturbance concluding that regeneration from vegetative fragments plays a crucial rule in vegetation development of grasslands after disturbance. There is evidence that vegetative propagation and regeneration throughout a long life-span may be a successful survival strategy in relatively stable grasslands (Bekker et al. 2000).

The regeneration process of the typical semi-natural grassland species after disturbance through rototilling was surprisingly fast. The direct impact of rototilling on plant individuals was less than expected, as vegetative regrowth was the main regeneration strategy (see above). Survival probability was a matter of the scale of observation. Considering all species, between 66 % and 96 % of the species were able to re-occur within eight weeks. Concentrating on the abundant species alone, all were found to re-occur within such a short time after disturbance.

In conclusion, re-occurrence of semi-natural grassland species after disturbance happens very fast, rather due to vegetative regrowth than to generative regeneration. The low seed bank density of the whole plant community, the low densities of most character species of semi-natural grasslands, the dissimilarity between seed bank and above-ground vegetation as well as the missing persistent seed banks for most species indicate that the potential for regeneration from soil seed banks is very limited. Although rototilling is a severe treatment with consequences for plant individuals, causing death to almost all established individuals, most species are able to exceed the loss of biomass by vegetative regrowth. This study reveals that semi-natural grassland communities are able to withstand disturbance by rototilling. The investigations into the regeneration potential of a semi-natural grassland community for the first two successive years indicate that succession after rototilling may lead species composition similar to that observed before disturbance, depending on disturbance frequencies (Chapter 5) and above-ground vegetation dynamics (Box 3). The study highlights the importance of analysing seed bank composition and seed persistence on the local scale for the conservation of plant communities.

Box 3

Plant community response after a change in management strategy

Box 3

Plant community response after a change in management strategy

Background and aims

Disturbances can bring about both stability and non-equilibrium conditions (White & Jentsch 2001). Periodically introduced disorder may lead to a new patch trajectory, or back to a stable pre-disturbance community (Jentsch 2004). The direction of this development depends not only on abiotic and biotic factors and the previous development of the site (site history), but in fact mainly on the recolonisation and regeneration potential of the given community (Fig. B3.1).

Two disturbance systems (annual mowing versus rototilling once) were studied within this project on semi-natural grassland communities. Although mowing temporarily increases resources (first of all light) by removal of above-ground biomass, the treatment itself has little effect on meadow community composition. Plant species abundances fluctuate from year to year, within limited boundaries defined by weather conditions, but in the long-term, populations are (more or less) at equilibrium, due to functional adaptations to this kind of disturbance (Klapp 1971, DeAngelis & Waterhouse 1987, Leps 1990, Briemle et al. 1991, White & Jentsch 2001). Vertical vegetation cover is mostly maintained. On the other hand, rototilling may cause disruption to the established equilibrium on the patch scale. It is unknown whether all grassland species survive this kind of impact, or whether there will be shift to a more ruderal community. Thus, information regarding early successional effects on vegetation structure, species diversity and species abundances are required to understand future development of such disturbed sites. This understanding is especially important when it comes to the assessment of management practices which aim to maintain special plant communities of grasslands.

Currently, the most popular way to describe changes in vegetation composition and structure in species-rich grasslands is the periodical monitoring of vegetation on the community level within permanent plots, using vegetation releves or frequency analysis (Bühler & Schmid 2001). Repeated observations of permanent plots provide insights into the dynamics of population processes, and are probably the most reliable tool with which to demonstrate the course of succession (Leps et al. 2000). Investigation into successional processes after disturbance have a long tradition e.g. Clements (1916), Tilman (1988) and Osbornova et al. (1990). Recent examples of studies on successional processes after ground disturbance include Austrheim & Olsson (1999), Wilby & Brown (2000), Leps et al. (2000) and Jentsch (2004). Jentsch (2004) e.g. analysed the vegetation response of small-scale experimental soil disturbances within various successional stages on island sand dunes.

This box is concerned with early succession processes after soil disturbance by rototilling. Key questions are: (1) How does the vertical and horizontal vegetation structure change after rototilling? (2) How does species composition change following treatment and during succession? (3) Are there changes in plant dominance after a change in management strategy (4) Will succession lead back to the pre-disturbance plant community composition?

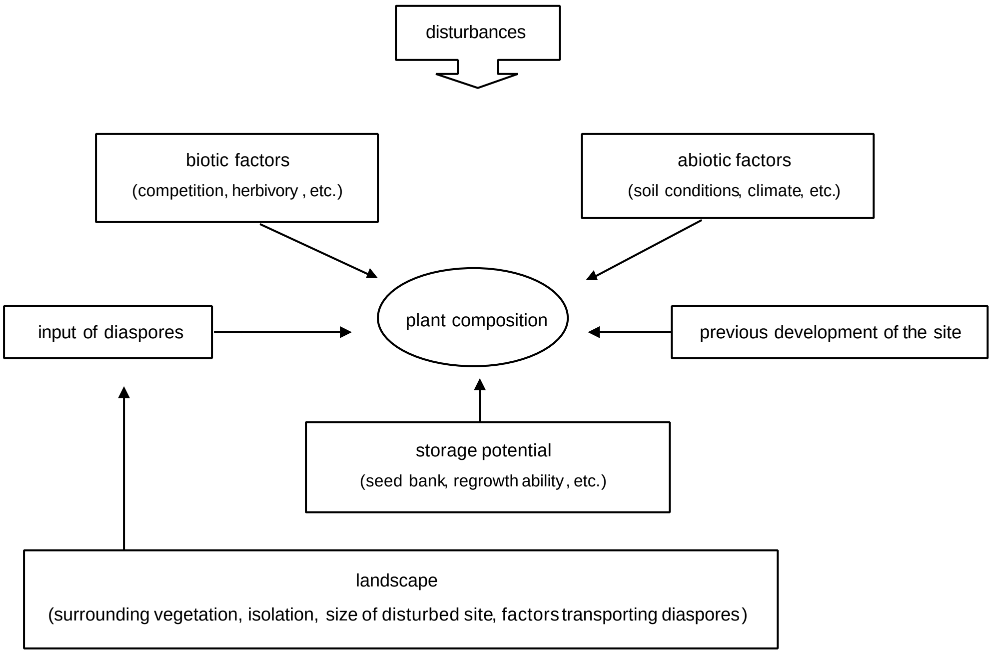


Fig. B3.1 Main factors controlling succession (modified after Prach 1990b).

Methods

Floristic composition was obtained from eight 1 x 1 m permanent subplots on rototilled plots using frequency analysis. (For further information on the experimental design see Introduction). Each subplot was divided into 100 10 x10 cm cells. Presence or absence of each plant species was recorded to obtain a measure of frequency, which was calculated using the sum of cells of a subplot in which the species occurred. Since the rototilled plots lay beside each other in a successional gradient, data on frequency for the first two successional years were taken from the year 2002 only.

To analyse changes in horizontal vegetation structure during yearly successional stages after rototilling, data on the percentage cover of the vegetation, bare soil, herbs, and bryophytes on 10 permanent plots of 2 x 2 m was recorded prior to the experiment, 8 weeks after treatment, and continued once a year in the following two years. The vertical vegetation density was calculated using the weighted average vegetation height (GMV; Barkman 1988, Sundermeier 1999). This was done by recording the height and densities of the herb layers at various levels:

$$GMV = \frac{\sum_{i=1}^{k} d_i h_i}{\sum_{i=1}^{k} d_i} \tag{B3.1}$$

with d_i = vegetation density in layer i; h_i = average height of layer i; k = number of layers.

Data on vegetation cover was estimated visually within each subplot. For data analysis average values were calculated. Data were tested for normality (Kolmogorov-Smirnov-test). If such conditions were not met, statistical comparisons among treatments were based on non-parametric tests (H-test, U-test). To analyse and compare plant species composition on mown and rototilled plots during early successional stages, principal components analysis (PCA) was carried out for each site, using the program Pc-ord 4. PCA was used because the short gradient of the scales allow the use of ordination techniques that relate to a linear response model in which the abundance of species either increases or decreases with the value of the latent environmental variables (Jongman et al. 1995).

Results

Effects of rototilling on vegetation structure

Contrary to mown plots, on which vegetation cover was constant over time, rototilled plots showed remarkable changes in vegetation structure (Fig. B3.2). Vegetation cover of recently rototilled plots decreased on average by more than 50 %, but plots of all four sites quickly recovered (point 4, Fig. B3.2b). In the second year of succession, plots were close to reaching pre-disturbance vegetation cover. Since all sites showed equal progression, data were pooled for further analysis.

The effects of rototilling on both vertical and horizontal structure were evaluated. Bare soil and the weighted average vegetation height (GMV), calculated to act as an indicator for vertical vegetation density, showed differential progression during succession (Fig. B3.3). Bare soil area increased (see Fig. B3.2b) in the first year after rototilling, but quickly gaps vanished in early successional years. This decrease in bare soil area was for the most part not due to an increase in moss cover but rather to an increase in herbs cover (Fig. B3.4), as mosses recovered more slowly than the herbs after rototilling. On the other hand, GMV at first decreased strongly as a direct consequence of vegetation destruction, but increased in the second year to a level that even exceeded the initial conditions (Fig. B3.3b).

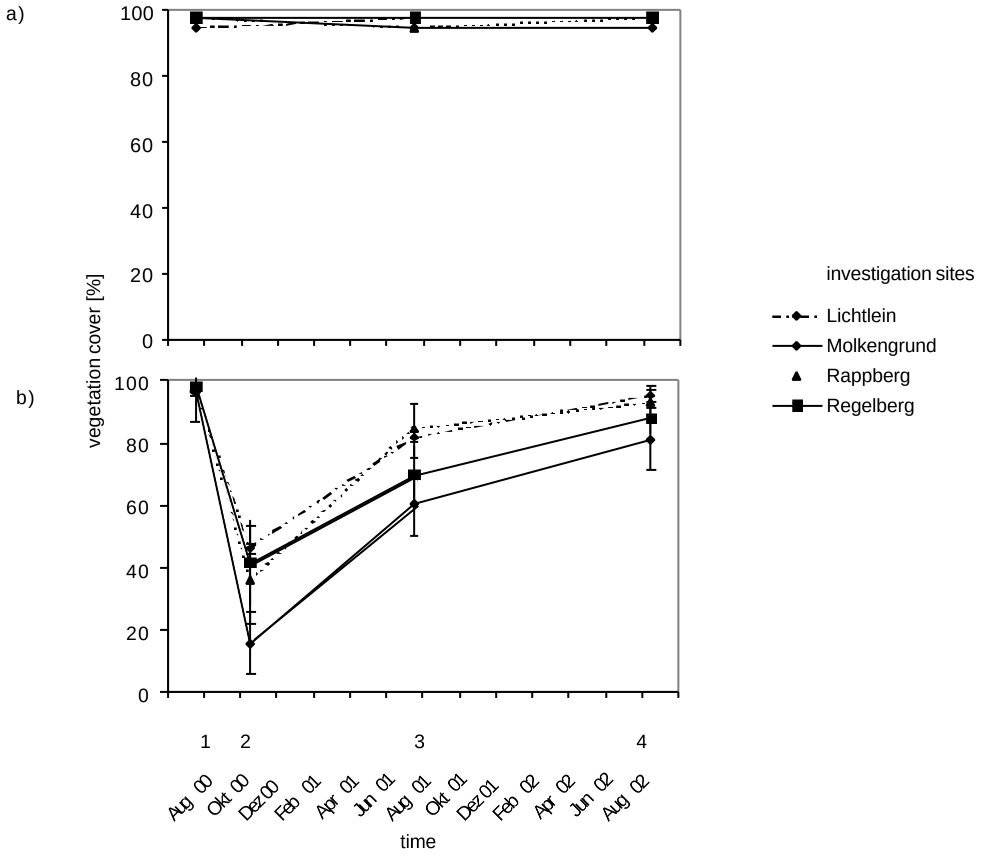


Fig. B3.2 Development of the vegetation cover [%] over time on (a) mown and on (b) rototilled plots on the four investigation sites Lichtlein, Molkengrund, Rappberg and Regelberg. Mean values and standard deviation are given. N = 10 plots per investigation point. Investigations began in the year 2000 prior to the experiment and 8 weeks after in case of rototilled plots, and were carried on once a year in the two years following. In case of rototilling, rototilling stages: 1 = initial stage (prior rototilling), 2 = recently rototilled plots, 3 = first year of succession, 4 = second year of succession.

The vertical vegetation density decreased with disturbance by rototilling, but biomass accumulated over time (Fig. B3.3b). In the second successional year, the weighted average vegetation height was higher than that of the initial stage. Furthermore, rototilling caused a change in the proportion of vegetation densities in different vegetation heights. There was a tendency towards an increase in mainly the upper vegetation layers (Fig. B3.5). In the first successional year, density was comparable to the initial stage, but in the second year after rototilling, density of the highest layer was already about 5 times higher than in the initial stage (point 4, Fig. B3.5).

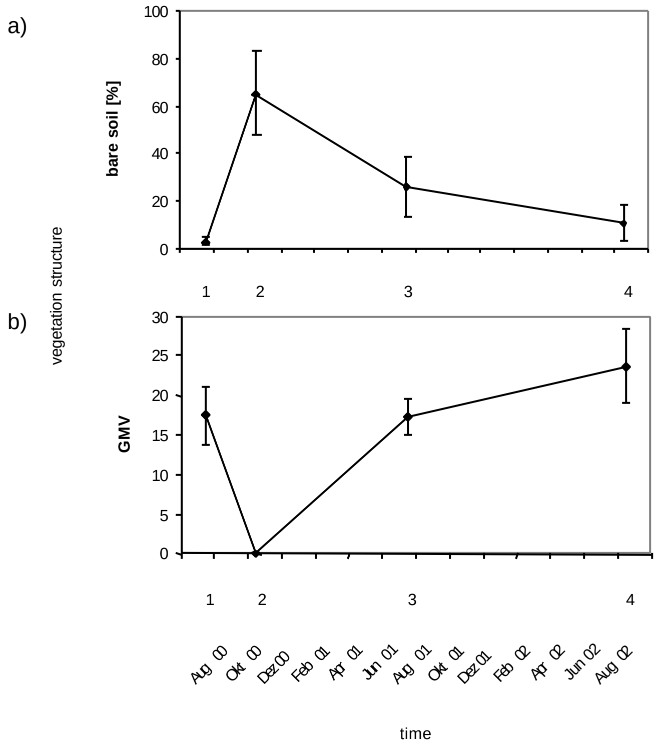


Fig. B3.3 Changes in vegetation structure (a) bare soil and b) average weighted height (GMV)) during succession on rototilled plots. Data of the four sites were pooled. Given are mean values ± standard deviation, n = 40 plots. Rototilling stages: 1 = initial stage (prior rototilling), 2 = recently rototilled plots, 3 = first year of succession, 4 = second year of succession.

