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**Effects of mowing,
sod-cutting, and
drift sand on
development of
soil and vegetation
in Grey Dunes**



Effects of mowing, sod-cutting, and drift sand on development of soil and vegetation in Grey Dunes

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Managementsamenvatting

Rapport titel:

Effecten van maaien, plaggen en verstuiving op de ontwikkeling van bodem en vegetatie van Grijze Duinen

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Samenvatting:

Duinwaterbedrijven hebben een grote opgave op het gebied van beheer en herstel van droge duingraslanden (Grijze Duinen), zowel vanuit nationale regelgeving (Programmatische Aanpak Stikstof; PAS) als EU-regelgeving (Natura 2000). De afgelopen decennia is de ecologische kwaliteit van deze graslanden afgenomen: ze vergrassen en er treedt struweelvorming op. Daarom is in 2012 een meerjarige onderzoekslijn gestart naar de mogelijkheden voor ecologisch herstel van Grijze Duinen. Dit onderzoek richt zich op de invloed van processen in de bodem, atmosferische N-depositie en de effectiviteit van beheer- en herstelmaatregelen. Het voorliggende onderzoeksrapport bevat drie deelstudies die in 2015 zijn uitgevoerd:

1. De effecten van maaien en plaggen op grijze duinen in de Middel- en Oostduinen;
2. Een meta-analyse van de effecten van maaien, plaggen en struweelverwijdering op Grijze Duinen;
3. Effecten van verstuiving door kleine stuifkuilen op de bodem en vegetatie in de Luchterduinen.

Het rapport beschrijft deze drie studies afzonderlijk in hoofdstukken met elk een discussie en conclusies. Bij het afsluiten van deze onderzoekslijn (ca. 2017) zal een uitgebreidere synthese van de resultaten worden gemaakt. Voorlopig zijn de belangrijkste resultaten:

Plaggen verlaagt het organische-stofgehalte en verhoogt de pH van de bodem. Het is een effectieve manier voor herstel van karakteristieke duingraslandsoorten.

Maaien leidt tot een opener vegetatiestructuur en heeft in een deel van de onderzochte gebieden een positief effect op de vegetatie.

Herstel van duingrasland door verwijdering van struweel lijkt een langere ontwikkeltijd (> 4-7 jaar) te vergen.

De instuiving van zand vanuit kleine stuifkuilen in aangrenzend duingrasland met een ontkalkte bodemtoplaag zorgt op een lokale schaal (enkele tientallen meters) voor een hogere basenrijkdom van de bodemtoplaag en heeft daarmee een positief effect op basenminnende duingraslandsoorten. Het effect op de vegetatie is afhankelijk van de ontkalkingsdiepte van de bodem en de kalkrijkdom van het instuivende zand. Het bevorderen van verstuiving biedt perspectief voor herstel van duingraslanden met een hoge kwaliteit. Daarom is vervolgonderzoek naar de effecten van kleinschalige verstuiving zinvol. Daarbij kan meer aandacht worden besteed aan de tijdsduur waarin ecologische effecten voortduren nadat de eolische activiteit (verstuiving) is gestopt. Belang voor DPWE:

Om effectief en efficiënt herstel en reguliere beheer uit te voeren, is kennis nodig over de effectiviteit van de onderzochte maatregelen. Meer inzicht in de invloed van kleinschalige verstuiving is nodig om (re)activatie van kleinschalige verstuiving op een zinvolle manier te plannen in tijd (over meerdere decennia) en ruimte. Verwerven van bovenstaande kennis is zeer urgent gezien de implementatie van de PAS vanaf 2015, die voorziet in veel maatregelen om verstuiving te bevorderen.

Van belang voor:

- Medewerkers van duinwaterbedrijven die beheer- en herstelmaatregelen plannen en evalueren en belast zijn met de implementatie van PAS en Natura 2000.
- Beheerders en boswachters die beheer- en herstelmaatregelen uitvoeren.
- Beleidmakers bij provincies op het gebied van natuurbeheer en implementatie van Natura 2000 en PAS.
- Ecologen die kennis over Grijze Duinen ontwikkelen en toepassen.

Trefwoorden:

duingrasland, Grijze Duinen, bodem, vegetatie, ecologische herstel, maaien, plaggen, struweel verwijderen, verstuiving

Samenvatting

Duinwaterbedrijven hebben een grote opgave op het gebied van beheer en herstel van droge duingraslanden (Grijze Duinen), zowel vanuit nationale regelgeving (Programmatische Aanpak Stikstof; PAS) als EU-regelgeving (Natura 2000). De afgelopen decennia is de ecologische kwaliteit van deze graslanden afgenomen: ze vergrassen en er treedt struweelvorming op. Daarom is in 2012 binnen het DPWE onderzoeksprogramma een meerjarige onderzoekslijn gestart naar de mogelijkheden voor ecologisch herstel van Grijze Duinen. Dit onderzoek richt zich op de invloed van processen in de bodem, atmosferische N-depositie en de effectiviteit van beheer- en herstelmaatregelen. Het voorliggende onderzoeksrapport bevat drie deelstudies die in 2015 zijn uitgevoerd:

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De effecten van maaien en plaggen op grijze duinen in de Middel- en Oostduinen

In de Middel- en Oostduinen zijn op basis van een analyse van gedetailleerde, ruimtelijk informatie over beheerhistorie 4 beheercategorieën geselecteerd: nooit gemaaid, voorheen gemaaid (periode 1995-2004), recent gemaaid (periode 1995-2014, d.m.v. chopperen) en geplagd in 2000/2001 + recent gemaaid. Al deze categorieën werden ook beweide. In elk categorie is op 10 locaties het bodemprofiel beschreven (humus, pH, kalk), zijn bodemonsters van 0-5 en 5-15 cm diepte geanalyseerd op pH, kalkgehalte, en organische stofgehalte en werd de vegetatie opgenomen. Omdat de ontkalkingsdiepte in het onderzoekgebied sterk varieert en deze variatie niet gelijkmatig was verdeeld over vier categorieën, zijn de effecten van beheer op bodem en vegetatie statistisch gecorrigeerd voor de invloed van ontkalkingsdiepte.

Plaggen verlaagde het organische-stofgehalte en verhoogt de pH van de bodemtoplaag. Het was een effectieve manier voor herstel van karakteristieke duingraslandsoorten en stimuleerde eenjarige soorten en basenminnende pioniersoorten van duingraslanden. Plaggen stimuleerde ook het verschijnen van houtige soorten (op kalkrijke bodem vooral Duindoorn). Om de ontwikkeling naar struweel tegen te gaan was het daarom nodig om na het plaggen maaien als nabeheer toe te passen. Ten opzichte van de andere 3 beheercategorieën was de soortenrijkdom 13 jaar na het plaggen geringer. Voor de ontwikkeling van een soortenrijker duingrasland op geplagde bodems is vermoedelijk een langere ontwikkeltermijn (2-4 decennia) nodig waarbij een duidelijk humusprofiel ontstaat.

