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Disturbance Effects on Plant and Mycorrhizal Communities in Sandy Grasslands

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”Ta hand om er och glöm inte att idéer också är vapen”

- *Subcomandante Marcos*

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Abstract

Many ecosystems have historically been disturbed, either naturally or as part of a cultural management. Due to loss of species as a result of too little disturbance, disturbance must be considered as a potential tool for conservation and restoration in various ecosystems. In this thesis work, disturbance effects on a grassland system were studied. The studied grassland had traditionally been severely disturbed, both by grazing animals and wind erosion, and through agricultural practices. By experimentally disturbing the soil in the dry sandy grassland, disturbance-induced effects on plant and arbuscular mycorrhizal communities in sandy grasslands was studied.

Ploughing and harrowing had no effects on soil pH and only small effects on available phosphorous was found. A positive effect on plant species richness and abundance of red-listed annuals in dry calcareous grasslands was found. The plant species richness shifted towards one comprised mainly of early successional species, but during the four years of this study, the succession went towards the pre-disturbance state rather than the restoration target defined for the area. It was found that a functional trait approach to evaluate disturbance effects was not sufficient to fully explain the reasons for the disturbed plots to diverge from the target areas. However, the functional approach showed that disturbance increased the incidence of nitrogen favoured species in the system.

By using Sanger sequencing it was shown that ploughing had a negative effect on the abundance and species richness of arbuscular mycorrhiza two years after disturbance. However, in a second experiment, at a different site and using pyrosequencing, small-scale disturbances was not shown to affect either species richness or composition of arbuscular mycorrhizal fungal communities 4.5 months after disturbances. Carbon flows through arbuscular mycorrhizal fungi was negatively affected by disturbance, mainly due to a decreased abundance of arbuscular mycorrhizal fungi and potential host plants.

In summary, disturbance was shown to have both positive and negative effects on the studied organisms in dry sandy grasslands. Ploughing and harrowing were not good options for restoring this specific dry calcareous grassland type although some of the wanted annual targets increased in incidence. Mycorrhizal abundance could potentially be decreased following disturbance and with it the potential soil carbon sequestration. Using disturbance for restoration purposes involves complex responses with potentially disparate responses in different organisms within the same community.

Key words
Arbuscular mycorrhiza, dry calcareous grasslands, functional trait, pyrosequencing, restoration, sanger sequencing, soil mechanical disturbance, species richness

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Disturbance Effects on Plant and Mycorrhizal Communities in Sandy Grasslands

Tim Krone Schnoor

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid naturvetenskapliga fakulteten vid Lunds Universitet, kommer att offentligen försvaras i Ekologihuset, Sölvegatan 37, Lund, fredagen den 23 september 2011 kl. 10.00.

Fakultetens opponent: Dr. Nancy Collins Johnson, Northern Arizona University, USA.

Avhandlingen kommer att försvaras på engelska.

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

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CONTENTS

THE THESIS IS BASED ON:

I - Schnoor, TK., Olsson PA. (2010) **Effects of soil disturbance on plant diversity of calcareous grasslands**. Agriculture, Ecosystems & Environment 139 (4): 714-719.

II - Schnoor, TK., Bruun, HH., Olsson, PA. **Soil disturbance as a grassland restoration measure: evaluating success with plant functional traits**. Submitted.

III - Schnoor, TK., Lekberg, Y., Rosendahl, S., Olsson, PA. (2011) **Mechanical soil disturbance as a determinant of arbuscular mycorrhizal fungal communities in semi-natural grassland**. Mycorrhiza 21 (3): 211- 220.

IV - Lekberg, Y., Schnoor TK., Kjøller R., Gibbons SM., Hansen, LH., Abu Al-Soud W., Sørensen SJ., Rosendahl, S. **454 sequencing reveals stochastic local reassembly and high disturbance tolerance within arbuscular mycorrhizal fungal communities**. Journal of Ecology (in press).

V - Schnoor, TK., Mårtensson, LM., Olsson PA. **Soil disturbance alters plant community composition and decreases mycorrhizal carbon allocation in a sandy grassland**. Oecologia (in press) DOI: 10.1007/s00442-011-2020-2.

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My contribution to the papers:
I performed the fieldwork, laboratory work as well as statistical analyses of paper I, II, III, V. I have written the manuscripts for these papers and been responsible for the coordination and submission processes. To papers I, II, III, and V, the co-authors have contributed with assistance in the field and with comments on the manuscripts. In the work for paper IV I took part of the planning, field and laboratory work and writing, and I was responsible for multivariate statistical analyses.

I INTRODUCTION

Disturbance is an important part of all ecological systems. Any process of removing biomass or death of individuals, from the most severe volcanic eruptions to trampling by animals, could fall within the concept of disturbance. The type and properties of disturbance influence establishment and death of all types of organisms within a system. Given the importance of disturbance, many have studied how systems react on different types and regimes of disturbance. To date, we have built an understanding of the concept and made hypotheses regarding how different types of disturbances affect species richness and community composition in a range of different habitats and at a range of scales, from fires in forests to trampling in grasslands. In the light of climate change, changing land use, and loss of biodiversity, increasing attention is given to restoration and conservation of threatened habitats and ecosystems. Many ecosystems have historically been disturbed, either naturally or as part of cultural use, which is why disturbance must be considered as a tool for conservation and restoration. In my thesis, I have studied how disturbance can be employed to restore a grassland system, which has traditionally been severely disturbed, both naturally by grazing animals and wind erosion, and culturally through agricultural practices. By experimentally disturbing the soil in a degraded calcareous grassland, we could both study plant ecological effects, as well as impacts on microbial communities and carbon cycling. By combining multiple disciplines within ecology we believe that a more complex picture of the effects of disturbance emerges. This thesis focuses on disturbance-induced effects on plant and arbuscular mycorrhizal communities in sandy grasslands. This thesis is meant to introduce the reader to the concept of disturbance as well as the effects of disturbances found within the different fields covered in the doctoral project. The thesis covers the following questions:

1. How does mechanical soil disturbance affect the vegetation in degraded calcareous sandy grasslands, in which natural and cultural soil disturbances have been shaping the ecosystem?

2. What are the effects of disturbance on arbuscular mycorrhizal (AM) communities in dry grasslands?

3. How do the applied disturbances affect plant functional trait composition and carbon allocation to arbuscular mycorrhiza?

2 DISTURBANCE ECOLOGY

2.1 Disturbance – defining the concept

The concept of disturbance is often poorly defined among ecologists. It can refer to either the external force or agent that induces damage to a system, or to the effect of that force, e.g. altering of function or species composition of an ecosystem. Several authors have tried to clarify the definition of disturbance in order to make it easier to discuss. Grime (1977) defines disturbance as the removal of biomass from a given system. This is partly in accordance with the definition by Sousa (2001), who narrowly defines disturbance as the damage, displacement or the mortality that is caused either by a physical agent (abiotic) or accidentally by a biotic agent, e.g. trampling by grazers (but not grazing per se). Sousa's definition only includes the processes that will have an effect on the interactions between populations or communities. By narrowing the concept, Sousa potentially creates a research field in ecology that only covers disturbance effects and not other already studied fields, for example grazing.

Pickett *et al.* (1989) define disturbance as: ‘a change in the minimal structure caused by a factor external to the level of interest’. With such a mechanistic definition, Pickett and his colleagues tried to objectively define disturbance as an altering of a pre-defined structure by the physical destruction of the parts of the structure. The structure is defined from case to case and can be on several levels such as community, individual or even cellular and atomic levels. For example, if we want to study biomass production of a plant community, our minimal structure might be the interacting individuals. Disturbances will thus be anything that destroys or damages individuals to such an extent that changes in interactions between species occurs.

The disturbance definitions by Grime, Sousa and Pickett are somewhat similar in that they all refer to the effect of the external force, i.e. damage or mortality. Sousa (2001), with his narrow definition, does not include grazing as a disturbance since it is not an accidental biological effect. I argue that one should include such biological effects in disturbance studies to understand the mechanisms by which biological interactions function.

In ecology the term disturbance regime is a combination of the defining elements of disturbance; severity, frequency, area disturbed, timing and distribution. Severity is the amount of initial effect of the disturbance (Sousa 2001) or the degree to which the vegetation has been altered in function and composition (Runkle 1985). Severity is distinguished from the size of the disturbance force or agent itself. To measure severity one must have a good knowledge about the pre-disturbance state of the system of study. Severity is influenced by the temporality and spatial pattern of disturbance as well as abiotic environmental factors. Frequency is the mean number of events per time period, distribution refers to the spatial distribution of the disturbances, timing to when (during the year) the event takes place and area is the physical area affected by disturbance. To accurately describe a system’s dependency on disturbance and the effects of disturbance on systems, the regime needs to be described. Moreover, one important distinction in disturbance ecology is the one between abiotic and biotic agents of disturbances (Sousa 2001). Abiotic agents are those of physical character such as strong winds, fire and tillage, while biotic are effects of disturbance by living organisms such as animals or humans, e.g. grazing, clear-cutting and digging. The biotic effects can be further divided into 'natural' or anthropogenic. Disturbances with an anthropogenic origin are often considered to have a negative effect on ecosystems since they are habitually perceived as 'unnatural' although their effect on ecosystems can be the same as 'natural' disturbances.