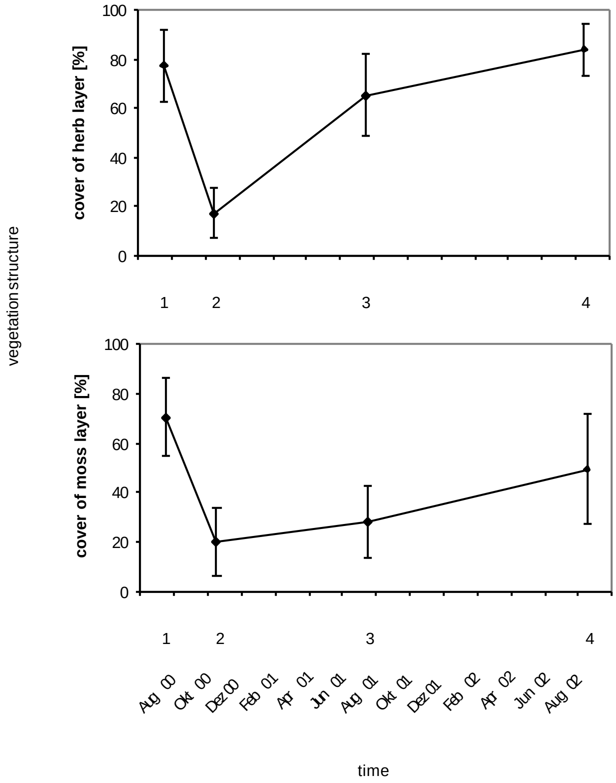


Fig. B3.4 Changes in vegetation structure (cover of moss and herb layer) during succession on rototilled plots. Data of the four sites were pooled. Given are mean values ± standard deviation, n = 40 plots. Rototilling stages: 1 = initial stage (prior rototilling), 2 = recently rototilled plots, 3 = first year of succession, 4 = second year of succession.

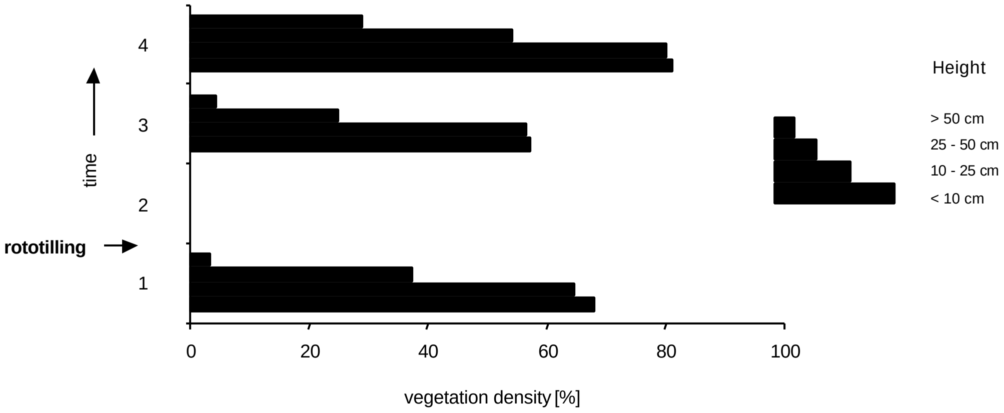


Fig. B3.5 Change of vegetation structure during succession presented as the change of proportion of vegetation densities in different vegetation heights. Rototilling stages: 1 = initial stage (prior rototilling), 2 = recently rototilled plots, zero height, all vegetation destroyed, 3 = first year of succession, 4 = second year of succession. Data were pooled for all sites.

Effects of rototilling on species turnover

The impact upon species composition was surprisingly low. In the first year after disturbance, 15 additional species appeared (Table B3.1). All species can be characterised as either typical pioneer species (e.g. *Echium vulgare*) or agricultural weeds (e.g. *Bromus sterilis*, *Fumaria officinalis*, *Papaver dubium*, *Viola arvensis*). Two out of 8 species introduced in the second year after disturbance were typical dry grassland species (*Cirsium acaule, Linum catharticum*). No species were found to have been lost as a direct consequence of the treatment, and only *Valerianella locusta* was found to be lost in the second successional year (Table B3.1).

Table B3.1 Species turnover as a consequence of rototilling within the first two successional years. To be considered in the analysis species have to be present in at least one plot. Sites were pooled.

time since rototilling	species gained after rototilling	species lost after rototilling
first year	*Anthyllis vulneraria, Bromus sterilis, Daucus carota, Echium vulgare, Epilobium spec., Fallopia spec., Fumaria officinalis, Galium aparine, Lactuca serriola, Melilotus spec., Papaver dubium, Potentilla reptans, Senecio jacobaea, Trifolium campestre, Viola arvensis*	
second year	*Carduus acanthoides, Cirsium acaule, Clinopodium vulgare, Festuca pratensis, Linum catharticum, Melilotus officinalis, Sonchus oleraceus, Vicia spec.*	*Valerianella locusta*

Recovery performance of particular species

The frequencies of 102 characteristic dry grassland species were taken in order to investigate changes in abundances brought about by rototilling (Table A6, Appendix). For 18 % of these species, significant differences in frequency were found between treatments (H-test, $p < 0.05$). Figure B3.6 shows the course of changes in frequency for 12 of these species. As a consequence of a change in management strategy, the frequency of some species such as *Achillea millefolium*, *Poa angustifolia* and *Ranunculus bulbosus* initially fell, wheras for others such as *Erophila verna* and *Medicago minima,* frequencies rose at first. In fact, by two years post-rototilling, eight species no longer shoed any differences in frequency between treatments. For the remaining 10 species, three different trajectories of frequency change were identified (Table B3.2): (1) Frequency in the second year after rototilling was low relative to that found in mown plots (*Festuca rupicola, Thymus pulegioides*). Rototilling would potentially lead to local extinction within the following successional years; (2) Frequency is high relative to that found in mown plots (*Elymus repens, Viola hirta*).

Species supported by a change in management strategy and frequency may possibly increase during following successional years; (3) Although significant differences remained between rototilled and mown plots, the course of frequency change indicated that initial conditions will be re-obtained within the following successional years (*Arenaria serphyllifolia, Thlaspi perfoliatum*).

Table B3.2 The course of frequency change in both mown and rototilled plots for all species with significant differences between treatments in the second year of succession. Frequency of species on rototilled plots either increased, decreased or reached the initial level within the following successional stages.

tendency of frequency	increase	decrease	initial size
number of species	3	3	4
species	*Elymus repens* *Hypericum perforatum Viola hirta*	*Avenula pubescence* *Festuca rupicola* *Thymus pulegioides*	*Arenaria serphyllifolia* *Euphorbia cyparissias* *Lotus corniculatus* *Thlaspi perfoliatum*

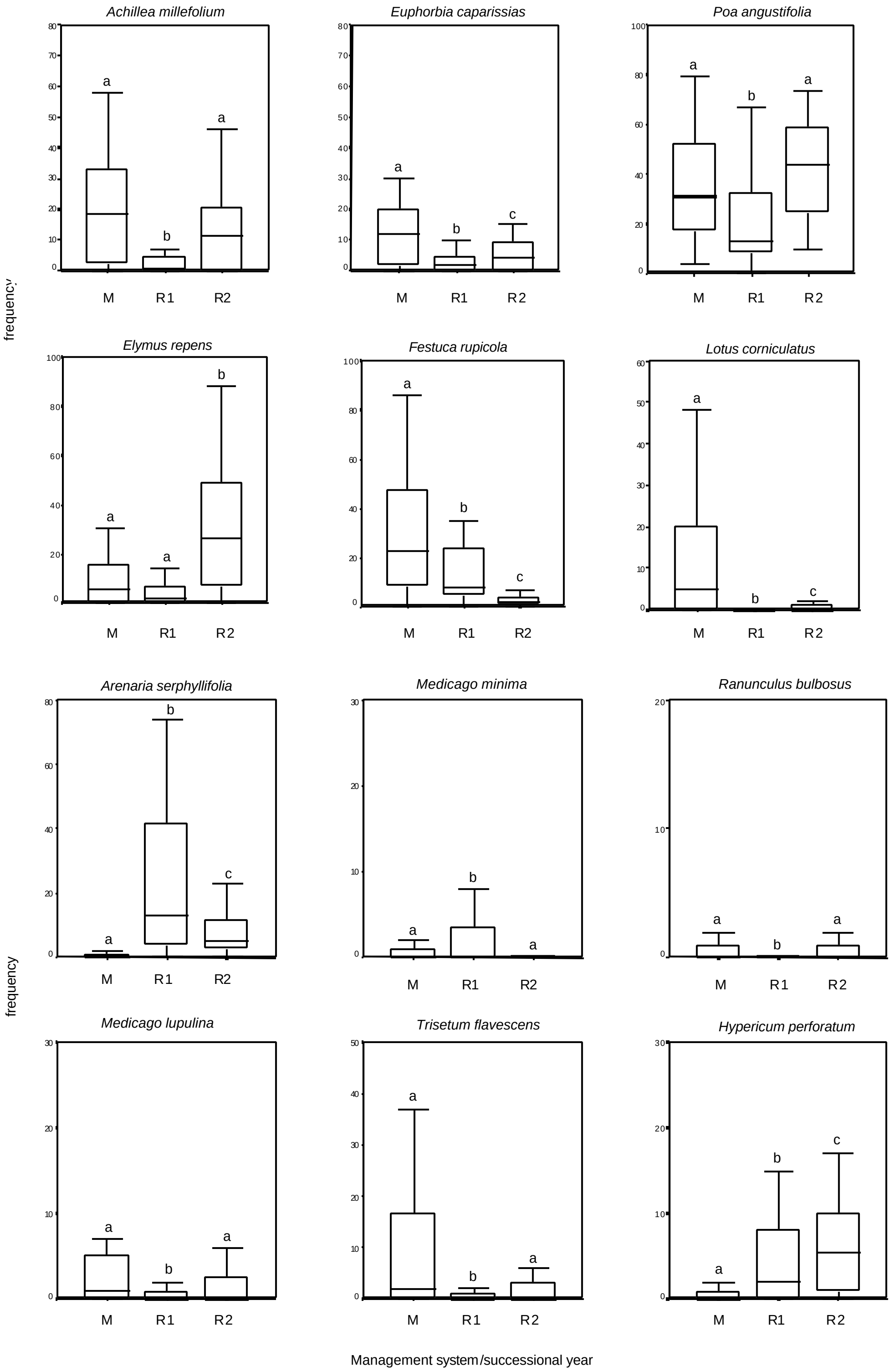


Fig. B3.6 Comparison of the frequency of 12 dry grassland species on mown (M) and rototilled plots during the first (R1) and second (R2) successional year. The same species used for seed bank analysis (see box 2) were selected and will appear in the same sequence. Given are mean values ± standard deviation, n = 32 plots. Data were pooled for all sites. Differences between treatment were tested using non-parametric tests (H-test for overall comparisons and U-tests for pairwise comparison). Significant differences between mown and rototilled plots are indicated by different letters. Please note that the scales differ for each species.

Effects of a change in management strategy on the plant community composition

To address the question of whether succession will lead back to the pre-disturbance plant species composition on rototilled plots, PCAs were generated for each site (Fig. B3.7 - B3.10). The eigenvalues, the percentage explanations of variance, and the cumulative percentage of variance of the first 2 axes for all analyses are shown in Table B3.3 - B3.6.

One each site, plots of the different treatments and successional stages (M/R1/R2) separated very well, whereas the development of species composition was not equal for all sites (Fig. B3.7 - B3.10). The species composition of rototilled plots shifted back to that on mown plots (M) by the second successional year on the site Lichtlein (Fig. B3.7). 22.68 % of the variation in the data could be explained by the first axis (Table B3.3). Annual species such as *Thlaspi perfoliatum*, *Medicago minima* and *Papaver dubium* were supported in the first year after rototilling, and went on to increase in frequency in the second successive year. Differences between mown and rototilled plots were mainly characterised by an increase in *Bromus sterilis* and/or a decrease in *Veronica arvensis* in the second year, respectively (Fig. B3.7).

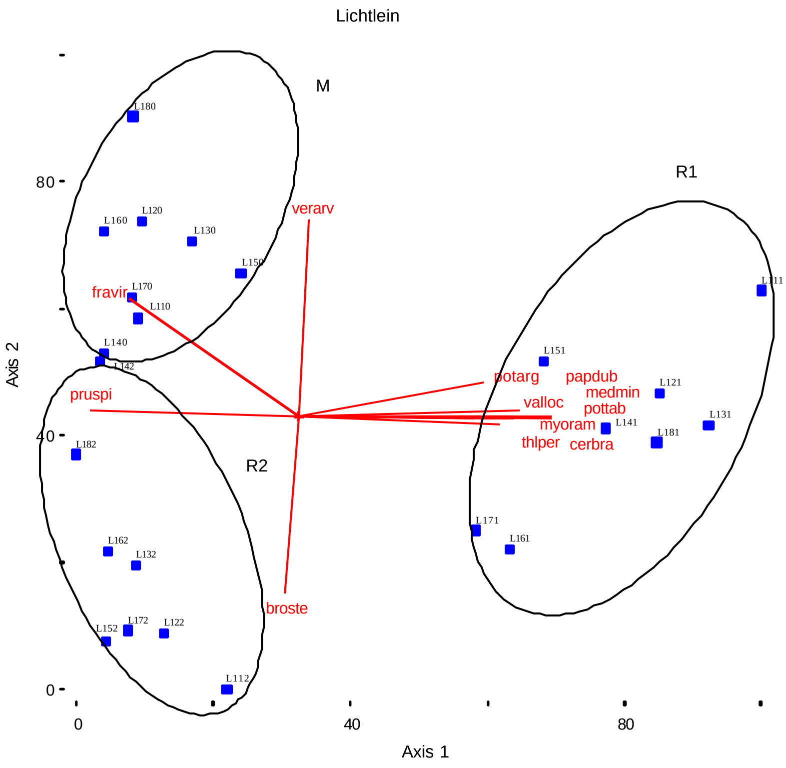


Fig. B3.7 Ordination biplot of axis 1 and 2 of the PCA for the site Lichtlein showing the relative position of the treatment plots concerning species composition and species frequencies. N = 8 plots. Abbreviations used: M = mown plots, R1 = rototilled plots, first year of succession, R2 = rototilled plots, second year of succession. broste = *Bromus sterilis*; cerbra = *Cerastium brachypetalum*; fravir = *Fragaria viridis*; medmin = *Medicago minima*; myoram = *Myosostis ramosissima*; papdub = *Papaver dubium*; potarg = *Potentilla argentea*; pottab = *Potentilla tabernaemontana*; pruspi = *Prunus spinosa*; thlper = *Thlaspi perfoliatum*; valloc = *Valerianella locusta*.