Maaien had een geringer effect op de vegetatie dan plaggen. Effecten op de organische stofvoorraad en zuurgraad konden niet worden vastgesteld. Zelfs bij het chopperen, waarbij ook veelal de strooisellaag werd verwijderd, had dus geen merkbaar effect op organische stofvoorraad. De soortenrijkdom verschilde niet tussen niet maaïen, langer geleden maaïen en recent maaïen. De laatste twee categorieën vertoonden wel een gering effect op de vegetatiestructuur: t.o.v. niet gemaaid was de bedekking van de kruidlaag iets lager. Het geringe effect van maaïen op de vegetatie heeft de volgende oorzaken: 1) alle categorieën werden al langere tijd beweïd, 2) het maaibeheer werd in het gebied juist gepland (ruimtelijk en frequentie) op plekken met vergrassing en struweelvorming. Bovendien ontbrak in de studie een 'referentie' die niet werd gemaaid en waar vergrassing en struweelvorming was opgetreden. Effecten op de vegetatiesamenstelling waren: minder houtige soorten in voorheen en recent gemaïde delen; een hogere bedekking van soorten van zomen, bossen en struwelen in nooit gemaïde delen. Verder ging maaifrequentie samen met een sterkere indicatie voor relatief natte omstandigheden. Dit werd vermoedelijk veroorzaakt door het frequenter maaïen van delen met een grotere productiviteit als gevolg van invloed van grondwater (minder droogtestress). Een multivariate analyse gaf aan dat soortensamenstelling voor niet gemaïde, voorheen gemaïde en nooit gemaïde plots weinig verschilde. Gesteld kan worden dat selectieve inzet van maaibeheer in delen met een ontwikkeling naar een dichte grasvegetatie of struweel effectief is voor het in stand houden van duingraslanden met een korte, open kruidlaag. Omdat maaifrequentie geen sterk effect had op de soortensamenstelling, is laagfrequente inzet van maaibeheer voor het tegengaan van vergrassing en struweelvorming voldoende.

Een meta-analyse van de effecten van maaïen, plaggen en struweelverwijdering op Grijze Duinen

Het belangrijkste doel van deze deelstudie was om te bepalen of het maaïen, plaggen en verwijderen van struweel in gedegradeerde duingraslanden, effectief de ontwikkeling van een vegetatie kenmerkend voor het doeltype Grijze Duinen bevordert: namelijk een lage vegetatie, zonder bomen en weinig of geen struiken, bestaande uit een grote verscheidenheid van (korte) grassen, mossen, korstmossen en kruiden. Van 10 herstelprojecten in duingebieden in Zuid- en Noord-Holland met monitoringgegevens werden de effecten van maaïen, plaggen en verwijdering van struweel geëvalueerd. Van elk project werden plots met een maatregel op een tijdstip 4 tot 7 jaar na de maatregel vergeleken met controle plots (geen maatregel). Er werd gekeken naar de effecten op de bedekking van vegetatielagen, de soortenrijkdom (vaatplanten, mossen+korstmossen), de verzadigingsindex voor het doeltype op basis van soortensamenstelling en de abundantie van Duinriet en Grijs kronkelsteeltje. Voor elke variabele werd het effect van een maatregel door het verschil tussen de controle en maatregel uit te drukken met de log response ratio (RR; Lajeunesse 2011) en statistisch te toetsen.

In het algemeen hadden maaïen, plaggen en de combinatie van maaïen en plaggen het 'verwachte' effect op de soortenrijkdom, verzadigingsindex en abundantie van ongewenste soorten. Daarentegen hadden deze maatregelen op de vegetatiestructuur niet altijd het verwachte effect (afname bedekking van de kruidlaag en toename bedekking moslaag). De waargenomen positieve effecten varieerde sterk tussen de geëvalueerde projecten. Een oorzaak kan zijn dat de berekende RR-waarden gebaseerd zijn op de toestand van de controle plots. Deze kon sterk verschillen tussen locaties (bv. wel en niet vergrast). Daarnaast is maaibeheer voor verschillende beheerdoelen toegepast: deels voor het terugdringen van sterke vergrassing in onbeweïde gebieden

en recent vaak voor het terugdringen van opslag van struiken, terwijl vergrassing geen probleem is. Het effect van maaien op de vegetatiestructuur verschilt dan sterk. In het laatste geval is het effect op de kruid- en moslaag gering.

Herstel van duingrasland door verwijdering van struweel gaf na 4 tot 7 jaar geen significante respons van de geanalyseerde variabelen. Op sommige locaties had struweel verwijderen een ongewenst effect: minder soorten, een lagere verzadigingsindex en een toename van Duinriet). Mogelijke verklaringen hiervoor kunnen zijn: 1) betere lichtcondities voor de kruidlaag na verwijdering van de struiklaag en 2) een relatief goede nutriëntenbeschikbaarheid door betere opwarming van de bodem die de mineralisatie stimuleert. Om effecten van struweel verwijderen beter te duiden zijn langere monitoringreeksen nodig.

Plaggen is een snelle en effectieve maatregel om de vegetatiebedekking te verminderen en leidt in de meeste gevallen tot een hogere soortenrijkdom en toename van de kenmerkende soorten van Grijze duinen. Echter, na plaggen kan herstel van duingrasland lang duren (langer dan 4-7 jaar de hier bestudeerde periode). Door een groot effect op de bodem (verwijderen van organische stof) kan herstel naar een soortenrijk duingrasland ook lang duren. Wanneer geplagd wordt, zou met een geringe plagdiepte (ca. 5 cm) herstel sneller kunnen optreden, omdat dan nog in de bodemtoplaag organische stof achterblijft. Op basis van dit onderzoek zou een goede alternatieve maatregel bestaan uit maaien, omdat maaien vaak net zo effectief is als plaggen bij het bereiken van een lagere vegetatiebedekking (= opener) en het onderdrukken van vergrassing en struweelvorming. Chopperen is dan een optie om locaties met veel strooisel en sterke struweelopslag aan te pakken (zo lang dit niet te hoog is). Bovendien, zorgt maaien voor meer positieve effecten (soortenrijkdom, verzadigingsindex) dan plaggen in geval van geanalyseerde termijn van 4-7 jaar na de behandeling. De maaienfrequentie kan worden aangepast aan de lokale toestand van het grasland: frequent maaien (eens in de 1-3 jaar) in geval van meer vergrassing en opslag van struiken, en minder frequent in geval de vegetatiestructuur snel verbeterd.

Effecten van verstuing door kleine stuifkuilen op de bodem en vegetatie in de Luchterduinen

Kleinschalige verstuing is in kustduinen een belangrijk proces dat bijdraagt aan de dynamiek van duinecosystemen en daarmee zorgt voor kleinschalige ruimtelijke variatie in successiestadia en een hoge biodiversiteit. Stuifkuilen kunnen door zanddepositie in omliggend oud duingrasland sterke invloed hebben op de kwaliteit van deze graslanden. In niet of ondiep ontcalcite duingebieden eroderen uitstuifzones veelal tot de kalkhoudende zandlaag. Zulke kleinschalige verstuing heeft dan invloed op de basenhuishouding in de depositiezones. Er is echter weinig (kwantitatief en kwalitatief) bekend over de invloed van stuifkuilen op duingraslanden. Tegelijk is het reactiveren van kleinschalige verstuing een maatregel in de PAS die veelvuldig en in korte periode is gepland. De behoefte aan meer kennis over de effectieve inzet van deze maatregel op Grijze Duinen is daarom zeer urgent. In 2014 zijn 4 stuifkuilen en hun omgeving in de Luchterduinen onderzocht die minstens 35 jaar actief waren en een diameter hadden van >20 m. Er werden 2 stuifkuilen geselecteerd in relatief diep ontcalcite achterduin en 2 stuifkuilen in het oppervlakkig ontcalcite middenduin. Van elke stuifkuil werden de bodem en vegetatie beschreven in 4 transecten (NO, ZO, ZW, NO) in het omliggende duingrasland. Ook werd de geochemie in de uitstuifzone geanalyseerd.