2.2 Disturbance and its relation to species richness

Two of the most influential hypotheses regarding the relationship between disturbance and diversity are the intermediate disturbance hypothesis (IDH) (Connell 1978) and the model of dynamic equilibrium (DE) (Huston 1979; 1994).

The IDH states that diversity will be highest at a moderate rate of disturbance (Figure 1a). The disturbance factor can either be the frequency of disturbance (time between disturbances), time since last disturbance, or the severity of disturbance, together referred to as the disturbance regime (Sousa 2001). The IDH assumes that a system is in non-equilibrium, with interspecific interactions and abiotic constraints interacting to structure ecological systems. At high disturbance, the system can only hold a few species that are able to endure the environment. However, after a disturbance event, propagules from different organisms arrive to the system and occupy the open spaces and resources that the disturbance created, steadily increasing species richness with every new species arriving. As time since the latest disturbance event passes, or if only low intensity and small-scale disturbances occur, competition between species becomes stronger, eventually leading to competitive exclusion of species.

The IDH has been tested vigorously, with studies showing results in accordance with the hypothesis (e.g. (Fensham, Holman & Cox 1999; Vujnovic, Wein & Dale 2002). However, there are studies that show a more complex disturbance response than stated by the IDH. For example, Li *et al.* (2004) studied the response of plant communities to different levels of disturbance. When applying generalized models to their data set, they found seven different diversity-disturbance response patterns. Only 6.7 % of the responses were in accordance with the IDH. Fifteen % showed maximum diversity at highest disturbance intensity, 12.5 % at the lowest, and about 50 % of the responses showed no response at all. Although these are results from only one study, they indicate that the relationship between diversity and disturbance proposed by the IDH might not be valid for all systems at all times.

Huston (Huston 1979; 1994) formulated the model of dynamic equilibrium (DE). The DE hypothesizes that species richness is affected by disturbance as well as community productivity (Figure 1). According to the DE, these two factors interact to determine species richness. At low productivity, the system can only maintain a few species able to cope with the high stress. As productivity increases, the possibility for both specialist and generalist species to survive in the system increases, as a result increasing the species richness. As productivity increases further, a few strong competitors are able to dominate the system through effective resource use and competitive exclusion, thereby decreasing species richness. Considering only disturbance, the relationship between disturbance and species richness is the same as for the IDH. However, combining the two hypotheses gives a more complex picture where the species richness is a function of both the level of disturbance and the productivity. For example, at high productivity and low disturbance,

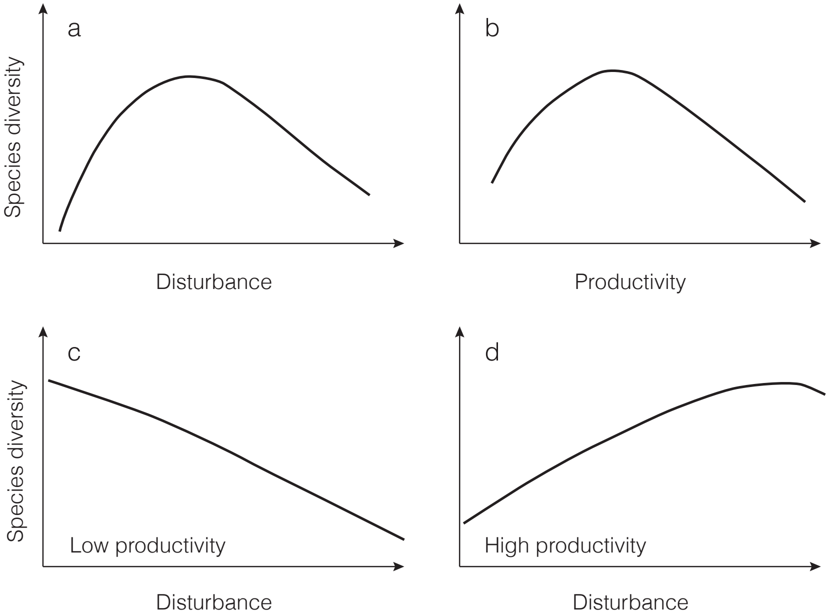

Figure 1 Conceptual plots of a) the relationship between disturbance and species diversity according to the intermediate disturbance hypothesis (Connell 1978) b) between productivity and species diversity according to the dynamic equilibrium hypothesis (Huston 1994). c) and d) shows how the relationship between disturbance and species diversity varies with productivity at a site according to the dynamic equilibrium model. The figure is based on a figure by Huston (1994).

dominant competitors will exclude many species resulting in a species poor system. But, as disturbance increases, the dominants disappear, resulting in more available space and resources. This may then lead to higher species diversity. In the case of low productivity, the pattern is the opposite, that is, a decline in species richness as disturbance increases. This shifting response points at the importance of including productivity in disturbance theory.

The IDH and the DE are two theories regarding the causal relationship between species diversity and disturbance. However, disturbance also affects community composition of species. Ecosystems undergoing change in abiotic properties or disturbances of different kinds, may respond differently depending on the systems resilience and resistance. The resistance of a system is defined as how well it can withstand a changing agent, e.g. disturbance. Resilience is the systems capacity, or speed, to recover to a pre-disturbance state (Folke *et al.* 2004; Walker & Meyers 2004). If the disturbance is intense or frequent, a system might exceed a threshold, which is higher than the systems resilience. This can lead to regime shifts, with large alterations in ecosystem function, plant community structure, diversity and composition (Romme *et al.* 1998; Folke *et al.* 2004). Some systems might respond with small changes as the disturbance intensity increases. A regime shift can also be the result of lack of disturbance, when succession leads to a restructuring of the ecosystem or possibly, from a conservation point of view, degrades it. Regime shifting disturbances can also be used as a conservation tool, deliberately pushing a system towards a certain state. However, to be able to make use of this knowledge in conservation one must know the response of a certain ecosystem to the applied disturbance.

2.3 Disturbance effects on plant communities

Plant communities are subjected to a wide range of different disturbance agents. The effect on a plant community will vary depending on the timing and severity. Ecologists try to find patterns in the community responses to be able to predict what kind of changes that are likely to take place. Plant communities have been subjected to a massive amount of studies regarding the response to disturbance. Grazers affect the dynamics between colonization and extinction. They create disturbance by consumption of plant individuals, cause soil disturbance through trampling and local deaths of individuals due to dung piles (Gurevitch, Scheiner & Fox 2002). Grazing is one of the agents that numerous times has been shown to increase the species richness of plant communities (Collins *et al.* 1998; Valone & Kelt 1999; Dupre & Diekmann 2001; Vujnovic, Wein & Dale 2002; Harrison, Inouye & Safford 2003; Jacquemyn, Brys & Hermy 2003; Altesor *et al.* 2005) and alter the species composition (Peco, Sanchez & Azcarate 2006). However, the timing (Hadar, Noy-Meir & Perevolotsky 1999), severity (McIntyre & Lavorel 1994), and grazer species (Suess & Schwabe 2007) might play a large role in determining the outcome of grazing. Mowing, that is cutting and removing vegetation, can also increase the species diversity, either by itself or in combination with grazing (Beltman *et al.* 2003). Moreover, plant species diversity can increase as a response to fire (Harrison, Inouye & Safford 2003; Fynn, Morris & Edwards 2004), tilling (Dolman & Sutherland 1994) and more 'modern' disturbances as the use of vehicles (Brown & Schoknecht 2001). However, if these agents of disturbance become too frequent or too severe, the system could experience degradation (e.g. increased erosion) and loss of species richness (Petraitis, Latham & Niesenbaum 1989; McIntyre & Lavorel 1994; Bengtsson *et al.* 2000; Milchunas, Schulz & Shaw 2000). If the disturbance is infrequent or a one time event, the system might return to an initial state of low species diversity relatively quickly (Lavorel 1999). The results of most of these studies are clear; the species diversity or richness declines when no disturbances occur, whatever the type of disturbance needed.

There is a suite of mechanisms behind the effects on species richness. Disturbance opens up space, or microsites, in a community, thereby providing physical space for new individuals to occupy. However, if this leads to an increased diversity depends on which species that establishes in the space. The propagule supply in turn depends on which propagules are present in the community or arrive from the outside, which in turn is determined by the regional and local species pool (Foster & Dickson 2004). Disturbance also influences the recruitment in a community. Different kinds of soil disturbances have been shown to increase seedling emergence, and frequent clipping increases seedling survival in grasslands

(Hofmann & Isselstein 2004), partly due to the increased light on the soil surface. Jutila & Grace (2002) found that litter inhibited germination due to a combination of lowering light penetration and altering of the microclimate. Also, many systems which are low in disturbance are dominated by species that are strong competitors, resulting in a low richness. Disturbances decrease intra- and interspecific competition by removal of competitively superior species, which may increase the abundance of inferior competitors.