Table B3.3 Eigenvalues, the percentage explanation of variance, and the cumulative percentage of variance of the first 2 axes of the PCA for the site Lichtlein (Fig. B3.7)

axes	eigenvalue	% of variance	cumul. percent. var.
1.	14.288	22.679	22.679
2.	5.976	9.485	32.164

On the Molkengrund site, differences in species composition between mown and rototilled plots could be explained mainly by changes in the frequency of five particular species: firstly, an increase in the frequencies of *Hypericum perforatum* and *Geranium sanguineum* and secondly, a decrease in the frequencies of three frequent semi-natural grassland species *Festuca rupicola*, *Lotus corniculatus* and *Euphorbia cyparissias* (Fig. B3.8). 16.48 % of the variation in data could be explained by the first axis (Table B3.4). Differences between rototilled plots in different successional years comprised an increase of *Arenaria serphyllifolia* in the first year only, whilst the second year was characterised by an increase of dominance of *Anthemis tinctoria* (Fig. B3.8).

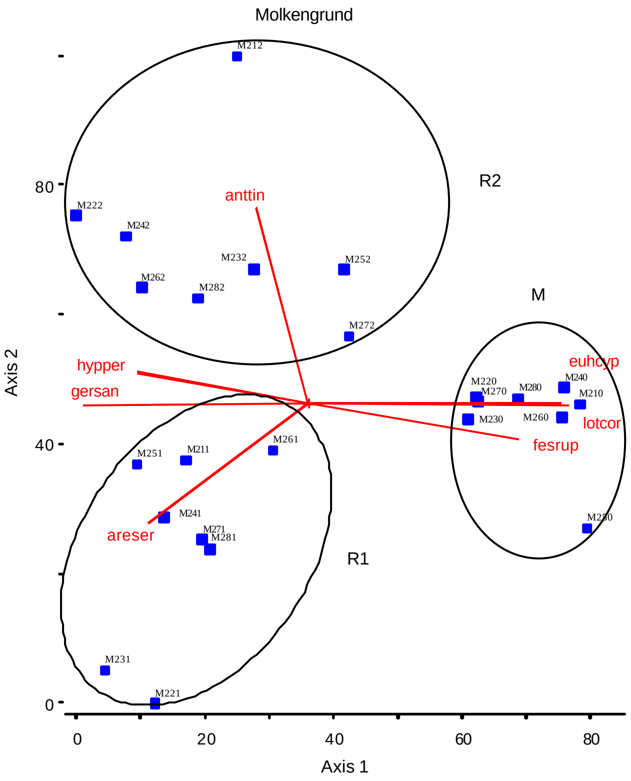


Fig. B3.8 Ordination biplot of axis 1 and 2 of the PCA for the site Molkengrund showing the relative position of the treatment plots concerning species composition and species frequencies. N = 8 plots. Abbreviations used: M = mown plots, R1 = rototilled plots, first year of succession, R2 = rototilled plots, second year of succession. anttin = *Anthemis tinctoria*; areser = *Arenaria serphyllifolia*; euhcyp = *Euphorbia cyparissias*; fesrup = *Festuca rupicola*; gersan = *Geranium sanguineum*; hypper = *Hypericum perforatum*; lotcor = *Lotus corniculatus*.

Table B3.4 Eigenvalues, the percentage explanation of variance, and the cumulative percentage of variance of the first 2 axes of the PCA for the site Molkengrund (Fig. B3.8)

axes	eigenvalue	% of variance	cumul. percent. var.
1.	8.733	16.478	16.478
2.	6.142	11.589	28.067

The pattern of plant community composition change at the Rappberg site differed from that of the other three sites. Dissimilarity increased during succession, mainly due to the increasing dominance of three species *Elymus repens*, *Sanguisorba minor*, and *Viola hirta* (Fig. B3.9). The analysis showed 15 % and 12 % of the variance in plant composition to be found on the first and second axes, respectively (Table B3.5).

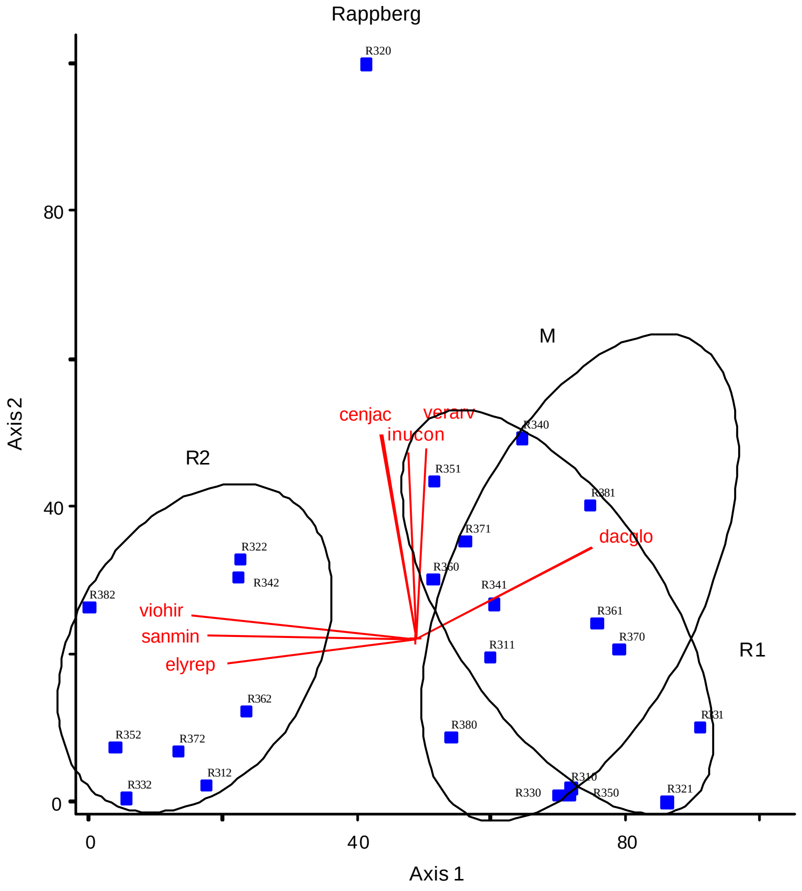


Fig. B3.9 Ordination biplot of axis 1 and 2 of the PCA for the site Rappberg showing the relative position of the treatment plots concerning species composition and species frequencies. N = 8 plots. Abbreviations used: M = mown plots, R1 = rototilled plots, first year of succession, R2 = rototilled plots, second year of succession. cenjac = *Centaurea jacea*; dacglo = *Dactylis glomerata*; elyrep = *Elymus repens*; inucon = *Inula conyza*; sanmin = *Sanguisorba minor*; verarv = *Veronica arvensis*; viohir = *Viola hirta.*

Table B3.5 Eigenvalues, the percentage explanation of variance, and the cumulative percentage of variance of the first 2 axes of the PCA for the site Rappberg (Fig. B3.9)

axes	eigenvalue	% of variance	cumul. percent. var.
1.	7.090	15.085	15.085
2.	5.483	11.666	26.751

The Regelberg and Molkengrund sites showed similar patterns of change in species composition after rototilling (see Fig. B3.8, Fig. B3.10). Ordination indicated a shift in species composition from rototilled plots towards the pre-disturbance composition on mown plots. Differences between treatments were characterised by a decrease in the frequency of typical semi-natural grassland species such as *Potentilla tabernaemontana* or *Bupleurum falcatum*. The analysis showed nearly 42% of the variance in plant composition to be found on the first two axes (Table B3.6).

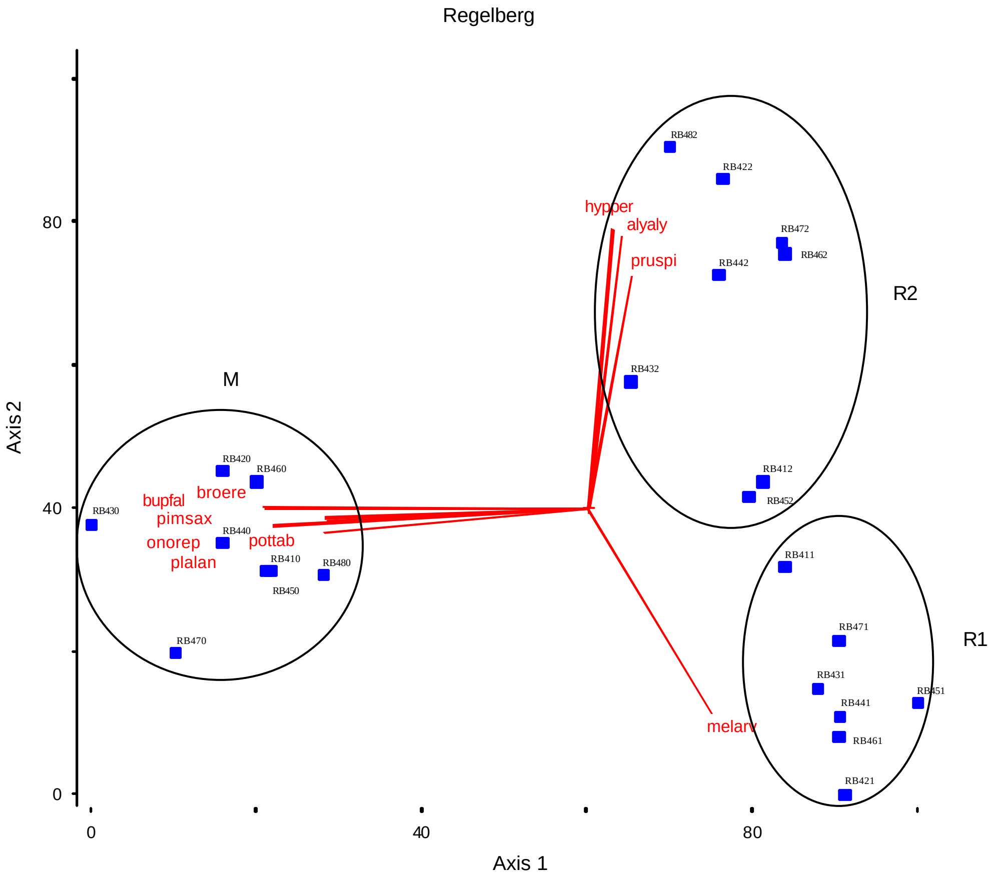


Fig. B3.10 Ordination biplot of axis 1 and 2 of the PCA for the site Regelberg showing the relative position of the treatment plots concerning species composition and species frequencies. N = 8 plots. Abbreviations used: M = mown plots, R1 = rototilled plots, first year of succession, R2 = rototilled plots, second year of succession. alyaly = *Alyssum alyssoides*; broere = *Bromus erectus*; bupfal = *Bupleurum falcatum*; hypper = *Hypericum perforatum*; melarv = *Melampyrum arvense*; onorep = *Ononis repens*; pimsax = *Pimpinella saxifraga*; plalan = *Plantago lanceolata*; pottab = *Potentilla tabernaemontana*; pruspi = *Prunus spinosa.*

Table B3.6 Eigenvalues, the percentage explanation of variance, and the cumulative percentage of variance of the first 2 axes of the PCA for the site Regelberg (Fig. B3.10)

axes	eigenvalue	% of variance	cumul. percent. var.
1.	15.555	27.776	27.776
2.	7.941	14.181	41.957

Discussion and conclusions

The present study aimed to characterise the course of succession on patches disturbed by rototilling, in comparison to those disturbed by mowing. The results emphasise the differential nature of the two disturbances applied: mowing as a more slight, preservational management method and rototilling as a severe disturbance with an initially strong impact on vegetation composition and structure.

Effects of rototilling on vegetation structure

Comparisons of mown and recently rototilled plots have found distinct shifts in vegetation structure following treatment, but this impact was to some extent of short duration. Succession on rototilled plots started from bare ground, but vegetation completely recovered within two vegetation periods, although the recovery by mosses was slower. Pre-disturbance cover levels were not attained within the period of observation, even though shoot fragments were left after disturbance to allow regeneration. This difference in recovery speed, with herbs being faster than mosses, is in accordance with that found by Rydgren et al. (1998), who analysed the revegetation of vascular plants, bryophytes and lichens following experimental disturbance in a boreal forest. Rydgren et al. (1998) suggested that climate constrains the process of bryophyte recolonisation considerably, whereby the colonisation of disturbed patches may be more rapid in a humid climate. This could explain the low recovery of mosses in the present study, since rototilling was applied during the summer drought.

In contrast to the comparably low effects on the horizontal vegetation structure, the present study assessed obvious changes in the vertical vegetation structure during the first successional years. It was found that rototilling leads to a higher and more dense plant species stock. This finding is supported by observations of successional processes in abandoned meadows (Falinska 1991) and chalk grasslands (Hakes 1987). This state likely continues until succession is restored by repetition of the disturbance.

Effects of rototilling on species turnover

The low species-turnover rate of typical dry grassland species within the first two years after rototilling was surprising, and differed from observations for other sites after below-ground disturbance e.g. Jentsch (2004). In the present study, no species was lost as a direct consequence of rototilling. In total 15 species were gained in the first year after disturbance. Most of these can be characterised as typical pioneer species or agricultural weeds which became established owing to their presence in the seed bank, which was stimulated by the treatment. Species gained in the second successional year occurred due to colonisation, though for example seed dispersal, from undisturbed patches. This initial increase in species diversity within the first year after disturbance caused by seed bank activation has often been observed for old fields (Grime 1979, Lavorel et al. 1994, Prach 1990a) and grasslands (Grubb 1976, Poschlod & Jordan 1992). However, the population of such pioneer species will slowly decline with increasing competition during subsequent succession. The observation that no species were lost after treatment suggests a high regeneration and recolonisation potential of the plant community. This suggestion is verified in Box 2, indicating that vegetative regrowth rather than seed bank activation is responsible for the maintenance of semi-natural grassland species after rototilling.