De instuiving van zand vanuit kleine stuifkuilen in aangrenzend duingrasland met een ontkalkte bodemtoplaag zorgt op een lokale schaal (enkele tientallen meters) voor een hogere pH en basenrijkdom van de bodemtoplaag en ruimtelijk gezien was dit effect het sterkst aan de noordoostzijde (tegenover de overheersende windrichting). De ruimtelijke omvang hangt sterk samen met de omvang van de uitstuiwzone. Gemiddeld was de zone waarvan de pH van de bodemtoplaag was verhoogd 8.7 keer zo groot in oppervlakte als de uitstuiwzone. Deze verhouding was in stuifkuilen met kalkrijk zand in het middenduin hoger dan in stuifkuilen met kalkarm zand in het achterduin. Voor de zone waarvan de basenrijkdom sterk werd beïnvloed is dit verschil nog sterker. Verschillen in afstand tot de kust kunnen ook bijdragen aan deze verschillen, omdat de windsnelheid in het middenduin vaak hoger is dan in het achterduin. De patronen in basenrijkdom werken sterk door in het patroon van de vegetatie. Dichter bij de uitstuiwzone worden duingraslandsoorten van basenrijke omstandigheden en die indifferent zijn voor basenrijkdom bevorderd. Opvallend is dat de invloed van instuivend zand in de 'kalkarme' stuifkuilen meer tot expressie kwam in de vegetatie dan in de kalkrijke stuifkuilen van het middenduin. Een verklaring hiervoor is dat bij de kalkarme stuifkuilen het effect optreedt in sterk verzuurde omgeving, terwijl in het middenduin de achtergrond relatief basenrijk is. Het effect op de basentoestand van de bodemtoplaag neemt af bij toenemende afstand van de stuifkuil. Hier voor zijn twee oorzaken: bij toenemende afstand is (1) de instuiving van kalkhoudend zand geringer en (2) het organische stofgehalte van de bodemtoplaag hoger. Om de basenverzadiging te verhogen is meer aanvoer van kalk nodig naar mate het organische stofgehalte hoger is.

Dit onderzoek laat zien dat secundaire stuifkuilen een aanzienlijk ruimtelijk en positief effect hebben op de kwaliteit van omliggende oude duingraslanden met een oppervlakkig en dieper ontkalkte bodem. De sterkte van de effecten hangt af van de kalkrijkdom van het zand in de uitstuiwzone, de basenrijkdom en ontkalkingsdiepte van de bodem en ook van het organische stofgehalte van de bodemtoplaag. In duingebieden waarin stuifkuilen kalkrijk zand verplaatsen is het bevorderen van kleinschalige verstuiwing een effectieve maatregel voor het bevorderen van basenrijke vormen van het habitatype Grijze Duinen. Omdat deze studie stuifkuilen met een langdurige eolische levensduur heeft onderzocht vormen de gevonden effecten een bovengrens. In stuifkuilen die kortere tijd actief zijn, zullen de effecten geringer zijn. Door grote variatie in duinlandschappen en eolische levensduur van secundaire verstuiwingen is verder onderzoek aan de effecten van stuifkuilen op duingraslanden zinvol. Daarbij is aandacht nodig voor zaken als ontkalkingsdiepte van de omgeving, de geochemie van het stuifzand, de eolische levensduur en de duurzaamheid van effecten nadat verstuiwing is gestopt. Daarnaast is meer inzicht nodig in de dynamiek van stuifkuilen binnen uiteenlopende type duinlandschap en welke factoren van invloed zijn op de dynamiek.

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1 General introduction

1.1 Background

This reports deals with research on conservation and restoration of Grey Dunes in the Dutch coastal dunes. It was conducted in the DPWE research program of the four Dutch dune water companies (Dunea, PWN, Waternet and Evides), which operate as nature managers of large coastal dunes areas in the province Zuid-Holland and Noord-Holland. The research reported here is part of a multiple year research line for restoration of Grey dunes, which started in 2012.

Dry dune grasslands in Netherlands host various ecosystems with high plant diversity, including those designated as target habitats by national nature policy as well as priority habitat types (e.g. Grey dunes) by the Habitat Directive of the European Community (Natura 2000). Biodiversity of these ecosystems declined strongly in the last decades due to grass and shrub encroachment, which is attributed to elevated atmospheric N deposition [Kooijman et al., 1998; Remke et al., 2009] as well as changes in management [Brunbjerg et al., 2014]. Atmospheric N deposition may also increases accumulation rates of soil organic matter and mineralization rates of nutrients, accelerating the speed of succession [Sparrius and Kooijman, 2012]. The level of atmospheric N deposition has decreased since 1990's, However, dune ecosystems remain being threatened by grass encroachment, because the critical loads for N-deposition are still exceeded. Moreover accumulated SOM from the past keeps is still releasing nutrients via mineralization [Kooijman et al., 2012]. Because of the low critical loads of Grey dunes N-deposition is currently still a major threat.

In the Netherlands, the dune water companies, which operate production sites in the coastal dunes (Evides, Dunea, Waternet and PWN) have approximately 3700 ha of Grey Dune habitat in their management area. This represents 25 % of the Dutch area. EC nature legislation (Habitat Directive) obligates the Netherlands to realize a favourable conservation status of this and other protected habitats. Last years this EU-legislation (Natura 2000) is implemented in the Netherlands. Therefore the dune water companies have a strong responsibility for management and restoration of dune grasslands on as well a national level as EU level. Because of the large area of Grey Dune habitat, and large scale treats, 'regular' nature management and restoration of Grey Dunes requires a strong effort. Meanwhile the Netherlands is implanting special legislation for dealing with exceedance of critical N deposition loads of habitats (Programmatische Aanpak Stikstof; PAS). It regulates how to deal with negative effects of a high N deposition load. Besides regulation of N emissions on a national and regional level, also local measures are proposed in Nature 2000 areas in order to mitigate negative effects of a high N deposition. For Grey dunes these measures consist of measures which stimulate processes (e.g. aeolian activity) beneficial for Grey Dunes as well local management and restoration affecting soil and vegetation structure (e.g. sod cutting, mowing, grazing). These measures should counteract deterioration of the habitat, and contribute to restoration. Coming years many measures are planned for Grey Dunes in the PAS program. This program will intensify the restoration practice conducted in the last decennia.

Because of the strong effort needed for conservation and restoration of Grey Dunes, in 2012 a research line was launched on restoration of Grey Dunes as a part of the DPWE research program. The research line focus on processes which rule the abiotic conditions of dune grasslands, and on the effectiveness of restoration measures and nature management. Special attention is given to processes in the soil and N deposition. The outcomes will contribute to knowledge on a more effective and efficient ecological restoration.

This report deals with three sub-studies conducted in 2014:

1. The effects of mowing and sod cutting on the soil and vegetation in the Middel- and Oostduinen (area managed by Evides);
2. A meta-analysis of the effects of mowing, sod cutting and shrub removal of restoration projects in Dutch coastal dunes (including projects in areas of Evides and Waternet);
3. The effects of small-scale blowouts on the soil and vegetation of dune grasslands in the Luchterduinen (managed by Waternet).

These three sub-studies are reported separately in chapters 2, 3 and 4. Each chapter contains a full description with introduction, methods, results, discussion and conclusion. Because synthesis of the studies in the research line on restoration of Grey Dunes is planned for later (foreseen at ca. 2017), this report does not present an integration of the findings of these sub-studies.

1.2 Involvement of students

Two students contributed each on a sub-study. Bart Crezee (University Utrecht) worked on sub-study 1 and contributed much to the analyses of management history, selection of sites, soil fieldwork, time consuming lab analyses of soil samples, and statistical analyses. Marten Annema (Evides) was involved in analysing management history and site selection. The second student, Ester Dielissen (University Utrecht), worked on the meta-analysis of restoration projects. She put a strong effort in data processing and analyses. Esther was guided by Prof. Jos Verhoeven (University Utrecht), Luc Geelen (Waternet) and Camiel Aggenbach (KWR). Yuki Fujita supported both students in statistical analyses.

A third student, Ko Melis (University Utrecht) evaluated the effectiveness of restoration measures in Grey Dunes by reviewing literature. The results of this review are not presented in this report, but will be used for the planned synthesis mentioned above.

1.3 Operational guidance

The research was guided on an operational level by staff members of the dune water companies dealing with nature management. These were:

- Marten Annema (Evides)
- Harrie van der Hagen (Dunea)
- Mark van Til (Waternet)
- Luc Geelen (Waternet)
- Hubert Kivit (PWN)
- Dick Groenendijk (PWN)

We thank them for their input and comments of the draft report.

