PLANTS AND MYCORRHIZAL FUNGI
IN WIND EROSION CONTROL

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SUMMARY

Soil erosion by wind is a natural process which has been enhanced in recent years by anthropogenic activities such as the destruction of native vegetation and inadequate agricultural practices, particularly in arid and semi-arid regions. Increased wind erosion often results in land degradation, with adverse effects on soil resources, agricultural productivity, air quality, human health and climate. A common strategy to restore degraded soils is to re-establish a vegetation cover, because plants are able to protect the soil from wind erosion in various ways, e.g. by sheltering the soil from the erosive force of the wind and by stabilizing the soil with their roots. Most plants form symbiotic associations with mycorrhizal fungi which have the potential to improve both plant growth and soil aggregation. Mycorrhizal fungi are therefore expected to be of key importance for wind erosion control. However, their effect on wind erosion has never been quantified and the mechanisms involved in the interactions between vegetated surfaces and wind are still poorly understood.

The present thesis experimentally addresses selected aspects of using plants and mycorrhizal fungi in wind erosion control, with emphasis on alpine plant species. The overall aim of the thesis is to improve the understanding of the mechanisms by which plants and mycorrhizal fungi influence wind erosion. The thesis contains three wind tunnel studies and a plant growth experiment.

The focus of the first study (chapter 2) is on the above-ground processes by which vegetation protects the soil against wind erosion. The test section of a laboratory wind tunnel was furnished with 8 m of plant trays to perform experiments with a bare sand surface and three canopy densities of Perennial Ryegrass (*Lolium perenne*). The use of live plants allowed mimicking the behavior of a naturally grown vegetation canopy more accurately than any previous wind tunnel study, since vegetation canopies have traditionally been simulated by plant imitations. The aim of this study was to compare the total sediment mass flux $Q$, the vertical distribution of sediment mass flux and the PM$_{10}$ concentration in the air stream in the different plant configurations. The results suggest that both total sediment mass flux $Q$ and PM$_{10}$ concentration in the air
decreased exponentially with increasing canopy density. In the large-density canopy (frontal area index \( \lambda = 0.58 \)), \( Q \) and PM\(_{10}\) concentration were reduced to 0.01% and 0.4% compared to the unplanted configuration. In the medium-density canopy (\( \lambda = 0.16 \)), \( Q \) and PM\(_{10}\) concentration were reduced to 6.6% and 48.5%. In the small-density canopy (\( \lambda = 0.03 \)), however, \( Q \) and PM\(_{10}\) concentration were increased to 117.5% and 145.6%. This is attributed (i) to elevated shear stress on the sand bed, caused by flow acceleration around the tussocks and vortical structures in their lee, and (ii) to oscillating movements of the grass blades at the ground surface. The vertical profiles of sediment mass flux in the medium- and large-density canopy strongly deviated from the exponential decay curve of the unplanted configuration, showing a local maximum at approximately twice the canopy height.

The second study (chapter 3) refers to the same wind tunnel experiments as the first study, but presents observations on spatial patterns of sediment deposition within the small-, medium- and large-density grass canopy. Colored quartz sand was used to identify and locate areas experiencing net deposition. In the small- and medium-density canopy, the wake areas downstream of the tussocks were the main locations of sediment deposition. In the medium-density canopy, these wedge-shaped wake deposits overlapped with the adjacent downstream tussocks, while in the small-density canopy they did not, indicating a wake-interference flow and an isolated roughness flow, respectively. In the large-density canopy, only few sand grains were entrained by the wind and they were deposited mainly within reach of the grass tussocks. The deposited sand grains were evenly distributed around the tussocks, without pronounced accumulations on their upstream, downstream or lateral sides, suggesting a skimming flow regime. The fraction of the sand surface which was potentially exposed to erosion (\( EP_{nc} \)) was substantially smaller than the area which was not covered by grasses. It accounted for 67-78% of the non-covered surface in the small-density canopy, and for 44-77% in the medium-density canopy. This finding indicates that wind erosion models overestimate the sediment source area if they approximate the erodible area with the surface not covered by roughness elements.

The focus of the third study (chapter 4) is on the below-ground processes by which mycorrhizal fungi and plant roots protect the soil against wind erosion. It addresses the question of whether mycorrhizal fungi can decrease the soil susceptibility to wind.
erosion and thereby increase the protective effect of newly seeded plants. Wind tunnel experiments were conducted with mycorrhizal and non-mycorrhizal root balls of Perennial Ryegrass (*Lolium perenne*) and Kidney Vetch (*Anthyllis vulneraria ssp. alpestris*). The entire root balls were exposed to an erosive wind event, and then analyzed for their total root length and the percentage of root length colonized by mycorrhizal fungi. For both plant species, the wind-induced soil loss was found to decrease significantly with increasing percentage of root colonization by mycorrhizal fungi. The mean soil loss of non-mycorrhizal control samples was more than twice as high as the one of mycorrhizal samples for *A. vulneraria*, while no significant difference was observed for *L. perenne*. These results are all the more remarkable because there was no mycorrhiza-induced plant growth enhancement. On the contrary, mycorrhizal plants had significantly smaller root systems than non-mycorrhizal plants in both species. Above-ground biomass was significantly smaller in mycorrhizal plants than in non-mycorrhizal plants for *L. perenne*, but only slightly smaller for *A. vulneraria*. This study demonstrates that mycorrhizal fungi are able to help newly seeded plants to decrease the wind erodibility of soil, even in cases when they do not increase plant growth.

The fourth study (chapter 5) focuses on the question of whether mycorrhizal fungi are able to improve plant establishment under adverse soil conditions. In a laboratory plant growth experiment, seedlings of four alpine grass species were subjected to extreme nutrient and water stress. The grasses were grown on four types of nutrient-depleted mineral sand, inoculated with a mycorrhizal fungus (*Glomus intraradices*) and additionally subjected to a drought treatment. After a growth period of three months, plant survival, above-ground biomass and mycorrhizal colonization were assessed. The proportion of inoculated grass tussocks that established a symbiosis was significantly lower under drought-conditions (23-58%) than under non-drought conditions (33-100%). The proportion of surviving tussocks was also significantly lower under drought conditions than under non-drought conditions. It decreased from 86% to 38% in the inoculated tussocks, and from 72% to 32% in the non-inoculated tussocks. Inoculation of *G. intraradices* had no significant effect on either plant survival or above-ground biomass. However, there was a trend towards higher survival and biomass in inoculated tussocks compared to non-inoculated tussocks.
The present four studies demonstrated in several ways that plants and mycorrhizal fungi have the potential to substantially reduce wind erosion. However, they also revealed limitations of using plants and mycorrhizal fungi in wind erosion control, e.g. the enhancement of wind erosion below a critical canopy density, the negative impact of drought conditions on mycorrhiza formation and the dependence of the mycorrhizal effect on the host plant species.


Die erste Studie (Kapitel 2) fokussiert auf die oberirdischen Prozesse, mit denen Pflanzen den Boden vor Winderosion schützen. Die 8 m lange Teststrecke eines Labor-Windkanals wurde mit bepflanzbaren Kisten beladen um Experimente mit drei verschieden dichten Bepflanzungen aus Englischem Raygras (Lolium perenne) sowie mit
unbepflanzten Sandoberflächen durchzuführen. Im Gegensatz zu früheren Windkanal-Untersuchungen, in denen üblicherweise Pflanzen-Imitate verwendet wurden, kamen in der vorliegenden Studie lebende Pflanzen zum Einsatz, mit denen das Verhalten einer natürlichen Pflanzendecke besser simuliert werden konnte. Das Ziel der Experimente bestand darin, den totalen Sediment-Massenfluss \( Q \), die vertikale Verteilung des Sediment-Massenflusses sowie die PM\(_{10}\)-Konzentration in der Luft in den verschiedenen Pflanzen-Konfigurationen zu vergleichen. Die Resultate deuten darauf hin, dass sowohl \( Q \) als auch die PM\(_{10}\)-Konzentration in der Luft mit zunehmender Pflanzendichte exponentiell abnehmen. In der stark bepflanzten Konfiguration wurde \( Q \) auf 0.01% reduziert und die PM\(_{10}\)-Konzentration auf 0.4% im Vergleich zur unbepflanzten Konfiguration. In der mittelstark bepflanzten Konfiguration wurde \( Q \) auf 6.6% reduziert und die PM\(_{10}\)-Konzentration auf 48.5%. In der schwach bepflanzten Konfiguration hingegen wurde sowohl \( Q \) als auch die PM\(_{10}\)-Konzentration auf 117.5% bzw. 145.6% erhöht. Dies kann damit erklärt werden, dass auf der Sandoberfläche lokal erhöhte Scherspannungen auftraten als Folge von erhöhten Windgeschwindigkeiten seitlich der Grasbüschel und Turbulenzen in deren Windschatten. Ausserdem wurde beobachtet, wie die Grasalme durch vibrierende Bewegungen auf der Sandoberfläche Erosion verursachten. Die Vertikalprofile des Sediment-Massenflusses in der stark und mittelstark bepflanzten Konfiguration zeigten ein lokales Maximum auf doppelter Pflanzenhöhe und wichen damit deutlich ab vom Profil der unbepflanzten Konfiguration, bei dem der Massenfluss mit zunehmender Höhe exponentiell abnahm.

Die zweite Studie (Kapitel 3) bezieht sich auf die gleichen Windkanal-Experimente wie die erste Studie, fokussiert jedoch auf die räumlichen Verteilungsmuster der Sandablagerungen innerhalb der schwach, mittelstark und stark bepflanzten Konfiguration. Mit Hilfe von gefärbtem Quarzsand konnten Zonen identifiziert werden, in denen Netto-Deposition auftrat. In der schwach und mittelstark bepflanzten Konfiguration lagerte sich der Sand vor allem im Windschatten der Grasbüschel ab. In der mittelstark bepflanzten Konfiguration überlagerten diese trichterförmigen Depositions-Zonen die windabwärts benachbarten Grasbüschel, während sie in der schwach bepflanzten Konfiguration nicht bis zu den benachbarten Grasbüscheln reichten. Diese Beobachtung deutet darauf hin, dass in den beiden Konfigurationen verschiedene Strömungs-Regimes herrschten, und zwar ein sogenannter wake-

durch Bildung einer Symbiose mit Mykorrhizapilzen in der Lage sind, die Resistenz des Bodens gegen Winderosion zu erhöhen, sogar in Fällen wo sich dadurch das Pflanzenwachstum nicht verbessert.


1 General Introduction

1.1 Background

1.1.1 Wind erosion

The process of wind erosion involves the entrainment and transport of soil particles by the action of wind, as well as subsequent deposition. Wind erosion is a geological and climatic phenomenon which mostly proceeds unnoticed over long periods of time in arid and semi-arid regions, where the ground surface typically lacks a continuous vegetation cover (Shao, 2008). However, wind erosion can also produce most spectacular outcomes such as dust storms or shifting sand dunes. Wind erosion is an important mechanism for the formation and evolution of sand seas and the long-range transport of sediment from continent to ocean (Shao, 2008). On geological time scales, it contributes greatly to the global mineral and nutrient circulation and to the evolution of surface topography (Greeley and Iversen, 1985). Large amounts of minerals and organic matter are carried with the dust particles and redistributed around the world. Particles suspended in the atmosphere (aerosols) play an important role in the climate system, as they influence the atmospheric radiation balance directly, through scattering and absorbing various radiation components, and indirectly, through modifying the optical properties and lifetime of clouds (Shao, 2008). The global dust emission is estimated to amount to 3000 Mt yr$^{-1}$, with estimates varying between 1’000 and 10’000 Mt yr$^{-1}$ (Duce et al., 1991).

The occurrence of wind erosion is the result of a complex interplay between a variety of factors, including soil properties, atmospheric conditions and land surface topography. In general, wind erosion occurs when the erosivity of the wind exceeds the erodibility threshold of the surface (Okin et al., 2006). The erosivity of the wind, i.e. the potential of the wind to cause erosion, is typically quantified by the friction velocity of the wind, a measure of the shear stress transported downwards to the surface by the wind (Gromke and Burri, 2011). The erodibility of the surface, i.e. the potential of the surface to be eroded, is typically related to the threshold friction velocity, the friction velocity...
below which erosion will not occur. The threshold friction velocity of soils is largely determined by their texture, moisture, and the amount of coverage by vegetation, surface crusts or non-erodible elements such as rocks. Bagnold (1941) distinguished three modes of aeolian sediment transport, each depending primarily on the size of the particles. Suspension refers to the floating motion of dust-sized particles (<70 µm) that are light and therefore easily kept in the atmosphere over relatively long distances, ranging from a few meters to thousands of kilometers. Saltation refers to the hopping motion of sand-sized particles (70-500 µm), in which they follow nearly parabolic trajectories. Typical saltation distances are in the order of a few meters with maximum trajectory heights of 0.1-0.2 m. Surface creep refers to particles that are too heavy to be lifted by the wind (>500 µm) and therefore are pushed or rolled along without losing contact with the ground.

Human activities such as excessive clearing of native vegetation, overgrazing and inadequate agricultural practices can substantially increase soil erodibility. In the recent history, such activities have caused profound disturbances of soils and vegetation, resulting in increased frequency and intensity of wind erosion in many parts of the world with adverse effects on soil resources, crop productivity, environmental quality, human health and climate (Lal, 1994; Tegen and Fung, 1995; Montgomery, 2007). During the 1930s, for example, a period of prolonged drought coupled with intensive agricultural activities lead to severe dust storms in the Great Plains of the United States, which became known as the “Dust Bowl” (Schubert et al., 2004). Accelerated wind erosion often results in land degradation, because it preferentially removes fine soil particles which hold most of the nutrients and organic matter, leaving coarser and less fertile material behind. This process decreases soil productivity and soil water-holding capacity, changes the composition and spatial patterns of vegetation, and potentially causes a loss in biodiversity (Okin et al., 2006; Ravi et al., 2010). Furthermore, wind erosion processes are responsible for the movement of sediments and agricultural pollutants into water bodies, thereby affecting scarce fresh water resources in drylands (Lal, 2001). Wind erosion also causes air-quality hazards which pose a threat to public health. Mineral aerosols can cause respiratory diseases, and often, they are associated with various health-threatening contaminants, including metals, pesticides, dioxins and radionuclides (e.g. Chi et al., 2008; Wu et al., 2010). Besides these negative effects on
human health, aeolian dust also affects the global climate and hydrological-biogeochemical cycles (Ramanathan et al., 2001; Hui et al., 2008).

Due to these negative impacts on environmental quality and human health, land degradation in drylands is regarded as one of the major environmental issues of the 21st century (MEA, 2005; UNCCD, 1994; UNEP, 1995). With the climate change scenarios predicting increased aridity and higher frequencies of droughts in drylands around the world, the impact of aeolian soil erosion processes on land degradation may become even stronger in the future (Ravi et al., 2010). Therefore, it is of great importance to develop and implement sustainable strategies against wind erosion. The research community is challenged to improve the knowledge about wind erosion processes, and in particular, to identify the responsible factors, to quantify the risks of wind erosion on different temporal and spatial scales, and to develop sustainable strategies for wind erosion control (Shao, 2008).

1.1.2 Plants in wind erosion control

Plants play a key role in wind erosion control measures all over the world, because they are able to protect the soil in various ways. The above-ground parts of vegetation modulate wind erosion processes primarily through three mechanisms: i) vegetation can shelter the soil from the force of the wind by covering a fraction of the surface and providing lee-side wakes in which the average wind velocity and friction velocity are substantially reduced, ii) vegetation can extract momentum from the wind, thus reducing the erosivity of the wind, and iii) vegetation can trap windborne particles, thereby reducing total sediment flux and providing loci for sediment deposition (Wolfe and Nickling, 1996). Plants protect the soil also by below-ground mechanisms, i.e. by stabilizing the soil structure and by affecting near-surface soil and air humidity (Namikas and Sherman, 1995; Lyons, 2002; Eldridge and Leys, 2003; Kimura et al., 2006). Plant roots stabilize soil structure by enmeshing individual soil particles and by releasing glue-like exudates, thereby contributing to the formation of stable soil aggregates (Tisdall and Oades, 1982). Wind erosion has been shown to decrease significantly with increasing level of soil aggregation (Eldridge and Leys, 2003). Soil and air humidity are important determinants of the erodibility of the soil and the
erosivity of the wind, respectively, which plants can affect through various mechanisms, including evapotranspiration, changes in near-surface air temperature and wind velocities (e.g. McKenna Neuman, 2003; Cornelis et al., 2004; Ravi et al., 2006; McKenna Neuman and Sanderson, 2008).

Humans have made use of these beneficial plant effects to protect the soil against wind erosion for hundreds of years. Vegetation - in the form of cover crops, wind strips or postharvest residues - is traditionally used as a means of protecting agricultural soils from wind erosion (Wolfe and Nickling, 1996). On grazing land, farmers try to minimize and prevent wind erosion by appropriate land-use practices such as rotational grazing, limiting livestock numbers and fencing highly erosive areas. Early research on the use of plants in wind erosion control focused on developing and evaluating strategies for agricultural soils, probably because these soils are especially susceptible to wind erosion and because the consequences are particularly evident (e.g. Siddoway et al., 1965; Greb, 1979; Skidmore et al., 1979; Tibke, 1988). Other situations where humans have traditionally used vegetation in wind erosion control include planting trees or shrubs as windbreaks to protect roads and fields, or to stabilize mobile sand surfaces in coastal and arid regions (Wolfe and Nickling, 1996).

1.1.3 Mycorrhizal fungi in wind erosion control

While the early research on the role of plants in wind erosion control has primarily aimed at developing specific practical solutions to protect cultivated land or human infrastructures, the focus of recent research has shifted towards a more holistic and conceptual perspective. A large number of recent studies deals with ecological interactions and feedbacks between wind erosion, vegetation, climate and degradation processes on different spatial and temporal scales, focusing not only on cultivated land but also on grazing land and natural ecosystems (e.g. Breshears, 2009; Field et al., 2009; Ravi et al., 2010). In this context, it has been recognized that the loss of protective vegetation cover is often accompanied or preceded by changes in physico-chemical and biological soil properties, such as soil structure, plant nutrient availability, organic matter content and microbial activity (Jeffries et al., 2003). With regard to wind erosion control, it has thus been acknowledged to be of critical importance to address not only
vegetation cover, but also these biological and physico-chemical soil qualities (Miller and Jastrow, 1992; Jeffries and Barea, 2001). In particular, wind erosion processes have been found to reduce the inoculum potential of mutualistic microbial symbionts that are key organisms in governing the cycles of major plant nutrients and hence in sustaining the vegetation cover in natural habitats (Requena et al., 2001). There are several groups of symbiotic rhizosphere micro-organisms, such as mycorrhizal fungi, plant growth promoting bacteria or dark septate endophytes (Jeffries et al., 2003; Rodriguez et al., 2009).

In terms of ubiquity and partnerships throughout the plant kingdom, mycorrhiza is the most significant plant-microbe symbiosis and the study of its ecology has thus a long tradition (Jeffries et al., 2003; Smith and Read, 2008). Since several years, there is an increasing interest in making use of mycorrhizal fungi to improve revegetation processes in desertified ecosystems, by inoculating the soil or seedlings with mycorrhizal propagules, or by implementing soil managing practices that reduce the loss of mycorrhizal fungi (Miller and Jastrow, 1992; Perumal and Maun, 1999; Enkhtuya et al., 2003; Estaun et al., 2007).

Mycorrhizal fungi form symbiotic associations with the roots of most terrestrial plant species and they are a keystone to the productivity and diversity of natural plant ecosystems (Smith and Read, 2008). They improve the water and nutrient supply of their hosts, protect them against pathogens, toxic compounds and herbivores, and are a driving force of plant successional processes (Van der Heijden et al., 1998; Smith and Read, 2008). Furthermore, mycorrhizal fungi essentially contribute to the process of soil aggregation by various mechanisms on different hierarchical levels (reviewed in Rillig and Mummey, 2006). Two key mechanisms are i) physical stabilization through entanglement of individual soil particles by vast hyphal networks, and ii) chemical stabilization by glue-like fungal exudates (Tisdall and Oades, 1982; Miller and Jastrow, 1990; Wright and Upadhyaya, 1998; Bearden and Petersen, 2000). Mycorrhizal hyphae physically stabilize the soil in a similar way as roots, but at a smaller scale, i.e. they enmesh and entangle soil primary particles, organic materials and small aggregates, thereby facilitating macro-aggregate formation (Tisdall and Oades, 1982; Rillig and Mummey, 2006). With regard to chemical stabilization by mycorrhizal exudates, several compound groups have been suggested to contribute to the binding and coating
of soil aggregates due to their glue-like and hydrophobic characteristics, such as mucilages, polysaccharides and other extracellular compounds, hydrophobins and related proteins, as well as glomalin or glomalin-related soil proteins (e.g. Chenu, 1989; Tisdall, 1991; Tagu et al., 2001; Rillig, 2005). Among these compounds, the glomalin-related soil proteins (GRSP) have recently gained particular attention (Wright and Upadhyaya, 1996; Rillig, 2004). Several studies have found a strong positive correlation between GRSP and soil aggregate stability for a wide variety of different soils (e.g. Wright and Upadhyaya, 1998; Wright and Anderson, 2000; Harner et al., 2004; Wright et al., 2007; Bedini et al, 2009). However, this evidence remains correlative, and the mechanisms involved are still unclear (Rillig and Mummey, 2006). GRSPs are hypothesized to act as a glue with hydrophobic properties, perhaps sealing soil pores and thereby slowing down penetration of water, but direct biochemical evidence for this is lacking (Rillig and Mummey, 2006).

Due to these effects on soil structure and plant physiology, mycorrhizal fungi offer a twofold benefit with regard to wind erosion control, i.e. they potentially improve both soil stability and plant growth. However, although this potential is widely recognized, it is difficult to address experimentally. Similarly to the effects of plants, the effects of mycorrhizal fungi on wind erosion can hardly be separated from the various other factors affecting wind erosion, e.g. humidity and temperature of the soil and air, surface topography, as well as soil texture, composition, aggregation and crusting (Shao, 2008). Furthermore, the effects vary greatly among different plant and fungal species, and even within the same species, they depend on the ecotype as well as on the biotic and abiotic context. Therefore, field studies addressing the effects of plants and mycorrhizal fungi on wind erosion produce highly site-specific data, which makes it difficult to draw general conclusions. One way to simplify the system and to control specific factors is to perform experiments in a wind tunnel.

1.1.4 Wind tunnel research

Wind tunnels are an essential and commonly used tool for simulating quasi-natural wind erosion processes under controlled conditions (Bagnold, 1941; Maurer et al., 2006). Data gained from wind tunnel experiments constitute a major part of wind
erosion research (Shao, 2008). Wind tunnels need to satisfy several aerodynamic criteria to ensure that they acceptably reproduce the atmospheric flow which causes wind erosion in natural environments (Raupach and Leys, 1990). An important prerequisite for creating quasi-natural aerodynamic forces on the soil in a wind tunnel is the establishment of a logarithmic wind profile, i.e. the simulation of an atmospheric boundary layer. Furthermore, it is important to minimize undesired turbulences in the air stream caused by rotor blade movement or irregularities in the wind tunnel construction (Maurer et al., 2006). Two main types of wind tunnels are distinguished, i.e. stationary wind tunnels used for research under laboratory conditions and mobile wind tunnels for research under field conditions. Stationary laboratory wind tunnels are usually larger, and thus allow for a better approach to natural conditions, while the size of mobile wind tunnels is often limited due to financial or logistic restrictions (Maurer et al., 2006). However, many surface conditions that essentially influence soil erodibility in natural environments (e.g. surface crusting or vegetation) are difficult to simulate with stationary wind tunnels, while mobile wind tunnels can easily be used to examine the impact of wind on natural surfaces in the field.