The effects of rototilling on the recovery performances of particular species

The recovery performance of typical semi-natural grassland species after disturbance is of particular interest with respect to nature conservation. The present study revealed that species show different patterns of recovery after disturbance by rototilling. Surprisingly, the impact of this disturbance regime on plant species frequency is mostly short-term. Most species regained their initial plot frequency within two years of the treatment. This corresponds to the experimental evidence of Jentsch (2004), who analysed the effects of various small-scale disturbances on species composition and abundance in early successional stages of dry acidic grasslands. However, single plant species show significant changes in frequency even two years after rototilling. The promotion of certain species and the consequently depression of others may be problematic, e.g. if frequencies of matrix species decline and more competitive species become dominant. The results showed that the matrix grass species *Festuca rupicola* suffered immediate decline under the rototilling treatment, continuing through subsequent succession, and might be lost in later successional years. On the other hand, the frequency of the competitive ruderal *Elymus repens* increased. Similar shifts in dominance favouring clonal species have been investigated in the case of *Brachypodium pinnatum* (Hakes 1987), which is known to suppress typical dry grassland species and eventually bring about their loss (Bobbink 1989). Nevertheless, since both species differ in clonal growth strategy with regard to the occupation of space, *Elymus repens* is unlikely to bring about similar effects. *Elymus* *repens* represents the guerilla strategy with relatively greater distances between, and a loose aggregation of modules, whereas *Brachypodium pinnatum* represents the phalanx strategy, with short distances between modules and a tight packing of modules within genets (Schmid & Harper 1985, Doust & Doust 1988, Klimeš & Klimešová 1999). Thus, suppression of typical semi-grassland species might not be as severe as for patches on which *Brachypodium pinnatum* occurred.

Effects of a change in management strategy on the plant community composition

The low differences found in species composition and species abundance between mowing and rototilled plots in different successive years are reflected in the PCAs. Nevertheless, each treatment (M, R1, R2) separated very well on all four investigation slopes. However, only few species, specific to each site, are responsible for this separation. The ordination plots show, that the course of succession is strongly dependent on initial conditions and that revegetation patterns are linked to species composition before disturbance (Dzwonko & Loster 1998). Strong differences were found in site conditions, in part due to depth and soil type (Vetterlein 2002, unpubl., Chapter 2 Table 2.1). Species composition ranged from Mesobromion communities with different degrees of shrub encroachment (Lichtlein, Molkengrund, Regelberg) to a dry sub-community of the Arrhenatheretum elatioris (Rappberg, for further information see Chapter 2). Clearly, the pathway of succession was not equal for all sites, although the results for three out of four sites indicate a trajectory of succession towards the initial stage (Fig. B3.7 - B3.10).

Conclusions

Several general conclusions can be drawn from the present study. I have demonstrated that the impact of rototilling on horizontal vegetation structure is generally short-term. Herb layers recover quickly, whereas mosses take longer to regenerate. Vascular plant cover is fully restored within two vegetation periods. The impact of rototilling on the vertical structure of vegetation is intense and ongoing during succession. Rototilling affects vertical vegetation structure in that it leads to higher and denser stocks, but effects upon species composition were less notable. No species was lost as a direct consequence of treatment, and changes in species frequencies within the first successional years were low. A few species were supported by rototilling and subsequent succession, while others were depressed. However, frequency of the most species reverted to initial levels within two years.

The ordination plots have shown that the course of succession is strongly dependent on the initial conditions. The analysis reveals that revegetation patterns are linked to species composition before disturbance. In general, rototilled plots move in the ordination space along trajectories of different lengths (according to species regeneration potential) but more or less towards the initial stage. Nonetheless, as shown in the present study, there are exceptions to this rule. In cases in which for instance the characteristic matrix species suffer under a change in management strategy and frequencies decline, other more competitive species may become dominant. Thus, succession will not necessarily lead back to the pre-disturbance plant composition and the appearance of sites may change.

Chapter 6

Main results and overall discussion

Chapter 6
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It was hypothesised that despite the destructive nature of rototilling, characteristic plant species of disturbed patches can immediately return after rototilling due to their good regeneration potential. It was further predicted that annual plant species are temporary supported after rototilling, but become endangered during succession phases. Only high rototilling frequencies ensure the persistence of populations of annual plant species. Perennials with a high vegetative regrowth potential or species with multiple regeneration strategies may be at an advantage after rototilling, but a larger disturbance return interval than that which is optimal for annuals has to be applied if such species are to be maintained. Nevertheless, it was suggested that a rototilling frequency by which all characteristic semi-natural grassland species will survive can be found, preventing shrub redevelopment through reduction of regeneration vigour after treatment. To verify this hypothesis, the impact of disturbance on plant species and community at the patch level within experimental fields was analysed at community and population level. The consequences of cyclic disturbances by rototilling on temporal population dynamics are explored through simulation models, for the focal species *Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia pratensis*. I hence assessed the risk of population extinction for plant species with different life histories under different disturbance frequencies, and evaluated the optimal rototilling return interval for maintaince of each focal species. Furthermore, I used sensitivity analyses to provide practical information for model builders and users, by highlighting the parameters that have the greatest influence on the model output (McCarthy et al. 1995).

The impact of management change at the community level

The investigations at the community level revealed differences in the impact of rototilling between vegetation structure, below-ground, and above-ground population of a semi-natural grassland community (Box 2 & 3). The impact on the vertical structure was intense and continuous through succession, leading to more dense and higher stocks (Hakes 1988, Falinska 1991), whereas the impact on the horizontal structure was short in duration. Succession after rototilling started from bare ground, but plots had been completely recovered by herbs within two years. Most characteristic semi-natural grassland plant species were able to regenerate immediately after rototilling. For most species, re-occurrence was completed within eight weeks after treatment. This was because the vegetative regrowth potential of most grassland species was high (Eriksson 1989, Crawley 1990, Rogers & Hartnett 2001, Amiaud & Touzard 2004), whereas the analysis of seed bank characteristics of the grassland community revealed that the regeneration potential out of the soil seed banks was very limited. Several other studies reveal a similar relationship between vegetative and generative regeneration on grasslands (Edwards & Crawley 1999, Jentsch 2004, Bossuyt & Hermy 2003). The seed bank was characterised by a low seed density of the whole plant community, low densities of most characteristic semi-natural grassland species, high dissimilarity between seed bank and above-ground vegetation and a short longevity of seeds in the soil for most species. Below-ground (seed bank) and above-ground population dynamics on rototilled plots were linked. Increasing abundancy of a species in the established vegetation due to rototilling caused a delayed rise in seed abundancy in the soil, whereas a decrease in abundance in the vegetation caused a delayed decline of seeds in the soil. Changing treatment had no significant impact on either seed bank density or on the composition of below- and above-ground vegetation. No species was lost as a direct consequence of a change in treatment. For most species, seed densities in the soil and abundancies in the above- and below-ground vegetation approximated the mowing values within two years after rototilling. The trajectory of succession on rototilled fields tended mostly towards the pre-disturbance plant composition, depending upon initial conditions, above all species composition before disturbance. Nevertheless, some species showed buoyancy in above-ground frequency after rototilling, others a decline in abundancy. Further succession may promote such tendencies. In cases when dominancies of matrix species (e.g. *Festuca rupicola*) are overtaken by other more competitive species, succession will not necessarily lead back to the pre-disturbance plant composition, since such a change may alter the overall appearance of sites and lead to further loss of typical semi-natural grassland species.

The impact of management change at the population level

The investigations at the population level revealed parameters which determine population attitude after a change in the management regime (Chapter 3 & 4, Box 1). According to theory (Salisbury 1942, Harper 1977), fitness parameters and demography of annual plant species should be especially influenced by a change in environmental conditions due to rototilling. Winter annuals such as *Thlaspi perfoliatum* profit from the gaps brought about through rototilling by germinating when recently rototilled plots have not fully recovered. As hypothesised, annuals responded to the reduced competition and higher resource availability caused by the treatment by vigorous branching and seed set in the following spring. Furthermore, seedling survival was significantly higher on rototilled in comparison to mown plots. However, these differences in demography were mostly of short duration since values for fecundity and germination declined during the second successional year after rototilling (Canales et al. 1994).

Dispersal distance has previously been related to mean height of individuals (Abs 1999). Given that *Thlaspi perfoliatum* grows higher on rototilled plots, and that, especially in the first year after rototilling, the habitat is more open, a change in management might be expected to influence the dispersal range. Nonetheless, no differences were found between the treatments. *Thlaspi perfoliatum* seeds have no morphological accessories for long-distance dispersal, and most seeds germinated in the immediate vicinity of the mother individual (about 10 cm). Thus, *Thlaspi perfoliatum* is a poor coloniser by long-distance dispersal. The same has been shown for several relevant grassland species (Primack & Miao 1992, Poschlod et al. 1996, Kollmann 1997, Poschlod et al. 1997) and also for the two perennials studied in this thesis (see below). For annual plant species, density-dependent fecundity and mortality through self-thinning have been observed frequently in a range of habitats (Symonides 1988, Watkinson et al. 1989, Buckley et al. 2001, Silvertown & Lovett Doust 2001). For *Thlaspi perfoliatum* seedlings, an increased mortality as a result of crowding has been found on rototilled plots. Such mortality has been similarly reported for other annual species e.g. Maxwell et al. (1986) and Symonides (1983). Density-dependent seedling mortality through self-thinning is mainly caused by intraspecific competition for limited resources. The level of herbivorous and pathogenic activities can also be expected to be affected by the level of crowding (Symonides 1988). No density-dependence was found for fecundity (Grein 2003).

In summary, annuals are able to take quick advantage of opened gaps, but as week competitors suffer through increasing competition and litter accumulation during early successional stages (see Box 3). The most strongly affected parameters were seed production, germination and seedling survival.

The impact of a change in management on biological traits and demographic parameters for perennials was less than for annual plant species, and differed between the two focal species (*Sanguisorba minor*, *Salvia pratensis*). In general, the responses of *Salvia pratensis* and *Sanguisorba minor* to destructive disturbance differ initially. *Sanguisorba minor* takes a seeding strategy which relies almost exclusively on increased seed production and germination in the first year after rototilling, when competition with established plants is still low, whereas *Salvia pratensis* resprouts from the bud bank. However, since *Salvia pratensis* also produces a high number of seeds per plant, it provides a counter-example to a trade-off between vegetative performance and generative reproduction in perennial plants (Doust & Doust 1988, Chaloupecka & Leps 2004). Nonetheless, the generative pathway plays only a minor role in recruitment, due to seed predation and low germination. Recruitment from a bud bank may be competitively advantageous, because the Relative Growth Rate of a shoot emerging from regenerative buds will usually be higher than that of a seedling (Klimešová & Klimeš 2003). *Sanguisorba minor* likewise displays no such trade-off. Even though for *Sanguisorba minor* there is an increase in vegetative reproduction in the first year after rototilling, and a simultaneous decrease in the probability of flowering for adults, these differences were not significant. High standard errors indicate that they may more likely be explained by site conditions than by management. However, in contrast to *Salvia pratensis*, the change from mowing to rototilling has a positive effect on the germination of *Sanguisorba minor*. In accordance with studies compiled by Thompson et al. (1997) *Sanguisorba minor* was able to build up a short-term persistent seed bank. Rototilling increased seedling appearance, due to activation of seeds germinating from the soil seed bank. The relative activation of the seed bank was calculated to be 3 %.

Resprouting after rototilling differed significantly between the two species even though shoots and roots were expected to have been destroyed in similar magnitude. *Salvia pratensis* recovered very well after disturbance (see above), *Sanguisorba minor* did not. Clonal spread and vegetative regeneration can be an effective method for survival on disturbed patches (Fahrig et al. 1994). Evidence suggests that under a mowing or trampling regime, species having a protected bud bank either below or near the soil surface responded less than plants with upright growth form and exposed buds (Maschinski 1996). However, both species have similar compressed rhizomes with regenerative buds, and belong to the same clonal growth type according to Klimeš et al. (1997). Thus, clonal growth is not responsible for differential response to rototilling. *Salvia pratensis* has a continuously renewed cork layer which makes the species highly drought resistant (Kutschera 1982). Thickened clonal growth organs of *Salvia pratensis* may store accumulated resources better than those of *Sanguisorba minor*. This indicates that it may be not bud bank distribution but storage efficiency that makes *Salvia pratensis* a superior resprouter.

During secondary succession in the years following rototilling, seed production of *Sanguisorba minor* decreased and was negatively correlated to vegetation height and density. Similarly, Hegland et al. (2001) and Sundermeier (1999) demonstrated that both vegetation height and density were negatively related to reproduction parameters, such as seed production, number of inflorescences, and the proportion of flowering to non-flowering individuals, for some species of semi-natural grasslands. The former author hypothesises an effect of vegetation structure and open ground on the proportion of adults flowering in grasslands for *Salvia pratensis*. Their results indicate that a higher proportion of adults flower in open habitats. My results do not support these findings. The number of inflorescences produced per rosette did not differ between treatments for either species and there were no differences in the proportion of vegetative to generative rosettes for *Salvia pratensis* on mown or rototilled pots. On the contrary – although vegetation cover is especially reduced in the first successional year – I found a lower proportion of *Sanguisorba minor* rosettes flowering on recently rototilled plots. For *Salvia pratensis* no correlations were found between fecundity and any of the tested parameters of vegetation height and density. Seed production did not differ between mown and rototilled plots.

I could not find differences in seedling mortality between the two management systems, although studies on *Salvia pratensis* seedlings indicated that establishment is generally unsuccessful in tall undisturbed grasslands because of litter accumulation (Rich et al. 1999). Evidence suggests that seedlings become reproductive more quickly in disturbed systems (Bazzaz 1983, Maschinski 1996, Hautekeete et al. 2002). Studies concerning seedling development have shown both (i) that plants subjected to disturbance flower early in their life-cycle, and (ii) that plants that suffer from resource limitation, favour vegetative growth and biomass accumulation rather than flowering (reviewed in Kobayashi 2001). Since rototilling has a more severe impact on biomass than mowing, one may expect that changing the disturbance regime would influence this life-cycle parameter. Nevertheless, no differences were found for either focal species. Age at first flowering does not differ between mown and rototilled plots. Thus, seed production and seed germination can be identified as the most responsive traits, hence setting the pattern of population dynamics of *Sanguisorba minor* on rototilled sites.

The differential effects of a change in management strategy on the demographic data for the two focal species were reflected in the population structure, with consequences for future population dynamics (see below). The consequences of a change in management strategy are relatively lower in *Salvia pratensis* than in *Sanguisorba minor,* since a large number of adult rosettes of *Salvia pratensis* were able to persist in the face of rototilling, fecundity did not differ between both management treatments, and germination was a rare event in both mown and rototilled populations*. Salvia pratensis* populations were dominated by adult individuals on both mown and rototilled plots. Nevertheless, as a consequence of the treatment, the proportion of seedlings and juveniles to generative adults ((S + J)/G ratio see Hegland et al. 2001) decreased from 1.28 on mown plots to an average ratio of 0.46 on recently rototilled plots. According to the classification of Hegland et al. (2001), who clustered *Salvia pratensis* populations into three groups (dynamic, normal and regressive) based on the relative proportions of the different life stages, populations on mown plots can be described as ‘dynamic’ and populations on rototilled plots as ‘normal’. In this study, the results for mown plots support the findings of Hegland et al. (2001), who also observed higher proportions of young stages when a late mowing regime was applied, leading to the conclusion that conservation of the remaining populations of *Salvia pratensis* in Dutch dry floodplain grasslands would be best achieved by late mowing with hay removal. The (S + J)/G ratio for *Sanguisorba minor* populations shifted from 1.05 on mown plots to 9.28 on recently rototilled plots, due to the loss of most of the juvenile and adult rosettes after rototilling. Populations of this focal species were dominated by seedlings. One may suggest that rototilling is a better management regime than mowing for maintenance of *Sangiusorba minor* populations, but this suggestion only holds if the return interval is not too small (see below).