1.4 Acknowledge

This research was possible because several persons provided data. Besides members of the operational guidance team, nature managers and researchers provided data of monitoring projects for the meta-study. We thank therefore Wouter van Steenis (Natuurmonumenten), Marijke Van der Heiden (Natuurmonumenten), Menno van Zuijlen (Natuurmonumenten) and Annemiek Kooijman (University Amsterdam).

2 Effect of mowing and sod-cutting on grey dunes in Middel- and Oostduinen

2.1 Introduction

The Middel- and Oostduinen are an important grey dune ecosystem located on the Dutch island of Goeree-Overflakkee. Grey dune habitat (classification H2130 in the European Natura 2000 habitat system) is dry grassland on coastal dunes, bordering the dynamic first ridge of White dunes. Because of differences in decalcification depth and humus thickness, grey dune habitats are very diverse ecosystems [Van Haperen, 2009]. Typically, a distinction is made between calciumcarbonate-rich (H2130A), calciumcarbonate-poor (H2130B) and moist (H2130C) habitats [Smits *et al.*, 2012]. Vegetation of these grasslands is normally characterized by a species-rich variety of grasses, mosses, lichens and herbs [Arens *et al.*, 2009b]. Phytosociologically, all these species typically fall in the Koelerio-Corynephoretea class of dry grasslands on sandy soil [Weeda *et al.*, 2002]. Due to the presence of multiple strong gradients in acidity, trophic level and moisture content, the Middel- and Oostduinen area is one of the most valuable of these grasslands in the Netherlands [Weeda *et al.*, 2002].

Recently, species-rich grey dune habitats are threatened by grass and shrub encroachment, which is the strong increase in dominance of some tall-growing grasses and shrubs, such as sea-buckthorns (*Hippophae rhamnoides*) [Doody, 2013]. The spread of these grasses leads to reduced light and nutrient availability for other, smaller plants, and causes a decline in species-richness [Kooijman *et al.*, 2005; Veer and Kooijman, 1997]. Grey dune vegetation thus shifts from a species-rich, mosaic pattern to a uniform, tall-grass climax state. The cause of this increased succession is partly sought in the high levels of atmospheric N-deposition over the past few decades, yet also related to almost simultaneously decreased rabbit populations and a reduction in the number of sand-drifts [Arens *et al.*, 2009b].

Within the Netherlands, dune systems are of great importance for nature conservation, as they are home to almost 70% of the Dutch flora species and form the main distribution area of most of the species on the Dutch Red List of endangered plant species [Grootjans *et al.*, 2002; Veer and Kooijman, 1997]. Within the European context of Natura 2000, the Netherlands is home to 18% of the total European grey dune habitat [Houston, 2008]. This makes restoration and protection of the Dutch grey dunes a vital goal for Dutch and European nature conservation [Aggenbach *et al.*, 2013].

In order to do so, mowing and sod-cutting have been proposed as effective management measures, [among others; Kooijman *et al.*, 2005; Kooijman *et al.*, 2009]. Mowing is a traditional management technique to open canopy and restore chances for lower vegetation types to obtain light, space, nutrients and water. Sod-cutting takes away the first layer of topsoil in order to interrupt succession and give new chances to pioneer species. This has a much more drastic effect on the system [Jungerius *et al.*,

1995]. Historically, these measures have been used extensively already, albeit sometimes with other (economic) purposes in mind [Van Haperen, 2009]. For example in Middelduinen, sod cutting has been carried out during World War II by the Germans, because they used the sods for covering bunkers.

In studying the effectiveness of these management techniques, it is particularly important to pay attention to soil conditions, as vegetation diversity depends strongly on the heterogeneity of the soil as growth medium [Rorison, 1990]. One particular deterministic factor to take into account is the spatial patterning of calcium carbonate (CaCO_3). The presence of calcium carbonate strongly affects species composition through impacting the plant's nutrient balance, and, via pH, nutrient availability [Rorison, 1990]. As such, decalcification depth is a critical factor in studying soil conditions. Other important factors are acidic level (pH) and soil organic matter (SOM) content. Over time, succession causes an accumulation of soil organic matter. This plays a key role in managing grey dune systems, as accumulation of SOM is thought to increase nutrient levels (particularly available N) [Aggenbach *et al.*, 2013; Fujita *et al.*, 2014] and cause further grass encroachment [Arens *et al.*, 2009b]. Also, pH will decrease due to the dissolution of calcium carbonate and leaching of base cations from the soil exchange complex [Grootjans *et al.*, 2013; Stuyfzand, 1993]. It is thought that these processes are increased by high levels of atmospheric N- and acid-deposition [Kooijman *et al.*, 2009]. In general, high nutrient levels and acidified topsoil form a significant threat to valuable Red List species. Sod-cutting significantly reduces this threat by removing large amounts of topsoil and thus lowering organic matter content and reducing acidification. This is likely to be most effective on calciumcarbonate-poor soils, as those are more prone to acidification [Aggenbach *et al.*, 2013]. However, regular mowing might actually speed-up the acidification of the soils, by removing base cations stored in the hay (C. Aggenbach, pers. comm., 2014). It does not, however, remove below-ground organic matter. The primary effect of mowing on soil conditions might come from its physical disruption of soil from vegetation structure. Ecological disturbances are found to have a positive effect on grassland diversity [Collins and Barber, 1986], and can reduce soil carbon [Silveira *et al.*, 2009]. The intensity of mowing is thus thought to affect soil conditions as well through disturbance of the system.

However, the long-term effect of these techniques is still largely unknown. Melis [2014] showed that long-term monitoring of management measures is often lacking, and that scientific literature on sod-cutting in dune systems in particular is very rare. As both techniques are expensive and labour-intensive measures, better understanding of their effectiveness over different time scales is therefore much required [Aggenbach *et al.*, 2013; Doody, 2013].

The aim of this research is to evaluate the effects of mowing and sod-cutting on soil and plant diversity of grey dunes. This research only focused on effects on dry dune grasslands, as wet dune slacks have traditionally been given much research attention already [Grootjans *et al.*, 2002; van der Hagen *et al.*, 2008; van Dijk and Grootjans, 1993], while protection and restoration of dry dune grasslands have a high conservation priority as well. In this research we examine how mowing and sod-cutting affect soil characteristics and vegetation characteristics of calciumcarbonate-rich (H2130A) and calciumcarbonate- poor (H2130B) dry dune grasslands in the Middel- and Oostduinen, at short to medium timescales. This area is particularly interesting because from 1990 the mowing was carried out by 'chopping off' (Dutch: 'chopperen' or 'maaizuigcombi') instead of regular mowing. With this mowing technique both above

ground vascular plant biomass and a part of litter is removed. In Middel- and Oostduinen the rotating chains were adjusted close to the soil, and therefore a greater part of the litter was removed. Because of small scale relief the choppinging also removes a part of the mineral top soil at patches. This type of mowing therefore has a stronger impact on the vegetation structure and top soil than regular mowing, and is expected to have an intermediate impact between mowing and sod cutting. An additional effect of sod cutting, mowing, and 'choppinging' might be compaction of the top soil, because of the pressure of machinery tires. Therefore the bulk density can increase. Moreover sod cutting, and to a less extent 'choppinging', removes a part of the top soil which has a lower bulk density than the subsoil.

In this study, soil characteristics are defined in terms of bulk density, organic matter, calcium carbonate and acidity profiles. Vegetation characteristics are defined in terms of vegetation structure (i.e. cover of different functional groups of plants), plant species richness, and plant species composition. We are primarily interested in the old successional stages of dune grasslands (at least several centuries). Because sod cutting was conducted in 2000-2001 in the study areas, medium successional stages were examined too. The timescale of management effect that we examined varied from 1 to 34 year depending on the history of mowing. For this research question, the following hypotheses were proposed:

- H1) Sod-cutting leads to higher pH of the new topsoil in comparison with the old topsoil. This effect is depended on the decalcification depth and the pH depth profile;
- H2) Sod-cut and intensively mowed grasslands have less organic matter content in soils compared with less-intensively mowed soils;
- H3) Sod-cutting results in less competition for light among plant species and thus increases plant species richness;
- H4) Mowing results in less competition for light among plant species and thus increases plant species richness. This effect will be less strong than sod cutting.