Laboratory wind tunnel experiments have been carried out primarily to investigate the physics of wind erosion processes, such as the threshold friction velocity for different particle sizes, the erosion intensity under various wind and surface conditions, dust-emission mechanisms, and the impacts of surface roughness elements on wind erosion (e.g. Cornelis et al., 2004; Argaman et al., 2006; Liu et al., 2006; Roney and White, 2006; Shao, 2008; Sutton and McKenna-Neuman, 2008). Several laboratory wind tunnel studies have investigated the effects of vegetation on wind erosion, but no studies exist on the effects of mycorrhizal fungi. Most early studies on vegetation effects have simulated plants with wooden cylinders (e.g. Musick et al., 1996; Raupach et al., 1980). However, plants are porous and flexible, and thus affect aeolian sediment transport differently than solid, rigid roughness elements (Gillies et al., 2002; Udo and Takewaka, 2007). Hence, more recent studies have used porous, flexible plant imitations or clipped plant parts (Gillies et al., 2002; Kim et al. 2000; Molina-Aiz et al., 2006; Udo and Takewaka, 2007). These studies have provided important information on the ability of different plant types to absorb momentum from the wind and on the effectiveness of vegetation cover in reducing sand transport and PM$_{10}$ emission from the soil. However,
although many functions of vegetation in wind erosion control can be appropriately simulated with artificial imitations or clipped plant parts, this approach is not able to address the effects of plant roots and associated soil micro-organisms. Consequently, these below-ground effects have been neglected in wind tunnel research so far, although they constitute important ecological factors of wind erosion control, particularly in environments where the above-ground vegetation cover is inherently sparse.

1.2 Aims and investigations

This thesis addresses some ecological aspects of wind erosion control which have been disregarded in wind tunnel research so far. The overall aim of the thesis is to improve the knowledge about the mechanisms by which plants and mycorrhizal fungi can contribute to reduce wind erosion, including both above- and below-ground processes (Fig. 1.1). The thesis is structured in four investigations, i.e. three wind tunnel studies and a plant growth experiment (Fig. 1.2):

**Chapter 2:**

The focus of chapter 2 is on the above-ground processes by which vegetation protects the soil against wind erosion. It describes wind tunnel experiments with grass canopies of four different planting densities, presenting results on the total sediment mass flux, the vertical distribution of sediment mass flux and the PM$_{10}$ concentration in the air stream.

**Chapter 3:**

Chapter 3 refers to the wind tunnel experiments presented in chapter 2, but focuses on observations on spatial patterns of sediment deposition within grass canopies. These patterns were visualized by using colored sand.

**Chapter 4:**

The focus of chapter 4 is on the below-ground processes by which mycorrhizal fungi and plant roots protect the soil against wind erosion. It addresses the question of whether mycorrhizal fungi can contribute to decrease soil erodibility and presents results from wind tunnel experiments with mycorrhizal and non-mycorrhizal root balls of two plant species.
**Chapter 5:**

Chapter 5 focuses on the question of whether mycorrhizal fungi are able to improve plant growth and survival under adverse soil conditions. It reports on a laboratory plant growth experiment in which seedlings of four alpine grass species were inoculated with a mycorrhizal fungus and subjected to extreme nutrient and water stress.

Fig. 1.1: Schematic of the above- and below-ground mechanisms by which plants and mycorrhizal fungi protect the soil against wind erosion.

Fig. 1.2: Impressions from the four investigations of the present thesis: Wind tunnel experiments with continuous plant canopies (chapters 2 and 3, pictures A and B). Wind tunnel experiments with single root balls (chapter 4, picture C). Plant growth experiment (chapter 5, picture D).
1.3 References


Wu TY, Lin YC, Chen YM, Chang-Chien GP. 2010. Impacts of dust storms on PCDD/Fs and regulated harmful matter in a basin area. Atmospheric Research 97, 279-293.
Chapter 2

**Aeolian Sediment Transport over Vegetation Canopies: A Wind Tunnel Study with Live Plants**

Katrin Burri, Christof Gromke, Michael Lehning, Frank Graf

In press, “Aeolian Research”
2. Aeolian sediment transport over vegetation canopies: A wind tunnel study

Abstract

This wind tunnel study examines aeolian sediment transport in live plant canopies, whereas most previous studies have used model plants for this purpose. Experiments were performed with three canopy densities of Perennial Ryegrass (*Lolium perenne*) and with bare sand surfaces. The results suggest that both total sediment mass flux $Q$ and PM$_{10}$ concentration in the air decreased exponentially with increasing canopy density. In the large-density canopy (frontal area index $\lambda = 0.58$), $Q$ and PM$_{10}$ concentration were reduced to 0.01% and 0.4% respectively, compared to the unplanted configuration. In the medium-density canopy ($\lambda = 0.16$), $Q$ and PM$_{10}$ concentration were reduced to 6.6% and 48.5%. In the small-density canopy ($\lambda = 0.03$), however, $Q$ and PM$_{10}$ concentration were increased to 117.5% and 145.6%. This is attributed to elevated shear stress on the sand bed caused by flow acceleration around the tussocks and vortical structures in their lee. Furthermore, the grasses were observed to trigger erosion by oscillating movements at the ground surface. It was also found that the vertical profiles of sediment mass flux in the medium- and large-density canopy strongly deviated from the exponential decay curve of the unplanted configuration, showing a local maximum at approximately twice the canopy height.
2.1 Introduction

Vegetation plays an important role in reducing soil erosion by wind in arid and semi-arid environments. The effect of vegetation on wind erosion is attributed to several mechanisms: i) sheltering of the ground surface from the erosive force of the wind, both by creating wakes of reduced mean wind velocity and by covering a proportion of the ground and thereby limiting the erodible area, ii) momentum extraction from the wind by absorbing a part of the total shear stress of the wind and thereby decreasing the shear stress acting on the ground and on the downstream plants, and iii) trapping of windborne soil particles (Wolfe and Nickling, 1993). Furthermore, plants reduce wind erosion by altering soil and atmospheric characteristics, such as soil structural stability and near-surface air moisture (Namikas and Sherman, 1995; Eldridge and Leys, 2003).

Re-establishing an intact vegetation cover is a common measure to counteract soil degradation by wind erosion. To develop efficient revegetation strategies for degraded soils and to improve the predictive capabilities of wind erosion models, the effectiveness of different vegetation covers in reducing wind erosion must be known (King et al., 2005). However, studies of wind erosion in the presence of vegetation are complicated by the variability of vegetation characteristics and their dynamic interactions with different soil properties, atmospheric conditions and land-surface-characteristics, e.g. humidity and temperature of the soil and air, topography, soil texture, composition, aggregation and crusting (Shao, 2008).

Field studies offer the possibility to address the full complexity of a particular wind-erosion situation. In many parts of the world, field measurements of wind erosion in vegetated areas have been carried out on different scales and these studies have contributed greatly to understanding the role of specific vegetation types in wind erosion control, as for example mesquite-dominated desert grasslands (Gillette and Pitchford, 2004; King et al., 2006). However, the results of such field measurements are highly site-specific which makes it difficult to draw general conclusions.

As an alternative to field investigations, wind tunnel experiments in the laboratory offer the ability to control the wind speed and to address the physics of selected wind erosion mechanisms by simplifying the system. However, wind tunnel studies often lack significance for real ecosystems. In conventional wind tunnel studies, vegetation has
been simulated by rigid roughness elements (e.g. Raupach et al., 1980; Musick et al., 1996). Recent research has shown that aeolian sediment transport in flexible vegetation canopies is significantly different from that in solid roughness elements (Udo and Takewaka, 2007). Plants have a greater potential to absorb momentum from the wind than solid elements due to their porosity and flexibility (Gillies et al., 2002). Hence, more recent studies have used flexible plant imitations, clipped plants or plant parts (Kim et al. 2000; Gillies et al., 2002; Molina-Aiz et al., 2006; Udo and Takewaka, 2007). Although imitations of vegetation have become increasingly sophisticated, they are likely to perform differently than live plants due to differences in material properties and streamlining behavior. The mechanical properties of living plant tissue are governed largely by the intracellular turgor pressure, i.e. the pressure of the cell contents exerted outward on the plant cell walls. The turgor pressure depends on the water status of the plants and is responsible for the degree of rigidity or flaccidity of the plants. It influences the flexibility and the morphological architecture of the plants which both affect the plant form response to wind as well as the particle impaction and trapping efficiency of the plants. Farquhar et al. (2000) performed wind tunnel experiments on the effect of aeroelasticity on the aerodynamics of wheat and found that flaccid spikes experienced lower lift and drag forces than rigid spikes.

Although artificial plant imitations cannot account fully for the behavior of real plants, there are hardly any studies using live vegetation for studying wind erosion in a laboratory wind tunnel (e.g. Li et al., 2004). A reason for this might be the fact that live plants are much more complicated to control in their appearance and behavior than artificial imitations. Li et al. (2004) conducted wind tunnel experiments with excavated field soil samples of different vegetation covers. However, their vegetated samples were not large enough to create a sufficiently developed boundary layer flow and an equilibrium sediment flux in the wind tunnel.

In the present study, we used live vegetation cultivated under controlled conditions and planted in regular arrays of different densities. We furnished the test section of a boundary layer wind tunnel with 8 m of plant trays. This setup mimicked the behavior of a naturally grown vegetation canopy more accurately than previous wind tunnel studies that used artificial plant substitutes or limited numbers of clipped plants. The objective of this study was to compare the total sediment mass flux, the fine dust
concentration and the vertical profile of sediment mass flux in three different canopy densities of Perennial Ryegrass (*Lolium perenne*) and on bare sand surfaces. This paper presents (i) a description of the boundary layer flow characteristics of the four experimental conditions, i.e. vertical profiles of mean wind velocity and shear stress velocity, (ii) results of total sediment mass fluxes, (iii) increases in PM$_{10}$ concentration above the test section, and (iv) vertical profiles of sediment mass flux.

### 2.2 Material and methods

#### 2.2.1 Vegetation

Wind tunnel experiments were performed with three levels of canopy density of Perennial Ryegrass (*Lolium perenne*), namely 5.25, 24.5 and 91 tussocks per square meter, and with bare sand surfaces. In the following, these four configurations will be referred to as the small-, medium- and large-density configuration, and as the unplanted configuration. The arrangement of the plants followed the same pattern of staggered rows in all experiments (Fig. 2.1).

*Lolium perenne* was grown in a commercial horticulture nursery substrate (Topferde 140, Ricoter, Switzerland) in plant cultivation trays with integrated conical cells (20 ml). After seedlings reached a height of approximately 6 cm, they were removed from the cultivation trays with their entire root balls and planted into wooden trays (98 x 99 cm). The trays were filled with a 3:1 mixture of crushed limestone sand (grain sizes 0-3 mm, pH = 8.4) and soil (grain sizes 0-2 mm, pH = 7.5), which allowed firm rooting of the plants and provided a high water-retention capacity. To create a readily erodible surface, a 1 cm thick layer of quartz sand was spread over the planted soil (Table 2.1).
Table 2.1: Grain size distribution of the quartz sand used in this study.

<table>
<thead>
<tr>
<th>Grain size class [mm]</th>
<th>Percentage [%]</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; 0.80</td>
<td>4</td>
</tr>
<tr>
<td>0.63 - 0.80</td>
<td>54</td>
</tr>
<tr>
<td>0.40 - 0.63</td>
<td>40</td>
</tr>
<tr>
<td>&lt; 0.40</td>
<td>2</td>
</tr>
</tbody>
</table>

Vegetation density was quantified by two parameters, i.e. the frontal area index $\lambda$ and the horizontal vegetation cover $Cv$. The frontal area index $\lambda$ was calculated as $\lambda = na/A$, with $n$ being the number of tussocks with a mean frontal area $a$ occupying the ground area $A$ (Marshall, 1971). This index - also known as lateral cover or roughness density - quantifies how much roughness the flow will encounter on a surface. It is thus commonly used to describe the sheltering effect of vegetation in aeolian research, although it is not capable of characterizing how the roughness is distributed (Okin, 2008). The horizontal vegetation cover $Cv$ refers to the percentage of ground area covered by a vertical projection of the canopy onto the ground surface. The two parameters $\lambda$ and $Cv$ were determined based on frontal view images of individual plants and top-down images of whole plant trays, respectively. The images were converted to binary format, with black and white pixels representing the presence or absence, respectively, of vegetation. The binary images were analyzed with image analysis software to quantify the fraction of the trays covered by plants, the frontal area $a$ and the height $h$ of single plants. The height $h$ of the tussocks was determined by measuring the height of the second highest grass blade, which represented approximately the bulk height of the tussocks. At the time of the wind tunnel tests, the small-, medium- and large-density configuration had horizontal covers $Cv$ of 4, 16 and 47%, and frontal area indices $\lambda$ of 0.03, 0.16 and 0.58, respectively. The tussocks had a mean height $h$ of 10 cm (sd = 1, n = 20) and a mean frontal area $a$ of 64 cm$^2$ (sd = 18, n = 20).
Fig. 2.1: Left: The grasses were planted in staggered rows with various streamwise and lateral inter-plant spacings \(d\) (here \(d = 28\) cm and \(\lambda = 0.16\)). Right: Test section of the wind tunnel.

### 2.2.2 Wind tunnel facility

The experiments were performed in the boundary layer wind tunnel of the WSL Institute for Snow and Avalanche Research SLF in Davos, Switzerland, located at 1650 m a.s.l. (Clifton et al., 2006). The wind tunnel has a nominal cross-section of \(1\) m \(\times\) 1 m and a total length of 15 m, with a 2 m contraction section (4:1), a 5 m inlet duct and an 8 m test section. It operates in suction mode, drawing air from outside through a honeycomb.

For each experiment, eight wooden trays (98 x 99 cm) were aligned in the test section of the wind tunnel, planted with either 91, 24.5, 5.25 or 0 tussocks per square meter (Fig. 2.2). The height of the wind tunnel roof was adjusted for each configuration to provide a zero streamwise pressure gradient and to establish a turbulent boundary layer with an equilibrium inertial sublayer in the test section (Clifton et al., 2008; Walter et al., 2009). The measurement instrumentation in the wind tunnel consisted of a traversable 2D hotwire anemometer, two aerosol particulate monitors and a modified WITSEG sediment sampler (Dong et al., 2004).
2.2.3 Wind tunnel experiments

The first experiment was done with 91 plants per square meter. Subsequently, plants were removed from the trays to conduct experiments with 24.5 plants, 5.25 plants and finally 0 plants per square meter. After each experiment, the 1 cm quartz sand layer was renewed to provide consistent surface conditions, i.e. the eroded sand was replaced by new sand and the sand bed was flattened. The time between experiments was at least 24 hours, which allowed the plants to return to an upright position. The plants showed no visual evidence of sandblast injury. During the whole period of experimental work, we have not observed any cell damages or necrotic tissue in the plants.

First, a vertical profile of horizontal mean wind speed $U(z)$ and shear stress velocity $( - u'w' )^{1/2}$ was measured for each configuration using a traversable 2D hot wire anemometer. These profiles were taken at free stream velocities $U_\delta$ below the threshold for sediment transport in order not to damage the hot wire anemometer. In the experiments with plants, measurements were taken only above the canopies. Second, the hot wire anemometer was positioned 1 cm above the plant canopy to measure shear stress velocity over a range of different free stream velocities $U_\delta$. In the unplanted configuration, the anemometer was positioned analogously 1 cm above the sand surface. Next, each configuration was subjected to an erosive wind event, consisting of three phases. The wind tunnel motor was programmed to accelerate within 120 s to a free stream wind velocity $U_\delta$ of approximately 15.5 m/s, then, this velocity was maintained some time and finally the motor decelerated to 0 m/s within 100 s. Depending on the
intensity of erosion in a given experiment, the duration of constant wind velocity was
varied to yield a sufficient amount of sand in the sediment sampler without overloading
it and not to deplete the loose quartz sand on the beds. The experiments are summarized
in Table 2.2.

To measure aeolian sediment mass flux, a WITSEG sampler was constructed according
to Dong et al. (2004). With 60 sand chambers of 1 cm height each, the sampler allowed
measurements of the vertical profile of sediment mass flux in each experiment. Instead
of using 0.5 mm steel as proposed by Dong et al. (2004), the sampler was constructed of
1 mm steel, resulting in 6.5 x 5 mm openings of the sand chambers. The sampler was
set into the quartz sand near the end of the test section, so that the opening of the lowest
sand chamber was flush with the sand surface. It was positioned in a central plant row at
a cleared plant position to ensure the same relative location within the plant pattern for
all configurations (Fig. 2.2). The distance between the nearest plant upstream and the
sediment sampler varied according to the canopy density.

Sediment was collected during the whole time when wind speed exceeded the threshold
for sediment transport. The total sediment mass flux $Q$ [kg m$^{-2}$ s$^{-1}$] was calculated for
each experiment as

$$Q = \frac{1}{t_8} A_{tot} \sum_{i=1}^{60} m(z_i)$$  \hspace{1cm} (2.1)

with $m(z_i)$ [kg] being the sediment mass at height $z_i$ [m], $A_{tot}$ [m$^2$] being the total area of
openings of the sand chambers, and $t_8$ [s] being the time period during which the free
stream velocity $U_\delta$ was higher than 8 m/s (Eq. 2.1). At this wind speed, first grain
movements were observed visually in the unplanted experiment.

To compare the vertical profiles of sediment mass flux among the different experiments,
a flux fraction $q_f$ was calculated for each height level $z_i$ by dividing the flux at a given
height $q(z_i)$ by the total flux $Q$ as $q_f = q(z_i)/Q$. 
<table>
<thead>
<tr>
<th>Frontal area index $\lambda$</th>
<th>0.00</th>
<th>0.03</th>
<th>0.16</th>
<th>0.58</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment no.</td>
<td>U1</td>
<td>U2</td>
<td>U3</td>
<td>L1</td>
</tr>
<tr>
<td>Horizontal vegetation cover $C_v$ [%]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Planting density [plants/m$^2$]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5.25</td>
</tr>
<tr>
<td>Streamwise and lateral inter-plant spacing $d$ [cm]</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>56</td>
</tr>
<tr>
<td>Mean canopy height $h$ [cm]</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td>Mean free stream velocity $U_\delta$ [m/s]</td>
<td>15.4</td>
<td>15.3</td>
<td>15.3</td>
<td>15.4</td>
</tr>
<tr>
<td>Duration of erosive event $t_e$ [s]</td>
<td>120</td>
<td>124</td>
<td>124</td>
<td>256</td>
</tr>
<tr>
<td>Air temperature $T$ [°C]</td>
<td>-6.6</td>
<td>-6.4</td>
<td>-2.5</td>
<td>12.2</td>
</tr>
<tr>
<td>Relative air humidity $\varphi_{air}$ [%]</td>
<td>81.8</td>
<td>84.4</td>
<td>76.6</td>
<td>58.1</td>
</tr>
<tr>
<td>Specific air humidity $q_{air}$ [g/kg]</td>
<td>2.3</td>
<td>2.4</td>
<td>3.0</td>
<td>6.2</td>
</tr>
<tr>
<td>Relative humidity of soil pore air $\varphi_{pore}$ [%]</td>
<td>89.8</td>
<td>70.2</td>
<td>80.2</td>
<td>81.1</td>
</tr>
<tr>
<td>Matrix potential of the sand $\Psi$ [MPa]</td>
<td>-34.0</td>
<td>-45.0</td>
<td>-27.7</td>
<td>-27.8</td>
</tr>
</tbody>
</table>

$^a$ Experiment no. H2 was conducted at a higher free stream velocity $U_\delta$ to obtain measurable amounts of sediment over the whole height of the sediment sampler.
PM$_{10}$ concentrations $C_{PM10}$ [mg m$^{-3}$] were measured using TSI DustTrak instruments (model 8520). At the end of the test section, PM$_{10}$ concentrations were measured in the free stream whereas the measurements at the beginning of the test section were taken at a height of 10 cm. Sampling frequency was 1 Hz. The increase in PM$_{10}$ concentration over the test section $\Delta C_{PM10}$ [mg m$^{-3}$] was calculated by taking the difference in the mean concentration between the beginning and the end of the test section over the 40 s interval starting 10 s after the free stream velocity exceeded 15.2 m/s.

For the large-density configuration, an additional experiment (experiment no. H2) was conducted at a higher wind velocity (21.2 m/s) to have sufficient sediment flux for yielding weighable amounts of sand over the whole height of the sediment sampler. Thus, the vertical profile of sediment mass flux for the large-density canopy was derived from experiment no. H2, whereas $Q$ and $\Delta C_{PM10}$ were determined in experiment no. H1 at 15.6 m/s (Table 2.2).

Capacitive humidity sensors (SHT11, Sensirion AG) were used to measure the relative humidity $\varphi_{\text{soil}}$ of the soil pore air in the 1-5 mm top layer of the sand bed as well as the relative humidity of the atmospheric air $\varphi_{\text{air}}$ before and after each wind tunnel experiment. To protect the sensors from water and soil, they were wrapped with a breathable membrane. The matric potential $\Psi$ [Pa] of the sand was calculated using the Kelvin equation (Eq. 2.2):

$$
\Psi = \left( \frac{RT}{V_w} \right) \ln \left( \frac{\varphi_{\text{soil}}}{100} \right)
$$

(2.2)

where $R$ is the ideal gas constant [8.314 J mol$^{-1}$K$^{-1}$], $T$ is the temperature of the soil pore air [K], $V_w$ is the molar volume of water [1.8 x 10$^{-5}$ m$^3$ mol$^{-1}$], and $\varphi_{\text{soil}}$ is the relative humidity of the soil pore air [%]. In order to allow comparison to earlier research (e.g. McKenna Neuman, 2003), we give atmospheric air humidity as specific humidity $q_{\text{air}}$. Specific air humidity $q_{\text{air}}$ [g/kg] was calculated from the water vapour partial pressure $e$ [hPa], expressed as $e = \varphi_{\text{air}}/100 e_v$, and the ambient atmospheric pressure $p$ [hPa]:

$$
q_{\text{air}} = 0.622 \frac{e}{p - e} * 1000
$$

(2.3)
with 0.622 being the ratio of the molecular weights of water vapour to air and \( \varphi_{air} \) being the relative humidity of the air [%]. The saturation vapour pressure \( e_s \) was calculated according to Buck (1981). For the ambient atmospheric pressure \( p \), an estimated mean value of 840 hPa was used. In addition to \( q_{air} \), we also present relative humidity values \( \varphi_{air} \) because the sign of the latent heat flux (wetting or drying conditions) is determined by the relative humidity \( \varphi_{air} \) and a potential temperature difference between the surface and the air rather than by specific humidity \( q_{air} \).