In summary, it has been shown that the two perennial plant species react to rototilling with different levels of severity. The effects of a change in management strategy on biological traits, demographic data and population structure differed strongly between the two perennial species, although their regeneration ability had been hypothesised to be similar. It has been shown that both species are able to persist through rototilling by compensating for the loss of individuals from population, but comparison of regeneration strategies employed after rototilling showed that the species survived due to different pathways. *Salvia pratensis* survived mainly via resprouting from a bud bank, while *Sanguisorba minor* survived through generative regeneration by seedlings and seed bank activation. These results demonstrate very clearly that species within plant communities often employ a multitude of strategies (Semenova & van der Maarel 2000, Westoby et al. 2002) which cannot be lumped per site as it often happens in plant functional trait studies. Given their overall similarity in readily recordable traits such as canopy height, seed mass, SLA, clonal growth organ, etc. (Kühner & Kleyer, in prep). *Sanguisorba minor* and *Salvia pratensis* would probably be assigned to the same plant functional type. The only trait perceivable on the level of trait – environment studies that would allow for discrimination between the two species is seed bank longevity. Thus, this study shows the added value of a population based approach to plant functional trait studies in understanding plant – environment relations.

Alteration of management strategy could be problematic, since reduced management implies colonisation by shrub vegetation with negative consequences, especially for Mesobromion and Brometalia species. Thus, intensive studies on the regeneration vigour of *Prunus spinosa* after rototilling were carried out (Box 1). The investigations confirm the hypothesis that rototilling dimishes the resprouting of shrubs. Most of the above-ground and below-ground biomass is removed through rototilling. Since there is evidence that the mobilisation of below-ground plant resources is essential for resprouting (Bellingham 2000), it was assumed that resprouting vigour may be reduced because of declining plant resource availability. Even though there is no direct evidence for a relationship between environmental conditions and the efficiency of management strategies in reducing shrub shoots, climatic data on precipitation for the two investigation years supported this assumption. No time-lag concerning resprouting was found, i.e. the percentual increment of both the number of shoots and the number of basal stems was lower than 1 % in the second year following rototilling. Furthermore, this study revealed that a change in management influenced the growth form of *Prunus spinosa,* supporting the assumption that there is a relationship between growth form and disturbance (Halle et al. 1978) and productivity gradients resulting from competition (Bellingham

2000). Rototilling decreased basal stems and initially supported a more single-stemmed architecture. Mowing, on the other hand, supported multi-stemmed resprouting - a growth form by which the most rapid recovery of canopy area is achieved (Bellingham 2000). Elongation of branches during succession after rototilling increased canopy extension and thus implied a competitive advantage.

In summary, since woody plants became competitively weaker with increasing frequency of severe disturbance, it seems that only a frequent cyclic disturbance by rototilling is able to bush back *Prunus spinosa* cover and to prevent canopy extension. According to these results, a combination of the two management strategies, mowing and rototilling, may be a conceivable option. Rototilling with a disturbance return interval of three or four years and mowing once in between may be effective.

The impact of a change in management strategy on future population dynamics for three plant strategies

Analysis revealed large differences in sensitivity between the models employed, emphasising the importance of achieving accurate data regarding certain parameter values, which are different for each of the three models. These are, namely, data on seed bank depletion and germination for the dormant annual species (*Thlaspi perfoliatum*), data on the mortality rates of juveniles and adults for *Sanguisorba minor* and data on the germination rate in the first year after rototilling for *Salvia pratensis*. Furthermore, my results indicated that the predictions of the *Salvia pratensis* model are comparatively the most robust. Changes in even the most sensitive model parameter resulted in only little variation in model output. The modelling results reveal a strong but life-history dependent impact of rototilling frequency on species dynamics and population survival, and in accordance with disturbance level and plant persistence theories, support the suggestion that only high disturbance levels select for short-lived plant species with a high population growth rate e.g. (McArthur 1962, McArthur & Wilson 1967, Grime 1977, see Chapter 3 & 5). In cases where frequent and severe disturbance is the dominant influence upon vegetation, it is likely that those genotypes (species) in which rapid growth and early reproduction allow production of sufficient offspring for survival and reestablishment of populations have been favoured (Grime et al. 1988). The annual *Thlaspi perfoliatum* is a regular member of the community species pool of managed dry grasslands and rocky outcrops in Central Europe (Oberdorfer 1978). It is rarely seen in fields or ruderal habitats. In mown semi-natural grasslands, it apparently profits from a regeneration niche on small-scale open microsites (Grubb 1977), conforming to the short-lived interstitial – strategy in the matrix-interstitial model of Grubb (1986). After rototilling, the matrix of perennials is erased, and small-scale microsites become large-scale open space. My results show that *Thlaspi perfoliatum* populations dramatically increase after rototilling in an almost weedy habit. However, high recruitment lasts only for one year. Reasons for a decline in the following years are decreases in fecundity, germination and establishment under ongoing succession, with values falling far below those in mown plots (Chapter 3). In terms of Grubb (1986), restoration of the matrix slowly closes off the regeneration niche of *Thlaspi perfoliatum*, in contrast to yearly mowing. Storage effects (Warner & Chesson 1985) in the form of a seed bank allow storage of some reproductive capacity until the next rototilling event. However, as the seed bank depletes over time, no recruitment is possible at larger rototilling return intervals (> 6 years). The sensitivity analysis identified seed bank depletion as most important trait. This is in accordance with simulations of the dynamics of annual grass species by Canales et al. (1994) and Silva et al. (1991). Both emphasise changes towards lower disturbance frequencies as the major reason for the decline of populations of annual plant species.

My simulations reveal that the maximum number of adult individuals of *Thlaspi perfoliatum* increases with decreasing disturbance frequency. This pattern can be explained by density-dependent seedling mortality. There is evidence that, for annual plant species, density-dependent fecundity and mortality through self-thinning is common in a range of habitats (Symonides 1988, Watkinson et al. 1989, Buckley et al. 2001, Silvertown & Lovett Doust 2001). I incorporated an increased mortality of *Thlaspi perfoliatum* seedlings, due to crowding, into the model by putting a ceiling of 55 on the maximum number of seedlings that can survive in one cell, using logarithmic functions based on field observations (Chapter 3). At low disturbance frequencies (e.g. every third year), a higher amount of cells are occupied by seedlings than at lower frequencies (e.g. every sixth year), since both seed dispersal over short distances and seed bank stimulation following each disturbance resulted in higher seedling appearance. Higher seedlings densities per cell resulted in higher seedling mortalities, and consequently in lower population sizes of adults.

On the other hand, a change in the disturbance return interval towards lower frequencies ensured or prolonged population survival of the perennial plant species. With respect to life cycle, *Sanguisorba minor* takes an intermediate position between the annual *Thlaspi perfoliatum* and the perennial *Salvia pratensis.* Individuals of *Sanguisorba minor* need two years to reach the reproductive stage. Thus, age at first flowering is responsible for extinction if the rototilling return interval is lower than three years, as offspring can no longer be produced. Enlarging the disturbance return interval prolonged population survival for both *Sanguisorba minor* and *Salvia pratensis*. *Sanguisorba minor* is able to build up larger populations due to two reasons: firstly establishment is not as much affected by higher vertical canopy density as it is in *Salvia pratensis* (although seed weight is comparable), and secondly stimulation of seeds to germinate from the soil seed bank adds to recruitment following each year with rototilling. Seed bank activation does not occur under mowing. Taken this results into account, for *Sanguisorba minor* high recruitment exceeds high adult mortality following rototilling. However, litter production may seriously hamper recruitment in later successional years (Tilman 1988).

Compared to *Sanguisorba minor*, *Salvia pratensis* populations exhibit a continuous decline under all disturbance return intervals that were simulated. Although adult mortality is considerably lower than in *Sanguisorba minor* due to effective resprouting following rototilling, an almost complete lack of establishment of new individuals under ongoing succession leads to extinction. Since the seed bank of *Salvia pratensis* is transient germination rates are low in the first year after rototilling. Thus, in the long term, *Salvia pratensis* declined due to overaged populations.

Population viability analysis has often shown that decreasing environmental variation increases the likelihood of population extinction (Menges 2000, Menges & Quintana-Ascencio 2003). Replacing a regular and light disturbance such as annual mowing by a more severe but infrequent disturbance such as rototilling increases shifts in habitat qualities, as species encounter both biomass loss when disturbed and risk of competitive exclusion under ongoing succession following disturbance. However, for those species exhibiting storage effects via a persistent seed bank, increasing environmental variation leads to population increase instead of decline (Higgins et al. 2000). A persistent bud bank as in *Salvia pratensis* is obviously not as effective if recruitment rates during disturbance intervals are low.

Through simulation modelling, Schippers et al. (2001) made a theoretical evaluation of the role of three important plant life history traits (adult longevity, seed longevity, and seed mass – seed mass as an indicator of dispersal distance and seedling vigour) in relation to different levels of disturbance. Concerning adult mortality, their results show a clear range in the disturbance gradient in which perennials exclude annual plant species. The authors explained this segregation by the fact that disturbance affects the adults but not the seeds. Thus, under increasing disturbance levels, the strategy to invest in seeds is more profitable than investment in adult life span. According to Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987), dormancy (i.e. persistent seed banks) and dispersal are alternative ways of coping with disturbance. Schippers et al. (2001) conclude from simulation results that dormancy is a better way to cope with disturbance, i.e. that escape in time is better than escape in space. According to dispersability traits such as appendices of the dispersule, none of the species analysed in my study should be good dispersers. Simulations of Schippers et al. (2001) show a general sequence of dominance of non-dormant perennials, followed by dormant perennials, non-dormant annuals, and dormant annuals with increasing disturbance level. My simulation results are in accordance with these findings, showing a sequence of extinction probability of the non-dormant perennial, followed by the dormant perennial and finally the dormant annual, with increasing disturbance frequency.

Chapter 7

Final conclusions and implications for nature conservation

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A major goal of nature conservation is to ensure the preservation of the unique floristic and faunistic diversity of semi-natural grasslands, which are continously threatened by land use change, such as afforestation, fertilisation and abandonment owing to their low agricultural productivity (Poschlod & Schumacher 1998). Abandonment causes successional processes which result in the loss of species. The need to find alternative management regimes to replace the traditional, uneconomical systems, has prompted several studies on management treatments in recent decades (Schiefer 1981, Briemle et al. 1991, Plachter 1995, Schreiber 1997). Nevertheless, there still is a need for management experiments which are more flexible, less expensive and take into account former dynamics by which these systems were maintained and the viability of many characteristic species (Poschlod & WallisDeVries 2002). The authors highlight the need for conservation management practices which provide a dynamic and process-oriented approach. To this end, this thesis tests the usefulness of a rototilling regime for the maintenance of semi-natural grasslands, bearing in mind that in the neolithic agriculture cultivation was followed by an indefinite time of succession (Abel 1978, Briemle et al. 1991, Bonn & Poschlod 1998). At this time period, most grassland species either entered the Central-European flora or extended their populations from refuges that they had occupied in the Ice Age. The hypothesis was that many grassland species would have been able to tolerate mechanical cultivation due to adapted regeneration strategies.

Although the analysis of the impact of a change in management (from mowing to rototilling) revealed only very little short-term impact on the plant community, analysis of the long-term consequences via simulation models revealed a great effect of disturbance frequency. This result shows the added value of using simulation models to predict long-term population dynamics in order to determine population viability. The concept of population viability analysis (PVA), i.e. assessing the likelihood that populations will persist, is one of the most central questions of conservation biology (Schwartz & Brigham 2003). The modelling results for the effects of rototilling frequencies on the population dynamics and extinction probabilities of three plant strategies highlighted a serious dilemma in the conservation of semi-natural grasslands community by rototilling. The models predict increasing extinction probability for non-dormant (i.e. lacking a persistent seed bank) and dormant perennial plant species under high disturbance frequencies. Dormant annuals, however, only survive at high disturbance frequencies. Therefore, mowing can not be satisfactorily replaced by a rototilling regime, if the object of the conservation management is to maintain the overall species composition. Thus, the task is to find a solution that provides the best compromise between ecological (i.e. the maintenance of the plant community) and economical (i.e. low costs for the treatment) aspects. This ranking of alternative management approaches is a central issue in conservation biology (Lindenmayer & Possingham 1996).

From an economical point of view, rototilling is possibly advantageous over mowing (Kögl & Piotraschke 2004), but the costs depend strongly on site conditions, particulary the local institutional conditions. If the machines used to apply rototilling are working to full capacity, i.e. large areas are rototilled, then rototilling is economically speaking a real alternative management regime compared to a annually mowing regime (Kleyer & Mosaik-Projekt, in press). On the other hand, from an ecological point of view, there is no doubt that mowing once a year is the best management regime to ensure the protection and maintenance of these semi-natural grasslands. This thesis reveal that no rototilling return interval is able to ensure the survival of the whole plant community. However, it has to be taken into account that rototilling with an intermediate frequency may cause the loss of species, but, abandonment would nonetheless cause more species to suffer through succession (Hobbs & Mooney 1986, Kollmann 1997, Poschlod & WallisDeVries 2002, Tasser & Tappeiner 2002, Bouchard et al. 2003, Chapter 1 & 2). Furthermore, conservation managers may have to take into account the state and the scarcity value of the species which might be lost by applying rototilling.

In sum, disturbance is an omnipresent force in vegetation dynamics, and disturbance frequency and magnitude play a major rule in conservation biology (White & Pickett 1985, Tilman 1996, White & Jentsch 2001). The results of this thesis demonstrate that maintenance of semi-natural grasslands is dependent on the constant initiation of dynamic processes: Frequent, but slight disturbances are the key factors for the persistence of biodiversity of semi-natural grasslands (Jentsch 2004). By applying an intense, but less frequent disturbance regime, species diversity suffer under the indirect effects of succession due to increasing biomass and competition, rather than under the direct effects of the severity of the treatment itself. Since successional processes due to missing disturbances are the major threat, a combination of the two disturbance regimes mowing and rototilling is conceivable. Rototilling applied every 3 - 4 years and mowing once in between in order to prevent biomass accumulation may be an appropriate management regime for the protection of plant communities on semi-natural grasslands. Considering these facts, research on a mixture of the two treatments mowing and rototilling may provide a rewarding avenue for future research.