2.2 Methods

2.2.1 Selection of study locations

A study was performed on different management measures in the Middel- and Oostduinen nature reserve on the Dutch island of Goeree- Overflakkee. The Middel- and Oostduinen area is historically and up to the present used for drinkwater infiltration, but has a protected nature reserve status as well. An aerial overview of this study site can be found in Appendix (Figure 6-1).

Firstly, a spatial analysis of cartographic data of management measures was conducted. This was possible because mowing management from 1985 for every year (field data in GIS), and sod cutting and filling up with sand from 1934 (fielddata in GIS, interpretation of aerial photographs) has been documented by Marten Annema of Evides Drinkwater Company. Spatial data on management measures was also obtained from Marten Annema of Evides in the form of geo-tagged GIS files. Because of the fine spatial resolution of the data (2-3 m) the management history is very well known. Using these data, areas with single, uniform management combination measures over time were identified for comparison. This analysis was done using ArcGIS mapping software. The results of these analyses were discussed with Marten Annema and were used for selecting management types to be investigated. The selection was based on the

practical possibilities and the interest in a distinction between effects of previous and recent mowing. The area also differed in grazing management. However, because of limitation in resources, we selected only management categories in the area with cattle grazing. Grazing with cattle was reintroduced in 1993 for Middelduinen and in 2001 for Oostduinen. Grazing is done from early summer until (late) autumn. In most years the end of the grazing season was adjusted depending on the crop yield of the year, in order to realize short above-ground biomass before the start of winter.

Map areas were categorized according to their mowing history and sod-cutting history. We defined three categories of mowing: category M0 is “never mown”, category M1 is “previously mown” (i.e. one or more times mown in the period 1995-2004 and not after 2004) and category M2 is “recently mown” (i.e. mown after 2004 as well) (also see Table 2.1). For sod-cutting, we define two categories: S0 is never sod-cut, and S1 is sod-cut. For simplicity, only areas that had been sod-cut within the so-called OINS-project from 2000/2001 were taken into account. The depth of the sod cutting was variable among sites: the top soil was removed until the humus-poor layer appears. Since the sod-cut sites are all categorized into the mowing categories M2, we ended up with four groups of management types: never mown & not sod-cut (M0_S0), previously mown & not sod-cut (M1_S0), recently mown & not sod-cut (M2_S0), and recently mown & sod-cut (M2_S2). We used the combination of sod cutting and mowing, as these measures are typically combined to suppress shrub encroachment. The reason for the combined measures is because during the first years after sod cutting a strong encroachment of shrubs (especially *Hippophae rhamnoides*) cannot be suppressed by cattle grazing only, but needs a combination with mowing.

For each of the four management types, we selected 10 locations (i.e. 40 sampling locations in total). These locations were on dry dune grasslands only. This selection for dry areas was done by real colour comparison of aerial photographs, as cartographic data on moisture classification was unreliable. Originally we divided each management class in 5 calciumcarbonate-poor and 5 calciumcarbonate-rich sites, based on a map of decalcification depth in 2005. However, because the pattern of decalcification was more complex than indicated by the map, the pre-set calciumcarbonate classification poorly matched with measured calciumcarbonate- and pH-profiles. Therefore we did not use this distinction between calciumcarbonate poor and rich in further analyses. For each location, ‘duration not mown’ and ‘mowing intensity’ was calculated. ‘Duration not mown’ is the duration in years since the location was last mown (i.e. 2014 minus the last mown year). ‘Mowing intensity’ was defined as the total amount of mowing events during the period of 1995- 2014.

At all locations mowing consisted of a technique called ‘chopping’, which means close cutting of tall-growing plants, after which both the soil litter and the cut-off plant materials are removed from the site.

Table 2.1. Description of codes of mowing and sod-cutting. Codes used in this study deviate from the original dataset of management combinations. Original codes are indicated in column ‘Code_orig’.

Code	Code_orig	Short name	Description
<i>Mowing</i>			
M0	M0	Never mown	Never mown
M1	M2	Previously mown	one or more times mown in the period 1995-2004 and not after 2004; mostly chopping ('maaizuigcombi')

M2	M3	Recently mown	one or more times mown both in the period 1995-2004 and 2005-2014; mostly chopping ('maaizugcombi')
<i>Sod-cutting</i>			
S0	P0	Not sod-cut	Never sod-cut
S1	P5	Sod-cut	Sod was cut in 2000/2001

2.2.2 Field sampling

At each location, a permanent quadrant (PQs) was installed as a circle of 4 m² around a central peg in the ground. X,Y and Z coordinates were measured using GPS-RTK (2-3 cm accuracy). On the edge of each PQ, 3 sub locations were chosen for soil profiling and sampling. Soil profiles were taken using a so-called 'humushapper', a rectangular device that cuts out ca. 10 cm broad samples up to a depth of ± 30 cm (Wardenaar, 1987). Firstly, a description of each humus profile was made. In situ pH profiles were then taken by measuring pH at 2.5, 7.5, 12.5, 17.5, 22.5, 27.5 and – if possible – 32.5 cm depth in the field using a Hanna soil pH electrode (Hanna H199121). When dry, the soil was wetted with MilliQ (very mineral poor water). Calcium carbonate profile was then established by identifying calcium carbonate presence using a 10% hydrochloric acid test. We distinguish three classes: K0: no fizzing, K1: weak fizzing visible or audible, K2: strong fizzing visible. With this method, decalcification depths up to 120 cm were obtained for each sub location by using both the humushapper profile and an Edelman soil auger. The decalcification depth was defined as the depth of the top of the first layer with class K1 or K2.

At each sub-location, soil samples were then taken from 0-5 and 5-15 cm depth. Bulk density (BD) samples were taken at both depths using a round metal tube of 38,10 mm diameter. The 0-5 cm sample was corrected for topsoil compaction by measuring both the in and out ground level height at 3 locations around the rim of the metal tube. BD samples of each sub-location were stored and analysed separately in plastic bags. Using the 'humushapper', chemistry (CH) samples were taken at both 0-5 and 5-15 cm depth as well. CH samples of each sub location were put together in plastic bags for both depths, and analysed as mixed sample.

Vegetation was recorded within the circle plot of 4 m². Abundance of vascular plants, mosses, and lichens were recorded with Londo scale. Moreover, cover of shrubs, vascular plants, mosses, litter, and bare sand were also recorded. The height of the higher layer of the vascular plants was also recorded.

2.2.3 Soil chemical analysis

Chemical analysis was carried out at KWR Watercycle Research Institute in Nieuwegein. Firstly, bulk density was measured by drying each BD sample plus plastic bag at 65°C and subtracting the average mass of a plastic bag. Dry mass was then divided by the standard volume of a sample in the metal tube, according to the following formula:

$$BD \text{ (g/cm}^3\text{)} = \text{dry mass}_{65^\circ\text{C}} / V$$

where $\text{dry mass}_{65^\circ\text{C}}$ is dry weight at temperature 65°C (g), V is the volume of the soil (cm³).

Bulk density for each PQ was calculated by averaging bulk density results of each of the

three sub-locations. Also, decalcification depth of each location was calculated by averaging the decalcification depths of each of the three sub locations. The decalcification depth was calculated as the depth of the highest soil layer with calcium carbonate. Some soil profiles had a layer with calcium carbonate above a layer without calcium carbonate because of bioturbation by ground ants.