Disturbance effects on plant communities in sandy grasslands in southern Sweden – Paper I and II

In agricultural areas, species adapted to high disturbance can suffer a negative population trend due to both too much and too little disturbance (McLaughlin & Mineau 1995). Some semi-natural grasslands depend on frequent disturbance, and changes in land use pose a threat to the disturbance dependent areas remaining today (Olsson 1994; WallisDeVries, Poschlod & Willems 2002). In these types of systems, re-initiating soil disturbance, such as ploughing, could function as a restoration measure. In Sweden, the habitat referred to as sand steppe (Andersson 1950), which is part of the habitat type ‘xeric sand calcareous grasslands’ in the European habitat directive (habitat code N612; EU habitat directive 92/43/EEC), is threatened by insufficient disturbance, proceeding decalcification, and increased nitrogen deposition (Bobbink & Willems 1987; Roem & Berendse 2000; Olsson, Mårtensson & Bruun 2009; Mårtensson & Olsson 2010). Given the threat status of this specific habitat type, as well as the fact that sandy grasslands exist worldwide, studying the effects of disturbances in these grasslands can be of both local and global importance. Several of our studies were performed on a degraded sand steppe habitat in south-eastern Scania, Sweden. The purpose of one of these studies (Paper I) was to unravel the response of the vegetation to mechanical soil disturbances. We wanted to study how these grasslands respond to what can be considered to be the historical disturbance regime. The historical soil disturbances were presumed to be a kind of low-intensive cultivation with long periods of fallow (Emanuelsson 2002). We mimicked these disturbances through ploughing and rotavation in a replicated field experiment (Figure 2). In accordance with the above outlined disturbance effects in plant communities we found that both disturbance types increased species richness, but the result depended on at which scale we performed our studies and the length of the time period since disturbance (Figure 3, Table 1). There were only small differences between the two types of disturbance, although we observed that rotavation created a more heterogeneous habitat than did ploughing.

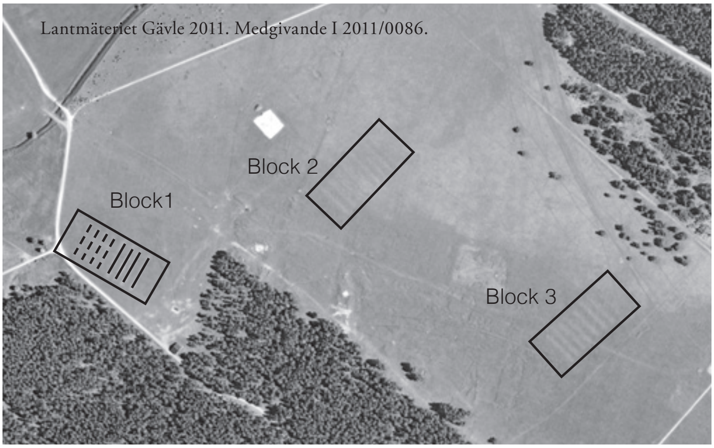

Figure 2 Aerial photo of Rinkaby experimental site. On the photo the placing of the three blocks of the experiment are shown. Within each block there are ploughed plots (continuous lines in block 1) and rotavated plots (dashed lines). Each treatment was applied in plots measuring 5 x 60 m, replicated four times within each block. Between these treatments are the controls, also five meters wide.

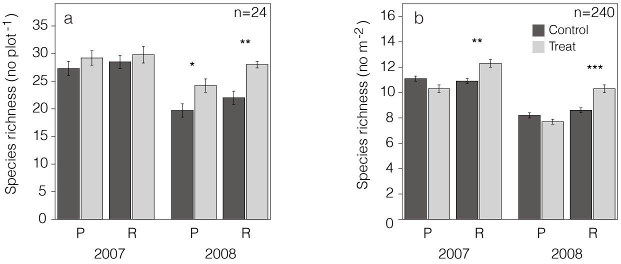

Figure 3 Data from the vegetation surveys in Paper I. Plots show both years including results of linear mixed model testing. Species richness denotes the number of unique species found either on a) plot scale (sum of 10 one m^2 quadrats) or on b) $1m^2$ scale (one quadrat). n = the number of plots or quadrats, included in each analysis; P = ploughed areas, R = rotavated areas. Bars denote SE. * $p<0.05$; ** $p<0.01$; *** $p<0.001$

One of our purposes was to evaluate the effectiveness of the disturbances from a restoration perspective. Both disturbance types increased the incidence of some threatened annual species (Figure 4, Table 1) (threatened species within this habitat type are referred to as target species, that is, species that define the sand steppe habitat and which we want to increase the abundance of), but the studied time span was not long enough in order to make any conclusions on the effects on perennial, later establishing species. In Paper II we compared a species focused analysis and a functional analysis by using one selected block in the experimental area. From the species focused analysis we found that the positive effects on species richness were sustained during the four years of study (Table 1), but more so for the rotavated plots than for ploughed. We also observed that the positive effects on some target annual species mainly took place during the first three years after disturbance. The later establishing target species *Koeleria glauca* seemed to respond weakly positive from year two and onward, demonstrating that we need long-term studies to evaluate treatment effect on later establishing target species.

These studies show that soil disturbance is positive for species richness in these habitats and thus could function as a restoration method,

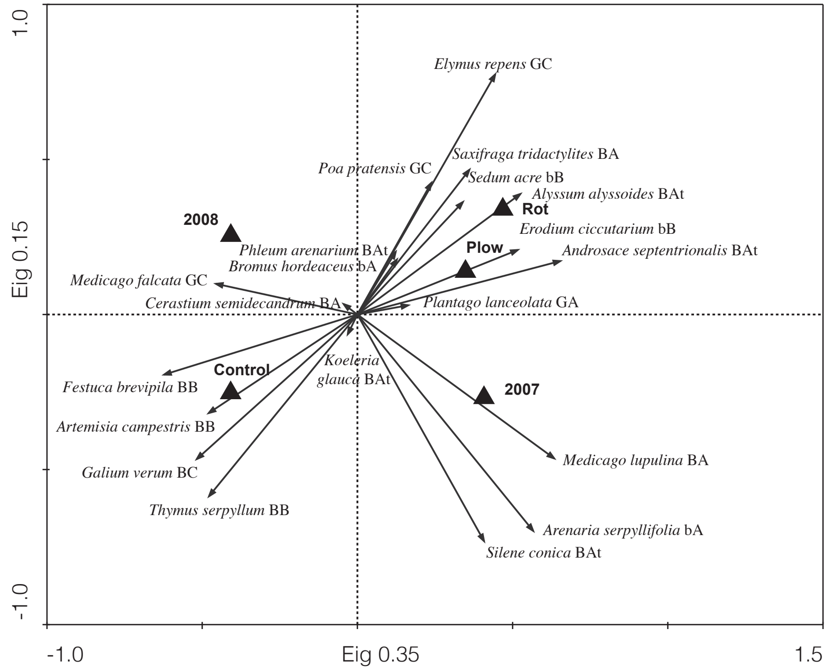

Figure 4 Ordination diagram (PCA) including treatments and year (black triangles) and the 15 most abundant species (both years, all treatments) and target species in Block 1 at Rinkaby. Treatment and year are significant environmental variables (p=0.002, 499 Monte-Carlo permutations, for both). Abbreviations after species name refer to preferred habitat classification where first letter refers to grazing adaptation (B = grazed habitats, b = grazed and non-grazed, G = general grasslands) second letter for successional stage (A = continuous hard disturbance, B = intermediate disturbance preference, C = infrequent/low disturbance) and t denotes restoration target species for sand steppe. rot = rotavation.

although the success of the restoration can be limited by factors other than disturbance, e.g. a lack of a proper seed bank and/or differences in abiotic properties compared with the target habitat. The effect on species composition was greatest the first years following disturbance, with a slow and steady return to a species composition similar to before disturbance. No large regime shifts can be concluded from the treatments, probably due to the history of disturbance in the area.

Table 1 Vegetation response to soil disturbances applied in our studies. All differences are noted as differences in means without considering the variation. The species for which the response is noted are those that are considered restoration target species. Y refers to which year following treatment the response was noted.

Source	Duration/Size	Response: plant species richness		Positive response target species	
		Ploughed	Rotavated	Ploughed	Rotavated
Paper I	2 seasons/3 blocks	+23% plot scale (Y2)	+27% plot scale (Y2); + 20% m^2 scale (Y2)	*Alyssum alyssoides* -Y1,2 *Androsace septentrionalis* -Y1 *Phleum arenarium* -Y1,2 *Saxifraga tridactylites* -Y1,2	*Alyssum alyssoides* -Y1,2 *Androsace septentrionalis* -Y1 *Koeleria glauca* -Y2 *Saxifraga tridactylites* -Y1,2
Paper II	4 seasons/1 block	+16 % (mean Y1-4)	+32 % (mean Y1-4)	*Alyssum alyssoides* -Y1-3 *Androsace septentrionalis* -Y1,(3-4)[a] *Saxifraga tridactylites* -Y1,(2)[a]	*Alyssum alyssoides* -Y1-3 *Androsace septentrionalis* -Y1,3 *Koeleria glauca* -Y2-4 *Saxifraga tridactylites* -Y1 *Silene conica* -Y1,3-4

[a] Year 3-4 this species occurred in very low abundance.