Summary

Summary

Semi-natural grasslands are major components of the landscape. Many of these rank among the most species-rich habitats within Central Europe (Poschlod & WallisDeVries 2002), and major goal of nature conservation is to ensure the preservation of their unique floristic and faunistic diversity. To achieve this goal, succession has to be resisted via the application of management regimes (Poschlod & Schumacher 1998). In recent decades, many systems such as extensive grazing, burning, and mulching have been tested, with a view to finding alternatives to traditional uneconomical management regimes (Schiefer 1981, Briemle et al. 1991, Plachter 1995, Schreiber 1997). Nevertheless, there still is a need for management experiments which are more flexible and less expensive.

In this thesis, I investigate plant performance in semi-natural grasslands, in order to be able to predict species composition after a change in management (from mowing to rototilling). Empirical studies were done at two different levels. On the community level population response due to a change in management is presented without explaining the underlying processes. Although investigations into the regeneration potential of all characteristic semi-natural grassland species can account for plant community response after disturbance, only life-cycle analysis for individual species, based on the observations of individuals within that species, can link population dynamics and environmental factors and hence provide useful insights into the underlying pattern and mechanisms. In this study, plant response of focal species after disturbance is extrapolated in time using simulation models, and population survival/extinction is forecasted for given disturbance return intervals.

The empirical investigations were done on a semi-natural grassland community in the nature reserve 'Hohe Wann' situated in Lower Franconia using experimental fields with different management histories. One of these, the reference field (M), was mown once a year. The remaining three fields were rototilled (R) once, each in a different year beginning in 2000 (R2000, R2001, R2002). After rototilling, fields were left alone to allow succession to take place.

Investigations at the community level revealed that recovery of rototilled plots was very fast. Within eight weeks, nearly all character species of semi-natural grasslands were already detectable. Species re-occurrence was due rather to vegetative than to generative regeneration strategy. The low seed bank density for the whole plant community, the low densities for the most characteristic dry grassland species, the dissimilarity between seed bank and above-ground vegetation as well as the missing persistent seed banks for most species indicated that potential for regeneration directly from soil seed banks is very limited.

The impact of rototilling on the horizontal vegetation structure was high, but generally short in duration. Herb and moss layer both recovered quickly, although of the two, the latter took longer to regenerate. Vascular plant cover was fully restored to pre-rototilling levels within two vegetation periods. Impact on the vertical vegetation structure was however intense and ongoing during succession, culminating in higher and more dense stocks in rototilled plots.

A change in management regime had less impact on species composition. No species was lost as a direct consequence of the treatment, and changes in frequencies within the first successional years were low for most species. Some species were supported by rototilling and subsequent succession, while others were repressed, but most returned to pre-rototilling frequencies within two years.

The course of succession was strongly dependent on the initial conditions. Revegetation patterns were linked to pre-disturbance species composition. Mown and recently rototilled plots tended to show more differences in species composition than mown and rototilled plots did in later successional years. Succession hence leads back towards the initial stage of vegetation. There were however exceptions to this rule, for example, in such cases in which a change in management strategy brings about a decline in frequency of the characteristic matrix species, competitively stronger species may become dominant. Thus, succession will not necessarily lead back to the pre-disturbance plant composition and the appearance of sites may change.

On the second level, investigations into the life histories and biological traits of three species (*Thlaspi perfoliatum*, *Sanguisorba minor*, *Salvia pratensis*) were carried out in mown and rototilled fields. The individual models are based on these results. In order to assess the level of encroachment by shrubs after rototilling, investigations into the regeneration potential of *Prunus spinosa* were performed.

A change in management strategy has a strong effect on population dynamics and on the population viability of annual plants. At first, annuals take advantage of reduced competition and increased resource availability, but as weak competitors they later suffer during ongoing succession. The most strongly affected parameters were fecundity, germination, and establishment (seedling survival). Sensitivity analysis highlighted the importance of information on seed bank depletion and germination for the prediction of population viability. Modelling the population dynamics of *Thlaspi perfoliatum* revealed that a rototilling disturbance return interval of less than eight years has to be applied if annuals with similar biological traits and demography are to be maintained.

Perennials reacted to disturbance by rototilling with different levels of severity. Effects on biological traits, demography and population structure can be quite different, even though regeneration ability is hypothesised to be similar. The investigations have shown that perennial species are able to compensate for the loss

of individuals after rototilling by using different pathways of regeneration. *Salvia pratensis* survived mainly owing to resprouting from a bud bank, while *Sanguisorba minor* survived due to generative regeneration by seedlings and seed bank activation.

Investigations into *Prunus spinosa* have shown that rototilling diminishes the resprouting vigour of shrubs after disturbance. Weather conditions (moisture) have a great impact on the efficiency of management. The numbers of shoots per m^2 and the number of basal stems per shoot were reduced. There was no time-lag concerning resprouting. Shrub cover reached initial levels or even more dense stocks within only two successional years, owing to massive lateral spread in later successional years.

The thesis highlights the value of simulation models as an aid to management decisions regarding the conservation of plant composition under changing disturbance frequencies. The influence of disturbance frequency on population dynamics and extinction probabilities was tested for three plant strategies. Using individual-based models for each strategy, I aimed to verify theories about disturbance and plant persistence. The models predicted increased extinction probability for non-dormant (species lacking a persistent seed bank) and dormant perennial plant species under high disturbance frequencies. Dormant annuals only survived at high disturbance return intervals. No disturbance return interval allows for survival via all strategies.

Combining the results of both investigations on the population and the community level provides an estimation of community performance after a change in management strategy, and can be used to recommend management practice on semi-natural grasslands. This thesis suggests that rototilling may be an effective strategy for short-term maintenance of semi-natural grassland species. Nonetheless, the results of the simulations models show that there is no rototilling return interval by which all species can be maintained and shrub recovery can be prevented. A high disturbance return interval should be applied if both the reduction of shading by shrubs and the maintainance of dormant annual species, are to be obtained. However, high disturbance frequencies endanger non-dormant perennial species. These results reveal that rototilling cannot be used as an alternative management method to preserve plant Mesobromion communities and dry sub-communities of the Arrhenatheretum elatioris communities without accepting the loss of plant species.

Zusammenfassung

Zusammenfassung

'Halb-natürliche' Magerrasen sind bedeutsame Landschaftsbestandteile. Die meisten Typen dieser Magerrasen gehören zu den besonders artenreichen Habitaten in Mitteleuropa (Poschlod & WallisDeVries 2002). Die Erhaltung der für diesen Lebensraum typischen und einzigartigen Diversität von Pflanzen- und Tierarten ist ein wesentliches Ziel des Naturschutzes. Dieses Ziel kann nur mit Pflegemaßnahmen erreicht werden, die die Sukzession auf den potenziellen Waldstandorten immer wieder aufhalten und zurücksetzen (Poschlod & Schumacher 1998). In den letzten Jahrzehnten wurden zahlreiche Pflegemaßnahmen wie z.B. extensive Beweidung, mulchen und brennen (Schiefer 1981, Briemle et al. 1991, Plachter 1995, Schreiber 1997), als Alternative zu den traditionellen, unökonomischen Maßnahmen (meist jährliche Mahd) erprobt. Doch noch immer ist Bedarf an Managementvarianten, die flexibler und weniger aufwendig sind.

Die vorliegende Arbeit untersucht das Verhalten von Pflanzenarten auf Magerrasenflächen mit dem Ziel, die Artenzusammensetzung nach Änderung des Störungsregimes (einschürige Mahd versus Fräsen) einschätzen zu können. Die empirischen Untersuchungen wurden auf zwei verschiedenen Ebenen durchgeführt. Die erste Ebene (Gemeinschaftsebene) stellt die Reaktion von Populationen in Folge von Nutzungswandel dar, ohne jedoch die zugrunde liegenden Prozesse erklären zu können. Untersuchungen zum Regenerationspotential aller charakteristischen Arten tragen dabei zum Verständnis des Verhaltens der Artengemeinschaft nach einer Änderung im Störungsregime bei. Nur die Analysen der Lebenszyklen von Einzelarten auf der Basis von Individuen (Populationsebene) sind jedoch geeignet, um Zusammenhänge zwischen Populationsdynamik und Umweltfaktoren aufzudecken und somit Einblicke in die zugrunde liegenden Muster und Mechanismen zu gewähren. Mit Hilfe von Simulationsmodellen wird die Reaktion von ausgewählten Arten auf Störung in die Zeit extrapoliert und das Überleben bzw. Aussterben von Populationen bei gegebenen Störungsrhythmen prognostiziert.

Die empirischen Untersuchungen dieser Arbeit fanden auf eigens angelegten Pflegeparzellen auf Magerrasen im Naturschutzgebiet 'Hohe Wann' in Unterfranken statt. Hierbei diente eine Pflegeparzelle (9 x 15 m) als Referenzfläche, auf der die traditionelle Nutzung, eine einschürige Mahd im Spätsommer, weitergeführt wurde. Drei weitere Parzellen wurden in unterschiedlichen Jahren (2000-2002) einmalig im Sommer gefräst und anschließend der Sukzession überlassen.

Mit Hilfe der Untersuchungen auf Gesellschaftsebene konnte gezeigt werden, dass die Wiederbesiedlung gefräster Flächen durch Magerrasenarten sehr schnell verläuft. Innerhalb von acht Wochen waren fast alle typischen Magerrasenarten wieder auf den gefrästen Flächen nachweisbar. Dabei erfolgte die Wiederbesiedlung eher

durch vegetative als generative Regeneration der Arten. Die geringen Gesamtdichten von Samen in der Diasporenbank, die geringen Diasporendichten der meisten charakteristischen Magerrasenarten, die große Unähnlichkeit der etablierten Vegetation mit der Diasporenbank sowie die Kurzlebigkeit der meisten Samen im Boden deuten auf ein geringes Regenerationpotenzial aus dem Boden hin.

Der Einfluß des Fräsens auf die horizontale Vegetationsbedeckung ist groß, aber nur von kurzer Dauer. Die horizontale Vegetationsbedeckung wird durch Fräsen zunächst komplett zerstört. Die Wiederbedeckung erfolgte rasch. Innerhalb von zwei Jahren hat sich die Krautschicht wieder vollständig regeneriert. Im Gegensatz dazu beeinflußt Fräsen die vertikale Vegetationsstruktur stark und langanhaltend. Nach einmaligem Fräsen entwickeln sich höhere und dichtere Bestände.

Die Artenzusammensetzung wird durch Fräsen wenig verändert. Keine der Magerrasenarten stirbt als direkte Konsequenz der Störung aus, und es sind nur geringe Veränderungen der Frequenz in den ersten beiden Sukzessionsjahren nachweisbar. Es gibt Arten die durch Fräsen gefördert werden, während andere weniger häufig auftreten. Die meisten Arten traten jedoch schon im zweiten Jahr der Sukzession mit der gleichen Häufigkeit wie vor dem Fräsen auf.

Die Sukzessionsentwicklung auf den gefrästen Flächen hängt stark von der Ausgangssituation ab. Die Wiederbesiedlung ist eng mit der Artenzusammensetzung vor der Störung verknüpft. Generell ist ein Trend erkennbar, daß sich gemähte und frisch gefräste Flächen stärker unterscheiden als gemähte und gefräste Flächen im späteren Sukzessionsjahr. Allerdings wurde auch gezeigt, dass es Flächen gibt auf welchen keine Rückentwicklung zum Ausgangszustand stattfindet. Werden z.B. Matrixarten in ihrer Häufigkeit stark zurückgedrängt und andere konkurrenzstärkere Arten übernehmen deren Dominanz ändert sich die Vegetationsausprägung drastisch.

Vergleichende, detaillierte Untersuchungen auf der Populationsebene, zu Lebenszyklen und biologischen Merkmalen von drei Pflanzenarten (*Thlaspi perfoliatum*, *Sanguisorba minor*, *Salvia pratensis*) wurden auf gemähten und gefrästen Parzellen durchgeführt. Die Ergebnisse sind Grundlage für die Initialisierung und Parametrisierung der individuenbasierten Modelle. Zusätzlich wurde das Regenerationsvermögen von *Prunus spinosa* ermittelt, um den Verbuschungsprozess auf gefrästen Flächen abschätzen zu können.

Die Populationsdynamik annueller Arten (Beispielart: *Thlaspi perfoliatum*) wird durch eine Änderung der Pflege wesentlich beeinflußt. Wie angenommen, profitieren Annuelle zunächst nach Störung, da einerseits die Konkurrenz vermindert und andererseits das Ressourcenangebot erhöht ist. Bei fortschreitender Sukzession, d.h. bei einer Zunahme an Konkurrenz und einer damit einhergehenden Abnahme der Ressourcen sind sie durch ihre Konkurrenzschwäche benachteiligt. Die am stärksten beeinflußten Parameter sind Fruchtbarkeit, Keimungsrate und Keimlingsetablierung.

Die Sensitivitätsanalyse des Modells legt dar, daß Informationen über Diasporenbankabbau und Keimung besonders wichtig sind, wenn das Überleben von Populationen nach Störung prognostiziert werden soll. Um annuelle Pflanzenarten mit ähnlichen Merkmalen und Demographie wie *Thlaspi perfoliatum* zu erhalten, müssen Störungen von einem Rhythmus, der kürzer als acht Jahre ist, erfolgen.

Obwohl die Regenerationsfähigkeit nach Störung für beide untersuchten Arten (*Sanguisorba minor* und *Salvia pratensis*) ähnlich eingeschätzt wurde, war der Einfluß auf biologische Merkmale, Demographie und Populationsstruktur sehr verschieden. Beide Arten sind in der Lage einmaliges Fräsen zu überleben, aber bedingt durch unterschiedliche Regenerationsstrategien. *Salvia pratensis* überlebt aufgrund von vegetativem Austrieb. *Sanguisorba minor* überlebt aufgrund von erhöhtem Keimlingsaufkommen und Anregung der persistenten Diasporenbank.

Fräsen reduziert die Regenerationskraft von *Prunus spinosa*, allerdings hat die Bodenfeuchte einen großen Einfluß auf die Wirksamkeit der Pflegemaßnahme. Sowohl die Anzahl der Sprosse pro m² als auch die Anzahl der basalen Austriebe pro Sproß wurden durch Fräsen reduziert. Es konnte kein zeitverzögerter Austrieb festgestellt werden. Problematisch ist allerdings die massive laterale Ausdehnung schon im zweiten Jahr der Sukzession nach Fräsen. Die Bedeckung mit *Prunus spinosa* nimmt zunächst ab, erreicht im zweiten Jahr der Sukzession allerdings schon die Ausgangswerte oder liegt sogar darüber.