The three sub samples for chemistry of each location were homogenized by removing living plant material and manually mixing the samples until a uniform colour was reached. Soil moisture content of these samples was measured by separating 20-30 g of homogenized sample into a beaker via handpicking of small volumes. Wet mass was then immediately measured. Dry mass was measured after drying each sample at 105°C for 48 hours. Soil moisture was then calculated according to:

Soil moisture = (wet mass – dry mass_{105°C})/dry mass_{105°C}
where wet mass is the fresh weight of the soil (g).

Soil pH of each sample was obtained from measuring both H₂O (demi water) and 1M KCl extracts of 10 g (±0,3) homogenized, fresh CH sample for each location. These samples were prepared by handpicking small volumes of the homogenized CH sample into 50 ml Greiner tubes. 25 ml MiliQ H₂O or 1M KCl was added via a pipette. The extracts were then mechanically shaken for 2 hours, after which pH was immediately measured using a Hanna pH electrode.

Soil organic matter (SOM) content and calcium carbonate content were determined using Loss-on- Ignition (LOI) method. In this method, samples are heated to very high temperatures so that volatile substances escape from hydrates and carbonates. For this, homogenized CH samples were first dried at 65°C for 48 hours. Large pieces of dried samples were then separated out using a 2 mm sieve. The remainder was grinded manually using a mortar and pestle for ca. 5 minutes or until a completely uniform colour was obtained. Sieve, mortar and pestle were cleansed after every sample with a paintbrush and high-pressure nitrogen gas.

Pre-ignited, ceramic crucibles were dried at 105°C after which tare weight was measured. Ca. 2.5 g of grinded sample was then added, after which this was again dried for 2 hours at 105°C. Dry weight was noted, after which the crucibles and samples were heated under air for 4 hours at 550°C in a calcining furnace. After cooling in a desiccator, dry mass was again measured. SOM content was then calculated as:

$$\text{SOM (\%)} = 100 \times (\text{dry mass}_{105^\circ\text{C}} - \text{dry mass}_{550^\circ\text{C}}) / \text{dry mass}_{105^\circ\text{C}}$$

In addition, SOM was corrected for clay content because strongly-bound water to clay may be released at high temperatures [Stuyfzand *et al.*, 2012]:

$$\text{SOM}_{\text{cor}} (\%) = \text{SOM} - 0.07 \times L$$

where L is the clay content (%). Due to the low clay content in this area (0.7%), the correction factor was very small (i.e. 0.049 % of SOM), Therefore, for the analysis, we will use the uncorrected values of SOM.

Samples were subsequently heated under air for 1 hour at 600°C. After cooling, dry mass was again measured. Samples were then heated under air for 2 hours at 1000°C.

Again after cooling, dry mass was measured. Calcium carbonate content was then calculated according to [Stuyfzand *et al.*, 2012]:

$$\text{CaCO}_3 (\%) = 100 \times (\text{dry mass}_{600^\circ\text{C}} - \text{dry mass}_{1000^\circ\text{C}}) / \text{dry mass}_{105^\circ\text{C}} \times \text{MW}_{\text{CaCO}_3} / \text{MW}_{\text{CO}_2} - 0.095 \times$$

where $\text{MW}_{\text{CaCO}_3}$ and MW_{CO_2} are the molecular weight of CaCO_3 and CO_2 ($\text{MW}_{\text{CaCO}_3} = 100.08935$, $\text{MW}_{\text{CO}_2} = 44.00995$).

Note that some soil samples had an increase in weight after burning at 1000°C compared to those at 600 °C, resulting in an estimate of negative calcium carbonate content for these soils. These values were converted to zero for the statistical analysis. These negative values of calcium carbonate content turned out to be caused by the flying dust in the oven at very high temperature (i.e. 1000°C). This means that our estimates of calcium carbonate content could be overestimated because of the measurement error. The overestimation, however, should not be too large, since maximum increase in soil weight was ca. 20 mg, which is equivalent to ca. 0.14% of calcium carbonate content. In a test with empty oven cups an average increase of 0.08 mg per cup was measured. For the calculations of the CaCO_3 content mass_{1000°C} was corrected with this average values. It should also be noted that the detection limit of the TGA method is rather high (ca. 1%). Therefore, estimates of SOM and calcium carbonate content in a low range are not very accurate.

Subsequently, by multiplying bulk density with SOM and calcium carbonate content, total SOM and calcium carbonate pools (in g/m²) were calculating for each location.

2.2.4 Data analysis

Recorded plant species were classified into five life span groups (annuals, biannuals, perennials, woody species, winterannuals) as well as ten ecological species groups for dry dunes based on their syntaxonomical preference [Aggenbach unpublished]. For each plot, number of species and cumulative cover of these species were calculated for each group. Furthermore, Ellenberg indicator values of nutrient (EII_N), acidity (EII_R), moisture (EII_F), and light availability (EII_L) was retrieved from the database GermanSL and average values were calculated for each plot.

The plots that we used involve two different restoration measures: sod-cutting and mowing. Since all sod-cut plots are mown, the design of the dataset is not fully factorial of the two measures. Therefore, to compare means among different restoration measures, we use one factor only ("management type": M0_S0 / M1_S0 / M2_S0 / M2_S1), instead of two factors (i.e. sod-cutting (S0/S1) and mowing (M0/M1/M2)). Prior to analysis, decalcification depth was log transformed to obtain approximately normal distribution. Depth-specific soil variables (pH_KCl, pH_H2O, SOM content, and bulk density) were analysed with 2-way ANOVA for the type of management (M0_S0, M1_S0, M2_S0, M2_S1) depth (0-5cm depth / 5-15cm depth), and their interactions. The assumed conditions of ANOVA, equality of variance and normal distribution of residuals, were tested with the Levene's test and Kolmogorov-Smirnov test, respectively. When the effect of management was significant, multiple comparison test was conducted using the Tukey Honest Significant Difference method. Also, when interaction effects of several factors were significant, the multiple comparison test was conducted among different combinations of these factors.

For the other soil variables (area-based SOM pool of 0-15 cm depth, log-transformed decalcification depth) and vegetation variables (number of plant species, herb cover,

moss cover, herb height, plot-mean Ellenberg values of light, nutrients, moisture, and acidity) was tested with 1-way ANOVA for the effect of management type, and their interactions. Note that cover of other vegetation structure (shrubs, bare sand, litter) could not be analysed due to frequent zero records for these variables.

Decalcification depth is not evenly distributed among the different management types, whereas decalcification depth can strongly and directly affect a number of soil and vegetation variables. Thus, to properly evaluate the effects of management effects, it is necessary to statistically control the effect of the possible confounding effects of decalcification depth. For that purpose, we conducted 2-way ANCOVA analysis for depth-specific soil variables (pH_KCl, pH_H2O, SOM content, and bulk density) with management type, depth, and their interaction as independent variables, and log-transformed decalcification depth as the covariate. For depth-non-specific variables (SOM pool, species richness, herb cover, moss cover, herb height, plot-mean Ellenberg values of light, nutrients, moisture, and acidity), we conducted 1-way ANCOVA with management type as the independent variable and log-transformed decalcification depth as the covariate. When the effect of the covariate is not significant, we use the results of ANOVA to evaluate the effect of management for the variables.

Since we expect interactive effects of decalcification depth and management type for some of the response variable (e.g. sod cutting effect would be stronger in decalcified areas; see Introduction), we conducted additional ANCOVA with an interaction term of covariance (i.e. decalcification depth) and independent variable (i.e. management type). Note that an assumption of ANCOVA is homogeneity of the slopes (i.e. there is no interaction between covariate and management type). However, one can conduct ANCOVA with the interaction term to check if the interaction effect is significant. When the interaction effect in ANCOVA is significant (i.e. slopes of regression against decalcification depth are not parallel among management types), we conducted multivariate regression analysis including interaction effects between management type and decalcification depth. The assumed model is:

$$y = \beta_0 + \beta_1 d_{M1_S0} + \beta_2 d_{M2_S0} + \beta_3 d_{M2_S1} + \beta_4 \ln(\text{decal}) + \beta_5 d_{M1_S0} \ln(\text{decal}) + \beta_6 d_{M2_S0} \ln(\text{decal}) + \beta_7 d_{M2_S1} \ln(\text{decal})$$

where y is the response variable, $\ln(\text{decal})$ is log-transformed decalcification depth, β_x is the regression coefficient, d_{M1_S0} , d_{M2_S0} and d_{M2_S1} are the dummy variables for management type M1_S0, M2_S0, and M2_S1, respectively.