### 2.3 Results

#### 2.3.1 Boundary layer flow characteristics

The vertical profile of the horizontal mean wind velocity \( U(z) \) over the unplanted sand surface indicated a boundary layer depth \( \delta \) of approximately 0.3 m at a free stream velocity \( U_\delta \) of 7.9 m/s (Fig. 2.3). With increasing canopy density, \( \delta \) steadily increased up to 0.4 m. The location of the inertial sublayer, identified by constant shear stress velocities, was highest in the large-density configuration, indicating that the depth of the roughness sublayer was greater than that in the small- and medium-density configuration (Fig. 2.4). The depth of the inertial sublayer, however, was not found to vary significantly with canopy density. It had a constant value of 0.04-0.05 m, corresponding to 10-15% of the boundary layer depth \( \delta \). Between the shear stress velocities measured 1 cm above the plant canopies and the free stream velocity \( U_\delta \), linear relationships were found (Fig. 2.5).
Fig. 2.3: Vertical profiles of normalised mean wind velocities $U/U_{max}$. $h =$ plant canopy height (10 cm). $z =$ height above ground.

Fig. 2.4: Vertical profiles of normalised shear stress velocities $( - u'w' )^{1/2} / ( - u'w' )^{1/2}_{max}$. $h =$ plant canopy height (10 cm). $z =$ height above ground.
Fig. 2.5: Shear stress velocity \( \left( - \overline{u'w'} \right)^{1/2} \) measured 1 cm above the plant canopies vs. free stream velocity \( U_\delta \).

### 2.3.2 Total sediment mass flux and PM\textsubscript{10} concentration

The data suggest that both total sediment mass flux \( Q \) and PM\textsubscript{10} concentration \( \Delta C_{\text{PM10}} \) decreased exponentially with increasing canopy density, with the relative decrease being larger for \( Q \) than for \( \Delta C_{\text{PM10}} \) (Fig. 2.6, Table 2.3). In the large-density canopy, \( Q \) was reduced to 0.01\% and \( \Delta C_{\text{PM10}} \) to 0.4\% compared to the unplanted sand surface. In the medium-density configuration, \( Q \) and \( \Delta C_{\text{PM10}} \) were reduced to 6.6\% and 48.5\%, respectively. In the small-density configuration, however, \( Q \) increased to 117.5\% and \( \Delta C_{\text{PM10}} \) to 145.6\% compared to the unplanted sand surface.

Air temperature and humidity differed among the experiments according to weather conditions. Relative air humidity \( \varphi_{\text{air}} \) varied between 84.4 and 54.5\%, specific air humidity \( q_{\text{air}} \) ranged from 2.3 to 6.2 g/kg and the matric potential \( \Psi \) of the sand varied between -10.8 and -45.0 MPa (Table 2.2). For the three experiments using unplanted sand surfaces (experiments no. U1, U2, U3), \( Q \) and \( \Delta C_{\text{PM10}} \) varied only slightly despite fluctuations in \( q_{\text{air}} \) and \( \Psi \) (mean \( Q = 0.262 \text{ kg m}^{-2} \text{ s}^{-1} \), sd = 5.6e-03; mean \( \Delta C_{\text{PM10}} = 0.274 \text{ mg m}^{-3} \), sd = 0.031).
Fig. 2.6: Total sediment mass flux $Q$ and PM$_{10}$ concentration $\Delta C_{PM10}$ vs. frontal area index $\lambda$.

Table 2.3: Total sediment mass fluxes $Q$ and increases in PM$_{10}$ concentration $\Delta C_{PM10}$ (n = 40).

<table>
<thead>
<tr>
<th>Frontal area index $\lambda$</th>
<th>0.00</th>
<th>0.03</th>
<th>0.16</th>
<th>0.58</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment no.</td>
<td>U1</td>
<td>U2</td>
<td>U3</td>
<td>L1</td>
</tr>
<tr>
<td>Total sediment mass flux $Q$ [kg m$^{-2}$ s$^{-1}$]</td>
<td>0.256</td>
<td>0.267</td>
<td>0.260</td>
<td>0.299</td>
</tr>
<tr>
<td>Increase in PM$<em>{10}$ concentration $\Delta C</em>{PM10}$ [mg m$^{-3}$]</td>
<td>0.241</td>
<td>0.302</td>
<td>0.279</td>
<td>0.388</td>
</tr>
<tr>
<td>Mean $C_{PM10}$ at the beginning of the test section ± sd</td>
<td>0.019 ±0.012</td>
<td>0.048 ±0.023</td>
<td>0.009 ±0.010</td>
<td>0.122 ±0.041</td>
</tr>
<tr>
<td>Mean $C_{PM10}$ at the end of the test section ± sd</td>
<td>0.260 ±0.111</td>
<td>0.350 ±0.135</td>
<td>0.288 ±0.107</td>
<td>0.510 ±0.244</td>
</tr>
</tbody>
</table>
2.3.3 Vertical profiles of sediment mass flux

The three vertical profiles of sediment mass flux measured in the unplanted configuration (experiments no. U1, U2, U3) decayed exponentially with height (Fig. 2.7). The profiles of the medium- and large-density experiments deviated strongly from the exponential decay curve of the unplanted configuration (Fig. 2.7). Only slight differences were found between the profiles of the small-density grass canopy and the unplanted configuration. In the medium- and large-density configuration, the sediment mass fractions \( q_f \) near the ground were much smaller than in the unplanted configuration. The decrease in \( q_f \) up to 20 cm was less pronounced in the medium-density configuration than in the unplanted one. In the large-density configuration, \( q_f \) increased with height up to 20 cm instead of decreasing. In both the medium- and large-density configuration, the profiles showed a distinct change in shape at a height of 20 cm, twice the canopy height. In the medium-density configuration, there is an abrupt increase in the decay rate at 20 cm height. In the large-density configuration, this height coincided with the peak in the sediment mass flux.

Fig. 2.7: Vertical profiles of sediment mass flux fractions \( q_f \). \( h \) = plant canopy height (10 cm). \( z \) = height above ground. The profile over the large-density canopy (\( \lambda = 0.58 \)) was conducted at a higher free stream velocity than the other experiments for yielding weighable amounts of sand over the whole height of the sediment sampler despite rather low sediment flux.
2.3.4 Observations of wind-induced changes in the elevation of the sand bed

The erosion and deposition processes during the wind tunnel experiments produced characteristic changes in the elevation of the sand bed, which was clearly visible when the plant trays were illuminated from one side (Fig. 2.8). Sand deposited and accumulated preferentially in the lee of the grass tussocks. In the small-density canopy, these accumulations did not meet with the adjacent downstream tussocks, while in the medium-density canopy, they did meet with the adjacent downstream tussocks. In the large-density configuration, no specific erosion or deposition pattern was found.

Fig. 2.8: Sand accumulations in the lee of grass tussocks. In the small-density configuration (left), these sheltered areas did not meet with the next tussocks downstream. In the medium-density configuration (right), they do reach the next tussocks downstream.
2.4 Discussion

2.4.1 Total sediment mass flux and PM$_{10}$ concentration

The exponential decrease in total sediment mass flux $Q$ with increasing canopy density found in this wind tunnel study is in accordance with field observations by Lancaster and Baas (1998), Hesse and Simpson (2006), Li et al. (2007) and Allgaier (2008). The relationship between horizontal plant cover $C_v$ and erosion reduction is similar to the one found for Salt Grass (*Distichlis spicata*) by Lancaster and Baas (1998). The data from the present study do not significantly differ from their model (p-value of two-sided Wilcoxon test $= 0.686$, Fig. 2.9).

The PM$_{10}$ concentration $\Delta C_{PM10}$ decreased exponentially with increasing canopy density, too, but at a lower rate than $Q$. This may be due to the fact that the threshold friction velocity for fine dust entrainment is lower than for sediment (Roney and White, 2004). Thus, the reduction in shear stress acting on the ground provided by the grass was more effective at reducing saltation than suppressing fine dust emission. Kim et al. (2000) empirically developed an exponential equation to predict PM$_{10}$ emission rate as a function of wind speed and horizontal vegetation cover $C_v$ for Owens (dry) Lake. Similar to the present study, they found that a very low horizontal vegetation cover $C_v$ of approximately 5% does not provide a significant sheltering effect, and may even slightly increases PM$_{10}$ concentration above the plant canopy. They attribute this phenomenon to enhanced turbulent mixing in the shear layer around the top of the canopy and oscillation of the grasses causing a sweeping-like action. However, higher canopy densities provided substantial shelter against dust entrainment. The medium- and large-density canopy in the present study reduced $\Delta C_{PM10}$ to 48.5% and 0.4%, respectively, compared to the unplanted configuration. These values are in the same order of magnitude as the decrease in emission rates found by Kim et al. (2000). However, direct comparison of the plants’ protection effect among studies is complicated by the fact that fine dust emissivity greatly depends on the soil substrate (Roney and White, 2006; Macpherson et al., 2008).
Fig. 2.9: Estimates of normalised sediment mass flux $Q_n$ using the predictive equation of Lancaster and Baas (1998) (dashed line) and measurements of $Q_n$ (circles). $Q_n$ is normalized with respect to the unplanted configuration.

The quartz sand used in this study was industrially sieved and washed to grain sizes ranging from 0.4 to 0.8 mm (Table 2.1). Hence, the fine dust emitted from the test section originated from remainders on the sand or was generated by impacting saltating sand grains. PM$_{10}$ concentrations $C_{PM_{10}}$ above the test section fluctuated evenly around a mean value, indicating that there was a sufficient supply of PM$_{10}$ during the whole duration $t_8$ of the experiments.

The nonlinearity of the relationship between canopy density on the one hand, and sediment mass flux $Q$ and PM$_{10}$ concentration $\Delta C_{PM_{10}}$ on the other hand, may be attributed to changes in the near-surface flow regime (Allgaier, 2008). Data suggest that the three planting configurations of this study represent the three flow regimes proposed by Morris (1955), i.e. an isolated-roughness flow in the small-density, a wake interference flow in the medium-density and a skimming flow in the large-density configuration. The plant spacing to height ratios $(d/h)$ and the frontal area indices $\lambda$ lie within the categories that Lee and Soliman (1977) propose for the three flow regimes. Evidence for these flow regimes was found by looking at how the wind changed the sand bed level during the experiments (Fig. 2.8). In the small-density configuration, the sand accumulations in the lee of the grass tussocks did not meet with the next tussocks.
downstream, indicating fully formed flow separation and wake regions. In the medium-density configuration, however, the wakes formed by the grass tussocks seemed not to be able to fully develop before the next tussock downstream was encountered. In the large-density configuration, no specific erosion or deposition pattern was found, suggesting a skimming flow regime, where the entire sand surface was sheltered from the above-canopy flow.

The isolated-roughness flow regime may also be responsible for the fact that sediment mass flux $Q$ and PM$_{10}$ concentration $\Delta C_{PM10}$ were higher in the small-density configuration than in the unplanted one. Isolated and sparsely arrayed roughness elements generate local surface shear stress peaks through speed-up effects and induce vortical structures on their lee side, which may cause enhanced local erosion (Logie, 1982; Sutton and McKenna Neuman, 2008). Another reason for the enhanced erosion in the small-density configuration may be the triggering of erosion by oscillating movements of grass blades on the sand surface. In the small-density experiment, there was clear evidence of this effect as the grass blades carved sickle-shaped hollows into the sand surface (Fig. 2.10). The occurrence of such local scouring processes and the observed temporal changes in the elevation of the sand bed (Fig. 2.8) indicate that the boundary conditions slightly changed in the course of the experiments. In addition to measuring the total sediment mass flux $Q$, it would thus be interesting to perform temporally resolved measurements of the sediment mass flux.

Fig. 2.10: Sickle-shaped hollows in the sand surface give evidence of erosion triggering by oscillating movements of grass blades.
As the wind tunnel facility used in this study did not allow climate control, air temperature and humidity differed slightly among the experiments according to weather conditions (Table 2.2). To what extent these fluctuations influenced the wind erosion processes in the experiments could not be determined and would require a much larger number of experiments under different conditions. It is well known that soil and air humidity affect the threshold shear stress for the entrainment of sediment (e.g. McKenna Neuman, 2003; Cornelis et al., 2004; Ravi et al., 2006), particularly in fine and tightly packed substrates (McKenna Neuman and Sanderson, 2008). However, the sand used in this study was rather coarse and weakly adhesive, and the wind speeds applied were well above the threshold for particle entrainment. Hence, it can be assumed that the differences in air temperature and humidity had only a minor effect on the amount of erosion. This is supported by the fact that $Q$ and $ΔC_{PM10}$ varied only slightly in the three experiments on unplanted sand surfaces (experiments no. U1, U2, U3) despite fluctuations in the relative humidity of air $φ_{air}$ and the matric potential of the sand $Ψ$.

### 2.4.2 Vertical profiles of sediment mass flux

Whereas the vertical distribution of sediment mass flux over unplanted surfaces has gained considerable attention, there are hardly any studies on vegetated surfaces. Some literature exists on the filtering of aeolian sediment by natural windbreaks (Raupach et al., 2001; Cornelis and Gabriels, 2005; Bouvet et al., 2006; 2007). However, windbreaks are narrow, isolated strips of vegetation that affect the flow differently than continuous vegetation canopies.

On bare surfaces, the vertical profile of aeolian sediment mass flux follows an exponential decay function, with the flux at a given height depending mainly on wind velocity and the grain size distribution of the drifting sediment (e.g. Willliams, 1964; White, 1982; Nishimura and Hunt, 2000; Dong et al., 2002; Ni et al., 2002; Dong and Qian, 2007). The three profiles measured over unplanted sand surfaces (experiments no. U1, U2, U3) reflect this exponential nature of the decrease in sediment mass flux with height (Fig. 2.7).
The presence of vegetation alters the vertical distribution of aeolian sediment mass flux directly by trapping particles which impact on plants, and indirectly by changing turbulent flow properties. Direct impaction of particles on vegetation elements acts as a sediment sink, i.e. any particle hitting a plant surface will have a high probability of being removed from the air. Changes in turbulent flow structure, however, may locally enhance either upward or downward motion of particles and the shear stress available for erosion. Within the canopy, i.e. below 10 cm, the low sediment mass fractions $q_f$ in the medium- and large-density canopy may be primarily the result of the efficient trapping of particles by impaction on vegetation. Above the canopy, i.e. above 10 cm, the sediment flux was not obstructed by plants, but the sediment trapping within the canopy still affected the vertical distribution of sediment mass flux in this region. With the seven experiments discussed here and the flow sensor equipment available, we cannot offer a full mechanistic explanation of the processes leading to the observed mass flux profiles. In the following sections, however, we offer two possible explanations for the characteristic shapes of the profiles above the medium- and large-density canopy: first, the vertical distribution of shear stress velocity, and second, the selective filtering of particles with relatively small ejection angles.

Our data suggest that the vertical profile of $q_f$ above the plant canopy is linked to the vertical profile of shear stress velocities. The decrease in $q_f$ with height was smallest in regions of maximum shear stress (Fig. 2.4 and Fig. 2.7). High shear stress implies high lift forces on the sand particles acting against the gravitational settling force. This mechanism may be partly responsible for the peak in $q_f$ in the large-density configuration and the abrupt decrease in $q_f$ in the medium-density configuration at 20 cm height, as they coincide with the peak and an abrupt decrease in shear stress velocity, respectively. It has to be kept in mind that the vertical profiles of shear stress velocities were not measured simultaneously with the vertical profiles of $q_f$, but at free stream velocities below the threshold for sediment transport in order not to damage the 2D hot wire anemometer. We acknowledge that the shear stress velocity profiles may change in the case of particle erosion, especially in the presence of high particle fluxes close to the surface (Bagnold, 1941; Doorschot and Lehning, 2002). However, it is safe to assume that in the present experiments, the influence of the saltating particles on the flow was relatively small compared to the influence of the vegetation, particularly in the
large-density canopy. Therefore, we feel justified to claim that the sharp bends in the shear stress profiles of the medium- and large-density configuration at approximately twice the canopy height also existed when saltating particles were present. Another mechanism that may have contributed to the characteristic shapes of the vertical profiles of $q_f$ in the medium- and large-density canopies is the selective filtering of particles with small ejection angles. Considering a given location in the sand bed, particles may only be able to jump out of the canopy if they are ejected at an angle large enough not to impact on the downstream tussocks. Depending on the distance to the next downstream tussock and the height of the tussock, this mechanism leads to a selective filtering of particles with small ejection angles, and thereby, to a depletion of particles immediately above the grass canopy. Similarly, vegetation confines the range of angles for descending particles.

As mentioned in chapter 2.2, the profile of the large-density configuration was taken at a free stream velocity $U_\delta$ of 21.2 m/s (experiment no. H2) to yield weighable amounts of sand over the whole height of the sediment sampler, whereas all the other experiments were performed at around 15.5 m/s. Generally, higher wind velocities lead to greater streamlining of the plants which can affect the vertical profile of sediment flux. However, this effect was probably negligible in experiment no. H2 as the high vegetation density provided so much shelter for the individual grass tussocks that they were not observed to bend considerably in the wind. Based on the results of Dong and Qian (2007), who measured sediment mass flux profiles at different wind velocities, it can be assumed that this increase in free stream velocity led to a slightly steeper slope in the upper part of the profile but did not change the overall characteristic shape of the profile.

The use of live plants in laboratory wind tunnel experiments requires careful consideration of the plants’ needs for water and light. The present study provides only a limited number of experiments because the water status of the grasses did not allow conducting experiments over a long time period. The wind tunnel test series was stopped before the grasses became flaccid due to reduced turgor pressure. For future experiments, it is recommended to use plant species with a higher drought resistance or to choose a set-up that allows watering of the plants without wetting the soil.
2.5 Conclusions

We present for the first time results on aeolian sediment transport within and above plant canopies based on wind tunnel experiments with live grasses. In accordance with several field studies, our data suggest that sediment mass flux $Q$ and PM$_{10}$ concentration $\Delta C_{PM_{10}}$ in the air decrease exponentially with increasing canopy density. A rather low canopy density ($\lambda = 0.03$), however, increased both $Q$ and $\Delta C_{PM_{10}}$. So far, most studies exploring this phenomenon of erosion enhancement used sparsely arrayed rigid roughness elements and focused on the effect on the threshold velocity for sediment entrainment. The present study demonstrates a clear effect on the magnitude of sediment transport, based on experiments with live, flexible vegetation. It also provides information about the degree of canopy density associated with different flow regimes. The three canopy densities used in this study ($\lambda = 0.03$, 0.16 and 0.58) are likely to represent an isolated roughness flow, a wake-interference flow and skimming flow regime.

Medium- and large-density grass canopies ($\lambda = 0.16$ and 0.58) were found to strongly affect the vertical distribution of sediment mass flux. This effect may be partly explained by impaction of particles on plants and vegetation-induced changes in the vertical profile of shear stress velocity. However, the limited number of experiments in this study gives only a first insight into this issue. More extensive research is required to address the processes involved in detail.

The use of live plants in wind tunnel experiments offers the chance to study aspects of biological wind erosion control which are not observable when using artificial roughness elements. The focus of the present experiments was on the protective function of the above-ground vegetation against wind erosion. Ongoing research will consider additional below-ground effects of plant roots and micro-organisms, which play a key role in reducing the wind erodibility of soils in arid and semi-arid environments.
2.6 References


King J, Nickling WG, Gillies JA. 2006. Aeolian shear stress ratio measurements within mesquite-dominated landscapes of the Chihuahuan Desert, New Mexico, USA. Geomorphology 82: 229-244.


SPATIAL PATTERNS OF AEOLIAN SEDIMENT DEPOSITION IN VEGETATION CANOPIES:
OBSERVATIONS FROM WIND TUNNEL EXPERIMENTS USING COLORED SAND

Katrin Burri, Christof Gromke, Katherine Leonard, Frank Graf

In preparation
3. Spatial patterns of aeolian sediment deposition in vegetation canopies: Observations from wind tunnel experiments using colored sand

Abstract

In partly vegetated environments affected by wind erosion, plants act as a trap for aeolian sediment, which leads to a small-scale mosaic of depositional and erosional areas. In the present wind tunnel study, we used colored quartz sand to visualize spatial patterns of sediment deposition within grass canopies and to identify areas of net deposition. Wind tunnel experiments were performed with a large-, medium- and small-density canopy of Perennial Ryegrass (*Lolium perenne*), corresponding to horizontal vegetation covers *Cv* of 47%, 16% and 4%. In the small- and medium-density canopy, the wake areas downstream of the tussocks were the main locations of sediment deposition. In the medium-density canopy, these wedge-shaped wake deposits overlapped with the adjacent downstream tussocks, while in the small-density canopy they did not, indicating a wake-interference flow and an isolated roughness flow, respectively. In the large-density canopy, only few sand grains were entrained by the wind and they deposited mainly within reach of the grass tussocks. The deposited sand grains were evenly distributed around the tussocks, without pronounced accumulations on their upstream, downstream or lateral sides, suggesting a skimming flow regime. The fraction of the sand surface which was potentially exposed to erosion (*EPnc*) was substantially smaller than the area which was not covered by grasses. It accounted for 67-78% of the non-covered surface in the small-density canopy, and for 44-77% in the medium-density canopy. This finding indicates that wind erosion models overestimate the sediment source area if they approximate the erodible area with the surface not covered by roughness elements.
3.1 Introduction

Vegetation affects soil erosion by wind at multiple spatial and temporal scales (Okin et al., 2006). The above-ground parts of vegetation act as non-erodible roughness elements that modify the near-surface wind. Their effect on aeolian sediment transport is attributed to three mechanisms, as discussed in the following paragraphs: i) surface sheltering, ii) momentum extraction from the wind, and iii) trapping of windborne sediment (Wolfe and Nickling, 1993).

Surface sheltering is provided both by covering a proportion of the ground surface and thereby limiting the bare ground area available to be eroded, and by creating wakes of reduced mean wind velocity. Morris (1955) has defined three flow regimes depending on the wake development and the proportion of protected surface: i) isolated roughness flow, where there is no interaction between wakes and adjacent downstream roughness elements, ii) wake interference flow, where wakes from upstream elements intercept downstream elements, and iii) skimming flow, where wakes completely overlap and the entire ground surface is sheltered (Fig. 3.1). The type of flow regime depends on the size and spacing of roughness elements and is critical with regard to the amount of wind erosion (Morris, 1955; Lee and Soliman, 1977; Wolfe and Nickling, 1993; Breshears et al., 2009).

Momentum extraction from the wind by vegetation reduces the erosive force of the wind. By absorbing a part of the total shear stress of the wind, plants decrease the shear stress which acts on the ground surface.

Trapping of sediment by vegetation occurs when windborne particles are removed from the air stream as they hit plant surfaces and when the sediment transport capacity of the wind is reduced due to decreased wind velocities. By these means, plants cause particles to settle, which results in characteristic deposition patterns within vegetation canopies. A landscape experiencing wind erosion is thus a small-scale mosaic of depositional and erosional areas (Okin et al., 2006). These redistribution processes have important implications for the development of the surface morphology and for soil resource availability. Wind erosion leads to a depletion of nutrients from plant interspaces and to an increase within and around plants, a process known as the resource island phenomenon (Bielders et al., 2002).
Fig. 3.1: Schematic representation of the three flow regimes defined by Morris (1955). Figure modified after Oke (1988) and Gromke (2008).