Die Arbeit bestätigt die Nutzbarkeit von Simulationsmodellen, um Managemententscheidungen bezüglich der Erhaltung von Pflanzenbeständen bei unterschiedlichen Störungsrhythmen zu unterstützen. Für drei Pflanzenstrategien wurde der Einfluß von Störungsfrequenz auf Populationsdynamik und Aussterbewahrscheinlichkeit getestet. Die Modelle sagen eine steigende Aussterbewahrscheinlichkeit für nicht dormante (Arten ohne persistente Diasporenbank) und dormante perenne Arten bei kurzen Störungsrythmen voraus. Dormante annuelle Arten überleben nur bei kurzen Störungsintervallen.

Die Summe der Ergebnisse aus beiden Ansätzen, d.h. aus den populationsbiologischen Untersuchungen von Einzelarten und aus den Erhebungen auf der Gesellschaftsebene, ermöglicht es, das Verhalten der Artengemeinschaft bei Nutzungsänderung abschätzen zu können und Hinweise für das Pflegemanagement von Magerrasen zu geben. Dabei zeigte sich, dass Fräsen geeignet ist, auf kurze Sicht den Artbestand auf Magerrasenflächen zu erhalten. Allerdings gibt es keinen Fräsrhythmus bei dem alle Arten langfristig erhalten werden können und gleichzeitig eine Verbuschung der Flächen verhindert werden kann. Um Gehölzaufwuchs zu verhindern und annuelle Arten zu erhalten, muß eine häufige Störung erfolgen. Bei zu hohen Störungsfrequenzen sterben allerdings nicht dormante perenne Arten aus. So ist es nicht möglich, die Pflegemaßnahme einschürige Mahd durch Fräsen zu ersetzen, wenn es das Ziel ist, alle Arten der Magerrrasengesellschaften zu erhalten.

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Map

TK 5929 Haßfurt, Bayerisches Landesvermessungsamt München (1987).

Appendix

Appendix

Table A1 Coefficients for the lognormal or normal distribution fitted on field data for seed production of *Thlaspi perfoliatum*, *Sanguisorba minor*, and *Salvia pratensis* for mown plots (M) and rototilled plots in the first (R1) second (R2) and third (R3) year of succession. Abbreviations used: M = values for the mowing model, R1 = values for the rototilling model, first year of succession, R 2 = values for the rototilling model, second year of succession etc.

Thlaspi perfoliatum	a	w	c	y0
M	1736.439	1.145	16	-
R1	36613.56	1.177	358	-
R2	760.2840	1.456	16	-
R3	249.3891	10.494	20	3.026
Sanguisorba minor	a	w	c	y0
M	3607.498	1.7367	24	-
R1	6616.122	2.3836	52	-
R2	2508.306	1.4450	41	-
Salvia pratensis	a	w	c	y0
M	11675.14	547.5239	656	-
R1	11165.58	680.6438	669	0.702
R2	4872.701	423.7483	612	0.071

Table A2 Coefficients for weibull functions fitted to dispersal field data for *Thlaspi perfoliatum*, *Sanguisorba minor*, and *Salvia pratensis* for mown plots (M) and rototilled plots in the first (R1) and second (R2) year of succession. Abbreviations used: M = values for the mowing model, R1 = values for the rototilling model, first year of succession, R 2 = values for the rototilling model, second year of succession etc.

Thlaspi perfoliatum	Chi²	R²	a	b	c
M	4.4117	0.9964	100	0.0600± 0.0058	1.5453± 0.0505
R1	2.7714	0.9973	100	0.0392± 0.0035	1.7241± 0.0454
R2	13.380	0.9895	100	0.0565± 0.0109	1.7285± 0.1109
Sanguisorba minor	Chi²	R²	a	b	c
M	1.0120	0.9991	100	0.0104±0.0005	1.5690±0.0148
R1	3.0088	0.9980	100	0.0002±0.0001	2.6208±0.0473
R2	7.0682	0.9939	100	0.0104±0.0013	1.5985±0.0414
Salvia pratensis	Chi²	R²	a	b	c
M	3.4837	0.9971	100	0.0034±0.0004	1.8648±0.0338
R1	12.409	0.9906	100	0.0011±0.0003	2.1622±0.0755
R2	33.583	0.9799	100	0.0336±0.0124	1.2214±0.1303

Table A3 Biological attributes for the four focal plant species *Thlaspi perfoliatum*, *Sanguisorba minor*, *Salvia pratensis,* and *Prunus spinosa.* Abbreviations used: a = autumn, s = spring; data source: [1] = Grime et al. (1996), [2] = Rothmaler (1990), [3] = Rich et al. (1998), [4] = Rich et al. (1999) [5] = Krebs (1992), [6] = Hegland (2001), [7] = Kleyer (1995), [8] = Thompson et al. (1997), [9] = Thompson et al. (1998), [10] = Grunicke (1996), [11] = Ouborg & Treuren (1995), [12] = Cerabolini et al. (2003), [13] = Müller-Schneider (1986), [14] = exampling species for the clonal growth type according to the database of Klimeš et al. (1997), [15] = empirical data according to the present study (Chapter 3), [16] = Kühner (unpubl. data), [17] = empirical data according to the present study (Chapter 4), [18] = Tackenberg (2001), [19] = Maurer & Stöcklin (unpubl. data), n.i. = no information available, n.a. = not applicable.

	species			
	Thlaspi perfoliatum	*Sanguisorba minor*	*Salvia pratensis*	*Prunus spinosa*
life form	[1]therophyte	[1]hemicryptophyte	[1]hemicryptophyte	[1]phanerophyte
life span	[2,3]winter annual	[1]polycarpic perennial	[1]polycarpic perennial	[1]polycarpic perennial
canopy structure	[2]leaves basal	[2]leaves basal	[2]leaves basal	[2]leafy
releasing height [cm]	[14]8.15±3.16	[17]42.38±7.65	[17]62±10.9	[2]100-400
SLA	[16]22.69	[16]21.23	[16]18.85	[16]18.76
germination saison	[3]a	[1]a/s, main a	[4]a/s, main a	n.i.
age at first flowering	n.a.	[5,15]1-2 years	[6,15]3-5 years	[7]6-15 years
seed mass [mg]	[1]0.27	[1,12]2.84	[16]2.56	[1]427
seed number	[15]24±20	[17]656±264	[17]54±33	[7]<1000
terminal velocity $[m*s^{-1}]$	[18,19]2.93	[18]3.14	[18]2.96	[18]5.46
dispersal range	[3]short	[11,13,17]short	[11,13,17]short	[10]long
lateral spread [mm]	n.a.	[7]< 100	[7] < 100	[7]> 100
type of veg. regen.	n.a.	[1]regrowth by buds	[1]regrowth by buds	[1]regrowth by buds
clonal growth type	n.a.	[14]"Rumex obtusifolius"	[14]"Rumex obtusifolius"	[14]"Rumex acetosella"
seed bank longevity	[3]persistent	[8,9]persistent	[8,9]transient	[10]transient
	[15]long-term	[17]short-term	n.a.	n.a.

Table A4 Parameter values (%) of the mowing and rototilling models of *Thlaspi perfoliatum*, *Sanguisorba minor* and *Salvia partensis*. *Thlaspi perfoliatum* adult mortality means the transition of vegetative to generative adults. Abbreviations used: M = values for the mowing model, R1 = values for the rototilling model, first year of succession, R 2 = values for the rototilling model, second year of succession etc. The italic letters indicate estimated values.

	***Thlaspi perfoliatum* %**				***Sanguisorba minor* %**				***Salvia pratensis* %**			
	M	R1	R2	R3	M	R1	R2	R3	M	R1	R2	R3
germination	12.95	12.95	0.920	1.664	0.385	0.385	0.554	0.380	0.010	0.002	0.014	0.016
seedling mortality												
seedling mortality_autumn	66.66	55.48	94.19	95.04	51.11	45.92	70.21	70.21	61.40	69.81	89.11	89.11
seedling mortality_spring	-	-	-	-	69.71	52.55	61.70	61.70	50.00	20.00	*20.00*	*20.00*
juvenile mortality												
juvenile2 mortality_autumn	-	-	-	-	48.95	81.94	39.29	39.29	12.50	21.32	99.90	99.90
juvenile2 mortality_spring	-	-	-	-	45.45	81.94	37.52	37.52	66.7	21.32	25.00	25.00
juvenile3 mortality_autumn	-	-	-	-	*20.00*	81.94	*20.00*	*20.00*	*20.00*	21.32	*20.00*	*20.00*
juvenile3 mortality_spring	-	-	-	-	*20.00*	81.94	*20.00*	*20.00*	*20.00*	21.32	*20.00*	*20.00*
juvenile4 mortality_autumn	-	-	-	-	-	-	-	-	*20.00*	21.32	*20.00*	*20.00*
juvenile4 mortality_spring	-	-	-	-	-	-	-	-	*20.00*	21.32	*20.00*	*20.00*
adult mortality	4.672	2.506	1.375	8.333	6.865	81.94	1.104	3.910	2.632	21.32	3.817	0.733
seed bank germination	-	46.25	-	-	-	3.134	-	-	-	-	-	-
seed bank depletion												
first year	-	84	84	84	-	84	84	84	-	-	-	-
second year	-	25	25	25	-	50	50	50	-	-	-	-
third year	-	50	50	50	-	-	-	-	-	-	-	-
proportion of flowering	-	-	-	-	60.23	29.11	66.30	58.70	50.60	56.34	56.68	37.27
number of inflorescenses pe plant												
rosettes with 1 inflorescence	-	-	-	-	96.27	81.97	68.6	68.6	6807	86.59	93.75	93.75
rosettes with 2 inflorescences	-	-	-	-	3.31	13.11	16.53	16.53	16.3	6.50	3.91	3.91
rosettes with 3 inflorescences	-	-	-	-	0.41	3.28	8.26	8.26	5.42	3.25	2.34	2.34
rosettes with 4 inflorescences	-	-	-	-	0	1.64	4.13	4.13	6.02	2.03	0	0
rosettes with 5 inflorescences	-	-	-	-	0	0	0.82	0.82	3.01	1.21	0	0
rosettes with 6 inflorescences	-	-	-	-	0	0	0.82	0.82	0.60	0	0	0
rosettes with 7 inflorescences	-	-	-	-	0	0	0.82	0.82	0	0	0	0
rosettes with 8 inflorescences	-	-	-	-	0	0	0	0	0	0	0	0
rosettes with 9 inflorescences	-	-	-	-	0	0	0	0	0.60	0	0	0

Table A5 Number of seeds/m² in the seed bank at each investigation site (Lichtlein, Molkengrund) for two depth (0-5 cm and 5-10 cm) and three different treatments. M = mown plots, R1 = rototilled plots in the first year of succession, R2 = rototilled plots in the second successive year. One seed found in the soil seed bank corresponds with 16 seeds/m². Species labelled with an asterisk were used for the analysis of seed bank density.

Site	Lichtlein						Molkengrund					
Treatment	M		R1		R2		M		R1		R2	
soil depth [cm]	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10
*Achillea millefolium**	0	0	16	16	32	0	0	0	0	0	0	0
*Agrimonia eupatoria**	0	0	0	0	0	0	0	0	0	0	0	0
*Ajuga genevensis**	0	0	0	0	0	0	0	0	0	0	0	0
Alopecurus myosuroides	0	0	0	0	0	0	0	0	0	0	0	0
*Anthemis tinctoria**	0	0	16	0	16	0	16	0	0	0	112	0
Arabidopsis thaliana	16	0	0	0	0	0	0	0	0	0	0	0
*Arabis hirsuta**	0	0	16	0	0	0	0	0	0	0	0	0
*Arenaria serphyllifolia**	127	0	16	0	398	159	303	112	478	239	1928	191
Aruncus sylvestris	0	0	0	0	0	0	0	0	16	0	0	0
Betula pubescens	32	0	0	32	64	32	32	0	0	16	16	16
*Bromus erectus**	0	0	0	0	0	0	0	0	16	0	0	0
*Campanula rapunculus**	80	32	159	223	605	191	0	0	16	0	0	16
Cardamine hirsuta	0	16	16	0	0	0	48	0	0	0	0	0
*Centaurea jacea**	0	0	0	0	0	0	0	0	0	0	0	0
Chenopodium hybridum	32	16	0	0	0	16	0	0	0	0	0	0
*Convolvulus arvensis**	0	16	0	0	0	0	0	0	0	0	0	0
*Coronilla varia**	32	0	16	0	32	0	0	0	0	0	0	0
*Dactylis glomerata**	16	0	0	0	0	0	0	0	16	0	0	0
*Daucus carota**	0	16	0	16	0	16	0	0	0	0	0	0
*Dianthis carthusianorum**	32	16	0	0	16	0	32	0	0	32	48	0
*Echyum vulgare**	0	0	0	0	0	0	0	0	0	0	0	0
*Elymus repens**	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium spec.	0	0	16	0	0	0	0	0	16	0	0	0
*Erophila verna**	0	0	0	0	16	0	0	0	0	0	0	0
*Euphorbia cyperissias**	0	16	0	0	0	0	0	0	0	0	0	0
Euphorbia helioscopia	0	32	0	32	0	16	0	0	0	0	0	0
Fallopia spec.	48	0	0	0	16	16	0	0	0	0	0	0
Festuca rubra	0	0	0	0	0	0	0	0	0	0	16	0
*Fragaria viridis**	191	175	1529	1513	685	526	16	16	0	0	0	0
Fumaria officinalis	16	127	48	0	112	0	0	0	0	0	0	0
Gentianella spec.	0	0	0	0	0	0	0	0	16	0	0	0
Glechoma hederacea	0	0	0	0	0	0	0	0	0	0	0	0
Holcus lanatus	48	0	0	0	0	0	0	0	16	0	0	0
*Hypericum perforatum**	605	239	478	478	1529	1338	382	112	446	430	127	143
*Inula conyza**	112	16	32	0	64	32	271	64	16	64	112	48
Juncus spec.	0	0	0	0	0	0	16	16	0	0	0	0
*Knautia arvensis**	0	0	0	0	0	0	0	0	0	0	0	0
*Lathyrus nissolia**	0	0	0	0	0	0	0	0	16	0	0	0
*Leucanthemum vulgare**	0	0	0	0	0	0	0	0	0	0	0	0
Linaria vulgaris	0	0	0	0	0	16	0	0	0	0	0	0
*Lotus corniculatus**	0	0	0	0	0	0	48	16	0	0	0	0
*Medicago lupulina**	80	0	16	16	80	0	64	0	16	16	48	0