When the interaction effect of ANCOVA is not significant (i.e. slopes of regression against decalcification depth are parallel among management types), we conducted multivariate regression analysis without interaction term. The assumed model is:

$$y = \beta_0 + \beta_1 d_{M1_S0} + \beta_2 d_{M2_S0} + \beta_3 d_{M2_S1} + \beta_4 \ln(\text{decal}) + \beta_5 d_{M1_S0} \ln(\text{decal})$$

Tested response variables were area-based SOM pool of 0-15cm depth, soil pH_KCl of 0-5cm depth, and number of plant species, herb cover, moss cover, herb height, plot-mean Ellenberg values of light, nutrients, moisture, and acidity. Normality of the residual distribution of all regression models were tested with Kolmogorov-Smirnov test. For mown plots (N=30), effects of additional variables of mowing type (mowing intensity and duration not mown) were tested with multivariate regression analysis. Log-transformed decalcification depth and a dummy variable for sod-cutting were also included as an explanatory variable. Tested response variables were area-based SOM pool of 0-15cm depth, soil pH_KCl of 0-5cm depth, and number of plant species, herb cover, moss cover, herb height, plot-mean Ellenberg values of light, nutrients, moisture,

and acidity. Normality of the residual distribution of all regression models were tested with Kolmogorov-Smirnov test.

To analyse how management and site characteristics influence plant species composition, canonical correspondence analysis (CCA) was conducted using the package 'vegan' of the statistical program R. For management type, we included sod-cutting as a dummy variable and mowing types as two dummy variables (one for M0, the other for M2). To avoid multicollinearity, we selected two essential site variables which are not strongly correlated to each other ($-0.7 < r < +0.7$): area-based SOM pool of 0-15 cm depth and log-transformed decalcification depth. The significance of the relationship between species and site factors was tested with the Monte-Carlo permutation method by random permutations of the dataset for 499 times.

2.3 Results

2.3.1 Decalcification depth as a confounding factor

It was revealed that decalcification depth was not evenly distributed among the management types we studied (Figure 2-1). It was significantly lower in sod-cut & recently mown plots (M2_S1) than in plots with other management types. Therefore, location-specific decalcification depth may hinder finding the true effects of management type on soil and vegetation characteristics. Indeed, decalcification depth was strongly related to, for example, soil pH_KCl of 0-5 cm depth (Pearson's correlation coefficient $r = -0.82$, $p < 0.001$), soil pH_KCl of 5-15 cm depth ($r = -0.79$, $p < 0.001$) and SOM content at 0-5 cm depth ($r = 0.73$, $p < 0.001$). See Table 6.1 **Error! Reference source not found.** in Appendix for correlation coefficients of other variables. Therefore, for the following sections, we explicitly consider the confounding effect of decalcification depth in statistical analysis.

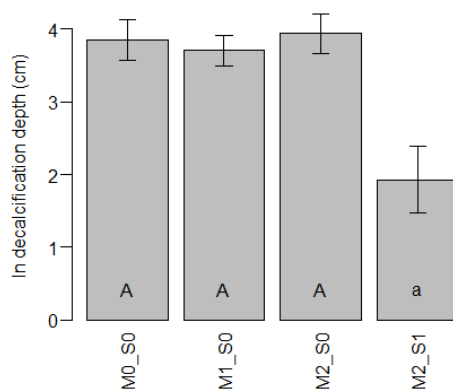


Figure 2-1. Log-transformed decalcification depth in plots with four different management types. Mean and standard errors of 10 plots are shown for each management type. Results of multiple comparison test among the four management types are shown with alphabet ($p < 0.05$). Groups with upper-case letters are significantly ($p < 0.05$) different from those with lower-case letters (e.g. 'A', and 'a').

2.3.2 Management effects on soil characteristics

Soil pH_KCl was significantly related to the covariate decalcification depth ($p < 0.001$ with ANCOVA, Table 2.2). Management type had a significant effect on soil pH_KCl ($p < 0.001$ with ANCOVA). It was significantly higher in sod-cut & recently mown plots (M2_S1) compared to the other management types ($p < 0.05$ with multiple comparison test), even when the effect of covariate was controlled (Figure 2-2a). Depth (either 0-5 cm or 5-15 cm) did not have significant effect on pH_KCl. The same patterns were observed in soil pH_H2O (Figure 2-2b, Table 2.2).

Organic matter content in soil was significantly related to the covariate decalcification depth ($p < 0.01$ with ANCOVA, Table 2.2). Both management type and depth had significant effects on SOM content ($p < 0.001$ with ANCOVA). It was significantly lower in 5-15 cm depth than in 0-5 cm depth, and lower in sod-cut & recently mown plot (M2_S1) compared to the others ($p < 0.05$ with multiple comparison test) (Figure 2-2c). The interaction effect of management type and depth was also significant ($p < 0.001$ with ANCOVA), reflecting that the difference in SOM content between depths was much smaller in M2_S1 plots (M2_S1) compared to the others.

Bulk density was not related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.2). Bulk density had opposite patterns to SOM concentrations. It was

higher in sod-cut & recently mown plots (M2_S1) than the other plots, and higher in 5-15 cm depth than 0-5 cm depth ($p < 0.001$ with ANOVA for both) (Figure 2-2d). The interaction effect of management type and depth was also significant ($p < 0.001$ with ANOVA), since the difference between the depths was small in M2_S1 plots. Calcium carbonate content in soil was not related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.2). It was not affected by management type nor depth ($p > 0.05$ with ANOVA). As mentioned in the Method section, our measurements of calcium carbonate were not very reliable. Correlation between pH_KCl and calcium carbonate content, which is expected to be very strong if the measurements are correct, was only marginal in our dataset ($r = 0.26$, $p < 0.05$ with Pearson's correlation test) (Also see Figure 6-2 **Error! Reference source not found.** in Appendix). Therefore, for the rest of the analysis, we will not use our data of calcium carbonate content.

Soil organic matter pool of 0-15 cm depth was significantly related to the covariate decalcification depth ($p < 0.01$ with ANCOVA, Table 2.3). Management type had a significant effect on SOM pool ($p < 0.001$ with ANOVA). It was significantly lower in sod-cut & recently mown plots (M2_S1) than others ($p < 0.05$ with multiple comparison test) (Figure 2-3).