Several methods have been used to study the small-scale spatial patterns of aeolian sediment deposition. Udo and Takewaka (2007) performed a wind tunnel study in which they used a laser displacement sensor to measure wind-induced bed elevation changes in flexible artificial plant canopies. They found that canopies of small height, high density and high flexibility promoted bed accumulation and reduced sand transport downstream of the canopy. In several field studies, small-scale erosion and deposition processes have been monitored by marking the changing level of the soil surface on steel rods driven into the ground (Wiggs et al., 1995; Hesse and Simpson, 2006). Other field studies used sediment traps to measure mass fluxes of windborne sediment in
heterogeneous plant canopies, thereby indirectly providing information about the spatial distribution of deposition and erosion processes at the bed level (Gillette and Pitchford, 2004; Gillette et al., 2006). Another approach to investigate aeolian sediment transport is the use of fluorescent tracer sand, but it has only sporadically been used on unvegetated surfaces (Berg, 1983; Willetts and Rice, 1988; Cabrera and Alonso, 2009).

More detailed information on deposition processes and wake development has been obtained from wind tunnel experiments with model canopies consisting of solid roughness elements (Sutton and McKenna Neuman, 2008a and b; Gillies et al., 2006). Various types of methods have been used to visualize bed-level flow and erosion patterns around solid roughness elements in wind tunnel experiments. Flow visualization techniques include different ink and oil methods (Langston and Boyle, 1982; Bullard et al., 2000; Sutton and McKenna-Neuman, 2008b), and a method based on the ammonia-manganese chloride reaction (Donat and Ruck, 1999). Sutton and McKenna Neuman (2008a) examined sediment transport initiation to the lee of solid roughness elements by placing strips of sand across the wind tunnel floor and observing where they had eroded after exposing them to a wind event.

However, results from experiments with solid roughness elements do not necessarily apply to live plant canopies. Since live plants are porous and flexible, they affect the wind flow and sediment flux differently than solid, rigid objects. Plants allow the wind and sediment particles to pass through them, and they have larger drag coefficients than solid objects, i.e. they produce greater overall flow resistance because they have a larger surface subject to skin friction (Gillies et al., 2002; Gromke and Ruck, 2008).

Our study differs from previous wind tunnel research in two respects. First, we used live vegetation instead of artificial roughness elements, and second, we used colored sand to visualize spatial patterns of sediment deposition in vegetation canopies. To our knowledge, colored sand has never been used for this purpose before. The objective of this study was to identify and locate areas experiencing net deposition in three canopy densities of Perennial Ryegrass (*Lolium perenne*). Based on a visual determination of net deposition areas, we estimated the proportions of sheltered and erodible ground surface within the grass canopies.
3.2 Material and methods

3.2.1 Wind tunnel facility

The experiments were performed in the boundary layer wind tunnel of the WSL Institute for Snow and Avalanche Research SLF in Davos, Switzerland, located at 1650 m a.s.l. (Clifton et al., 2006). The wind tunnel has a nominal cross-section of 1 m x 1 m and a total length of 15 m, with a 2 m contraction section (4:1), a 5 m inlet duct with a smooth wooden surface, and an 8 m test section. It operates in suction mode, with a fan downstream of the test section drawing air from outside through a honeycomb.

For each experiment, eight wooden trays (98 x 99 cm) were aligned in the test section of the wind tunnel, planted with different numbers of grass tussocks per unit ground surface (Fig. 3.2). The height of the wind tunnel roof was adjusted for each canopy density to provide a zero streamwise pressure gradient and to establish a turbulent boundary layer with an equilibrium inertial sublayer in the test section (Clifton et al., 2008).

Fig. 3.2: Wind tunnel test section with eight aligned plant trays (98 x 99 cm), the third and fifth tray downstream being filled with red and blue quartz sand. Small-density canopy (top left), medium-density canopy (top middle), large-density canopy (top right), and schematic representation (bottom). a = upstream part of the plant tray, b = downstream part of the plant tray, c = lateral parts of the plant tray close to the side walls of the wind tunnel.
3.2.2 Vegetation

Wind tunnel experiments were performed with three canopy densities of Perennial Ryegrass (*Lolium perenne* cv. Alligator, Alpine Garden Center Schutz Filisur, Switzerland), namely 5.25, 24.5 and 91 tussocks per square meter (Table 3.1). In the following, they will be referred to as the low-, medium- and large-density canopies. The arrangement of the plants followed the same pattern of staggered rows in all experiments (Fig. 3.2).

*L. perenne* was grown in a commercial horticulture nursery substrate (Topferde 140, Ricoter, Switzerland) in plant cultivation trays with integrated conical cells (20 ml). After seedlings reached a height of approximately 6 cm, they were removed from the cultivation trays with their entire root balls and planted into the eight wooden trays used for the wind tunnel experiments. The trays were filled with a 3:1 mixture of crushed limestone sand (grain sizes 0-3 mm, pH = 8.4) and soil (grain sizes 0-2 mm, pH = 7.5), which allowed firm rooting of the plants and provided a high water-retention capacity. To create a readily erodible surface, a 1 cm thick layer of quartz sand was spread over the planted soil. The grain size distribution of the sand is shown in Table 3.2. The third and fifth tray downstream were filled with red and blue resin-coated sand respectively, which was produced out of the uncolored sand presented in Table 3.2 (Carlo Bernasconi AG, Switzerland, Fig. 3.2). Effects of the resin-coating on the erodibility of the sand grains, e.g. via affecting grain size or inter-particle electrostatic forces, could not be considered in this study (Rasmussen et al., 2009).

Table 3.1: Characteristics of the three canopy densities and experimental conditions. The air temperature [°C], relative air humidity [%] and matric potential of the sand [MPa] were determined as described in Burri et al. (in press).

<table>
<thead>
<tr>
<th></th>
<th>Small-density</th>
<th>Medium-density</th>
<th>Large-density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planting density [plants/m²]</td>
<td>5.25</td>
<td>24.5</td>
<td>91</td>
</tr>
<tr>
<td>Horizontal vegetation cover Cv [%]</td>
<td>4</td>
<td>16</td>
<td>47</td>
</tr>
<tr>
<td>Frontal area index λ</td>
<td>0.03</td>
<td>0.16</td>
<td>0.58</td>
</tr>
<tr>
<td>Inter-plant spacing d [cm]</td>
<td>56</td>
<td>28</td>
<td>14</td>
</tr>
<tr>
<td>Mean canopy height h [cm]</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Mean free stream velocity [m/s]</td>
<td>15.4</td>
<td>15.7</td>
<td>15.6</td>
</tr>
<tr>
<td>Duration of erosive event [s]</td>
<td>174</td>
<td>610</td>
<td>7224</td>
</tr>
<tr>
<td>Air temperature [°C]</td>
<td>7.3</td>
<td>7.4</td>
<td>9.9</td>
</tr>
<tr>
<td>Relative air humidity [%]</td>
<td>81.3</td>
<td>68.3</td>
<td>54.5</td>
</tr>
<tr>
<td>Matric potential of the sand [MPa]</td>
<td>-10.8</td>
<td>-21.4</td>
<td>-25.1</td>
</tr>
</tbody>
</table>
The frontal area index $\lambda$ and horizontal vegetation cover $C_{v}$ were determined based on scaled frontal view images of individual plants and top-down images of whole plant trays. Images were binarized and analyzed with the software ImageJ (Version 1.39u, http://rsb.info.nih.gov/ij/). The frontal area index $\lambda$ was calculated as $\lambda = na/A$, with $n$ being the number of tussocks with a mean frontal area $a$ occupying the ground area $A$ (Table 3.1). At the time of the wind tunnel tests, the tussocks had a mean height $h$ of 10 cm ($sd = 1$, $n = 20$) and a mean frontal area $a$ of 64 cm$^2$ ($sd = 18$, $n = 20$).

### 3.2.3 Wind tunnel experiments

The wind tunnel experiments for this study were conducted in parallel to measurements of sediment mass fluxes that included collecting windborne sand particles with a segmented sediment sampler (Burri et al., in press). The first experiment was done with 91 plants per square meter. Subsequently, plants were removed from the trays to conduct experiments with 24.5 and 5.25 plants per square meter. After each experiment, the 1 cm quartz sand layer was renewed to provide consistent surface conditions, i.e. the eroded sand was replaced by new sand and the sand bed was flattened. The time between experiments was at least 24 hours, which allowed the plants to return to an upright position. During the whole period of experimental work, the plants did not grow observably and they showed no visual evidence of sandblast injury.

Each canopy was subjected to an erosive wind event consisting of three phases. The wind tunnel motor was programmed to accelerate within 120 s to a free stream wind velocity of 15.5 m/s, this velocity was maintained for a set time and finally the motor decelerated to 0 m/s within 100 s. Depending on the intensity of erosion in a given experiment, the duration of constant wind velocity was varied to yield a sufficient amount of erosion for recognising patterns in the colored sand but not to deplete the loose quartz sand on the beds (Table 3.1).

<table>
<thead>
<tr>
<th>Grain size class [mm]</th>
<th>Percentage [%]</th>
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<tbody>
<tr>
<td>&gt; 0.80</td>
<td>4</td>
</tr>
<tr>
<td>0.63 - 0.80</td>
<td>54</td>
</tr>
<tr>
<td>0.40 - 0.63</td>
<td>40</td>
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<tr>
<td>&lt; 0.40</td>
<td>2</td>
</tr>
</tbody>
</table>
3.2.4 Analysis of deposition patterns

The analysis of deposition patterns was restricted to the two trays with red and blue sand, subsequently referred to as the red and blue sections (Fig. 3.2). In these trays, sand deposits were expected to be most discernible because all the sand invading from upstream was of a different color than the sand with which the trays were originally filled. In the trays with white sand, on the contrary, the areas of sand deposition were expected to be less pronounced because the deposits contained not only colored grains, but also white grains. Upstream of the red section, there were 2 meters of white sand (Fig. 3.2). Thus, all white sand grains that were found in the red section after the wind tunnel experiment represented deposits originating from upstream. Upstream of the blue section, there were in total 3 meters of white sand and 1 meter of red sand (Fig. 3.2). Hence, the white and red sand grains in the blue section represented deposits. To describe the locations of sediment deposits, we divided the sand bed into the following zones, according to their position related to a given tussock (Fig. 3.3): a) the bleed flow zone, referring to the space within reach of the moving grass blades, projected on the ground, b) the lateral zones, c) the upstream area, and d) the wake area. The elongated bare soil areas that are oriented in the direction of the wind are referred to as ‘streets’ (Gillette and Pitchford, 2004).

![Fig. 3.3: Schematic flow areas around a tussock: a) bleed flow zone, b) lateral zones, c) upstream area, d) downstream area. The elongated bare soil areas that are oriented in the direction of the wind are referred to as ‘streets’ (dark shaded areas).](image-url)
To obtain information on the temporal development of deposition patterns in the red and blue section, image sequences were taken through the perspex roof of the wind tunnel during the experiments. In the low- and medium-density canopy, sediment flux was high and the amounts of deposited sediment were large enough to be clearly visible. In the large-density canopy, on the contrary, sediment flux was low and it was hardly possible to detect the isolated deposited sand grains in the images. Hence, two different strategies were applied to analyze the deposition patterns in the different canopy densities. In the low- and medium-density canopy, analysis was done based on a set of three consecutive images that were selected to represent an initial, intermediate and final stage of each experiment (Fig. 3.4 and Fig. 3.5). The deposition patterns were intensified by increasing contrast, saturation and brightness of these images with Adobe Photoshop CS4. In the large-density canopy, the analysis of deposition patterns was performed based on close-up images that were taken after the experiments in addition to the image sequences (Fig. 3.6). The individual deposited grains were automatically selected based on their color, marked in black and enlarged by using Adobe Photoshop CS4. The automatic selection was then checked manually to ensure that the marked areas corresponded to deposited grains.

In addition to qualitatively describing the location of sand deposits, we also analyzed them quantitatively in the small- and medium-density canopy. The aim of this quantitative analysis was to estimate the fraction of the ground surface which was sheltered from wind erosion, and the fraction which was potentially exposed to erosion. We defined the sheltered proportion $SP$ as the fraction of the total surface which was either covered by plants or net deposits. The remaining ground surface, which was potentially exposed to erosion, was defined as the erodible proportion $EP_{tot}$, if considered in relation to the total surface, and as $EP_{nc}$, if considered in relation to the non-covered surface, i.e. the surface not covered by grasses. The determination of $SP$ and $EP_{tot}$ was done visually by discriminating between the colors of the deposited sand and the colors of the sand with which the trays were filled originally, according to the following criteria and assumptions: Areas completely covered by upstream colored sand were attributed to $SP$, as they gave definite evidence that there was net deposition. Regions containing ripple patterns of alternating colors were attributed to $EP_{tot}$, even if a substantial proportion was covered by upstream colored sand, as this sand was
assumed to represent no net deposition, but only temporal deposition (Fig. 3.7). Areas completely covered by sand with which the trays were filled originally were also attributed to $EP_{tot}$, because these areas excluded the possibility that there was net deposition. However, they did not provide any conclusive evidence for or against the following scenarios: i) neither erosion nor deposition, ii) erosion equals deposition, iii) more erosion than deposition (net erosion). The sheltered ground proportions $SP$ were manually selected and marked in the images representing the final stages of the experiments by using Adobe Photoshop CS4 (Fig. 3.7).

Fig. 3.4: Image sequences of sediment deposition patterns in the small-density canopy (interspace = 56 cm). In the red section (A1-A3), white sand was invading from upstream. The dark spots at the top of image A3 are areas where erosion exposed the substrate underneath the red sand. In the blue section (B1-B3), red and white sand was invading from upstream. Wind direction: from left to right.
Fig. 3.5: Image sequences of sediment deposition patterns in the medium-density canopy (inter-plant spacing = 28 cm). In the red section (A1-A3), white sand was invading from upstream. In the blue section (B1-B3), red and white sand was invading from upstream. Wind direction: from left to right.

3.3 Results

3.3.1 Large-density canopy

In the large-density canopy, the bleed flow zones of neighboring tussocks overlapped and covered almost the whole surface. Because sediment flux was low, only isolated deposited sand grains were found (Fig. 3.6). Such grains were spread all over the canopy, with particularly high concentrations in the bleed flow zones and low concentrations in the plant interspaces. Within the bleed flow zones, the deposited grains were evenly distributed around the tussocks, without pronounced accumulations on the upstream, downstream or lateral sides of the tussocks.
3.3.2 Medium-density canopy

In the medium-density canopy, deposition occurred primarily in the bleed flow zones and the wake areas (Fig. 3.3 and Fig. 3.5). In some parts of the canopy, deposition was observed additionally in the lateral zones. In general, the sand deposits in the wake areas were wedge-shaped in plan view and overlapped with the adjacent downstream tussocks.

In the initial stage of the experiment (Fig. 3.5, A1 and B1), deposition was most intense in the upstream parts of the red and blue section, with less intense deposition occurring in the downstream parts (Fig. 3.2 and Fig. 3.5). In the intermediate stage (Fig. 3.5, A2 and B2), the deposition became more intense over the whole sections and the deposition areas in the wakes of the tussocks expanded in lateral direction. In the streets between the tussocks, rudimentary ripples evolved. In the final stage of the experiment (Fig. 3.5, A3 and B3), the deposition areas further increased in width, and in the central areas of the trays, they even expanded into the open streets between the tussocks. In the lateral parts of the plant trays, i.e. between the side walls and the second closest plant rows, there was less deposition than in the central areas in all three stages (Fig. 3.2 and Fig. 3.5).
The deposition areas were generally larger in the blue section than in the red section, which is most clearly visible in the final stage of the experiments (Fig. 3.5, A3 and B3). The visually determined sheltered ground surface $SP$ amounted to 33% in the red section, and to 62% in the blue section (Fig. 3.7, Table 3.3). The erodible proportion $EP_{nc}$ accounted for 77% of the surface not covered by grasses in the red section, and for 44% in the blue section (Table 3.3).

Table 3.3: Proportion of sheltered surface $SP$, and proportion of erodible surface in relation to the total surface $EP_{tot}$ and in relation to the surface which was not covered by grasses $EP_{nc}$.

<table>
<thead>
<tr>
<th></th>
<th>Small-density canopy</th>
<th>Medium-density canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red section</td>
<td>Blue section</td>
</tr>
<tr>
<td>Grass-covered proportion [%]</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Not-covered proportion [%]</td>
<td>97</td>
<td>95</td>
</tr>
<tr>
<td>Sheltered proportion $SP$ [%]</td>
<td>24</td>
<td>36</td>
</tr>
<tr>
<td>Erodible proportion $EP_{tot}$ [%]</td>
<td>76</td>
<td>64</td>
</tr>
<tr>
<td>Erodible proportion $EP_{nc}$ [%]</td>
<td>78</td>
<td>67</td>
</tr>
</tbody>
</table>

3.3.3 Small-density canopy

In the small-density canopy, deposition was observed in all four zones around the tussocks: a) the bleed flow zone, b) the lateral zones, c) the upstream area, and d) the wake area (Fig. 3.3 and Fig. 3.4). In contrast to the medium-density canopy, the deposits in the wake areas did not overlap with the adjacent downstream tussocks.

Already in the initial stages of the experiments (Fig. 3.4, A1 and B1), deposition was found in all four zones mentioned above. The deposits in the wake areas were wedge-shaped in plan view and their downwind ends could hardly be located in the initial stage. In the intermediate and final stages of the experiments (Fig. 3.4, A2-A3 and B2-B3), the wake deposits expanded laterally and a clearly discernible ripple pattern evolved in the streets between the tussocks. The downstream ends of the deposits in the
Spatial patterns of aeolian sediment deposition 71

wakes of the tussocks became more pronounced as they were marked by the occurrence of ripples approximately 10 cm upwind of the adjacent downstream tussocks.

Analogous to the medium-density canopy, there was more deposition in the blue section than in the red section, and more deposition in the central areas than in the areas close to the side walls of the wind tunnel in all three stages (Fig. 3.2 and Fig. 3.4). The visually determined sheltered ground surface $SP$ amounted to 24% in the red section, and to 36% in the blue section (Fig. 3.7, Table 3.3). The erodible proportion $EP_{nc}$ accounted for 78% of the non-covered surface in the red section and for 67% in the blue section.

Fig. 3.7: Visually determined proportion of sheltered surface $SP$ in the red and blue section of the small-density canopy (top, inter-plant spacing = 56 cm) and the medium-density canopy (bottom, inter-plant spacing = 28 cm). Wind direction: from left to right.
3.4 Discussion

The spatial patterns of colored sand found in this study provide evidence for different processes controlling aeolian sediment entrainment and deposition in vegetation canopies. One important process was sediment deposition in the sheltered wake areas of the tussocks. In the low- and medium-density canopy, such wake deposits were the main locations of sediment deposition (Fig. 3.4 and Fig. 3.5). The size of these wake deposits in relation to the plant spacing indicates that the two canopy densities represented an isolated roughness flow and a wake-interference flow regime, respectively. In the small-density canopy, the wake deposits did not intercept the adjacent downwind tussocks, while in the medium-density canopy, they overlapped with the downstream vegetation. In the large-density canopy, the lack of wake deposits and the even distribution of deposited sand grains within the bleed flow zones (Fig. 3.6) suggests a skimming flow regime with no individual wake areas, but the whole surface being sheltered.

In the immediate vicinity of the grass tussocks, i.e. within reach of the moving grass blades, windborne particles were trapped as they hit plant surfaces, thereby lost momentum and deposited. This process caused the sediment accumulations in the bleed flow zones of the tussocks. It was probably also responsible for the deposits in the upstream areas of the tussocks in the small-density canopy, which were best visible in the last pictures of the image sequences (Fig. 3.4 A3 and B3). Some of the windborne particles in the sand cloud approaching the tussocks may rebounded from the grass blades and came to settle in front of them (Bagnold, 1941). In the high- and medium-density canopy, the wake areas overlapped with the downstream tussocks and it could thus not be decided to what extent the deposits upstream of a given tussock were caused by this tussock itself or the adjacent upstream tussock (Fig. 3.5 and Fig. 3.6). Deposition upwind and laterally of an obstacle has been shown to strongly depend on its porosity. Walter et al. (unpublished) measured the bed level shear stress distribution around a single tussock of *L. perenne* and around a solid cylinder. Compared to a situation without a roughness element, they found increased shear stress laterally of both the grass tussock and the cylinder, with the peak shear stress being higher for the cylinder than for the grass tussock. This reflects the fact that flow acceleration around a solid
obstacle is higher than around porous obstacles (Bowker et al., 2008). Hence, more sediment entrainment is to be expected around a solid, rigid obstacle than around a porous, flexible obstacle. Accordingly, Leenders et al. (2007) observed in their field study that sediment accumulated upstream and laterally of a single shrub, whereas around a single tree trunk, sediment scouring occurred. In the present study, we found sediment deposits immediately laterally of the tussocks, indicating that the shear stress acting on the ground there was below the threshold for sediment entrainment. This is most clearly evident in Fig. 3.4 A3, where these lateral deposits are definitely larger than the bleed flow zones.

In the small-density canopy, the tussocks in the lateral parts of the plant trays close to the side walls of the wind tunnel produced asymmetric deposition without lateral deposition on their outer sides (Fig. 3.2 and Fig. 3.4). This phenomenon is probably caused by enhanced turbulences close to the side walls due to flow recirculation and corner vortices. Further evidence for enhanced erosion near the side walls of the wind tunnel was found in the medium-density canopy, where erosion was particularly intense in the streets adjacent to the side walls, i.e. between the outermost and second outermost plant rows (Fig. 3.5).

The areas of net deposition were generally smaller in the red section than in the blue section. Since the red section was closer to the upwind beginning of the test section, it had a smaller sediment fetch than the blue section. Aeolian sediment flux tends to increase up to saturation with the distance over which the erosion occurs, an effect known as the fetch effect (Gillette et al., 1996). Additionally, the characteristic flow regimes of the three canopy densities required some distance to fully develop, because the entering air encountered a change in surface roughness when it passed from the smooth inlet duct of the wind tunnel to the planted test section. The near ground wind velocities were thus highest at the beginning of the test section, and consequently, most efficient in entraining sediment, leading to higher erosion rates near the beginning of the test section than towards the downwind end. The changing erosive capacity of the flow along the test section offered an opportunity to study the development of deposition patterns under different erosion intensities. In the course of an erosive event, the deposited sand heap in the wake of an obstacle gradually increases in ground cover and height until its slopes stand at the limiting angle of repose (Bagnold, 1941). Once this
angle is reached, any additional sand slips down the slopes and thereby leaves the sheltered wake area, where it is entrained by the stronger wind outside. In the blue section where the erosive capacity of the wind flow was smaller than in the red section, this process enabled the deposition areas to spread even into the open streets between the tussocks (Fig. 3.4 B3 and Fig. 3.5 B3). In the red section, in contrast, there was only minor deposition in the streets (Fig. 3.4 A3 and Fig. 3.5 A3). Accordingly, the proportions of the erodible surface $E_{P_{tot}}$ were higher in the red section than in the blue section (Table 3.3).