2.4 Disturbance effects on AM fungal communities

Arbuscular mycorrhiza (AM) is one of the most important symbioses in terrestrial ecosystems, influencing plant productivity through the uptake of nutrients, mainly phosphorous (Smith & Read 2008). AM fungi have large hyphal networks that spread the fungi and increase nutrient uptake to host plants. However, these hyphal structures are sensitive to soil disturbances, which physically destructs hyphae. For example tillage, the most studied form of disturbance in relation to AM fungal communities, disrupts hyphal networks (Drijber *et al.* 2000; Gosling *et al.* 2006), decreases hyphal viability (Kabir 2005), decreases the number of AM fungal spores in soil (Galvez *et al.* 2001; Kabir 2005; Borie *et al.* 2006; Castillo *et al.* 2006) and decreases root colonization (Galvez *et al.* 2001; Kabir 2005; Castillo *et al.* 2006). Using fatty acids, Drijber *et al.* (2000) found that the AM fungal fatty acid signature increased in systems that were no longer exposed to tillage. In addition, Wortman *et al.* (2008) found that both AM fungi and saprotrophic fungi decreased as an effect of a one-time tillage, although saprotrophs (organisms living of dead organic matter) seemed less sensitive. Also, the diversity of AM fungi is often reported to decrease with increasing disturbance. Helgason *et al.* (1998) found that agricultural soils had lower diversity of AM fungi compared to woodland soils and concluded that this could be an effect of ploughing, pesticides and fertilization. These reports on disturbance effects on AM fungi were followed by several other studies confirming these results. E.g. Boddington and Dodd (2000) observed a decrease in AM fungal species richness in tilled soil, relative to untilled soil. Jansa *et al.* (2003) found 17 species of AM fungi in ‘no till’ managed soils (soil that was cultivated but not ploughed or harrowed), and 12 in ploughed soil and Antunes *et al.* (2009) observed a decrease in the number of AM fungal taxa (measured as terminal restriction fragments) following soil disturbance in a pot experiment. However, e.g. Castillo *et al.* (2006) did not find a significant increase in the number of species due to the cessation of tillage. However, this effect could also be an effect of slow AM fungal dispersal, rather than proof for a non-existing positive effect of cessation of tillage.

Tillage does not only have an effect on AM fungal abundance and species richness, it can also induce shifts in AM fungal communities. Tillage selects for a community with species that colonize roots from spores rather than from root fragments or extraradical hyphae (hyphae outside roots) (Gosling *et al.* 2006). This can induce an increase in abundance of species belonging to the genus *Glomus*, and a reduction of the abundance of species from the genus *Scutellospora* (Jansa *et al.* 2002; Jansa *et al.* 2003). However, Mathimaran *et al.* (2007) found that agricultural soils in Kenya were dominated by species belonging to the genus *Scutellospora* and *Acaulospora*, which may indicate differences in the outcome of disturbance between different ecosystems. These shifts in AM fungal species composition may have large effects on ecosystem properties such as carbon cycling and plant productivity given the large importance of AM for these features (Rillig *et al.* 2001).

Besides the direct effects of disturbance on AM fungi there are a range of indirect effects. These are often effects of a change in plant community composition following disturbance. Even though host-preference of AM fungi is generally considered to be low, studies show that the composition of the AM fungal community is affected by the plant species present. Jansa *et al.* (2002) found a significant effect of host-species identity on the abundance of the different AM fungal species. Castillo *et al.* (2006) found that AM fungi belonging to the genus *Acaulospora* associated with wheat produced a larger number of spores than those associated with oat. This implies that the disturbance effects on plant communities could spin off into an influence on the AM fungal community, thereby affecting which AM fungi species that re-establish in the community. In contrast, Van der Heijden *et al.* (1998) showed that the AM fungal community affects the plant community, with a positive relationship between AM fungal diversity and plant diversity. They argued that a low AM fungal diversity may have a detrimental effect on the biodiversity and productivity of plant communities. Kernaghan (2005) describes the relationship between plants and AM fungi as bi-directional, and emphasizes the possibility for positive feedback relationships enhancing both plant and AM fungal diversity. Clearly, disturbance affects both plant and AM fungal communities directly as well as indirectly.

Disturbance effects on AM fungi in sandy grasslands – Paper III and IV

We used the Rinkaby field site to study the disturbance effects on AM fungal communities. Individuals of the grass *Festuca brevipila* and the forb *Plantago lanceolata* from ploughed and control plots of Block 1 at Rinkaby (Figure 2) were sampled and subjected to molecular analysis (nested PCR followed by Sanger sequencing) of AM fungal species (Paper III). In accordance with above described studies we found that ploughing reduced the number of AM fungal OTUs (Operational Taxonomical Units defined as AM fungal phylogenetic groups with high similarity in rDNA) (Table 2). Likewise the AM fungal community was greatly affected by disturbance (Figure 5a), with an increase in presumably disturbance tolerant OTUs in ploughed areas. The increasing OTUs were closely related to *Glomus microaggregatum*, *G. mosseae* and *G. versiforme*, which are all reported to thrive in disturbed environments (Helgason *et al.* 1998; Sykorova *et al.* 2007). OTUs related to *G. intraradices* were present in both treatments and both plant species, which support earlier studies that suggest this fungus to be a generalist (Helgason *et al.* 2007; Sykorova *et al.* 2007). However, many of the *G. intraradices* OTUs were singletons, indicating a great deal of genetic variability within the clade, making it difficult to conclude whether all *G. intraradices* genotypes are generalists. We also found that disturbance was a stronger structuring force for the AM fungal community than host-preference (Paper III). From this we hypothesize that AM fungi are more or less host-plant generalists, which is in line with the view held by e.g. Smith and Read (2008). However, looking at only two species in the system and considering that the number of sequences per OTU and species were low in the study, we cannot conclude generality with any certainty.

A second disturbance experiment was performed at a dry sandy grassland at Melby in Denmark (Paper IV). Using 454 pyrosequencing we studied the response of AM fungi to small-scale disturbance (Figure 6) when growing with *P. lanceolata* as host plant. Melby has a lower pH than the site at Rinkaby, but despite this difference, molecular characterizations have shown that the AM fungal communities at the two sites share some taxa (Rosendahl & Stukenbrock 2004), albeit these taxa do not occur in the same proportions at the two sites. To our surprise, disturbance did not affect the AM fungal community in Melby. Neither species richness (OTU richness) nor species composition was affected by the applied disturbances (Figure 5b), and OTU abundances were positively correlated across treatments; i.e., OTUs that were common in undisturbed soil were also common in disturbed soils. The distribution of OTUs within and between plots was largely unpredictable, with approximately 40% of all sequences within a sample belonging to a single OTU, although the identity of the dominant OTU varied between plots. These results point towards competition playing a large role in this grassland, with abundant AM fungal OTUs dominating irrespective of disturbance treatments applied. These findings are somewhat controversial but may be explained by several factors. First, the AM fungal taxa in the grassland may all be well adapted to small-scale disturbances due to the habitat history of being kept open by grazing animals and wind blown sand. If most taxa present are well adapted, then it may be that the community assembly is more controlled by stochastic processes, such as small-scale pre-disturbance distribution patterns, than by the disturbance dynamic itself. Second, we used 454 pyrosequencing to study the AM fungal community

Table 2 Arbuscular mycorrhizal fungal community response to soil disturbances applied in our studies. All differences are noted as differences in means without considering the variation.

Source	Exp setup	Response: colonisation	Response: richness	Response: composition
Paper III	Ploughed/control Rinkaby Block 1	No effect of ploughing	- 45% for *P. lanceolata* - 29% for *F. brevipila* - 38% in total	Many taxa found in either control or plough. However, closely related taxa can have disparate preferences.
Paper IV	2 disturbance treatments replicated	0-20% increase dependant on which type of disturbance 12-16% increase in fine endophytes dependant on disturbance type	No effect on richness or phylotype dominance	No effect on composition

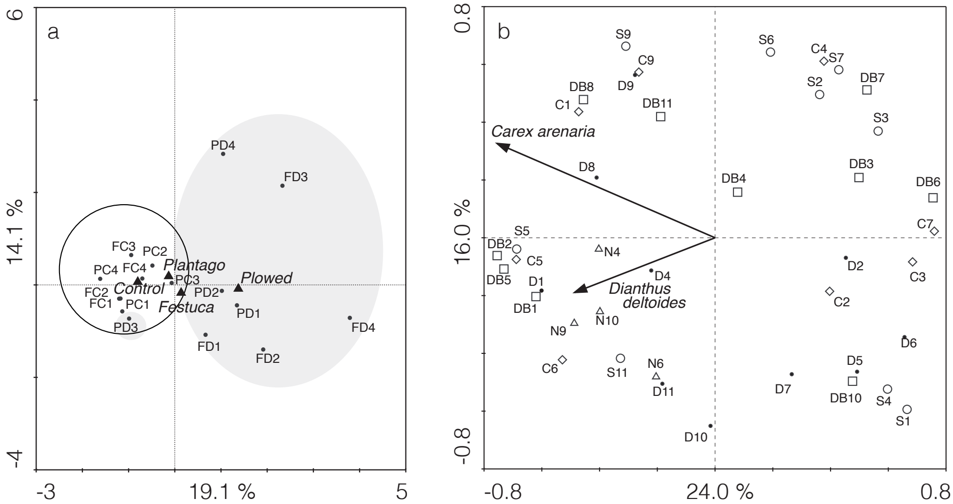

Figure 5 a) Correspondence analysis of the phylogenetic groups and their association with treatments and host species from Paper III. Circles denote plots and squares phylogenetic groups. Numbers of the groups refer to phylogenetic types. The ring encircles all control plots, and the shaded ovals cover all ploughed plots. Eigenvalue for axis 1 is 0.61 and for axis 2 0.45. Total inertia is 3.19. **b)** Principal component analysis plot of OTU composition in *P. lanceolata* roots in Paper IV. Plants were exposed to either minimal disturbance during planting (C), or to extensive disturbance where AMF surviving the disturbance and from outside the disturbed area could re-colonize (D), or where only AMF surviving the disturbance could colonize the roots (DB). OTU composition in these three treatments was compared to that in surrounding (S) plants found inside the eleven experimental plots and to native *P. lanceolata* found in four plots. The arrows indicate the plant species that explained a significant proportion of the OTU composition (using forward selection under a constrained – RDA – analysis). The N samples and 11S were excluded from the RDA because we lacked soil chemical data for those samples. Distance among samples approximates their OTU dissimilarity. PCA axis 1 accounts for 24.0% of the species variance, and PCA axis 2 accounts for 16.0% of the variance.