Site	Lichtlein						Molkengrund					
Treatment	M		R1		R2		M		R1		R2	
soil depth [cm]	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10
Melilotus *spec.*	80	48	0	0	0	0	64	32	0	0	64	48
*Myosotis ramosissima**	0	0	16	0	0	0	0	0	0	0	0	0
Myosotis spec.	159	16	112	16	1115	16	0	0	48	32	0	0
*Ononis repens**	16	16	0	0	0	0	0	0	16	0	0	0
*Origanum vulgare**	0	0	0	16	0	0	127	16	0	0	16	0
*Plantago lanceolata**	0	48	0	0	64	16	0	0	0	0	16	0
*Plantago media**	0	0	0	0	0	0	0	0	0	0	0	0
Poa pratensis agg*	159	127	64	48	255	175	143	48	191	191	175	48
*Potentilla neumanniana**	2198	1529	175	64	64	653	621	32	64	48	335	96
Salix *caprea*	0	16	0	0	0	0	0	48	0	16	0	0
Salix *spec.*	16	0	0	0	0	0	0	0	0	0	0	0
*Salvia pratensis**	0	0	0	0	0	0	0	0	0	0	0	0
*Sanguisorba minor**	0	0	16	0	16	0	64	16	48	16	64	0
Sagina procumbens	0	0	0	0	32	0	0	0	0	0	0	0
*Senecio jacobaea**	32	16	32	32	16	80	0	0	0	0	0	0
Senecio *vulgaris*	0	0	0	0	0	0	0	0	0	0	32	0
*Silene nutans**	0	0	0	0	0	0	64	0	0	0	16	0
*Silene vulgaris**	16	0	0	0	0	16	0	0	0	0	16	0
Sonchus asper	0	0	16	0	0	0	0	0	0	0	0	0
Sonchus oleratius	0	0	0	0	0	0	0	0	0	0	0	0
*Tanacetum corymbosum**	0	0	0	0	0	0	0	0	16	0	0	0
Taraxacum spec.	0	0	0	0	0	0	0	0	0	0	0	0
*Thlaspi perfoliatum**	127	64	96	32	350	32	32	0	32	16	335	64
*Thymus vulgare**	0	0	0	0	0	0	0	0	0	0	0	32
*Trifolium campestre**	112	0	16	0	0	0	0	0	0	0	366	143
Typha angustifolium	16	0	0	16	16	0	16	0	0	0	48	0
Urtica urens	0	0	0	0	0	0	0	0	0	0	0	0
Valerianella locusta	127	16	48	0	733	16	0	0	0	0	0	0
*Veronica arvensis**	143	32	48	0	478	191	16	0	16	0	16	0
Veronica spec.	430	48	159	32	1705	526	0	0	0	0	16	0
Vicia *spec.*	16	16	32	0	16	16	16	0	16	32	32	0
Viola arvensis	0	16	0	0	0	0	0	0	0	0	0	0
*Viola hirta**	16	0	0	0	0	16	0	0	32	0	0	0
Indet	32	0	32	0	0	0	0	0	0	16	0	0

Site	Rappberg						Regelberg					
Treatment	M		R1		R2		M		R1		R2	
soil depth [cm]	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10
Achillea millefolium	64	48	0	0	16	0	32	48	0	80	32	32
Agrimonia eupatoria	0	0	0	0	0	0	0	0	0	0	16	0
Ajuga genevensis	0	0	0	0	0	16	0	0	0	0	0	0
Alopecurus myosuroides	0	0	0	0	16	0	0	0	0	0	0	0
Anthemis tinctoria	0	0	16	0	0	0	32	0	0	0	0	16
Arabidopsis thaliana	0	0	0	0	0	0	0	0	0	0	0	0
Arabis hirsuta	0	0	0	0	0	0	0	0	0	0	0	0
Arenaria serphyllifolia	462	96	175	96	1179	32	48	32	16	127	303	96
Aruncus *sylvestris*	0	0	0	0	0	0	0	0	0	0	0	0
Betula pubescens	16	16	0	0	16	0	0	16	0	16	0	0
Bromus erectus	0	0	0	0	0	0	0	0	0	0	32	0

Site	Rappberg						Regelberg					
Treatment	M		R1		R2		M		R1		R2	
soil depth [cm]	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10
Campanula rapunculus	0	0	0	0	32	0	0	0	32	32	127	48
Cardamine hirsuta	0	0	0	0	0	0	0	0	64	16	0	0
Centaurea jacea	16	0	16	16	16	0	0	0	0	0	0	0
Chenopodium hybridum	0	0	0	0	0	0	0	0	0	0	0	0
Convolvulus arvensis	16	0	0	0	0	16	0	0	0	0	0	0
Coronilla varia	0	0	0	0	0	0	0	0	0	0	0	0
Dactylis glomerata	0	0	0	0	0	0	16	0	0	32	16	0
Daucus carota	16	0	32	0	80	48	32	64	0	0	48	16
Dianthis carthusianorum	0	0	0	0	0	0	0	0	0	0	16	0
Echyum vulgare	0	0	0	0	335	0	0	0	0	0	16	0
Elymus repens	0	0	0	0	16	0	0	0	0	0	0	0
Epilobium spec.	0	0	0	0	0	16	0	0	0	0	0	0
Erophila verna	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia cyperissias	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia helioscopia	0	0	0	16	0	0	0	0	0	0	0	0
Fallopia spec.	0	0	0	0	0	0	0	0	0	0	0	0
Festuca rubra	0	0	0	0	0	0	0	0	0	0	0	0
Fragaria viridis	0	0	64	0	0	0	16	32	80	96	16	112
Fumaria officinalis	0	16	0	0	0	0	0	0	0	0	0	0
Gentianella spec.	0	0	0	0	0	0	0	0	0	0	0	0
Glechoma hederacea	0	16	0	16	0	0	0	0	0	0	0	0
Holcus lanatus	0	0	0	0	0	0	0	0	0	0	0	0
Hypericum perforatum	64	32	16	16	32	64	0	112	0	0	335	350
Inula conyza	112	80	159	80	175	80	0	0	32	143	48	32
Juncus spec.	0	0	0	0	0	0	0	0	0	0	0	0
Knautia arvensis	0	0	0	0	16	0	16	0	0	0	0	0
Lathyrus nissolia	0	0	0	0	0	0	0	0	0	0	0	0
Leucanthemum vulgare	96	16	32	48	64	143	16	16	0	0	0	0
Linaria vulgaris	0	0	0	0	0	0	0	0	0	0	0	0
Lotus corniculatus	0	0	0	0	0	0	16	0	0	0	0	0
Medicago lupulina	0	48	0	0	0	16	0	0	16	0	0	0
Melilotus spec.	32	48	0	0	16	16	16	16	16	32	0	0
Myosotis ramosissima	0	0	0	0	0	0	0	0	0	0	0	0
Myosotis spec.	32	32	0	0	0	0	0	0	0	0	0	0
Ononis repens	0	0	0	0	0	0	32	0	0	0	0	0
Origanum vulgare	0	0	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	16	0	0	0	0	0
Plantago media	16	0	0	0	0	0	0	0	0	0	0	0
Poa pratensis agg	510	255	319	398	319	207	255	96	175	335	319	319
Potentilla neumanniana	0	0	16	0	16	16	589	366	64	239	16	112
Salix caprea	0	16	0	0	0	0	0	0	16	16	0	16
Salix spec.	0	0	0	0	0	0	0	0	0	0	0	0
Salvia pratensis	32	0	0	0	0	0	0	0	0	0	0	0
Sanguisorba minor	0	16	48	16	0	0	16	16	0	16	0	0
Sagina procumbens	16	0	0	16	0	0	0	16	48	0	16	0
Senecio jacobaea	143	207	0	0	0	0	0	0	0	0	0	0
Senecio vulgaris	0	0	0	0	0	0	0	0	0	0	0	0
Silene nutans	127	32	207	223	0	0	0	0	48	0	0	0

Site	Rappberg						Regelberg					
Treatment	M		R1		R2		M		R1		R2	
soil depth [cm]	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10	0-5	5-10
Silene vulgaris	0	0	0	16	0	0	0	0	0	0	0	0
Sonchus asper	0	0	32	0	127	0	0	0	0	0	0	0
Sonchus oleratius	0	0	0	0	0	0	0	0	0	0	16	0
Tanacetum corymbosum	0	0	0	0	0	0	0	0	96	64	0	0
Taraxacum spec.	0	0	0	0	0	0	0	0	0	0	32	0
Thlaspi perfoliatum	32	16	32	16	175	16	32	16	80	159	414	175
Thymus vulgare	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium campestre	0	0	0	0	0	0	0	0	0	0	0	0
Typha angustifolium	0	0	0	0	0	0	0	0	0	0	16	0
Urtica urens	0	0	0	0	16	0	0	0	0	0	0	0
Valerianella locusta	16	16	0	0	16	0	0	0	0	0	32	0
Veronica arvensis	64	16	16	0	0	0	0	0	0	0	0	0
Veronica spec.	80	16	0	0	0	0	0	0	0	0	16	0
Vicia spec.	0	0	32	0	16	0	16	0	0	16	48	0
Viola arvensis	0	0	0	0	0	0	0	0	0	0	0	0
Viola hirta	0	0	0	0	0	0	0	0	16	0	0	0
Indet	0	0	0	0	0	0	0	0	0	0	0	0

Table A6 List of species recorded in the vegetation within the plots used for frequency analysis. Bold letters indicate, that these species were used for the analysis of frequency on mown and rototilled plots.

Acer campestre L.
Achillea millefolium **L.**
Agrimonia eupatoria **L.**
Allium oleraceum **L.**
Alyssum alyssoides (L.) L.
Anthemis tinctoria **L.**
Anthyllis vulneraria **L.**
Arabidopsis thaliana L.
Arabis hirsuta L.
Arenaria serphyllifolia **L.**
Arrhenatherum elatius **(L.) J. et C.**
Avenula pubescens **(Huds.) Dum**
Brachypodium pinnatum **(L.) P.B.**
Bromus erectus **Huds.**
Bromus sterilis L.
Bupleurum falcatum **L.**
Camelina pilosa (DC.) Vassilcz.
Campanula rapunculus **L.**
Campanula rotundifolia **L.**
Carduus acanthoides L.
Centaurea jacea **L.**
Centaurea scabiosa **L.**
Cerastium arvense **L.**
Cerastium brachypetalum **Pers.**
Cirsium acaule **Scop.**
Clinopodium vulgare **L.**
Convolvulus arvensis **L.**
Conyza canadensis **(L.) Cronq.**
Cornus sanguinea **L.**
Coronilla varia **L.**
Crataegus spec.
Dactylis glomerata **L.**
Daucus carota **L.**
Dianthus carthusianorum **L.**
Echium vulgare L.
Elymus repens **(L.) P.B.**
Epilobium spec.
Erigeron acris **L.**
Erophila verna **(L.) Chevall**
Euphorbia cyparissias **L.**
Euphorbia helioscopia L.
Falcaria vulgaris **Bernh.**
Fallopia spec.
Festuca pratensis **Huds.**
Festuca rubra **L.**

Festuca rupicola **Heufel**
Fragaria viridis **(Duchesne) Weston**
Fumaria officinalis L.
Galium album **Mill.**
Galium aparine L.
Galium verum **L.**
Genista tinctoria **L.**
Geranium sanguineum **L.**
Hieracium pilosella **L.**
Hordeum distichon L.
Hypericum perforatum **L.**
Inula conyzae **DC.**
Knautia arvensis **(L.) Coulter**
Lactuca serriola L.
Lamium amplexicaule L.
Lathyrus nissolia **L.**
Lathyrus pratensis **L.**
Lathyrus tuberosus **L.**
Lepidium campestre (L.) R. Br.
Leucanthemum vulgare **Lamk.**
Ligustrum vulgare **L.**
Linum carthaticum **L.**
Lotus corniculatus **L.**
Medicago falcata L.
Medicago lupulina **L.**
Medicago minima **(L.) L.**
Medicago sativa **L.**
Melamphyrum arvensis **L.**
Melilotus alba Med.
Melilotus officinalis (L.) Pallas
Myosotis ramosissimum **Rochel**
Onobrychis viniifolia **Scop.**
Ononis repens **L.**
Origanum vulgare **L.**
Papaver argemone L.
Papaver dubium L.
Petrorhagia prolifera **(L.) Ball et**
Peucedanum cervaria **Vill.**
Pimpinella saxifraga **L.**
Plantago lanceolata **L.**
Plantago media **L.**
Poa angustifolia **L.**
Poa nemoralis L.
Polygala comosa **Schkuhr**
Polygonum aviculare L.

Potentilla argentea **L.**
Potentilla reptans **L.**
Potentilla tabernaemontana **Rchb.**
Prunella vulgaris L.
Prunus avium **(L.) Moench**
Prunus spinosa **L.**
Pyrus pyraster **(L.) Burgsdorf**
Quercus spec.
Ranunculus bulbosus **L.**
Rhamnus cathartica **L.**
Rhinanthus minor **L.**
Rosa canina agg.
Rosa spec.
Salvia pratensis **L.**
Sanguisorba minor **Scop.**
Sedum acre **L.**
Senecio jacobaea **L.**
Silene nutans **L.**
Silene pratensis **Rafn) Godr. Et**
Silene vulgaris **(Moench) Garke**
Sonchus asper (L.) Hill.
Sonchus oleraceus L.
Sorbus tormentalis **(L.) Crantz**
Tanacetum corymbosum **(L.)**
Taraxacum laevigatum (Willd.)
Taraxacum officinale Wiggers
Thesium barvarum **Schrank**
Thlaspi perfoliatum **L.**
Thymus pulegioides **L.**
Torilis japonica (Houtt.) DC.
Trifolium campestre **Schreb.**
Trifolium medium **L.**
Trisetum flavescens **(L.) P.B.**
Valeriana locusta Laterrade em. Betcke
Veronica arvensis **L.**
Veronica chamaedrys **L.**
Veronica teucrium **L.**
Vicia angustifolia **L.**
Vicia cassubica **L.**
Vicia hirtsuta **(L.) S.F. Grey**
Vicia pisiformis L.
Vicia sativa agg. **L.**
Vicia tertasperma **(L.) Schreber**
Viola arvensis Murray
Viola hirta **L.**

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Dank

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Erklärung

gemäß § 10 Abs. 2 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl-von-Ossietzky-Universität Oldenburg.

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen. Desweiteren erkläre ich, dass ich früher weder akademische Grade erworben habe, noch zu erwerben versucht habe.

Oldenburg, den 11.06.2004

(Katrin Fritzsch)