Regardless of these differences between the red and blue section, $E_{P_{tot}}$ was in any case substantially smaller than the ground surface which was not covered by grasses (Table 3.3). Many wind erosion models for vegetated surfaces, however, approximate the erodible area as simply the surface not covered by non-erodible elements (e.g. Marticorena and Bergametti, 1995). The present study supports the findings of Chappell et al. (2010) who showed that this approximation can lead to substantial over-estimates of aeolian sediment fluxes. Chappell et al. (2010) developed a model based on angular reflectance and estimated the erodible proportion for different arrays of solid hemispheres. For an array with a horizontal cover $C_v$ of 5% and a frontal area index $\lambda$ of 0.04, they estimated $E_{P_{nc}}$ to 83% of the non-covered surface. The visually determined $E_{P_{nc}}$ in the small-density canopy, which had a similar $C_v$ and $\lambda$ (Table 3.1), was 78% of the non-covered surface in the red section and 67% in the blue section (Table 3.3), suggesting that the erodible surface proportion in canopies of flexible, porous grass tussocks is even smaller than in comparable arrays of solid roughness elements.
3.5 Conclusions

The present study provides initial information about the degree of canopy density associated with different flow regimes, based on wind tunnel experiments with live grass tussocks. Previous research on the determinants of the air flow regimes has been based on experiments with solid roughness elements (Morris, 1955; Lee and Soliman, 1977; Wolfe and Nickling, 1993). Furthermore, we found that the fraction of the sand surface which effectively experienced erosion \( (EP_{nc}) \) was substantially smaller than the area which was not covered by grasses. It would be interesting to validate these findings under field conditions of continuously varying wind speed and direction and more heterogeneous vegetation cover. We suggest that the values of \( EP_{nc} \) and the boundary conditions for each flow regime found in this study may not be exactly consistent with what is observed in nature, but the general trend and the order of magnitude may be representative.

The present wind tunnel study was distinct from previous research in that colored sand was used to examine erosion and deposition processes in live plant canopies. Colored sand proved to be useful for this purpose, as it produced high-resolution bed-level data for the whole ground surface under investigation. This is of particular importance when dealing with live plants, as they are non-uniform complex structures that interact with the wind in more variable ways than solid artificial roughness elements. The sensitivity of the method, i.e. the detectability of colored sand deposits depends on several factors, such as the scale of the images, the applied image analysis procedure and the characteristics of the underlying surface. The application of colored sand is a relatively easy and low-cost method to study aeolian sediment transport in vegetation canopies, and it may therefore be useful not only for wind tunnel studies, but also for larger scale field studies. Previous field studies have used fluorescent tracer sand on unvegetated surfaces and transferred deposits via sticky tapes to the laboratory for analysis under ultraviolet light (Berg, 1983; Cabrera and Alonso, 2009). The use of colored resin-coated sand, in contrast, may be suitable to collect on-site data, by taking high-resolution close-up images directly in the field.
3.6 References


Chapter 4

**MYCORRHIZAL FUNGI PROTECT THE SOIL FROM WIND EROSION: A WIND TUNNEL STUDY**

Katrin Burri, Christof Gromke, Frank Graf

In press, “Land Degradation and Development”
4. Mycorrhizal fungi protect the soil from wind erosion: A wind tunnel study

Abstract

Mycorrhizal fungi form symbiotic associations with the roots of most vascular plant species and can improve both plant growth and soil structure. Therefore, they are expected to play an important role in reducing soil erosion by wind. However, direct evidence for this is lacking, since it is hardly possible to separate the mycorrhizal effect from all other factors that influence wind erosion in natural environments. Here we present laboratory wind tunnel experiments which indicate that mycorrhizal fungi have the potential to substantially increase the protective effect of newly seeded plants against wind erosion. For root balls of two plant species (Lolium perenne and Anthyllis vulneraria ssp. alpestris), we found that the wind-induced soil loss decreased significantly with increasing percentage of root colonization by mycorrhizal fungi. The mean soil loss of non-mycorrhizal control samples was more than twice as high as the one of mycorrhizal samples for A. vulneraria, while no significant difference was observed for L. perenne. These results are all the more remarkable because there was no mycorrhiza-induced plant growth enhancement. On the contrary, mycorrhizal plants had significantly smaller root systems than non-mycorrhizal plants in both species. Above-ground biomass was significantly smaller in mycorrhizal plants than in non-mycorrhizal plants for L. perenne, but only slightly smaller for A. vulneraria. This study demonstrates that mycorrhizal fungi are able to help newly seeded plants to decrease the wind erodibility of soil, even in cases when they do not increase plant growth.
4.1 Introduction

Wind erosion is a geological and climatic phenomenon which takes place over long periods of time in arid and semi-arid regions (Shao, 2008). Anthropogenic disturbances of the soil have increased the frequency and intensity of wind erosion in many places around the world. Hence, wind erosion and resulting land desertification have become most alarming processes of environmental degradation, causing tremendous losses of fertile soil and, thereby, increasing the content of mineral fine dust in the atmosphere. This has severe consequences for human health, the earth’s radiation balance and the productive capacity of soil (Griffin et al., 2001). The re-establishment of a protective vegetation cover is regarded as the most effective strategy against wind erosion and desertification. However, revegetation practices often face high seedling mortality because the conditions on eroded soils are extremely adverse to plant growth (Padilla and Pugnaire, 2006). There is an increasing interest in using mycorrhizal fungi to overcome this problem (Miller and Jastrow, 1992; Perumal and Maun, 1999; Enkhtuya et al., 2003; Estaun et al., 2007). Mycorrhizal fungi form symbiotic associations with the roots of most vascular plant species and play an essential role in ecosystem functioning. They exert various beneficial effects on their host plants, e.g. facilitation of nutrient and water acquisition, promotion of soil aggregation as well as protection against pathogens, toxic compounds and herbivores (Smith and Read, 2008). Mycorrhizal fungi occur abundantly in all types of ecosystems, but usually lack on severely degraded soils (Amaranthus and Trappe, 1993; Azcon-Aguilar et al., 2003). Therefore, the promotion of mycorrhizal fungi within the scope of land management and restoration activities is a promising approach to improve revegetation processes (Jeffries et al., 2003; Byers et al., 2006; King and Hobbs, 2006).

Mycorrhizal fungi affect soil aggregation processes by various mechanisms on different hierarchical levels (Rillig and Mummey, 2006). Two key mechanisms are the physical stabilization through entanglement of soil particles by fungal hyphae and chemical stabilization by glue-like fungal exudates (Tisdall and Oades, 1982; Miller and Jastrow, 1990; Wright and Upadhyaya, 1998). The size and stability of soil aggregates are important factors governing soil erodibility by wind. Several studies have shown that wind erosion decreases with increasing level of soil aggregation (Eldridge and Leys,
Large soil aggregates are less likely to be entrained by the wind than small primary soil particles. Therefore, the formation of aggregates increases the non-erodible soil fraction for a given wind force, and it also increases the roughness of the surface, thereby decreasing near-ground wind velocities (Chepil, 1950; 1951). The stability of soil aggregates is critical for their resistance to disruption by abrasion.

Several field studies demonstrated that inoculation of mycorrhizal propagules improves the physical, chemical and biological properties of soil and enhances the establishment of vegetation in degraded environments (Requena et al., 2001; Caravaca et al., 2003a, b). Laboratory studies have shown that mycorrhizal fungi are able to increase the soil resistance to water erosion and the fraction of water stable aggregates (Graf, 1997; Bearden and Petersen, 2000; Augé et al., 2001). However, there are no studies to our knowledge that have examined the effect of mycorrhizal fungi on the wind erodibility of soil.

In the present study, we addressed this topic experimentally by performing wind tunnel tests with root balls of mycorrhizal and non-mycorrhizal plants of Perennial ryegrass (Lolium perenne) and Kidney vetch (Anthyllis vulneraria ssp. alpestris) (Fig. 4.1). Wind tunnels are commonly used to investigate aeolian processes, as they allow conducting experiments under controlled wind flow conditions (Bagnold, 1941). There is a large body of wind tunnel research dealing with the effects of various soil and vegetation parameters on wind erosion (e.g. Eldridge and Leys, 2003; Ravi et al., 2006; Burri et al., in press), but the effect of mycorrhizal fungi has never been examined in a wind tunnel before. The present study was designed to explore the question whether mycorrhizal fungi increase the protective effect of newly seeded plants against wind erosion. In particular, the objectives were to test i) whether the soil loss decreases with increasing percentage of mycorrhizal root colonization, and ii) whether the soil loss through wind erosion is smaller in mycorrhizal root balls than in non-mycorrhizal root balls.
4.2 Material and methods

4.2.1 Sample preparation

The wind tunnel experiments were conducted with mycorrhizal and non-mycorrhizal root balls of Perennial ryegrass (*Lolium perenne*) and Kidney vetch (*Anthyllis vulneraria ssp. alpestris*). These two plant species were chosen in order to represent a fibrous and a tap root system. The plants were grown in square pots (195 cm$^3$) in a climate chamber with a 12 hour day/night cycle at a temperature of 20/15°C and a light intensity of 50'000/0 lux. Before seeding, stainless steel grid cylinders were put into the empty plant pots (cylinder diameter: 40 mm, mesh size: 8 x 8 mm, cylinder height: 65 mm, wire diameter: 0.8 mm). Grid cylinders were used because preliminary experiments had shown that the root balls become extremely fragile after drying and tend to collapse during handling if they are not reinforced. The pots were then half filled with autoclaved sand (pH 8.4, Table 1). Based on the results of preliminary experiments, it was decided to use sand rather than soil due to its higher erodibility which ensured sufficient amounts of erosion in the wind tunnel experiments. For each plant species, 20 half-filled pots were provided with 20 ml of a commercial mycorrhizal inoculum in vermiculite of 1-2 mm particle size (INOQ Agri, INOQ GmbH), and 20 pots were provided with 20 ml of autoclaved vermiculite. The inoculum contained a
mixture of three arbuscular mycorrhizal species (*Glomus etunicatum*, *Glomus intraradices* and *Glomus claroideum*). After the pots were entirely filled with sand, they were seeded and covered with mulch foil to reduce the formation of a surface crust on the sand. After germination, seedlings were reduced to four individuals of *L. perenne* per pot, but to only two individuals of *A. vulneraria* per pot, because *A. vulneraria* developed more extensive root systems than *L. perenne*.

The plants were watered and fertilized using permanently installed cones, buried approximately 2 cm in the sand. Each pot received 10 ml of Hoagland’s solution with a tenfold lower P-concentration once a week and 10 ml of tap water 2-3 times a week. After a growth period of 2 months, the plants were removed from the pots with their entire root balls. The sand and roots outside the grid cylinders were cut off with a knife. The root balls in the grid cylinders were then mounted on Styrofoam pieces with close-fitting cavities (Fig. 4.1). After a week of air drying, the plants were cut off at the surface of the sand and the root balls were further dried in an oven at 50°C for 12 hours. The above-ground plant parts were removed to avoid that they generate leverage effects and thereby weaken the stability of the root ball when they swing in the wind during the experiment.

<table>
<thead>
<tr>
<th>Grain size class [mm]</th>
<th>Cumulative percentage [%]</th>
</tr>
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<tbody>
<tr>
<td>&lt; 0.063</td>
<td>10</td>
</tr>
<tr>
<td>&lt; 0.125</td>
<td>25</td>
</tr>
<tr>
<td>&lt; 0.25</td>
<td>69</td>
</tr>
<tr>
<td>&lt; 1</td>
<td>99</td>
</tr>
<tr>
<td>&lt; 2</td>
<td>100</td>
</tr>
</tbody>
</table>
4.2.2 Wind tunnel experiments

The experiments were performed in the boundary layer wind tunnel of the WSL Institute for Snow and Avalanche Research SLF in Davos, Switzerland, located at 1650 m a.s.l. (Clifton et al., 2006). The wind tunnel has a nominal cross-section of 1 x 1 m and a total length of 15 m, with a 2 m contraction section (4:1), a 5 m flow conditioning section and an 8 m test section. It operates in suction mode, drawing air from outside through a honeycomb. Flow conditioning was done by mounting artificial roughness elements and spires upwind of the test section (Clifton et al., 2006). The test section was provided with wooden boards covered with fixed quartz sand to simulate a rough natural surface (Fig. 4.1). The height of the wind tunnel roof was adjusted to provide a zero streamwise pressure gradient and to establish a sufficiently developed turbulent boundary layer in the test section (Clifton et al., 2008).

Immediately before the wind tunnel experiments, the root balls were treated with a custom-made tool consisting of four wire needles attached to a metal disk in a square pattern. This tool allowed pushing the four needles simultaneously into the root balls along their whole vertical axis, which reduced the internal tension in the sand-filled grid cylinders and made them more susceptible to wind erosion.

In the wind tunnel, the root balls were mounted 6 m downwind of the beginning of the sand-covered test section. They were fit into a cavity in the sand-covered wooden board with the root balls protruding 5 cm into the wind flow (Fig. 4.1). In this position, the root balls were subjected to an erosive wind event consisting of three phases. The wind tunnel motor was programmed to accelerate within 120 s to a free stream wind velocity of 20 m/s, then, this velocity was maintained for three minutes and finally the motor decelerated to 0 m/s within 120 s.

After the experiments, the root balls were weighed again and the soil loss through wind erosion \( SL \) [%] was calculated as

\[
SL = \frac{m_1 - m_2}{m_1 - m_g - m_s} \times 100
\]
with \( m_1 \) and \( m_2 \) being the weight of the root ball before and after the wind tunnel experiment, \( m_g \) the average weight of the grid cylinders (9.08 g ± 0.09 SE, \( n = 20 \)) and \( m_s \) the average weight of the Styrofoam pieces (8.55 g ± 0.09 SE, \( n = 40 \)). To determine the gravimetric water content of the sand, a sample of about 20 g was taken from each root ball after the wind tunnel experiment and dried at 100°C for 12 hours.

### 4.2.3 Analysis of roots and mycorrhizal colonization

After the wind tunnel experiments, the roots were rinsed in water to remove sand. The cleaned roots were spread out in a water-filled transparent plastic container and analysed with a flat bed scanner. The total root length and average root diameter were determined using the software WinRhizo® (2000).

Roots were cleared in KOH (10%) and stained in an ink-vinegar solution to assess mycorrhizal colonization (Vierheilig et al., 1998). The proportion of root length colonized by mycorrhizal fungi was quantified according to McGonigle et al. (1990). Twenty randomly selected root pieces of approximately 1 cm length were mounted in glycerine on a microscope slide, aligned perpendicular to the long axis of the slides. At a 200-fold magnification, the slide was moved on the stage of the microscope parallel to its long axis to examine a total of 50 intersections between roots and the vertical eyepiece crosshair whether or not they cut any intraradical hyphae, vesicles or arbuscules. The number of intersections with either hyphae, vesicles or arbuscules was divided by the total number of intersections to calculate the percentage of mycorrhizal colonization.

### 4.2.4 Statistical analysis

To compare mycorrhizal and non-mycorrhizal plants within the two plant species, pairwise two-sided Wilcoxon tests were used (significance level = 0.05). The assumptions of linear regression models were checked by residual analysis (QQ plots, Tukey-Anscombe plots, leverage analysis). The variables of the linear regression models were transformed following the first-aid transformations after Mosteller and Tukey (1977).
4.3 Results

After the 2-month growth period, all inoculated plants of both A. vulneraria and L. perenne have formed mycorrhiza. The root colonization by mycorrhizal fungi was tendentially higher in A. vulneraria than in L. perenne (Table 4.2). In the non-inoculated control plants, no mycorrhizal structures were found except in one plant of A. vulneraria which was excluded from the analysis.

The influence of mycorrhizal plant colonization on the wind erodibility of soil was examined by i) using linear regression to analyze the correlation between the percentage of mycorrhizal root colonization and wind-induced soil loss in mycorrhizal root balls, and ii) performing pairwise two-sided Wilcoxon-tests to compare the soil loss of mycorrhizal root balls to the one of non-mycorrhizal control samples. Linear regression yielded a significant decrease in wind-induced soil loss with increasing percentage of mycorrhizal root colonization for the mycorrhizal root balls of both L. perenne and A. vulneraria (Fig. 4.2A, Table 4.3). Most plants with a mycorrhizal colonization >80% had a soil loss <10% in both species. Comparison between non-mycorrhizal and mycorrhizal samples showed a significant difference in soil loss for A. vulneraria, but not for L. perenne. In A. vulneraria, the wind-induced soil loss was 2.6 times smaller for the mycorrhizal root balls (14.7%) than for the non-mycorrhizal ones (38.8%, Fig. 4.2B). In L. perenne, no significant difference in soil loss between mycorrhizal (12.1%) and non-mycorrhizal root balls (10.9%) was found. The mean soil loss of non-mycorrhizal plants was significantly smaller for L. perenne than for A. vulneraria plants (Fig. 4.2B).
Table 4.2: Properties of root balls tested in the wind tunnel (means ± standard deviation). P-values refer to pairwise two-sided Wilcoxon tests. * p-value <0.05.

<table>
<thead>
<tr>
<th></th>
<th>Mycorrhizal</th>
<th>Non-mycorrhizal</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. perenne</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of samples</td>
<td>14</td>
<td>15</td>
<td>--</td>
</tr>
<tr>
<td>Sediment loss through wind erosion SL [%]</td>
<td>12.1 ± 10.6</td>
<td>10.9 ± 5.4</td>
<td>0.949</td>
</tr>
<tr>
<td>Total root length [cm]</td>
<td>379.6 ± 88.7</td>
<td>449.1 ± 86.4</td>
<td>0.026*</td>
</tr>
<tr>
<td>Average root diameter [mm]</td>
<td>0.237 ± 0.011</td>
<td>0.263 ± 0.015</td>
<td>1.3e-04*</td>
</tr>
<tr>
<td>Above-ground plant biomass [g]</td>
<td>0.124 ± 0.026</td>
<td>0.167 ± 0.019</td>
<td>3.2e-04*</td>
</tr>
<tr>
<td>Mycorrhizal colonization [%]</td>
<td>66.7 ± 18.6</td>
<td>0 ± 0</td>
<td>--</td>
</tr>
<tr>
<td>Gravimetric water content [%]</td>
<td>0.074 ± 0.026</td>
<td>0.085 ± 0.041</td>
<td>0.536</td>
</tr>
<tr>
<td>A. vulneraria ssp. alpestris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of samples</td>
<td>18</td>
<td>16</td>
<td>--</td>
</tr>
<tr>
<td>Sediment loss through wind erosion SL [%]</td>
<td>14.7 ± 12.9</td>
<td>38.8 ± 13.9</td>
<td>5.4e-05*</td>
</tr>
<tr>
<td>Total root length [cm]</td>
<td>743.2 ± 130.6</td>
<td>858.0 ± 231.4</td>
<td>0.030*</td>
</tr>
<tr>
<td>Average root diameter [mm]</td>
<td>0.454 ± 0.032</td>
<td>0.434 ± 0.038</td>
<td>0.144</td>
</tr>
<tr>
<td>Above-ground plant biomass [g]</td>
<td>0.510 ± 0.095</td>
<td>0.546 ± 0.128</td>
<td>0.144</td>
</tr>
<tr>
<td>Mycorrhizal colonization [%]</td>
<td>77.1 ± 10.9</td>
<td>0 ± 0</td>
<td>--</td>
</tr>
<tr>
<td>Gravimetric water content [%]</td>
<td>0.064 ± 0.040</td>
<td>0.062 ± 0.035</td>
<td>0.903</td>
</tr>
</tbody>
</table>

Table 4.3: Statistical characteristics of linear regression models with soil loss as the response variable (arcsin square root transformed) and mycorrhizal colonization as the explaining variable. * p-value <0.05.

|                     | Estimate  | Std. Error | t value | Pr(>|t|) |
|---------------------|-----------|------------|---------|---------|
| A. vulneraria ssp. alpestris |           |            |         |         |
| Intercept           | 2.09958   | 0.53479    | 3.926   | 0.00121*|
| Mycorrhizal colonization | -0.28206 | 0.08613    | -3.275  | 0.00476*|
| Residual standard error: 0.1591 on 16 degrees of freedom, adjusted R-squared: 0.3639, p-value: 0.004764 |
| L. perenne          |           |            |         |         |
| Intercept           | 1.27047   | 0.17620    | 7.210   | 1.07e-05*|
| Mycorrhizal colonization | -0.16642 | 0.03051    | -5.455  | 0.000147*|
| Residual standard error: 0.0973 on 12 degrees of freedom, adjusted R-squared: 0.6887, p-value: 0.000147 |
Mycorrhizal fungi protect the soil from wind erosion

Fig. 4.2: A) Wind-induced soil loss decreased significantly with increasing percentage of mycorrhizal root colonization in mycorrhizal root balls of both *Lolium perenne* and *Anthyllis vulneraria ssp. alpestris*. The results of the regression analysis with transformed variables are shown in Table 4.3. B) The mean soil loss of mycorrhizal samples was significantly smaller than the one of non-mycorrhizal samples for *A. vulneraria ssp. alpestris*, but not for *L. perenne* (p-values of pairwise two-sided Wilcoxon tests = 5.4e-05 and 0.949, respectively).

Growth performance was lower in mycorrhizal plants than in non-mycorrhizal plants. Total root length of mycorrhizal plants was significantly smaller than the one of non-mycorrhizal plants for both *L. perenne* and *A. vulneraria* (Table 4.2). Above-ground plant biomass of mycorrhizal plants was significantly smaller than the one of non-mycorrhizal plants for *L. perenne*, but only slightly smaller for *A. vulneraria* (Table 4.2). Within the groups of mycorrhizal plants, total root length increased significantly with increasing percentage of mycorrhizal root colonization for *L. perenne*, but decreased significantly for *A. vulneraria* (Fig. 4.3, Table 4.4).

The mean gravimetric water content of the root balls was 0.08% for *L. perenne* and 0.07% for *A. vulneraria*, without significant differences between mycorrhizal and non-mycorrhizal root balls (Table 4.2).
Fig. 4.3: Within the groups of mycorrhizal plants, total root length increased significantly with increasing percentage of mycorrhizal root colonization for *L. perenne*, but decreased significantly for *A. vulneraria ssp. alpestris*. The results of the regression analysis with transformed variables are shown in Table 4.4.