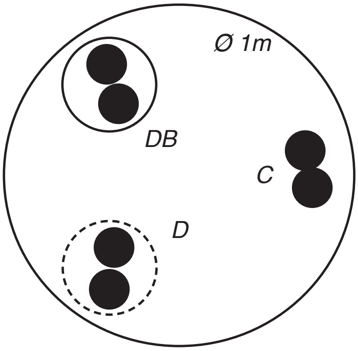

Figure 6 Experimental setup at Melby (Paper IV). Vegetation was exposed to either minimal disturbance (C) during planting of *P. lanceolata* individuals (black circles), or to extensive disturbance where AMF surviving the disturbance and from outside the disturbed area could re-colonize (D), or where only AMF surviving the disturbance could colonize the roots (DB). The experiment consisted of 14 replicated plots like the one showed here scattered randomly throughout the field site.

response. This high-throughput technology has the advantage of giving quantitative information that can be related to abundance of AM fungal phylotypes (Thomas *et al.* 2006). However, the technique is rather new, and more studies are needed before we can start comparing the results with results from common techniques, such as with nested PCR and Sanger sequencing as used in Paper III.

Our studies at Rinkaby showed that plant and AM fungal communities, or more specifically AM fungal species (or OTU) richness, have different disturbance optima, at least at the studied time span. Ploughing had a positive influence on the incidence of some target annual plants (Paper 1) and increased the plot plant species richness. This is in contrast to the reduced AM fungal richness observed following ploughing. This raises questions concerning structuring force differences between plant and AM fungal communities. It may be that ploughing increases competition for roots (possibly due to the overall lower plant abundance after disturbance) in AM fungal communities but decreases competition in plant communities. Not only does this contradict the positive relationship found between plant and AM fungal taxa richness (e.g. van der Heijden *et al.* 1998), but it also shows that a complex picture emerges when we expand our experimental systems from one to several organism groups.

In conclusion, we found that AM fungal richness and community composition were, like the plant community, affected by disturbance. Unfortunately, since we only looked at one disturbance type per study, a conclusion regarding which hypothesis (the IDH and DE) that best describes the effects is difficult to make. However, the two different studies gave two different disturbance responses. Paper III (Rinkaby) showed a clear effect of ploughing on both AM fungal species richness and composition, probably due to a combination of the severity and the size of the disturbance. Ploughing overturns the soil, thereby possibly diluting the AM fungal propagules and breaking the hyphal network over a large area (> 5 m Ø), which could affect the speed of recovery of the pre-disturbance AM fungal community. In Paper IV (Melby) the disturbance was performed at a smaller scale (20 cm Ø), and the soil was mixed rather than overturned. Potentially, this leaves a large amount of propagules in the upper soil layers, ready to spread rapidly over a small area. This could be one explanation to the different response, but we should also be aware of the large differences in abiotic properties at the two sites. At Rinkaby, we believe that there were large differences in heat and water availability between controls and ploughed plots. These differences are judged to be much smaller at Melby, due to the smaller plot scale, which could be one reason for the small differences observed in AM fungal response to disturbance.

2.5 Disturbance effects on plant functional composition

Besides affecting species richness and species diversity, disturbance may have a large influence on the functional richness or functional composition of a given system. A function can be defined as 1) a process or interaction between individuals; 2) states or sums of ecosystems, e.g. productivity; 3) objects having a specific role, e.g. plants as primary producers; 4) services provided to humans by ecosystems (Jax 2005). The concept can be used in a similar way as the species concept as it provides a description of ecosystem composition, but it also further complements the information from species composition with functional information. Ecosystem functioning research highlights the functions in an ecosystem, or the services that we as humans can get from ecosystems. Focus is put on which component of biodiversity that interacts with ecosystems functioning, and on differences in functioning between different systems, for example by using functional composition and functional diversity (FD) indices (Hooper *et al.* 2005; Diaz *et al.* 2007; Laliberté & Legendre 2010). Functional classifications measure what organisms and systems do, rather than the identity of the species in them, and are therefore suggested as measures to describe ecosystem processes and services (Hooper *et al.* 2005; Diaz *et al.* 2007). A functional type is a group of organisms with similar functional traits, with functional traits referring to any phenotypic property influencing ecosystem properties or an organism's response to its environment (Semenova & van der Maarel 2000; Hooper *et al.* 2005). FD can be defined as the 'value and range of those species and organismal traits that influence ecosystem functioning' (Tilman 2001). It is suggested to correlate with ecosystem functions such as productivity (Tilman *et al.* 1997; Hooper & Dukes 2004; Petchey, Hector & Gaston 2004) or resilience (Dukes 2001; Bellwood *et al.* 2004). A number of FD indices have been suggested (Villéger, Mason & Mouillot 2008; Petchey, O'Gorman & Flynn 2009; Laliberté & Legendre 2010), with different responses to changes in species composition and functions

(Petchey, O'Gorman & Flynn 2009). Choosing a suitable FD index is therefore a challenge.

Disturbance and plant traits

Disturbance has a number of effects on plant traits such as plant height, seed mass (Lavorel, McIntyre & Grigulis 1999), life-cycle length (Dupre & Diekmann 2001) and physiological traits such as specific leaf area and leaf dry matter content (Quetier, Thebault & Lavorel 2007). Grazing has been shown to increase the abundance of small (low) species with short life cycles (early flowering and seed set) and subsoil regeneration buds (Hadar, Noy-Meir & Perevolotsky 1999), although Dupre and Diekmann (2001) found that grazing negatively affected geophytes (plants with subsoil regenerative buds (Raunkiær 1905)), possibly as an effect of trampling. Hadar *et al.* (1999) showed that clearing of shrubs had a more general effect, increasing the abundance of species of many different functional types while grazing had a more selective effect on mainly plant growth form. High levels of disturbance has also been shown to favour annual plants, decrease age upon first reproduction, decrease height, decrease lateral extension, and increase the potential for long range dispersal (Kleyer 1999). Grazing has further been demonstrated to increase the time for decomposition of dead plant parts as it leads to increased leaf toughness and leaf dry matter content (Quetier, Thebault & Lavorel 2007). Grime (2006) argues that traits can either converge or diverge depending on the kind of disturbance. Convergence is considered to be a response of species in a disturbed community to increase fitness under certain circumstances, e.g. the yearly ploughing of an arable field, which increases abundance of species with early seed production. Divergence can be obtained if a system experiences many different disturbance agents, leading to a large heterogeneity (Grime 2006). Studies of responses in plant functions to disturbances reveal that many communities converge in their traits. The resulting plant communities are often dominated by species with typical disturbance adaptations, such as those described above. The traits that are most affected by disturbance are those that should be used in a functional analysis of disturbance effects.

Disturbance effects on functional composition in sandy grasslands

Using one block of the Rinkaby experimental setup, we studied the effects of soil disturbances on the functional composition and diversity of the plant community during four years following disturbance, and compared the functional response to the response in plant species composition (Paper II). We used functional trait databases and measured traits in field to collect traits related to disturbance, for example leaf dry matter content, specific leaf area, leaf tensile strength, seed mass. We then used a FD index and community weighed trait mean values to analyse the effects of disturbances on functional diversity and composition. We found that the disturbances increased FD and that a functional approach showed that the disturbances moved the system in a compositional direction towards the target communities (as mentioned before, target refers to the restoration target, the plant community that we want to find at the site) functional-wise, but not species-wise. During the first years following disturbances, the disturbed communities were associated with typical disturbance-induced traits such as low seed mass, leaf dry matter content and tensile strength. However, during succession the functional composition moved towards target areas but not completely so (Figure 7). The different treatment plots seemed more alike functionally than species-wise, which could be expected given the similarities in abiotic properties (dry, grazed and high pH). However, there were some fundamental differences in species composition that makes the target communities unique. Unfortunately, the disturbances did not manage to create the target vegetation, although the resulting communities were similar function-wise. Thus, other factors, such as either biotic limitations (such as seed bank and dispersal distance) or unmeasured abiotic properties, could be limiting the establishment of the target vegetation sand steppe. As a complement to the functional analysis we analysed disturbance effects on the community mean Ellenberg indicator values. This approach showed that disturbance increased the abundance of species that are associated with higher nitrogen availability compared to the target habitat. This is an indication of increased availability of nitrogen in the system following disturbance. It leads us to believe that one reason for the disturbed plots not being functionally equivalent to the target plots is an increase in nitrogen availability. In spite of this, we cannot distinguish between this effect and other effects such as seed limitation.