Table 4.4: Statistical characteristics of linear regression models with total root length as the response variable (log transformed) and mycorrhizal colonization as the explaining variable. * p-value <0.05.

|                          | Estimate | Std. Error | t value | Pr(>|t|)  |
|--------------------------|----------|------------|---------|-----------|
| **A. vulneraria ssp. alpestris** |          |            |         |           |
| Intercept                | 3.43764  | 0.23432    | 14.671  | 1.07e-10* |
| Mycorrhizal colonization | -0.09253 | 0.03774    | -2.452  | 0.0261*   |
| Residual standard error  |          |            |         |           |
|                          | 0.0697   |            | 16 degrees of freedom, adjusted R-squared: 0.2277, p-value: 0.02606 |

<table>
<thead>
<tr>
<th><strong>L. perenne</strong></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.03470</td>
<td>0.11906</td>
<td>17.09</td>
<td>8.67e-10*</td>
</tr>
<tr>
<td>Mycorrhizal colonization</td>
<td>0.09339</td>
<td>0.02061</td>
<td>4.53</td>
<td>0.000689*</td>
</tr>
<tr>
<td>Residual standard error</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.0658</td>
<td></td>
<td>12 degrees of freedom, Adjusted R-squared: 0.6003, p-value: 0.00069</td>
<td></td>
</tr>
</tbody>
</table>
4.4 Discussion

Previous studies have shown in various ways that mycorrhizal fungi stabilize soil structure (reviewed in Rillig and Mummey, 2006), but the present study provides the first experimental demonstration that they are able to increase soil resistance to wind erosion. Mycorrhizal fungi affect soil structure both directly through their hyphae and exudates, and indirectly by changing plant growth performance. The present study did not aim at disentangling the effects of the plant and the fungus, but addressed the resulting overall effect. Regardless of whether the correlation between mycorrhizal colonization and total root length was positive as in *L. perenne* or negative as in *A. vulneraria*, high mycorrhizal root colonization of 2 month-old plants resulted in lower wind-induced soil losses (Fig. 4.2A). This suggests that high mycorrhizal root colonization may decrease seedling mortality in erosive habitats by reducing the negative impacts of wind erosion on vegetation, i.e. plant burial caused by aeolian sand deposits, physical damages on the plant tissue caused by sandblasting, and plant pedestaling, the process whereby erosion lowers the soil surface and exposes plant roots (Perumal and Maun, 1999; Okin et al., 2006). However, seedlings on wind-eroded soils are often not or only poorly colonized by mycorrhizal fungi, because these soils are impoverished in mycorrhizal propagules and the process of spontaneous root colonization is relatively slow (Azcon-Aguilar et al., 2003). Caravaca et al. (2003a, b) analyzed 18 month-old shrubs on a degraded Mediterranean soil and found that less than 10 % of their total root length was colonized by mycorrhizal fungi. Requena et al. (2001) showed that inoculation of mycorrhizal propagules into the soil of a desertified Mediterranean ecosystem significantly increased the percentage of mycorrhizal root length of 10 month-old plants up to 90 %. In the present study, the percentage of mycorrhizal root length ranged from 55-95 % in *A. vulneraria* and from 25-95 % in *L. perenne*, thus covering the typical range of values found in field studies for newly seeded plants.

Comparing mycorrhizal plants to non-mycorrhizal control plants is common practice in ecological laboratory studies, although a complete absence of mycorrhizas is hardly found in natural plant communities. In the present study, the wind-induced soil loss of mycorrhizal root balls was significantly smaller than the one of non-mycorrhizal control
samples for *A. vulneraria*, whereas no difference was found between the mycorrhizal and non-mycorrhizal root balls for *L. perenne* (Fig. 4.2B). Since the total root length of mycorrhizal plants was significantly smaller than the one of non-mycorrhizal plants in both species, it can be excluded that mycorrhizal colonization decreased soil loss indirectly via enhanced root growth. The fact that the mean soil loss of mycorrhizal samples was not higher than the one of non-mycorrhizal samples indicates that the mycorrhizal fungi themselves exerted a direct stabilizing effect on the soil, which just outweighed the disadvantage of lower root growth in *L. perenne*, and overcompensated it in *A. vulneraria* (Fig. 4.2B). The mechanisms underlying this stabilizing effect were not addressed in the present study. However, based on previous research with sandy substrates, it is likely that mycorrhizal hyphae, together with the associated plant roots, have enmeshed sand grains by acting as a ‘sticky string bag’ (e.g. Clough and Sutton, 1978; Degens et al. 1996; Rillig and Mummey, 2006).

Plant growth response to mycorrhizal colonization is known to be highly variable and to depend on both abiotic and biotic context (Hoeksema *et al.*, 2010). In the present study, we found negative growth responses for the roots of both *L. perenne* and *A. vulneraria* as well as for the above-ground biomass of *L. perenne*. Several studies have documented such mycorrhiza-induced growth depressions for various plant species, including *L. perenne* (Buwalda and Goh, 1982; Grimoldi *et al.*, 2006; Chen *et al.*, 2007). Most of these studies were conducted under laboratory conditions with low phosphorus (P) supply and plants in the vegetative stage as in the present study (Bethlenfalvay *et al.*, 1982; Taweraya, 2003). Often, the growth depressions have been found to become smaller or reverse during the lifetime of the plant (Schroeder and Janos, 2004; Li *et al.*, 2005). Recent research suggests that these growth depressions are caused by a reduced P-supply to plants if the fungus suppresses plant pathways for P-uptake and does not provide a net gain via fungal pathways due to low root colonization or low hyphal development in soil (Li *et al.*, 2008; Grace *et al.*, 2009).

With regard to wind erosion control, negative growth responses due to mycorrhizal colonization in newly seeded plants may be disadvantageous, because wind erosion has been found to decrease exponentially with increasing density of the vegetation cover (Lancaster and Baas, 1998; Hesse and Simpson, 2006; Li *et al.*, 2007; Burri *et al.*, in
Mycorrhizal fungi protect the soil from wind erosion (press). However, in stressful environments, this possible disadvantage of mycorrhizal colonization is likely to be countered by several advantages such as a more stable soil structure or lower whole-plant transpiration rates. Since these mycorrhizal effects on plant growth and soil structure are highly species- and context-dependent, the presented results based on laboratory experiments with 2-month-old plantlets of *A. vulneraria* and *L. perenne* cannot be generalized. Therefore, it is necessary to comprehensively evaluate the performance of different plant and fungal species under the given conditions before using them in wind erosion control measures.

While both plant species showed a negative growth response to mycorrhizal colonization, they differed in their response with regard to soil erodibility. For *A. vulneraria*, the wind-induced soil loss was significantly smaller in the mycorrhizal samples than in the non-mycorrhizal samples, whereas no difference was found between the mycorrhizal and non-mycorrhizal root balls of *L. perenne*. In the following paragraphs, two possible explanations for this different extent of the mycorrhizal effect are discussed, referring to i) the root morphology of the two species, and ii) the discrimination capacity of the applied experimental procedure.

The strength of the mycorrhizal association and its relationship with soil structure depend on root morphology (Miller and Jastrow, 1990). Different root size classes and hyphae act at different hierarchical stages in the structural organization of soil aggregates (Tisdall and Oades, 1982). A mixture between root systems of various diameters and morphologies has been shown to be most effective in stabilizing the soil (Pohl *et al.*, 2009). In the present study, the average root diameter of *A. vulneraria* was approximately 3.5 times larger than the one of *L. perenne* (Table 2). Since mycorrhizal hyphae are many times smaller than plant roots, it can be speculated that the additional contribution of mycorrhizal hyphae to soil stability was greater for *A. vulneraria* than for *L. perenne*.

Another possible reason for the different extents of the mycorrhizal effect on soil erodibility for *A. vulneraria* and *L. perenne* may be related to the discrimination capacity of the applied experimental procedure. The way in which the experiments were conducted and erodibility was quantified determined a range where the method was able to discriminate different levels of erodibility. Defining erodibility as the fraction of the
weight loss to the initial weight of the sample implied that the discrimination capacity was best for intermediate levels. Since the soil loss of non-mycorrhizal root balls was significantly lower in *L. perenne* than in *A. vulneraria* (10.9 % vs. 38.8 %), the applied experimental procedure was better suited to detect a decrease in erodibility for *A. vulneraria* than for *L. perenne*. Not only was the measured mean soil loss of non-mycorrhizal *L. perenne* plants smaller than the one of *A. vulneraria* plants, but also the calculated soil loss per plant individual and per cm root length, indicating that *L. perenne* was more efficient in reducing wind erosion under the applied experimental conditions than *A. vulneraria*. It may be hypothesized that we could have detected a difference between mycorrhizal and non-mycorrhizal root balls of *L. perenne* if we would have modified the experimental procedure, e.g. higher wind speed, fewer grasses per pot or larger root balls.

Nevertheless, the applied experimental setup proved useful to study the effect of mycorrhizal fungi on the wind erodibility of soil. Due to the use of a large wind tunnel facility, the experiments could be conducted under atmospheric boundary layer conditions. Exposing root balls to the wind allowed focusing on the subsurface soil erodibility which is influenced essentially by mycorrhizal fungi. Surface erodibility, in contrast, may be influenced additionally by physical, chemical or biological soil crusts (Rice *et al.*, 1996), which were not the focus of this study. Although our experimental setup has no exact counterpart in nature, it partly represents the situation when wind erosion lowers the soil surface and exposes plant roots. Fig. 4.1C shows such a situation in the Death Valley (California), where severe wind erosion has exposed the root balls of shrubs. This figure is shown to illustrate that the wind sometimes acts not only on the surface soil, but also on the subsurface soil. The experimental setup of the present wind tunnel experiments constitutes a simplified system that does not cover all relevant aspects of natural wind erosion processes. In natural environments, plant pedestaling is a gradual process that typically takes place over several years. In the present experiments, in contrast, the roots were exposed instantaneously by artificially removing soil and they were subjected to the wind for only a few minutes. The experimental setup of the present study was primarily developed to satisfy the practical requirements of investigating the effect of mycorrhizal inoculation on the wind erodibility of soil under laboratory conditions. This means, for example, that the wind
speed was set to yield sufficient amounts of erosion and that the plant species were selected based on their ability to grow and establish mycorrhizal symbioses under the given laboratory conditions.

This study provides novel experimental evidence that mycorrhizal fungi have the potential to substantially increase the protective effect of newly seeded plants against wind erosion. For *Anthyllis vulneraria ssp. alpestris*, the reduction in soil loss was significant for the whole group of mycorrhizal plants. Although there was no such overall effect of inoculation for *Lolium perenne*, the mycorrhizal effect manifested itself in a significant reduction of soil loss with increasing percentage of mycorrhizal colonization. These results are all the more remarkable, because there was no mycorrhiza-induced plant growth enhancement. In contrast, mycorrhizal plants even had significantly smaller root systems than non-mycorrhizal plants. Hence, this study is a good example that plants can benefit from mycorrhizas beyond increased growth. Keeping soil erosion as low as possible is an essential advantage for plants to survive in erosive environments.

Further research is necessary to explore in more detail the environmental and practical circumstances under which mycorrhizas may best contribute to sustainable wind erosion control. It would be of particular interest to observe plant growth and soil erodibility over longer time periods, to examine the combined effects of below- and above-ground protection of mycorrhizal and non-mycorrhizal plants, and to test further plant-fungus-combinations. Since commercial inoculum products may contain non-mycorrhizal microbes, it would be interesting to conduct experiments with pure culture inoculum to exclude any effects of such organisms. In order to gain information on possible causes underlying the effect of mycorrhizal inoculation on the wind-induced soil loss, it would be useful to quantify extraradical hyphae and/or glomalin-related soil proteins.
4.5 References


Mycorrhizal fungi protect the soil from wind erosion


Mycorrhizal fungi protect the soil from wind erosion


Chapter 5

PLANT GROWTH AND MYCORRHIZA FORMATION UNDER NUTRIENT DEFICIENCY AND DROUGHT STRESS

Katrin Burri

In preparation
5. Plant growth and mycorrhiza formation under nutrient deficiency and drought stress

Abstract

The re-establishment of vegetation on severely disturbed soils often fails because plants are not able to grow under extreme nutrient deficiency and drought stress. Arbuscular mycorrhizal fungi (AMF) have been suggested to improve plant establishment success by enhancing the acquisition of nutrients and water. In the present study, we subjected seedlings of four alpine grass species to extreme drought and nutrient stress in a laboratory pot culture experiment. The grasses were grown on four types of nutrient-depleted mineral sand, inoculated with the AMF *Glomus intraradices* and additionally subjected to a drought treatment. After a growth period of 3 months, survival, above-ground biomass and mycorrhizal colonization of the grass tussocks were assessed. The proportion of inoculated grass tussocks that established a symbiosis was significantly lower under drought-conditions (23-58%) than under non-drought conditions (33-100%). The proportion of surviving grass tussocks was also significantly lower under drought conditions than under non-drought conditions. It decreased from 86% to 38% in the inoculated tussocks, and from 72% to 32% in the non-inoculated tussocks. Inoculation of *G. intraradices* had no significant effect on either plant survival or above-ground biomass. However, there was a trend towards higher survival and biomass in inoculated tussocks compared to non-inoculated tussocks.
5.1 Introduction

Arbuscular mycorrhizal fungi (AMF) are obligate symbionts that form associations with the roots of most terrestrial plant species. They have various beneficial effects on their host plants, including facilitation of nutrient and water acquisition, promotion of soil aggregation as well as protection against pathogens, toxic compounds and herbivores (Smith and Read, 2008). Plants dealing with abiotic stresses, such as low water or nutrient availability, have often been found to benefit particularly from AM symbioses (Smith et al., 2010; Augé et al., 2001).

Due to their role in alleviating water and nutrient deficiencies, there is an increasing interest in using AMF to improve the success of revegetation projects in extreme habitats, e.g. on steep mountain slopes affected by landslides, in desertification-threatened arid and semi-arid environments or in disturbed high-altitude grasslands (Miller and Jastrow, 1992; Perumal and Maun, 1999; Requena et al., 2001; Caravaca et al., 2003; Gai et al., 2006). Revegetation practices in such habitats are often confronted with poor plant establishment and high mortality, because seedlings face extremely harsh conditions at their sensitive earliest growth stages. However, a rapid and reliable plant establishment is of crucial importance for revegetation success in extreme environments with short growing seasons and recurrent disturbances. Recent research suggests that the introduction of symbiotic fungi together with indigenous plant species is a promising approach to initiate and promote autogenic recovery of disturbed ecosystems (King and Hobbs, 2006). Particularly in harsh, limiting environments, this approach bears the potential for a substantial increase in long-term revegetation success by creating synergies between abiotic and biotic processes (Jeffries et al., 2003; Byers et al., 2006).

Although numerous studies have demonstrated beneficial effects of AM symbiosis on plant growth, there is also an increasing number of reported cases where it had a negative effect (e.g. Koide, 1985; Jifon et al., 2002; Grimoldi et al., 2006). Such negative plant growth responses have often been found to be transient, followed by positive responses at later developmental stages of the symbiosis (Schroeder and Janos 2004; Li et al., 2005). While the AM symbiosis has traditionally been regarded as a clear example of mutualism, newer research shows that it might be better seen as a
continuum of outcomes ranging from mutualistic to neutral to antagonistic (Hoeksema et al., 2010). Whether or not a plant will benefit from being mycorrhizal depends on different variables, including host plant characteristics, fungal characteristics, soil biotic and abiotic conditions, and experimental procedures (Johnson et al., 1997; Jones and Smith, 2004). These findings demonstrate that the response of a specific plant species to mycorrhiza formation should be carefully evaluated under the given conditions before applying AMF in revegetation projects.

Abiotic soil conditions not only affect the mycorrhiza-induced plant growth response, but also the process of symbiosis formation. In undisturbed soils, colonization of roots by AMF can be initiated from spores, infected root fragments or hyphal networks (Smith and Read, 2008). Persistent underground hyphal networks associated with living plants are the main mean by which seedlings become rapidly colonized in many habitats. On disturbed soils, however, these hyphal networks are disrupted and the amount of spores and root fragments is decreased, which results in strongly reduced infectivity of the soil. This deficiency can be alleviated by adding industrially produced inoculum with high concentrations of spores and infected root fragments. However, hyphal growth from spores and root fragments is strongly restricted in contrast to the growth of extraradical hyphal networks (Smith and Read, 2008). Unfavourable soil conditions such as extreme pH or low soil water content may further limit the germination of spores and consequent hyphal growth, resulting in poor colonization of plants. In order to optimize the efficiency of AMF in revegetation projects, it is necessary to better understand how abiotic stresses affect the establishment of mycorrhizal symbioses. The existing knowledge is fragmentary and conflicting, partly caused by the wide variety of experimental procedures as well as species-specific responses and interactions of both plants and fungi.

In the present study, we investigated plant growth and mycorrhiza formation under extreme drought and nutrient stress in a laboratory pot culture experiment. We used Glomus intraradices, a commonly cultivated AMF species that occurs naturally in high-altitude grasslands (Gai et al., 2009), and four alpine grass species that are adapted to nutrient-deficient, poorly-structured soils. The grasses were grown on four types of mineral sand and subjected to a drought treatment in a full-factorial split-split-plot design. The aim of this study was to examine whether the inoculation of AMF under
extreme drought and nutrient stress leads to the formation of mycorrhizal symbioses and whether it improves plant survival and above-ground biomass. In particular, we addressed the following hypotheses: i) Drought reduces the formation of mycorrhizal symbioses. ii) Inoculated grass tussocks have a higher proportion of surviving tussocks than non-inoculated tussocks. iii) Inoculated tussocks produce more above-ground biomass than non-inoculated tussocks.

5.2 Material and methods

5.2.1 Plant cultivation

The experiment was performed with the following four alpine grass species: Poa alpina, Agrostis capillaris var. alpina, Bellardiochloa variegata and Festuca supina (Alpine Garden Center Schutz Filisur, Switzerland). The grasses were seeded on four types of autoclaved, fine-grained mineral sand, all of them having low water retention capacity and a lack of organic matter (Table 5.1).

The grasses were grown in 12 cultivation trays, each containing 150 cells of 33 ml (Quickpot® QP 150 RW). In each tray, 28 adjacent cells were first half filled with each of the four sand types. Half of the trays were then provided with 4 ml of a commercial mycorrhizal inoculum per cell (Glomus intraradices in vermiculite of 1-2 mm particle size, INOQ GmbH, Germany), resulting in an inoculum content of approximately 12 vol%. The other half of the trays were provided with 4 ml of autoclaved vermiculite (1-2 mm particle size). After the cells were entirely filled with sand, the four grass species were seeded alternately, resulting in 7 seeded cells per species, sand type and tray, and in a total of 1344 seeded cells. The plant trays were kept in a climate chamber with a 12 hour day/night cycle at a temperature of 20/15°C and a light intensity of 50’000/0 lux. After germination, seedlings were reduced to three individuals per cell. The plant trays were watered from below by placing them in larger trays that were periodically filled with water. Half of the trays were subjected to a drought treatment which included withholding watering until the grasses started to turn yellow. This resulted in drought periods of up to two weeks. The other half of the trays were irrigated 2-3 times a week. The water content of the sand was not measured, but it was observed that the drought
treatment resulted in extremely low water contents due to the low water retention capacity of the four sand types. With regard to nutrient supplementation, all plants were treated equally, i.e. they were grown without adding any fertilizer.

5.2.2. Analysis of plant growth and mycorrhizal colonization

After a growth period of 3 months, all grass tussocks were assessed whether they were alive or not. Additionally, the largest individual in each cell was harvested, except for the tussocks subjected to the drought treatment and the grasses grown on quartz sand. The harvested grasses were air dried for several weeks and then their dry weight was determined. The grasses subjected to the drought treatment and the grasses grown on quartz sand were excluded from the analysis of above-ground biomass, because they were hardly able to grow and experienced high mortality.

To assess mycorrhizal plant colonization, a sample of 74 inoculated and 69 non-inoculated tussocks were analyzed. The roots were washed, cleared in KOH (10%) and stained in an ink-vinegar solution (Vierheilig et al., 1998). The whole root systems were then systematically screened under a microscope at a 200-fold magnification to determine whether they contained any mycorrhizal structures, i.e. hyphae, vesicles or arbuscules. Root systems containing at least one of these mycorrhizal structures were classified as colonized, whereas all the others were classified as non-colonized.

| Table 5.1: Grain size distributions and pH of the four sand types used in this study. |
|-----------------|-----------------|-----------------|-----------------|
|                 | Quartz sand     | Granite sand    | River sand coarse |
| Sand (0.05-2 mm) [%] | 97.8            | 95.55           | 98.1            | 93.7 |
| Silt (0.002-0.05 mm) [%] | 0.4            | 3.65            | 0.75            | 5.1  |
| Clay (<0.002 mm) [%]  | 1.8            | 0.8             | 1.15            | 1.2  |
| pH               | 7.2            | 8.2             | 8.5             | 8.4  |
5.2.3 Statistical Analysis

The study was designed as a full factorial split-split-plot experiment with two 2-level whole-plot-factors (mycorrhizal inoculation and drought), a 4-level split plot factor (sand type), a 4-level split split plot factor (plant species), and three replicates.

Data were analyzed using three regression models generated with the software R (version 2.11.1). To test whether there was an effect of inoculation on plant survival, we used a generalized mixed-effects model with inoculation, drought, sand type and plant species as influencing variables (Eq. 5.1). All 4-factor and 3-factor interactions were excluded from the model. All 2-factor interactions with p-values >0.1 were removed stepwise from the model. To test the effect of inoculation on plant biomass, we used a linear mixed-effects model with the same influencing variables as in Eq. 5.1 except that the drought treatment was omitted, because biomass was measured only under non-drought conditions (Eq. 5.2). The biomass values were square-root-transformed according to the first-aid transformations after Mosteller and Tukey (1977). In the model statements, we accounted for the hierarchical split-split-plot design and tested the effect of each treatment against the residual variation associated with the units to which the treatment has been applied (Eq. 5.1 and Eq. 5.2). Analysis was based on the restricted maximum likelihood method to deal with unbalanced data. The assumptions of the regression models were checked by residual analysis. Post hoc multiple comparison was performed based on Tukey contrasts using the glht-function of the software R.

To test whether the drought treatment had an effect on the establishment of mycorrhizal symbioses, we used a generalized linear model with drought, sand type and plant species as influencing variables, and performed a chi-square test (Eq. 5.3). This model was based on a reduced dataset of 74 inoculated tussocks and did not account for the hierarchical design of the experiment because the sample was too small.

\[
glmer \text{ (survival ~ inoculation} \times \text{drought} \times \text{sand} \times \text{species}) \\
\quad + (1 | \text{tray/sand/species}), \text{family=binomial})
\]

\[
lme \text{ (sqrt(biomass) ~ inoculation} \times \text{sand} \times \text{species}, \\
\quad \text{random = ~ 1| tray/sand/species})
\]

\[
glm \text{ (mycorrhizal colonization ~ drought} \times \text{sand} \times \text{species, binomial})
\]
5.3 Results

5.3.1 Mycorrhizal plant colonization

In all plant species, the proportion of colonized tussocks was lower under drought conditions than under non-drought conditions (Table 5.2). The generalized linear model indicates that the drought treatment decreased the proportion of colonized tussocks significantly (p-value of chi-square test = 0.002, Table 5.3). Under non-drought conditions, the maximum proportion of colonized tussocks was obtained in *F. supina* (100%), and the minimum in *P. alpina* (33%). Under drought conditions, the proportion of colonized tussocks ranged from 58% in *A. capillaris var. alpina* to 23% in *P. alpina*. The non-inoculated plants were not colonized by mycorrhizal fungi.

Table 5.2: Proportions of colonized tussocks in the inoculated tussocks [%] and number of analyzed tussocks (in brackets).

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Non-drought conditions</th>
<th>Drought conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Poa alpina</em></td>
<td>33 (6)</td>
<td>23 (13)</td>
</tr>
<tr>
<td><em>Festuca supina</em></td>
<td>100 (7)</td>
<td>27 (11)</td>
</tr>
<tr>
<td><em>Agrostis capillaris var. alpina</em></td>
<td>67 (6)</td>
<td>58 (12)</td>
</tr>
<tr>
<td><em>Bellardiochloa variegata</em></td>
<td>86 (7)</td>
<td>42 (12)</td>
</tr>
</tbody>
</table>

Table 5.3: Statistical characteristics of a generalized linear model with mycorrhizal colonization as response variable (Eq. 5.3). Influencing variables: drought, sand type and plant species. * = p-value < 0.05.
5.3.2 Plant survival

The generalized mixed-effects model suggests that the effect of inoculation on plant survival was not significant (Table 5.4). However, there was a trend towards higher proportions of surviving tussocks in inoculated tussocks than in non-inoculated tussocks (Fig. 5.1). This tendency was more pronounced under non-drought conditions than under drought conditions. For the drought treatment, the model indicates a significant negative impact on survival. Across all species and sand types, the mean proportion of surviving tussocks was highest in the inoculated tussocks under non-drought conditions (86%), followed by the non-inoculated tussocks under non-drought conditions (72%), the inoculated tussocks under drought conditions (38%), and the non-inoculated tussocks under drought conditions (32%). Under non-drought conditions, the inoculation treatment increased survival in 13 out of 16 plant-sand-combinations. Under drought conditions, it increased survival in only 9 out of 16 plant-sand-combinations.