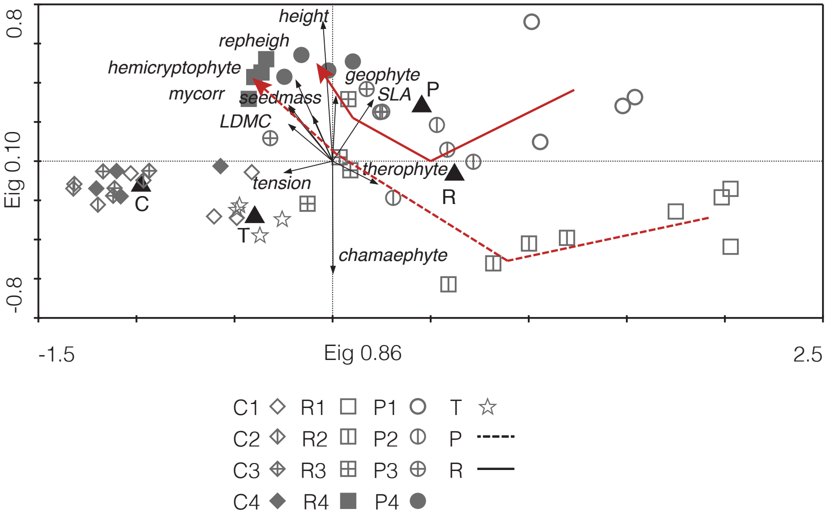

Figure 7 PCA plot showing the plant functional community composition based on community weighed means. Numbers in the legend refers to year after disturbance, C to control plots, P to ploughed plots, R to rotavated plots, T to target plots. Arrow text refers to the function in question. P/R lines indicate treatment development during the course of the experiment.

Disturbance had a positive effect on FD, which indicates that optimal disturbance for functional diversity is not prevailing in the control plots. Although we could not test for differences between target communities and our treatments, the limited data we have indicate that the treated plot FD is more like the one found in target plots than in the control plots. If that is the case, we could state that disturbance is successful in restoring FD, or at least it is a step in the right direction. However, we know from the differences in functional composition between disturbed and target plots that we probably did not restore the same functions as in the target areas.

We conclude that our functional approach is by itself not sufficient to say whether our disturbances are 'correct in function but wrong in species', but we get an indication that abiotic properties are affected in a way different from the target ecosystem.

2.6 AM fungal ecosystem function: carbon allocation

As described earlier, AM fungi is an important organism group in all grassland ecosystems, increasing plant nutrient uptake and possibly host plant water availability and pathogen resistance. In addition to these positive effects on plants, AM fungi play another important role as recipients of photo-assimilated carbon. Any change in the AM fungal community can thus affect the carbon flow through soil. It has been hypothesized that as much as 20-30% of the plant-assimilated carbon that is allocated below ground flows through the AM pathway (Jakobsen & Rosendahl 1990; Drigo *et al.* 2010). This carbon can be bound to AM fungi as e.g. building material for a growing mycelium. The structures of AM fungi (runner hyphae, residual hyphae and spore walls) contain organic molecules of different decomposability such as chitin and triacylglycerides (Bago, Pfeffer & Shachar-Hill 2000), some of which are recalcitrant or at least take weeks or years to decompose (Rillig 2004). AM fungi also produce glomalin, a protein complex which help to aggregate soil particles (Rillig, Wright & Eviner 2002). This protein complex has a slow turnover rate (Rillig 2004). The potential for AM fungi to bind carbon to soil through these molecules of slow decomposability makes the AM symbiosis interesting in a global warming context. Accordingly, we need to learn more about how much carbon that is sequestered in AM systems, and what effects the use of disturbance in shaping ecosystems have on carbon sequestering by AM fungi. As we observed in the part concerning disturbance effects on AM fungal communities (above), many types of soil disturbances have a direct effect on AM hyphal networks, e.g. by destroying the physical structures of AM fungi. Given the flow of carbon through the AM system, disturbance will in turn affect soil carbon sequestration, an important ecosystem service. The biomass of AM fungi, measured as the amount of fatty acid present, decreases as an effect of soil disturbance and thereby the carbon storage potential of AM fungi would be affected as well. Soil mechanical disturbances, e.g. tillage, also decrease the production of glomalin (Borie *et al.* 2006), with possible consequences for soil stability in turn affecting soil carbon decomposability.

Effects on AM fungal carbon allocation in sandy grasslands

At Rinkaby we evaluated the effect of ploughing and rotavation on carbon allocation through a carbon feeding experiment (Paper V). Using plastic hoods we fed isotopically labelled carbon to the vegetation. A fatty acid analysis of the labelled plants and surrounding soil showed that both ploughing and rotavation decreased the amount of AM fungal fatty acid marker concentration in both roots and soil. However, the fungi retained (or decreased in the case of rotavation) their level of ^{13}C enrichment, indicating that the rate of C allocation to AM fungal tissue was unaffected or lowered by disturbance. This means that soil mechanical disturbance decreased the potential for soil carbon storage by AM fungi through reducing the mass of AM fungi that could store carbon (Figure 8). This must be considered an effect of both the disturbance decreasing the abundance of AM host plants, and increase of expectedly non-mycorrhizal plants, and as a direct effect of hyphal destruction or dilution lowering the infection potential of the AM fungal hyphal network. The amount of saprotrophic fungi in soil was not affected by the disturbances and the level of ^{13}C enrichment in them tended to increase in disturbed plots, indicating that the relative importance of saprotrophs increased in disturbed habitats. This study shows clearly that soil disturbance has a negative effect on soil carbon sequestration via AM.

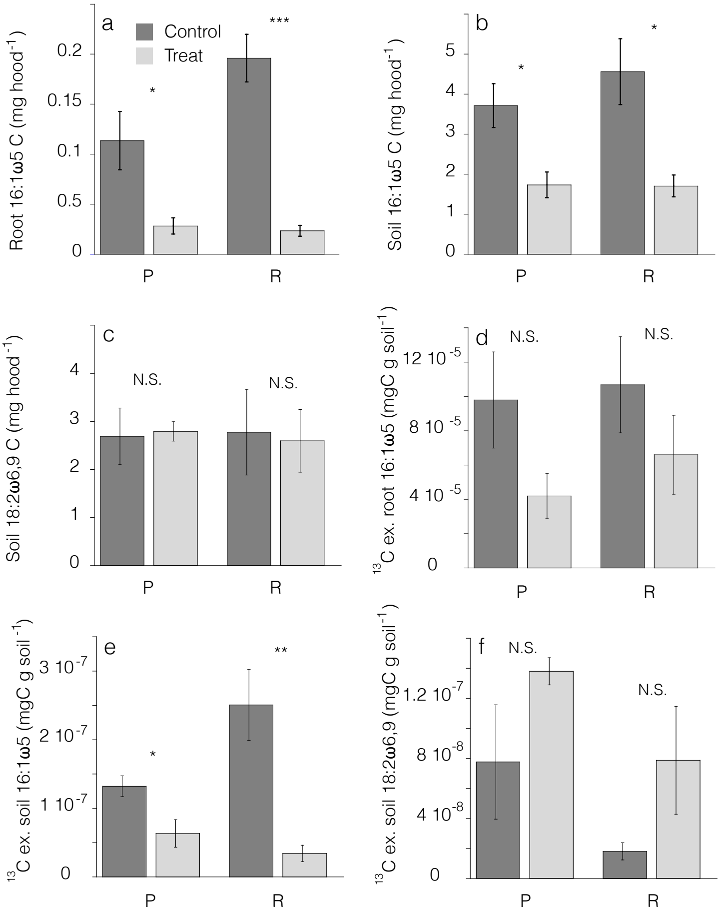

Figure 8 Plots showing responses to different kinds of disturbances for a number of carbon variables. Differences between ploughed plots and the associated control plots (category P), and between rotavated plots and the associated control plots (category R) were tested for. Dark grey bars show control plots and light grey treated plots. a) Total root neutral lipid fatty acid (NLFA) 16:1ω5 carbon per hood, b) soil NLFA 16:1ω5 carbon per hood, c) soil NLFA 18:2ω6,9 carbon per hood, d) ^{13}C excess in root NLFA 16:1ω5, e) ^{13}C excess in soil NLFA 16:1ω5, f) ^{13}C excess in soil NLFA 18:2ω6,9. Root values (a, d) are sums based on each plant species root mass and its corresponding NLFA concentration (a) or δPDB value (d). *$p<0.05$, **$p<0.01$, ***$p<0.001$.