The model suggests that the quartz sand had a significant negative effect on plant survival, while the fine river sand had a significant positive effect (Table 5.4). Across all treatments and plant species, the mean proportion of surviving tussocks was highest on the fine river sand (80%), followed by the granite sand (60%), the coarse river sand (54%), and the quartz sand (35%) (Fig. 5.1). The plant species had no significant effect on survival (Table 5.4). Across all treatments and sand types, survival was highest in *P. alpina* (73%), followed by *A. capillaris var. alpina* (59%), *B. variegata* (53%), and *F. supina* (43%).
Table 5.4: Statistical characteristics of a generalized mixed-effects model with plant survival as response variable. Influencing variables: inoculation, drought, sand type and plant species (Eq. 5.1). * = p-value < 0.05.

<table>
<thead>
<tr>
<th>Random effects:</th>
<th>Variance</th>
<th>Std. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species : (substrate : tray)</td>
<td>2.807</td>
<td>1.675</td>
</tr>
<tr>
<td>Substrate : tray</td>
<td>5.2e-13</td>
<td>7.2e-07</td>
</tr>
<tr>
<td>Tray</td>
<td>5.374</td>
<td>2.318</td>
</tr>
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<tr>
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<td>1.662</td>
<td>-3.190</td>
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</tr>
<tr>
<td>River sand fine</td>
<td>2.793</td>
<td>1.143</td>
<td>2.443</td>
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</tr>
<tr>
<td>Quartz sand</td>
<td>-3.571</td>
<td>0.778</td>
<td>-4.589</td>
<td>4.5e-06 *</td>
</tr>
<tr>
<td>River sand coarse</td>
<td>-0.721</td>
<td>0.750</td>
<td>-0.961</td>
<td>0.337</td>
</tr>
<tr>
<td>B. variegata</td>
<td>-0.488</td>
<td>0.807</td>
<td>-0.604</td>
<td>0.546</td>
</tr>
<tr>
<td>F. supina</td>
<td>-0.585</td>
<td>0.778</td>
<td>-0.753</td>
<td>0.452</td>
</tr>
<tr>
<td>P. alpina</td>
<td>0.527</td>
<td>0.839</td>
<td>0.628</td>
<td>0.530</td>
</tr>
<tr>
<td>Drought : river sand fine</td>
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<td>1.302</td>
<td>-0.432</td>
<td>0.666</td>
</tr>
<tr>
<td>Drought : quartz sand</td>
<td>2.266</td>
<td>1.008</td>
<td>2.249</td>
<td>0.025   *</td>
</tr>
<tr>
<td>Drought : river sand coarse</td>
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<td>Drought : B. variegata</td>
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<td>1.015</td>
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</tr>
<tr>
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<td>0.083</td>
</tr>
<tr>
<td>Drought : P. alpina</td>
<td>1.336</td>
<td>1.033</td>
<td>1.293</td>
<td>0.196</td>
</tr>
</tbody>
</table>
Fig. 5.1: Plant survival of the four grass species in the four treatments: control = not inoculated and non-drought conditions, drought = not inoculated and drought conditions, inoc = inoculated and non-drought conditions, inoc+drought = inoculated and drought conditions. Grey boxes: number of surviving grass tussocks. Black boxes: number of dead grass tussocks. Percentage numbers: proportions of surviving grass tussocks.
5.3.3 Above-ground plant biomass

Inoculation had no significant effect on above-ground plant biomass, as indicated by the linear mixed-effects model (Table 5.5). Compared to non-inoculated plants, the mean biomass of inoculated plants was higher in 6 out of 12 species-sand combinations, lower in 2 combinations, and the same in 4 combinations (Fig. 5.2). The mean biomass across all plant species and sand types was 0.005 g (sd = 0.005) in the non-inoculated plants and 0.006 g (sd = 0.005) in the inoculated plants. Although the linear mixed-effects model yielded no significant effect of inoculation on plant biomass, it suggested a nearly significant interaction effect between inoculation and plant species (Table 5.5). However, even if the model was run for each species separately, it yielded no significant effect of inoculation on biomass in any of the four plant species (Table 5.6).

The type of sand had a significant effect on plant biomass, both in the full model (Table 5.5) as well as in the four models separated by plant species (Table 5.6). In all four plant species, both the inoculated and non-inoculated plants yielded the largest biomass on the fine river sand (Fig. 5.2), but the multiple comparison test indicated no significant difference between any of the sand types (p-values river sand fine – granite sand: 0.258, river sand coarse – granite: 0.604, river sand coarse – river sand fine: 0.116). Plant species had a significant effect on biomass too (Table 5.5). *P. alpina* yielded the highest biomass on all three sand types used for comparison in both the inoculated and non-inoculated plants (Fig. 5.2). For the plant species, no multiple comparison test was performed because there was a significant interaction between inoculation and plant species in the full model, which could cause inaccurate results in post-hoc analyses.

Above-ground biomass was measured only for plants grown under non-drought conditions, exclusive of the plants grown on quartz sand, because plant growth and survival were extremely low under drought conditions and on the quartz sand (Fig. 5.2).
Table 5.5: Statistical characteristics of a linear mixed-effects model with plant biomass as response variable. Influencing variables: inoculation, sand type and plant species (Eq. 5.2). * = p-value < 0.05.

<table>
<thead>
<tr>
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<th>p-value</th>
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<td>381</td>
<td>213.645</td>
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<td>Inoculation</td>
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<td>4</td>
<td>0.443</td>
<td>0.542</td>
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<td>Sand</td>
<td>2</td>
<td>8</td>
<td>10.65371</td>
<td>0.006 *</td>
</tr>
<tr>
<td>Species</td>
<td>3</td>
<td>35</td>
<td>10.67417</td>
<td>&lt;.0001 *</td>
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<td>Inoculation : sand</td>
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<td>0.59058</td>
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<td>Inoculation : species</td>
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<tr>
<td>Sand : species</td>
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<td>0.42169</td>
<td>0.860</td>
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<tr>
<td>Inoculation : sand : species</td>
<td>6</td>
<td>35</td>
<td>0.39129</td>
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Table 5.6: Statistical characteristics of linear mixed-effects models with plant biomass as response variable, separated by plant species. Influencing variables: inoculation and sand type. * = p-value < 0.05.

<table>
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<tr>
<th>Plant Species</th>
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<tr>
<td><em>Agrostis capillaris var. alpina</em></td>
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<tr>
<td>(Intercept)</td>
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<td>101</td>
<td>103.406</td>
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<td>Inoculation</td>
<td>1</td>
<td>4</td>
<td>2.748</td>
<td>0.173</td>
</tr>
<tr>
<td>Sand</td>
<td>2</td>
<td>8</td>
<td>8.724</td>
<td>0.010 *</td>
</tr>
<tr>
<td>Inoculation : sand</td>
<td>2</td>
<td>8</td>
<td>1.102</td>
<td>0.378</td>
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<table>
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<td><em>Poa alpina</em></td>
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<td>(Intercept)</td>
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<td>89</td>
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<td>Inoculation</td>
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<td>Sand</td>
<td>2</td>
<td>7</td>
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<td><em>Festuca supina</em></td>
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</tr>
<tr>
<td>(Intercept)</td>
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<td>93</td>
<td>389.837</td>
<td>&lt;.0001 *</td>
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<td>2.293</td>
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<tr>
<td>Sand</td>
<td>2</td>
<td>8</td>
<td>23.634</td>
<td>4.0e-04 *</td>
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<tr>
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<td>2</td>
<td>8</td>
<td>5.024</td>
<td>0.039 *</td>
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</table>

<table>
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<td>8</td>
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<td>0.023 *</td>
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<tr>
<td>Inoculation : sand</td>
<td>2</td>
<td>8</td>
<td>1.040</td>
<td>0.397</td>
</tr>
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</table>
5.4 Discussion

5.4.1 Mycorrhizal colonization

In the present study, seedlings of four alpine grass species were inoculated with *G. intraradices* and grown under extreme nutrient and water stress. After a growth period of 3 months, the proportion of tussocks that did establish a symbiosis was significantly lower in the grasses grown under drought conditions than under non-drought conditions (Table 5.2). Previous research has produced contrasting results regarding the effect of low soil water contents on the level of root colonization by AMF. Augé (2001) reviewed over 150 studies and found that drought affected levels of root colonization in about half of the reports, increasing it more often than decreasing it, while in the other half, drought had no effect. Several studies showed that the level of colonization depends on the fungal species and genotypes (Ruiz-Lozano et al., 1995; Fagbola et al.,...
Plant growth and mycorrhiza formation

2001; Davies et al., 2002), indicating that the contrasting results may partly result from specific adaptations of certain AMF strains to drought conditions (Compant et al., 2010). Furthermore, interactions with other soil microorganisms have also been found to affect the outcome of mycorrhizal symbioses under drought conditions (Vazquez et al., 2001; Staddon et al., 2004).

The reduced proportions of colonized tussocks under drought conditions in the present study were probably due to reduced growth of plant roots and fungal hyphae, which decreased the likelihood that they would contact each other. Germinability and infectivity of AMF spores under drought conditions have been found to decrease or increase depending on the fungal species, the level of drought and the timing of sporulation (Jasper et al., 1993; Braunberger et al., 1996; Ruiz-Lozano and Azcon, 1996). For *G. intraradices*, Douds and Schenck (1991) found that the germinability of spores decreased with decreasing soil water content. In completely dry substrate, which was probably temporarily the case in the present study, Ruiz-Lozano and Azcon (1996) observed that the infective capacity of spores decreased considerably, including a species that had responded positively to moderate drought stress. Hence, it can be assumed that spore germination and hyphal growth of *G. intraradices* were reduced under the drought conditions of the present study, which consequently lead to reduced mycorrhiza formation. Root development of the grasses was not measured, but the significantly lower proportions of surviving tussocks under drought conditions than under non-drought conditions suggest that it was strongly reduced.

The fact that symbioses were observed in all four plant species showed that the plants and the mycorrhizal inoculum were compatible under the given circumstances. In such cases, i.e. pot cultures with limited soil volumes and high contents of compatible inoculum, the percentage of colonized tussocks is usually expected to be near 100%, as it was the case for *F. supina*. In the other species, however, the proportions of colonized tussocks were relatively low, even without drought treatment ranging from only 33% to 86%. These low proportions of colonized tussocks indicate that the experimental conditions of the present study were even more adverse than in comparable studies. The plants were grown on practically pure mineral sand without adding any fertilizer and the drought treatment was applied shortly after germination without waiting first for the symbioses to establish.
It is important to note that laboratory studies such as the present one can only cover a small part of the interactions that occur between AMF and plants in real environments. There, chronic or periodical drought may stimulate AMF to colonize roots more extensively or to develop adapted strategies such as rapid hyphal growth in response to increasing soil moisture and production of resilient spores in response to declining soil moisture (Augé, 2001). Furthermore, plants may become colonized by different types of mycorrhiza during longer exposure to drought (Querejeta et al., 2009; Compant et al., 2010).

5.4.2 Plant survival and above-ground plant biomass

The present study addressed the question of whether mycorrhizal inoculation improves the survival and growth of four alpine grass species under extreme nutrient and water stress. Contrary to our initial hypotheses, inoculation had no significant effect on either parameter. However, there was a consistent trend towards higher survival in inoculated tussocks than in non-inoculated tussocks across all combinations of plant species and sand types, which was more pronounced under non-drought conditions than under drought conditions. For above-ground biomass, there was also a slight tendency towards higher biomass in inoculated plants, except for *F. supina*, where the opposite was the case. The fact that the effect of inoculation on plant survival and biomass did not reach a significant level may be partly explained by the relatively low proportion of inoculated tussocks that established mycorrhizal symbioses. This may also explain why the trend towards higher survival was more pronounced under non-drought conditions, where the proportions of colonized tussocks were higher than under drought conditions.

Another reason for the lack of a significant response of plant survival and biomass to mycorrhizal inoculation might was that the experimental conditions of this study hardly allowed the fungi to enhance plant nutrition. Improved pant nutrition is regarded as the main cause of AMF enhanced plant growth under stressful conditions (Augé, 2001). The fungi absorb and transfer nutrients to their host plants, which can lead to a higher net-uptake of nutrients, due to the larger absorbing surface and the ability of hyphae to access extremely small soil pores that are not accessible to plant roots. In the present study, however, plants were grown on practically pure mineral sand with extremely low
nutrient availability, and it was thus hardly possible for the fungi to enhance plant nutrition. Under such circumstances, in which the fungi cannot make use of their potential in acquiring nutrients, they may not be advantageous for plant growth, or even disadvantageous as in *F. supina*. Mycorrhiza-induced growth depressions have been documented by several studies; most of them were conducted under laboratory conditions with low contents of phosphorus (P) in the soil and plants in the vegetative stage as in the present study (Bethlenfalvay et al., 1982; Taweraya, 2003). The conventional explanation for this phenomenon is that the fungal demand for organic carbon (C) from the host plant outweighs any benefit that the plant might get by acquiring P via the fungus (Stribley et al., 1980; Graham and Abbott, 2000). However, recent research has shown that growth depressions might be caused by regulation of P-uptake rather than C-demand (Li et al., 2008; Grace et al., 2009). Li et al. 2008 suggested that mycorrhizal colonization will result in lower P-supply to the plant if the fungus suppresses plant pathways for P-uptake and does not provide a net gain via fungal pathways due to low root colonization or low hyphal development in the soil. In previous studies, mycorrhiza-induced growth depressions have often been found to become smaller or reverse during the lifetime of the plant (Schroeder and Janos, 2004; Li et al., 2005), perhaps because the mycorrhizal P-pathway becomes more efficient with increasing age of the symbiosis. For ectomycorrhiza, Correa et al. (2006) found that the formation of the symbiosis had an adverse effect on plant growth if the plants were inoculated during their early establishment stages, while it had no adverse effect if the plants were older at the time of inoculation. With respect to the present study, it can thus be hypothesized that the only 3-month old grasses were still stressed by the establishment of the symbiosis, but that they would have benefited from the symbiosis at later growth phases.

Another circumstance that should be considered with regard to the lack of a positive inoculation effect on biomass refers to possible disadvantages of large plant size. While enhanced plant growth has commonly been regarded as advantageous, newer research shows that this is not necessarily the case in stressful environments (Smith et al., 2010). This is particularly obvious for water-limited environments, because large plants need more water than small plants, and thus have a disadvantage as long as reproductive success is not completely dependent on vegetative biomass (Smith et al., 2010).
Therefore, lacking or negative growth responses to AMF colonization could be a strategy to reduce whole-plant transpiration rate, and consequently water use. The same may hold true for nutrient-limited environments, because large plants need more nutrients than small plants.

Even though we found no significant effect of inoculation on plant survival, we still observed a consistent trend towards better survival of mycorrhizal plants under drought as well as under non-drought conditions. As mentioned above, improved nutrition is unlikely to have caused this trend. Mechanisms unrelated to plant size and plant nutrition that may be responsible for this trend are: i) effects on root architecture, e.g. increased branching or fineness, ii) reduction in root resistance to water flow within roots, and iii) improvement in soil structure, leading to a higher water retention capacity of the soil (Augé, 2001). Independent of any mycorrhizal influence, the sand types used in this study had different water retention capacities due to their different grain size distributions (Table 5.1). This was probably a major cause why the grasses yielded the highest survival and biomass on the fine river sand, which was the sand with the highest fraction of silt (Table 5.1). In future studies, it would be interesting to monitor the water and nutrient content of the growth substrates.

In the present laboratory study, grass seedlings were subjected to extreme nutrient and drought stress during their sensitive first growth phase just after emergence. The seedlings were hardly able to establish and grow, even though the species were adapted to nutrient-deficient, dry soils. It was also found that under such harsh experimental conditions, the establishment of mycorrhizal symbioses from industrially produced inoculum was severely impeded. Inoculation had no significant effect on either plant survival or above-ground biomass. With regard to revegetation measures in extreme habitats, these findings imply that the application of a commercial mycorrhizal inoculum may not necessarily improve plant establishment. Further research should explore whether plant establishment could be enhanced more effectively if inoculation is done with native adapted fungal strains, at later growth phases or in combination with other plant-growth promoting measures.
5.5 References


6 GENERAL CONCLUSIONS

6.1 Main findings

This thesis has addressed the effect of plants and mycorrhizal fungi on wind erosion processes by performing experiments in a laboratory wind tunnel (chapters 2-4). Furthermore, it examined how simulated eroded soil conditions affect plant growth and mycorrhiza formation in a pot culture experiment (chapter 5). In the following, seven main findings resulting from these experiments are presented and discussed in the context of current knowledge.

Enhancement of wind erosion in extremely sparse vegetation canopies

The above-ground parts of vegetation act as non-erodible roughness elements that modify the near-surface wind. Their effect on aeolian sediment transport is attributed to three mechanisms: i) surface sheltering, ii) momentum extraction from the wind, and iii) trapping of windborne sediment (Wolfe and Nickling, 1993). Therefore, wind erosion is generally lower on vegetated soil than on unvegetated soil and decreases with increasing vegetation density. The wind tunnel experiments presented in chapter 2 confirmed previous field studies that found an exponential decrease in sediment mass flux with increasing canopy density (e.g. Lancaster and Baas, 1998; Hesse and Simpson, 2006; Li et al., 2007). However, in our experiments with a grass canopy of rather small density (horizontal cover $C_v = 4\%$), we found that both total sediment mass flux and PM$_{10}$ concentration were increased to 117.5% and 145.6%, respectively, compared to an unplanted sand surface (chapter 2.3.2, Fig. 2.6, Table 2.3). This could be attributed to locally elevated shear stress on the sand bed caused by flow acceleration around the tussocks and vortical structures in their lee. Furthermore, the grasses were observed to trigger erosion by oscillating movements at the ground surface. So far, most studies exploring this phenomenon of erosion enhancement used sparsely arrayed rigid roughness elements and focused on the effect on the threshold velocity for sediment entrainment (Logie, 1982; Sutton and McKenna Neuman, 2008). The experiments
presented in chapter 2 used live, flexible vegetation and focused on the magnitude of sediment transport, which was found to be higher on a sparsely planted sand surface than over a bare surface.

Conclusion 1: A sparse canopy of isolated grass tussocks can increase aeolian sediment flux and fine dust emission compared to an unvegetated soil surface.

Peak in aeolian sediment mass flux at twice the canopy height

Over unvegetated soil, aeolian sediment mass flux decreases exponentially with increasing height above ground (e.g. White, 1982; Nishimura and Hunt, 2000; Dong et al., 2002). Vegetation modifies the vertical distribution of aeolian sediment mass flux both directly by trapping particles which impact on plants, and indirectly by changing turbulent flow properties. In the wind tunnel experiments presented in chapter 2, the vertical sediment mass flux profiles over medium- and large-density canopies were characterized by low flux proportions inside the canopy and a local maximum at approximately twice the canopy height (chapter 2.3.3, Fig. 2.7). This phenomenon may be caused by particles rebounding from plant surfaces and by vegetation-induced changes in the vertical profile of shear stress velocity.

Conclusion 2: The vertical profile of aeolian sediment mass flux over dense grass canopies exhibits a local maximum at approximately twice the canopy height.

Air flow regimes and vegetation canopy density

Plants provide a sheltered zone of reduced mean wind speed on their lee sides. The development of these sheltered wake zones depends on the size and spacing of the plants, resulting in different air flow regimes: i) isolated roughness flow, where there is no interaction between wakes and adjacent downstream vegetation, ii) wake interference flow, where wakes from upstream plants intercept downstream plants, and iii) skimming flow, where wakes completely overlap and the entire ground surface is sheltered (e.g. Morris, 1955; Wolfe and Nickling, 1993). The type of air flow regime is
critical with regard to the amount of wind erosion. The existing knowledge on the
determinants of the different air flow regimes is based on experiments with solid
The wind tunnel experiments presented in chapters 2 and 3 provide initial information
about the degree of canopy density associated with different flow regimes. Evidence
was found by analyzing spatial patterns of sediment deposition and wind-induced
changes in the sand bed level. In a small-density canopy (horizontal cover $C_v = 4\%$), the
wedge-shaped deposits in the wakes of the tussocks did not overlap with the adjacent
downstream tussocks, indicating a wake-interference flow (Fig. 3.4). In a medium-
density canopy ($C_v = 16\%$), in contrast, these deposits did overlap with the adjacent
downstream tussocks, suggesting an isolated roughness flow (Fig. 3.5). In a large-
density canopy ($C_v = 47\%$), only few sand grains were entrained by the wind and they
deposited mainly within reach of the grass tussocks. The deposited sand grains were
evenly distributed around the tussocks, without pronounced accumulations on their
upstream, downstream or lateral sides, suggesting a skimming flow regime (Fig. 3.6).

**Conclusion 3:** Canopies of uniformly spaced grass tussocks with horizontal covers
$C_v$ of approximately 4%, 16% and 47% are likely to produce an
isolated roughness flow, a wake-interference flow and a skimming
flow regime, respectively.

**Use of colored sand for visualizing aeolian deposition processes**

In partly vegetated environments affected by wind erosion, plants act as a trap for
aeolian sediment. This leads to a small-scale mosaic of depositional and erosional areas
and to a redistribution of soil resources (Bielders et al., 2002; Okin et al., 2006).
Previous studies have used various methods to visualize these erosion and deposition
patterns, such as measuring wind-induced changes in the level of the soil surface by
using laser displacement sensors or by marking the changing level of the soil surface on
steel rods driven into the ground (Wiggs et al., 1995; Hesse and Simpson, 2006; Udo
and Takewaka, 2007). On unvegetated soils, fluorescent tracer sand has sporadically
been used to investigate aeolian sediment transport (Berg, 1983; Willetts and Rice, 1988; Cabrera and Alonso, 2009).

The wind tunnel experiments presented in chapter 3 were distinct from previous research in that colored sand was applied to visualize spatial patterns of sediment deposition in vegetation canopies. The resin-coated sand used in these experiments proved suitable for this purpose. It produced high-resolution bed-level data for the whole ground surface under investigation and it allowed a quantitative estimation of the ground fraction which effectively experienced erosion. This fraction was found to be substantially smaller than the ground fraction which was not covered by vegetation.

The aerodynamic properties of the colored sand were not systematically evaluated and it thus remains unclear whether it performed slightly differently than the uncolored sand, e.g. due to differences in grain size distribution, electrostatic properties, surface characteristics or specific weight. However, we have not observed any differences in the behavior between colored and uncolored sand. The colored sand did not stick together to form aggregates, neither did it adhere to plant surfaces, and it thus satisfied the requirements of this primarily qualitative study. Furthermore, the application of colored sand is a relatively easy and low-cost method, and may therefore be useful not only for wind tunnel studies, but also for larger scale field studies. For quantitative purposes, however, it is recommended to further evaluate possible differences in aerodynamic properties of colored and uncolored sand.