3 LESSONS TO BE LEARNED FROM OUR STUDIES

3.1 What is an optimal disturbance regime for the plant community?

The studies that we performed at Rinkaby shows that applying soil mechanical disturbance will have a large effect on both the number of plant species present and the plant composition of both species and functions. The results could be discussed from the perspective of the theories on biodiversity and disturbance, the IDH (Connell 1978) and the DE (Huston 1979). Our studies encompassed three disturbance intensities: no disturbance, rotavation and ploughing. Out of these, ploughing was the most severe. In paper I we showed that there were only small differences in plant species composition between rotavation and ploughing, but the rotavated plots had higher species richness. In paper II we showed that both disturbance types affected species and functional composition in similar ways. However, as the disturbance regime encompasses more than just the severity of the disturbances, the frequency of these disturbance types should be considered. In our case we have performed a one-time tillage in order to mimic the disturbance type used in these areas as the habitat evolved. Given the unfertile, dry characteristics of the soils, and the cultural history of the area (Emanuelsson 2002), we believe that the area was severely disturbed with an interval of between 10-15 years. In that case we need to wait at least five more years before we could perform the next disturbance and even longer to evaluate the effect of this second disturbance. In paper II we have four years of data, which enables us to follow the succession of the communities. We see clearly that the differences we found between the two disturbances one and two years after disturbance have more or less diminished. This leads us to conclude that the two disturbance types are mainly separated by the initial environment created. Over time, the vegetation from the two disturbances more or less merge in species composition. So, regarding the IDH, we could state that during the first years following disturbance, rotavation seemed to be more optimal for plants in this grassland, but to be able to determine the final effects we would need to follow our plots over an even longer time span.

3.2 Productivity matters

The study was performed in an unfertile, calcareous and dry type of grassland. The high soil lime content make available phosphorous levels very low (Paper I; (Olsson, Mårtensson & Bruun 2009), and may be one limiting factor for plant growth. The DE states that the response of a habitat to disturbance is productivity dependant. Phosphorous levels in Block 1 at Rinkaby was much lower than in Block 2 and 3 (Paper I). For ploughed plots, the richness tended to increase in Block 1 but decreased in Block 2 and 3 the first year after disturbance, followed by a decrease or was unaffected in all blocks during the second year. For rotavated plots, the response was mainly positive in all blocks both years. That is, the productivity gave different patterns of response for the different disturbances. The species that increased in the ploughed plots of Block 1 are probably stress and disturbance tolerant and adapted to high pH. In the other blocks fewer species are adapted to open, dry, heavily disturbed habitats, also showing that low productivity promotes high species richness also in stressed habitats. We conclude that productivity matters, although unlike the relationship hypothesized by the DE, we saw that a disturbance event can have a positive effect not only in high productivity habitats but also in unfertile ones.

3.3 Restoration considerations

The IDH and DE are theories regarding species richness and diversity responses. However, no information or value is given to the identity of species. The sand steppe is a threatened habitat in need of restoration management. Although the main focus in the present thesis is on the general effects of soil disturbance, some conclusion regarding the restorational effects can be drawn. Paper I and II shows that the disturbance types applied do not lead to habitats with a species composition similar to the target habitat. Some target annuals increase as an effect of disturbance (Table 1), but over time the succession in the treated plots seem to move towards the degraded control plots rather than to a target habitat. However, using functional composition to evaluate disturbance gave a somewhat different picture. It seems as if the disturbance pushes the communities in the 'functional direction' of the targets, possibly indicating that the disturbance types applied are in some way positive, or in line with the historical land use in target areas. This suggests that they are optimal, at least when considering the increase in species richness following disturbance. The fact that the species composition in disturbed plots differs from the one in target areas could have several explanations. First, previous studies in calcareous grasslands have shown that the seed bank of the target species is poor in these areas (Bossuyt, Butaye & Honnay 2006). The dispersal distance of these species has also been shown to be short (Eichberg *et al.* 2010). This means that although disturbances are satisfactory, we need to have the right species in the area. We do not know if we have the right seed bank, but we do know that larger populations of the target species are far away from our field site. Secondly, we cannot guarantee that the disturbance types we applied create the correct abiotic properties. We do increase the amount of bare ground, and we do have high pH and low available P levels, but at the same time we affect the availability of N, which in turn seems to have an effect on plant species composition, as shown by the increased incidence of nitrogen thriving plants following disturbance.

Another more general reflection is that we cannot guarantee that the degraded control areas have not entered a so-called 'alternative state' (Hobbs *et al.* 2006; Hobbs, Higgs & Harris 2009). That is, although we would do all things exactly as done in historical times, other factors such as nitrogen deposition and acidification will have changed compared to what we consider being the original state. So, the response may very well be different from what we expect, and feedbacks in the system will also be different from what they were in the original habitats (Suding, Gross & Houseman 2004). This could e.g. explain the development of the functional composition in the treated plots diverging from both control and target plots, and why we get weedy grasses establishing in the treated plots. Basically, we can say that using ploughing and rotavation for restoring sand steppe is not successful if the right seed bank is not present or if the abiotic properties diverge from the target. This could for example be the case if calcium levels are not raised with the treatment (because the calcium layer is deeper down than the treatment reach), or if disturbance increases the level of available nutrients.

From a restorational perspective the results of the AM fungal taxa studies are of little guidance as we do not know about which species or genotypes that are threatened. However, the AM fungal community may prove to have an effect on threatened plant species as a high AM fungal diversity promotes a high plant diversity (van der Heijden *et al.* 1998). Future research in this area should for example study if restoring a specific habitat requires that we restore the AM fungal community as well, or just the function of AM fungi as such.

3.4 Functional considerations/thoughts

The result from the carbon study (Paper V) presents one type of functional information. The lowered levels of AM fungi due to disturbance signify that disturbance is negative for carbon sequestration in AM fungal structures; the total flow of carbon through AM fungi (per surface area) decreases. To what extent this affects carbon sequestration on an ecosystem level is less clear. However, soil mechanical disturbance destroys plant individuals and increases the speed of decomposition due to the destruction of plant material and aeration of compact soils. Soil mechanical disturbance has seldom been argued to be positive for soil carbon sequestration compared to e.g. low/no till systems. If there is less carbon entering the system via plants, and less roots for AM fungi to colonize, then the amount of carbon entering AM systems will decrease. In our study, the rate of allocation was not affected, but a lowered AM fungal abundance and no effect on the rates still signifies that the total amount of carbon in the soil will decrease as an effect of disturbance.

Recalling that disturbance increased the occurrence of some threatened annual plant species, we realized that there is a conflict of interest at Rinkaby. Basically, we see a conflict between two important goals: carbon sequestration and biological conservation. If we want to sequester carbon we cannot use mechanical disturbance over large areas. However, without the disturbance we will never be able to keep or restore our sand steppe areas or other disturbance-dependant habitats. The problem could seem trivial in a global perspective, given the small area where sands steppe potentially could be present, but it points out which types of considerations must be made in ecological management.

4 CONCLUSION

This thesis has demonstrated that altering the disturbance regime in sandy grasslands have a large impact on the species richness and composition of plant and AM fungal communities. These results fit well within the general theoretical framework, but also include some new experiences.

Both ploughing and rotavation had positive effects on the plant species richness although different species preferred different disturbances. If one wants to manage such grassland in a way which increases the number of threatened species, ploughing and rotavation could both be employed, but only if the abiotic properties are within the limits of those that you would find in the target habitat, and if the desired species are present nearby or in the seed bank. If these conditions are not fulfilled, then ploughing and rotavation could have detrimental effects such as paving the way for weedy grasses. More severe types of disturbances, for instance deep ploughing, digging, and topsoil removal, should be tested for comparison. We have also learnt that using a functional approach when evaluating vegetation management gives additional answers compared to the species focused approach alone. However, more studies in natural environments are needed before we know which traits to use, and which environmental variables to measure, in order to be able to interpret the results with more accuracy, and to compare the results from different environments. Combining the results from both species focused- and function focused investigations is a potentially powerful approach to describe restoration success. Such tools are essential to develop given the large need for biodiversity management posed by changing land use and climate.

AM fungal communities respond differently to disturbance depending on disturbance used and habitat type. Large-scale severe disturbance decreased the number of taxa, while small scale had no influence on the number of taxa present. These results highlight the different effects of disturbance depending on the dynamics of the disturbances. 454 sequencing should be used further in AM fungal research given the importance of acquiring quantitative abundance information. The abundance data generated by this method could then be used in conjunction with functional information to better describe the importance and functionality of AM fungi in natural environments. In Rinkaby we saw that decreased AM fungal abundance had a large influence on a potentially important ecosystem function, namely the amount of carbon fixed into AM fungal structures. This could have an influence on the amount of carbon fixed into soil, although to what extent this process is important for total carbon fixation in soil still remains to be studied. Still, the result points towards potential conflicts between biodiversity conservation on one hand and important ecosystem functions, such as carbon sequestration, on the other.