**Conclusion 4:** The use of colored sand is an effective and low-cost method for visualizing aeolian erosion and deposition processes in vegetation canopies.

**Methodological challenges in examining the mycorrhizal effect on soil erodibility by laboratory wind tunnel experiments**

The aim of chapter 4 was to investigate the effect of mycorrhizal fungi on the wind erodibility of soil in a laboratory wind tunnel. Since this has never been done before, the development of an appropriate experimental setup and procedure posed several challenges. A particular difficulty was to avoid unintended above-ground effects which
could mask the mycorrhizal effect on soil erodibility, such as soil surface crusting or irregular surface topography. We addressed this challenge by employing the following strategies for cultivating plants and conducting wind tunnel experiments: During the plant growth period, we shielded the sand surface from light by covering it with mulch foil to avoid the formation of a surface crust by micro-organisms (chapter 4.2.1). Furthermore, we watered the plants through permanently installed cones to avoid physical crusting by drop impacts or particle suspension.

Another difficulty was to match the erosivity of the applied wind force with the erodibility of the samples to yield appropriate amounts of erosion. Preliminary experiments had shown that root balls from pot cultures with sandy substrates become extremely fragile when they are removed from the pots and dried. To prevent them from collapsing during handling, they were reinforced with grid cylinders. However, the grid cylinders provided so much stability to the root balls, that there was hardly any erosion in the wind tunnel. Therefore, the root balls were treated with a custom-made tool consisting of four wire needles attached to a metal disk in a square pattern before they were subjected to wind tunnel experiments. This tool allowed pushing the four needles simultaneously into the root balls along their whole vertical axis, which reduced the internal tension in the sand-filled grid cylinders and made them more susceptible to wind erosion. Although this treatment served its purpose in the present study, it is recommended to avoid such an artificial intervention in future experiments, e.g. by using grid cylinders with larger mesh size or larger diameter. Further challenges associated with the present experiments were to ensure a similar air humidity and sand water content in all experiments, and to sample a representative amount of PM$_{10}$ emitted from the root balls (Appendix B).

Despite the methodological challenges mentioned above, the applied experimental setup proved useful to study the effect of mycorrhizal fungi on the wind erodibility of soil. Due to the use of a large wind tunnel facility, the experiments could be conducted under atmospheric boundary layer conditions. Exposing root balls to the wind allowed focusing on the subsurface soil erodibility which is influenced essentially by mycorrhizal fungi. Surface erodibility, in contrast, may be influenced additionally by physical, chemical or biological soil crusts.
Conclusion 5: Wind tunnel experiments with root balls allow the quantification of mycorrhiza effects on wind erosion.

Effect of mycorrhizal fungi on the wind erodibility of soil

Mycorrhizal fungi form symbiotic associations with the roots of most terrestrial plant species and play an essential role in promoting both plant growth and soil stabilization processes (Smith and Read, 2008). Several studies have demonstrated that mycorrhizal fungi are able to increase the soil resistance to water erosion and the fraction of water stable aggregates (Bearden and Petersen, 2000; Augé et al., 2001). Therefore, they can be expected to increase the soil resistance to wind erosion, too. However, direct evidence for this was lacking so far. The wind tunnel experiments presented in chapter 4 provide first experimental evidence that mycorrhizal fungi have the potential to substantially increase the protective effect of newly seeded plants against wind erosion. For root balls of two plant species (Lolium perenne and Anthyllis vulneraria ssp. alpestris), we found that the wind-induced soil loss decreased significantly with increasing percentage of root colonization by mycorrhizal fungi. The mean soil loss of non-mycorrhizal control samples was more than twice as high as the one of mycorrhizal samples for A. vulneraria ssp. alpestris, while no significant difference was observed for L. perenne. These results are all the more remarkable because there was no mycorrhiza-induced plant growth enhancement. On the contrary, mycorrhizal plants had significantly smaller root systems than non-mycorrhizal plants in both species.

Conclusion 6: Mycorrhizal fungi are able to help newly seeded plants to decrease the wind erodibility of soil, even in cases when they do not increase plant growth.

Plant establishment and mycorrhiza formation under drought and nutrient stress

In undisturbed ecosystems, the majority of plants live in symbiosis with mycorrhizal fungi, and new seedlings rapidly establish symbioses shortly after emergence (Smith and Read, 2008). On severely eroded sites, however, adverse soil conditions such as low
nutrient and water availability reduce plant and mycorrhizal growth, which affects the formation of mycorrhizal symbioses. In the laboratory growth experiments presented in chapter 5, we raised four alpine grass species on extremely nutrient-deficient sand which was incubated with a commercial mycorrhizal inoculum. Half of the seedlings were subjected to extreme drought stress. After a growth period of three months, it was found that the proportion of plants that established a symbiosis was significantly lower under drought-conditions (23-58%) than under non-drought conditions (33-100%). Furthermore, it was found that mycorrhizal inoculation had no significant effect on either plant survival or above-ground biomass. However, there was a trend towards higher survival and biomass in inoculated plants compared to non-inoculated plants.

Conclusion 7: Extreme water stress can impede the formation of mycorrhizal symbioses with industrially produced Glomus intraradices. Under such conditions, inoculation with G. intraradices may not improve plant survival and growth.

6.2 Synthesis

The novelty of this thesis was the use of live plants and mycorrhizal fungi in laboratory wind tunnel experiments. This offered the chance to study ecological aspects of wind erosion control which cannot be investigated by using artificial roughness elements. The new experimental approaches of exposing uniformly planted sand surfaces and entire root balls to the wind proved appropriate to investigate both above- and below-ground processes by which plants and mycorrhizal fungi protect the soil from wind erosion.

In particular, it was possible to provide initial experimental evidence that mycorrhizal fungi have the potential to substantially increase the protective effect of newly seeded plants against wind erosion (chapter 4). Although the ability of mycorrhizal fungi to improve soil structure has been known for some time, this is the first experimental demonstration of a mycorrhizal effect on soil resistance to the erosive force of the wind. The experimental setup of reinforcing root balls with grid cylinders and exposing them to the wind represented at least partly the situation when wind erosion lowers the soil surface and exposes plant roots, although it has no exact counterpart in nature. Hence, it
can be assumed that the mycorrhizal effect on soil wind erodibility found in this study also occurs in natural environments. Keeping soil erosion as low as possible is an essential advantage for newly seeded plants to survive in erosive environments. With regard to revegetation practices in such environments, it thus seems promising to ensure a sufficient availability of mycorrhizal propagules.

It is likely that the mycorrhiza-induced reduction in wind erosion entails a reduction in \( \text{PM}_{10} \) emission. However, the \( \text{PM}_{10} \) data collected within this thesis are not entirely consistent - probably due to methodological deficiencies - and thus do not provide clear evidence for this. Nevertheless, they still suggest that \( \text{PM}_{10} \) emission decreases with increasing percentage of mycorrhizal root colonization (Appendix B). This issue should be further explored in future studies, because air quality hazards caused by wind erosion are a major threat to public health.

With regard to revegetation practices, it is of particular importance to note that the mycorrhiza-induced decrease in soil erodibility was not associated with an increase in plant growth. On the contrary, mycorrhizal plants even had significantly smaller root systems than non-mycorrhizal plants. This is a good example that plants can benefit from mycorrhizas beyond increased growth and it implies that plant growth should not be used as the only indicator when evaluating mycorrhizal effectiveness in restoration measures.

Regardless of any mycorrhizal effect on plant growth, large vegetation cover of the soil is desirable for wind erosion control. The experiments presented in chapter 2 showed that sediment flux and \( \text{PM}_{10} \) emission decrease exponentially with increasing vegetation cover, without accounting for effects of plant roots or mycorrhizal fungi. In arid and semi-arid environments, vegetation cover is inherently sparse, but this does not mean that vegetation cannot provide adequate protection against wind erosion. The experiments with uniformly spaced grass tussocks presented in chapter 3 indicate that a cover of approximately 50% is sufficient to produce a skimming flow regime which prevents erosion almost completely.

However, specifications of percentage vegetation cover need to be treated with caution because they do not account for the spatial arrangement of vegetation. The spatial arrangement of vegetation is an important determinant of the predominant wind flow
regime and thus a critical factor for the intensity of wind erosion. In areas affected by wind erosion, vegetation is often not uniformly distributed but rather patchy. Isolated patches of vegetation may act to produce an isolated roughness flow regime, which can result in locally enhanced erosion. In the present thesis, this phenomenon of erosion enhancement was consistently observed in two independent wind tunnel test series (chapter 2 and Appendix A). Therefore, revegetation measures should try to avoid the occurrence of elongated patches of bare soil.

Prerequisites for achieving any benefit from plants and mycorrhizal fungi in wind erosion control are the establishment of viable plants and the formation of functional mycorrhizal symbioses. However, the laboratory growth experiment presented in chapter 5 indicated that adverse soil conditions such as drought and nutrient deficiency can severely impede plant growth as well as mycorrhiza formation. This finding highlights the importance of considering native adapted plant and fungal species for revegetation purposes. For future experiments, it would be interesting to test whether fungal strains originating from dryland habitats perform better than commercially available fungal strains with regard to the effect on both plant growth and soil erodibility.

This thesis includes only a limited number of experiments and plant-fungus-combinations. Further research is necessary to explore in more detail the environmental and practical circumstances under which plants and mycorrhizal fungi may best contribute to protect the soil from wind erosion. A sound scientific basis is needed to encourage and support practitioners and decision makers in applying plants and mycorrhizal fungi in sustainable wind erosion control.
6.3 References


Appendix A

In 2010, four wind tunnel experiments were performed within the scope of a partner PhD project at the WSL Institute for Snow and Avalanche Research SLF (Benjamin Walter “Sheltering effect of plants against soil erosion and snow transport”). This provided an opportunity to validate and extend the results of the wind tunnel experiments performed in 2008 (chapter 2). The basic conditions of the two test series were equal, using the same quartz sand (Table 2.1) and grass species (Lolium perenne). However, the inlet duct upwind of the test section in the wind tunnel was provided with artificial roughness elements for flow conditioning in 2010, while it was empty and smooth during the experiments in 2008. The planting densities in the two test series in 2008 and 2010 were the same, except that the densest canopy in 2010 comprised 55 instead of 91 tussocks/m², because sediment flux was extremely low in the canopy with 91 tussocks/m² in 2008. Furthermore, this allowed to obtain additional information on the relationship between canopy density and sediment flux, since the canopy density with 55 tussocks/m² represented an intermediate density level between the medium- and large-density canopy of the experiments in 2008.

The experimental procedure followed the one of the experiments conducted in 2008, except for the set-up of the plants (Table A.1). In 2010, the grasses were grown in plastic tubes and mounted on wooden tables (Fig. A.1). The planted tubes were placed into close-fitting boreholes, their upper edges flush with the table surface (Fig. A.1). A 1.5 cm thick layer of quartz sand was spread over the tables before conducting experiments.

Fig. A.1: Experimental set-up in test section of the wind tunnel. The grass tussocks were mounted on wooden tables with boreholes. The tables were covered with quartz sand before conducting experiments.
Measurements of the total sediment mass flux \( Q \), the increase in PM\(_{10} \) concentration \( \Delta C_{PM10} \) and the vertical distribution of the sediment mass flux confirmed the key findings of the experiments conducted in 2008:

- In the small-density canopy (5.25 tussocks/m\(^2\)), both \( Q \) and \( \Delta C_{PM10} \) were higher than over the bare sand surface (Table A.2 and Fig. A.2). The proportional increase was approximately the same size as in the experiments of 2008 (Table A.3).

- In the medium-density canopy (24.5 tussocks/m\(^2\)), both \( Q \) and \( \Delta C_{PM10} \) were lower than over the bare sand surface (Table A.2 and Fig. A.2). The proportional decrease was approximately the same size as in the experiments of 2008 (Table A.3).

- The absolute values of \( Q \) and \( \Delta C_{PM10} \) were in the in the same order of magnitude as in the experiments of 2008, despite slight differences in experimental conditions (e.g. flow conditioning in the inlet duct, air temperature and humidity, Fig. A.2).

- The distinct changes in profile shape at twice the canopy height, i.e. 20 cm above ground, in the canopies with 24.5 and 55 tussocks/m\(^2\) were essentially similar to the changes observed in 2008 in the canopies with 24.5 and 91 tussocks/m\(^2\), respectively: In the canopy with 24.5 tussocks/m\(^2\), the profile showed an abrupt increase in the decay rate, while in the canopy with 55 tussocks/m\(^2\), the profile showed a peak in the sediment mass flux (Fig. A.3).

Conclusively, the four experiments conducted in 2010 provided valuable additional data to demonstrate the repeatability and validity of the findings gained in 2008.
Table A.1: Summary of experimental conditions of the experiments conducted in 2010.

<table>
<thead>
<tr>
<th>Planting density [tussocks/m²]</th>
<th>0</th>
<th>5.25</th>
<th>24.5</th>
<th>55</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of tussocks / m²</td>
<td>-</td>
<td>56</td>
<td>28</td>
<td>14</td>
</tr>
<tr>
<td>Total sediment mass flux $Q$ [kg m⁻² s⁻¹]</td>
<td>0.145</td>
<td>0.166</td>
<td>0.011</td>
<td>0.002</td>
</tr>
<tr>
<td>Increase in PM$<em>{10}$ concentration $\Delta C</em>{PM10}$ [mg m⁻³]</td>
<td>2.976</td>
<td>5.169</td>
<td>1.424</td>
<td>0.156</td>
</tr>
<tr>
<td>Mean $C_{PM10}$ at the beginning of the test section</td>
<td>0.177</td>
<td>0.309</td>
<td>0.168</td>
<td>0.167</td>
</tr>
<tr>
<td>Mean $C_{PM10}$ at the end of the test section</td>
<td>3.153</td>
<td>5.477</td>
<td>1.593</td>
<td>0.323</td>
</tr>
</tbody>
</table>

Table A.2: Total sediment mass fluxes $Q$ and increases in PM$_{10}$ concentration $\Delta C_{PM10}$ of the experiments conducted in 2010.

<table>
<thead>
<tr>
<th>Planting density [tussocks/m²]</th>
<th>0</th>
<th>5.25</th>
<th>24.5</th>
<th>55</th>
</tr>
</thead>
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</tr>
<tr>
<td>Mean $C_{PM10}$ at the end of the test section</td>
<td>3.153</td>
<td>5.477</td>
<td>1.593</td>
<td>0.323</td>
</tr>
</tbody>
</table>

Fig. A.2: Total sediment mass flux $Q$ and PM$_{10}$ concentration $\Delta C_{PM10}$ vs. planting density in the experiments conducted in 2008 and 2010.
Fig. A.3: Vertical profiles of sediment mass flux fractions $q_f$ in the experiments conducted in 2008 and 2010. $h$ = plant canopy height (10 cm). For each configuration, one experiment was conducted, except for the unplanted configuration in 2008 (three experiments) and the canopy with 5.25 tussocks/m$^2$ in 2008 (two experiments). The profile over the canopy with 91 tussocks/m$^2$ was conducted at a higher free stream velocity than the other experiments for yielding weighable amounts of sand over the whole height of the sediment sampler despite rather low sediment flux (Table 2.2).

Table A.3: Proportional changes of the total sediment mass flux $Q$ and the PM$_{10}$ concentration $\Delta C_{PM_{10}}$ in the small-density canopy (5.25 tussocks/m$^2$) and the medium-density canopy (24.5 tussocks/m$^2$) compared to a bare sand surface.

<table>
<thead>
<tr>
<th></th>
<th>Experiments of 2008</th>
<th>Experiments of 2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase in $Q$ in the small-density canopy [%]</td>
<td>117.5</td>
<td>114.2</td>
</tr>
<tr>
<td>Increase in $\Delta C_{PM_{10}}$ in the small-density canopy [%]</td>
<td>145.6</td>
<td>173.7</td>
</tr>
<tr>
<td>Decrease in $Q$ in the medium-density canopy [%]</td>
<td>6.6</td>
<td>7.6</td>
</tr>
<tr>
<td>Decrease in $\Delta C_{PM_{10}}$ in the medium-density canopy [%]</td>
<td>48.5</td>
<td>47.9</td>
</tr>
</tbody>
</table>
Appendix B

The measurements of wind-induced soil loss in mycorrhizal and non-mycorrhizal root balls of *Lolium perenne* and *Anthyllis vulneraria ssp. alpestris* (chapter 4) were accompanied by PM$_{10}$ measurements. PM$_{10}$ concentrations [mg m$^{-3}$] were recorded with two TSI DustTrak instruments (model 8520), both at the beginning of the test section (10 cm above ground) and 17 cm downstream of the root ball position (7 cm above ground). PM$_{10}$ measurements were taken each second and the difference between the up- and downstream values (PM$_{10 diff}$) was used as an estimate of the dust emitted from the root ball. The accumulated PM$_{10 diff}$ over the full experiment was taken as an indicator of the total PM$_{10}$ emission. A similar procedure for measuring PM$_{10}$ concentrations has been applied within the scope of the wind tunnel experiments presented in chapter 2 (cf. Fig. 2.2).

Figure B.1 shows the PM$_{10 diff}$ values over time, averaged for the experiments with mycorrhizal and non-mycorrhizal root balls of *L. perenne* and *A. vulneraria*. In *A. vulneraria*, PM$_{10 diff}$ increased to approximately the same level in the mycorrhizal and non-mycorrhizal samples (Fig. B.1, top). However, in the mycorrhizal samples, the increase in PM$_{10 diff}$ started with a time delay of approximately 20 s. In *L. perenne*, PM$_{10 diff}$ increased simultaneously in the mycorrhizal and non-mycorrhizal samples (Fig. B.1, bottom). The peaks in PM$_{10 diff}$ were higher in the mycorrhizal samples than in the non-mycorrhizal samples.

Neither of the plant species showed a significant difference in the accumulated PM$_{10 diff}$ between mycorrhizal and non-mycorrhizal samples (Fig. B.2). However, the accumulated PM$_{10 diff}$ was significantly negatively correlated with mycorrhizal root colonization in the inoculated plants of both species (Fig. B.3). Likewise, a significant positive correlation was found between the accumulated PM$_{10 diff}$ and the soil loss SL (Fig. B.4).

In summary, the PM$_{10}$ measurements provided valuable data that seem to represent the PM$_{10}$ emission from the root balls, as indicated by the significant positive correlation between the accumulated PM$_{10 diff}$ and the soil loss SL (Fig. B.4). However, the accumulated PM$_{10 diff}$ did not reflect the significant difference between mycorrhizal and non-mycorrhizal samples found for the soil loss SL in *A. vulneraria* (Fig. 4.2B). This is probably partly due to the high variability of PM$_{10 diff}$ values over time (Fig. B.1) and
reflects the difficulty in finding an appropriate method to quantify the PM$_{10}$ emitted from the root balls. The magnitude and variability of $PM_{10}$ values strongly depend on the measurement location downstream of the root ball. This location should not be too close to the root ball in order to ensure a sufficient development of the dust plume and to thereby decrease the variability of the values. However, it should also not be too far away in order to catch a representative amount of dust originating from the root ball. For future experiments, it is recommended to systematically evaluate different measurement locations.

Fig. B.1: Time sequence of $PM_{10}$ values during the experiments, averaged for the mycorrhizal and non-mycorrhizal root balls of *Anthyllis vulneraria* ssp. *alpestris* (top) and *Lolium perenne* (bottom).
Fig. B.2: The accumulated $PM_{10\text{diff}}$ over the whole experiments showed no significant differences between mycorrhizal and non-mycorrhizal samples for *Anthyllis vulneraria ssp. alpestris* (p-value: 0.671) and *Lolium perenne* (p-value 0.345).

Fig. B.3: Significant negative correlation between the accumulated $PM_{10\text{diff}}$ and the percentage of mycorrhizal root colonization in the inoculated plants of both *Lolium perenne* ($R^2$: 0.310, p-value: 0.018) and *Anthyllis vulneraria ssp. alpestris* ($R^2$: 0.236, p-value: 0.017).
Fig. B.4: Significant positive correlation between the accumulated $PM_{10\text{diff}}$ and the soil losses through wind erosion $SL$ in both *Anthyllis vulneraria* ssp. *alpestris* (left) and *Lolium perenne* (right). Mycorrhizal samples of *A. vulneraria*: $R^2 = 0.784$, p-value = 6.3e-07. Non-mycorrhizal samples of *A. vulneraria*: $R^2 = 0.007$, p-value = 0.312. Mycorrhizal samples of *L. perenne*: $R^2 = 0.757$, p-value = 3.2e-05. Non-mycorrhizal samples of *L. perenne*: $R^2 = 0.371$, p-value = 0.009.
I completed this PhD thesis with the help of many people and the financial support of the Velux Foundation.

First of all, I would like to thank my supervisors for their help and support throughout the whole duration of my thesis. Frank Graf offered me the unique opportunity to do a PhD thesis which was tailored specifically to my research interests. It was only due to his enthusiastic effort that this thesis was initiated and successfully completed. Ottmar Holdenrieder kindly agreed to supervise this interdisciplinary and adventurous project. I greatly appreciated his genuine interest and involvement in the project, as well as his continued support in both scientific and administrative issues. Christof Gromke introduced me to the basics of fluid dynamics and I highly valued his positive attitude towards my ideas and work which was a great source of encouragement and motivation to me. Christine Alewell supported the idea of this thesis from the very beginning and I am very glad she agreed to be on my dissertation committee.

The SLF wind tunnel was the main experimental facility of my PhD thesis. Since wind tunnel work and fluid mechanic theory were completely new to me when I started with my thesis, I was extremely happy to be welcomed and supported so greatly by other wind tunnel researchers: Andrew Clifton, Michele Guala, Michael Lehning, Katherine Leonard, Costantino Manes and Benjamin Walter. I am very grateful that they shared their knowledge with me and entrusted me with filling the wind tunnel with ‘dirty’ soil and sand instead of snow. I very much appreciated being part of the wind tunnel team.

An essential part of my experimental work took part in the climate chamber of the SLF. I was very glad that I could use the climate chamber to grow plants at all times and I would like to thank the following people for their support: Martin Heggli, Matthias Jaggi, Martin Schneebeli and Stephen Steiner.
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undertake a very impressive field trip to Mt. Kailash. I hope that the amazing region of Mt. Kailash will benefit in some way from my research.

During my thesis, I was fortunate to benefit from the support and knowledge of many experienced professionals. I am very grateful for the continuous support of Caroline Schneider and Imke Hutter from the INOQ GmbH, who kindly provided mycorrhizal inoculum and shared their professional knowledge with me. I would like to thank Markus Schutz from the Alpine Garden Center Schutz Filisur for his expert consulting and the use of his plant nursery facilities, which greatly facilitated plant cultivation. Andreas Bättig and Ernst Lauper from the Lauper Instruments AG provided extremely valuable advice and technical support for conducting fine dust measurements in the wind tunnel. Klaus Oetjen from the Alpinum Schatzalp generously shared his expertise in plant cultivation with me. Furthermore, I would like to thank the following companies for supporting my research: Carlo Bernasconi AG, Holcim AG and Sensirion AG.

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