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SVENSK SAMMANFATTNING

Enligt ordboken betyder störning något som är avvikande från det normala. I den ekologiska begreppsvärlden är det tvärtom en del av det normala. Störning är en förutsättning för att många kulturmarker med hög biodiversitet ska kunna skapas och bevaras. I denna avhandling undersöktes hur markstörning i form av plöjning och harvning i torra gräsmarker påverkar mångfalden av växter och marksvampar i symbios med dessa växter, s.k. mykorrhizasvampar. Störningens påverkan på flödet av kol från växter till markens mikroorganismer undersöktes också.

Störning som ekologiskt begrepp syftar på något som dödar eller förstör levande varelser. Exempel på detta kan vara klippning av en gräsmatta, en ko som trampar sönder marken, trädfällning eller plöjning av en åker. Trots denna destruktiva definition är störning en naturlig del av alla ekosystem. Faktum är att utan störning skulle inte bilder av ängar dignande av färgglada blommor och lystna insekter finnas i våra sinnen. En äng skulle växa igen till skogsmark om inte någon eller något hindrade buskar och träd från att komma in. Arter knutna till ängar kräver mycket ljus och utan störning skulle de bli utträngda av växter som växer sig höga och skuggar. Störningen gör att dessa mer konkurrenskraftiga arter tas bort och möjliggör för de arter som är bättre på att klara sig i miljöer som får mer ljus och kanske därmed är varmare, torrare och blåsigare än miljön i skogen. För att maximera antalet arter i ett landskap krävs att det finns en blandning av olika förutsättningar; öppna trädlösa marker, skogsmarker, grustag, våtmarker.

Störning behövs alltså, men för mycket störning kan vara negativt för mångfalden av arter, biodiversiteten. Inom jordbruk utnyttjar man med framgång detta genom att använda sig av plöjning för att ta bort ogräs – eller för att beskriva det i ekologiska termer – för att minska antalet växtarter på en åker. Varken för lite eller för mycket störning är bra för biodiversiteten. Problemet är att vi inte riktigt vet hur mycket störning som är optimalt inom olika områden. Vi vet inte heller om man kan ersätta en typ av störning, t.ex. kotramp, med en annan störning som t.ex. någon typ av mekanisk markbearbetning.

Sandiga, kalkrika gräsmarker i östra Skåne har traditionellt brukats med mycket låg intensitet då sandiga jordar med lite näring är svårodlade. Marker av denna typ har troligen planterats med råg och bovete och efter det lämnats obrukade, "i träda", mellan 10 och 15 år. Kraftiga markomrörningar kombinerat med lång träda och hög kalkhalt har skapat en speciell naturtyp som kallas sandstäpp. Sandstäpp hotas idag av brist på markstörning och om inget görs kommer detta leda till att sandstäpperna så småningom växer igen. Dessutom försvinner kalken ur marken på grund av försurning och näringshalterna i marken ökar på grund av kvävenedfall. Både försurning och kvävenedfall härstammar från mänsklig industriell aktivitet. Till följd av minskad störning och luftutsläpp är sandstäppen idag på stark tillbakagång och många arter knutna till denna naturtyp är på väg att försvinna från Sverige.

Denna avhandling handlar om hur återinförande av markstörning på kalkrika sandmarker påverkar växter knutna till sandstäpp och vidare hur det påverkar mykorrhizasymbiosen och kolets kretslopp, samt om man genom denna störning kan motverka försurning och förhöjda kvävehalter. Vi plöjde och harvade om vartannat på Rinkaby skjutfält utanför Kristianstad i Skåne och utvärderade effekterna av detta under fyra års tid.

Effekter av plöjning och harvning på växtsamhällen

Störningen i experimentet på Rinkabyfältet hade ingen effekt på mängden kalk i marken men en liten ökning av tillgängligt fosfor kunde ses som en effekt av harvning. En minskning av kväve i form av ammonium blev en följd av störningen. Detta betyder att störning i form av plöjning och harvning inte höjer pH i vårt försöksområde och att vi istället riskerar att få mer tillgängliga näringsämnen i marken. Detta är inte positivt ur sandstäppssynpunkt då arter knutna dit kräver högt pH och låga näringshalter.

Två år efter störningen kunde vi se att vissa rödlistade eller ovanliga arter, främst annuella sådana (ettåriga växter), hade ökat i de ytor som var störningsbehandlade samt att artrikedomen hade gått upp. Efter fyra år hade effekterna av störningen börjat avta och de störda ytorna började återgå till hur de såg ut innan störningen. De rödlistade annuella arterna var då inte längre vanliga i störda ytor. Dock kunde man då se att ett rödlistat, flerårigt gräs hade etablerat sig i harvade ytor. Artrikedomen var fortfarande högre i störda ytor än i omkringliggande områden, med flest arter i harvade ytor. Tyvärr hade också näringsgynnade växtarter som kvickrot och storven etablerat sig i störda ytor.

Sammantaget hade störningen en viss positiv effekt genom att den ökade förekomsten av rödlistade annueller under de första åren, men tyvärr verkar också störningen frisätta näring i marken så att över tid återgår de störda områdena till att se ut som de gjorde innan störning, snarare än att likna sandstäppsområden. Plöjning och harvning är alltså inte en bra metod för att återskapa sandstäppsmiljöer i dessa områden eftersom det finns en risk att näringstillgängligheten ökar. Detta kan framförallt vara en risk i områden där det har bildats ett lager av matjord med bunden näring som frigörs vid en markbearbetning.

Mykorrhiza – växternas förlängda arm – påverkas negativt av störning

Marksvampar i symbios med växter, s.k. mykorrhizasavampar, är en grupp organismer som finns i ca 80% av alla jordens landlevande växter. I gräsmarker finns det en typ av mykorrhiza som lever inuti växtens rötter med trädliknande organ för utbyte av ämnen (arbuskler) och med blåsor fyllda av energirika oljor som energireservoar. I mykorrhizasymbiosen lever svampen i symbios med växten och får kol i utbytet mot att den förser värden med näring. Svampen kan, tack vare sitt stora hyfnätverk, mycel, ta upp näring från en större jordvolym än vad växten själv klarar. Som en mottagare av kol blir svampen en del av kolcykeln och därför blir det intressant att studera effekter av störning dels på själva svampsamhället och dels på hur kolflödena genom symbiosen förändras med störning. Mykorrhizasvampar är känsliga för markstörning eftersom deras mycel förstörs av den fysiska bearbetningen, hyferna slits helt enkelt sönder och därmed bryts flödena i dem.

I Rinkaby såg vi att plöjning minskar förekomsten och antalet arter av mykorrhizasvampar, samt ändrar artsammansättningen. Dessa effekter sågs två år efter störningen. I en annan studie på ett sandfält på norra Själland gjorde vi en småskalig störning om ca 20 cm i diameter. Här fann vi inga skillnader i förekomst, sammansättning eller artantal av mykorrhizasvampar fyra månader efter störning. Trots att platserna för undersökning och försöksupplägg skiljer sig åt mellan de båda försöken kan vi dra slutsatsen att störningens skala, alltså hur stort område som störs verkar spela en fundamental roll för effekten av markstörning på mykorrhizasamhällen. Däremot har vi ingen aning om vilken effekt en förlust av arter eller ett skifte i svamparter har på symbiosens funktion, d.v.s., hur växtsamhället eller flödet av näringsämnen påverkas. Vi såg dock att kolflödet genom svampen inte ändrar sig beroende på om det är stört eller inte. Detta leder till att den totala mängden kol som går in i mykorrhizastrukturer i en plöjd yta minskar eftersom förekomsten av mykorrhiza minskar kraftigt. Detta i sin tur kan ha en effekt på den mängden kol som kan lagras in i marken eftersom mykorrhizans fysiska strukturer tar lång tid att bryta ner. I förlängningen kan detta påverka hur effektiva gräsmarker är på att binda kol i marken, något som är en viktig ekosystemfunktion eftersom det kan hjälpa till att motverka effekterna av dagens höga mänskliga koldioxidutsläpp.

Sammanfattningsvis kan man konstatera att markstörning i sandmarker har både positiva och negativa effekter. Att plöja och harva ökar antalet växtarter och ökar förekomsten av rödlistade annueller kopplade till sandstäpp. Samtidigt finns det riskt för ökad näringstillgång i marken och växtsamhället visar få tecken på att utveckla sig mot det ur naturvårdssynpunkt eftertraktade habitatet sandstäpp. Antalet arter av mykorrhizasvampar kan minska och därmed också potentiellt minska inlagringen av kol i mark. Uppenbart är plöjning och harvning inte rätt metod för att återskapa sandstäppsmiljöer i detta område utan andra störningar som inte höjer näringshalten kan visa sig vara mer framgångsrika. Exempelvis kan man ta bort den näringsrika ytjorden eller gräva gropar så att bar sand blir exponerad. Dock kan man inte räkna med att man ska både kunna bevara sandstäpp och att effekten på mykorrhiza ska vara positiv. Det finns alltså en motsättning mellan att bevara sandstäpp och att lagra in kol i marken. Störning är en metod att bevara ett kulturlandskapet med öppna fält dignande av blomsterprakt, men det inte lika lätt att säga vilken störning eller hur ofta man ska störa för att återskapa de miljöer som idag är hotade. Det kan bara fortsatta studier inom området ge svar på.

Doctoral theses published at the Department of Ecology, Plant Ecology and Systematics, Lund University

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