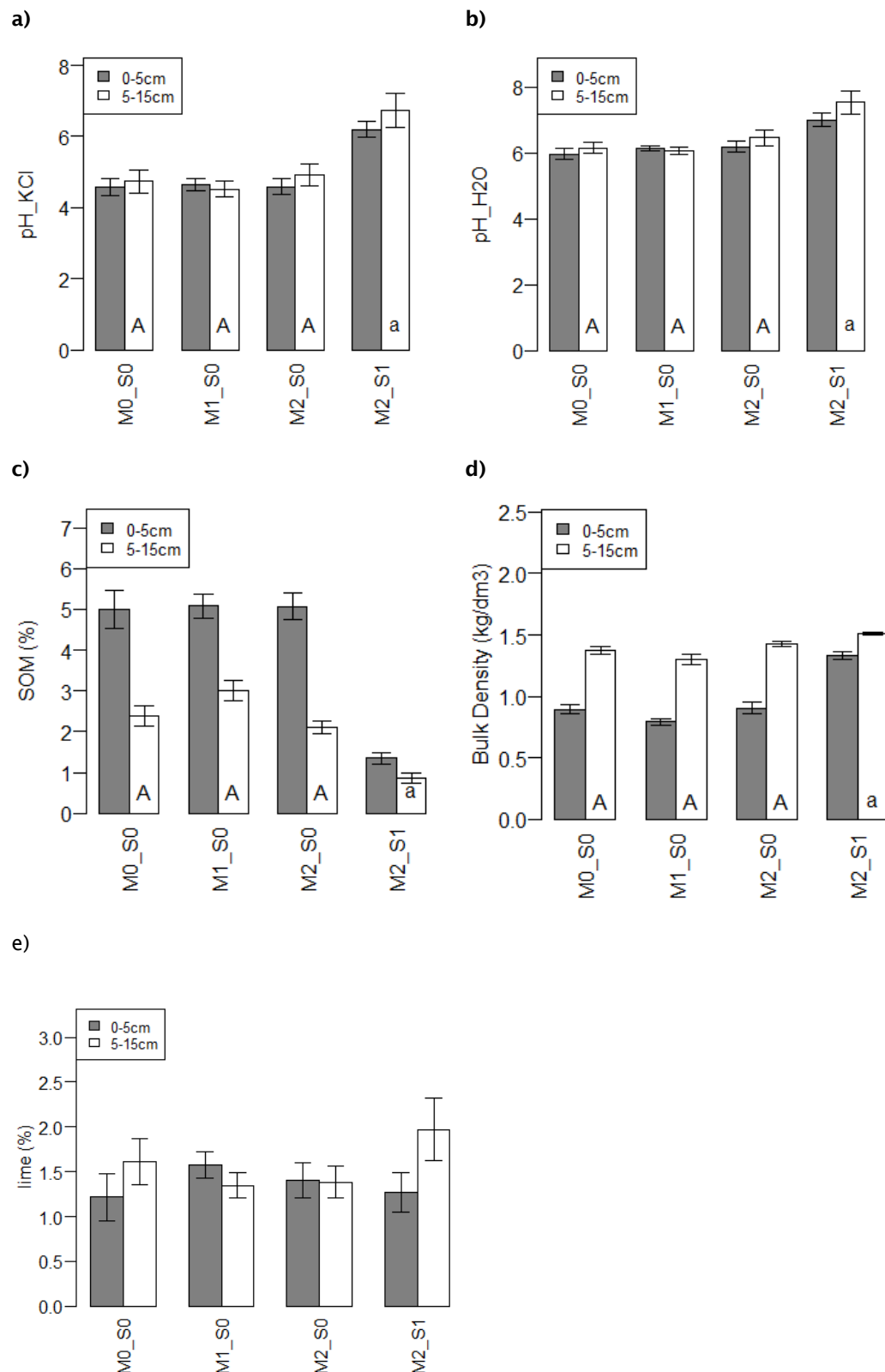


Figure 2-2. pH_{KCl} (a), pH_{H₂O} (b), concentrations of soil organic matter (c), bulk density (d), and calcium carbonate content (e) of soils in plots with four different management types. Measurements of 0-5cm depth and 5-15cm depth are separately shown. Mean and standard errors of 10 plots are shown for each management type. Alphabets show the results of multiple comparison test among four management

types (thus two depths were clumped) ($p < 0.05$). Groups with upper-case letters are significantly ($p < 0.05$) different from those with lower-case letters (e.g. 'A', and 'a'). For bulk density, which was not significantly related to the decalcification depth, multiple comparison test was conducted on response variable not adjusted for the covariate (i.e. ANOVA). For the rest, multiple comparison test was done after adjusted for covariate (i.e. ANCOVA).

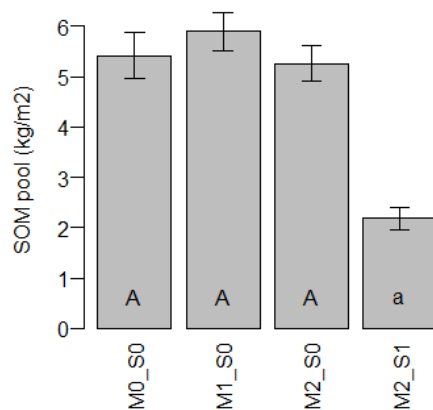


Figure 2-3. Soil organic matter pool of soils of 0-15cm depth (in plots with four different management types. Mean and standard errors of 10 plots are shown for each management type. Alphabets show the results of multiple comparison test, after adjusted for the covariate decalcification depth (i.e. ANCOVA), among the four management types ($p < 0.05$). Groups with upper-case letters are significantly ($p < 0.05$) different from those with lower-case letters (e.g. 'A', and 'a').

Table 2.2. Results of 2-way ANOVA (with management type and depth and their interaction as explanatory variables) and 2-way ANCOVA (with log-transformed decalcification depth as covariate) for depth-specific soil variables. Results of multiple comparison test for the effect of management are shown in Figure 2-2.

	pH_KCl		pH_H2O		SOM (%)		BD (g/cm³)		calcium carbonate (%)	
ANOVA	F	p	F	p	F	p	F	p	F	p
Mgt	19.60	***	15.82	***	48.65	***	46.54	***	0.41	ns
Depth	1.29	ns	2.64	ns	110.91	***	324.54	***	1.76	ns
M x D	0.51	ns	0.74	ns	8.04	***	11.76	***	1.64	ns
ANCOVA	F	p	F	p	F	p	F	p	F	p
Mgt	33.28	***	20.02	***	54.91	***	45.89	***	0.41	ns
Depth	2.18	ns	3.33	ns	125.20	***	320.06	***	1.74	ns
M x D	0.86	ns	0.93	ns	9.08	***	11.59	***	1.62	ns
log(decals)	51.23	***	20.07	***	10.27	**	0.01	ns	0.12	ns

Table 2.3. Results of 1-way ANOVA (with management type as explanatory variable) and 1-way ANCOVA (with log-transformed decalcification depth as covariate) for depth-specific soil variables. Results of multiple comparison test for the effect of management are shown Figure 2-3, Figure 2-4, and Figure 2-5.

	SOM pool (kg/m ²)		sp richness		Ell_light		Ell_nutrient		Ell_moisture	
ANOVA	F	p	F	p	F	p	F	p	F	p
Mgt	21.98	***	0.22	ns	35.48	***	0.28	ns	9.34	***
ANCOVA	F	p	F	p	F	p	F	p	F	p
Mgt	26.10	***	0.22	ns	37.66	***	0.29	ns	9.19	***
log(decal)	7.75	**	0.42	ns	3.21	ns	1.51	ns	0.42	ns
	Ell_acidity		herb cover		moss cover		Herb height			
ANOVA	F	p	F	p	F	p	F	p		
Mgt	2.49	ns	8.40	***	1.99	ns	1.80	ns		
ANCOVA	F	p	F	p	F	p	F	p		
Mgt	3.40	*	8.17	***	2.02	ns	1.78	ns		
log(decal)	14.21	***	0.00	ns	1.59	ns	0.62	ns		

2.3.3 Effect of management on plant species richness and vegetation structure

Plant species richness (vascular plants, mosses, and lichens) depth was not significantly related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.3). The effect of management type was not significant either ($p > 0.05$ with ANOVA, Figure 2-4a). None of the variables for vegetation structure (herb cover, moss cover, herb height) was related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.3). However, they were more sensitive to management effects. Cover of herbs was significantly influenced by management types ($p < 0.001$ with ANOVA). It was highest at not-mown plots (M0_S0), followed by recently-mown plots (M2_S0), previously-mown plots (M1_S0), and recently-mown & sod-cut plots (M2_S1) (Figure 2-4b). Neither cover of mosses nor average height of herb layer were significantly affected by management types ($p > 0.05$, Figure 2-4c, Figure 2-4d). Yet there was a trend, though not significant, that not-managed plots (i.e. M0_S0) had the lowest moss cover and tallest herb layer.

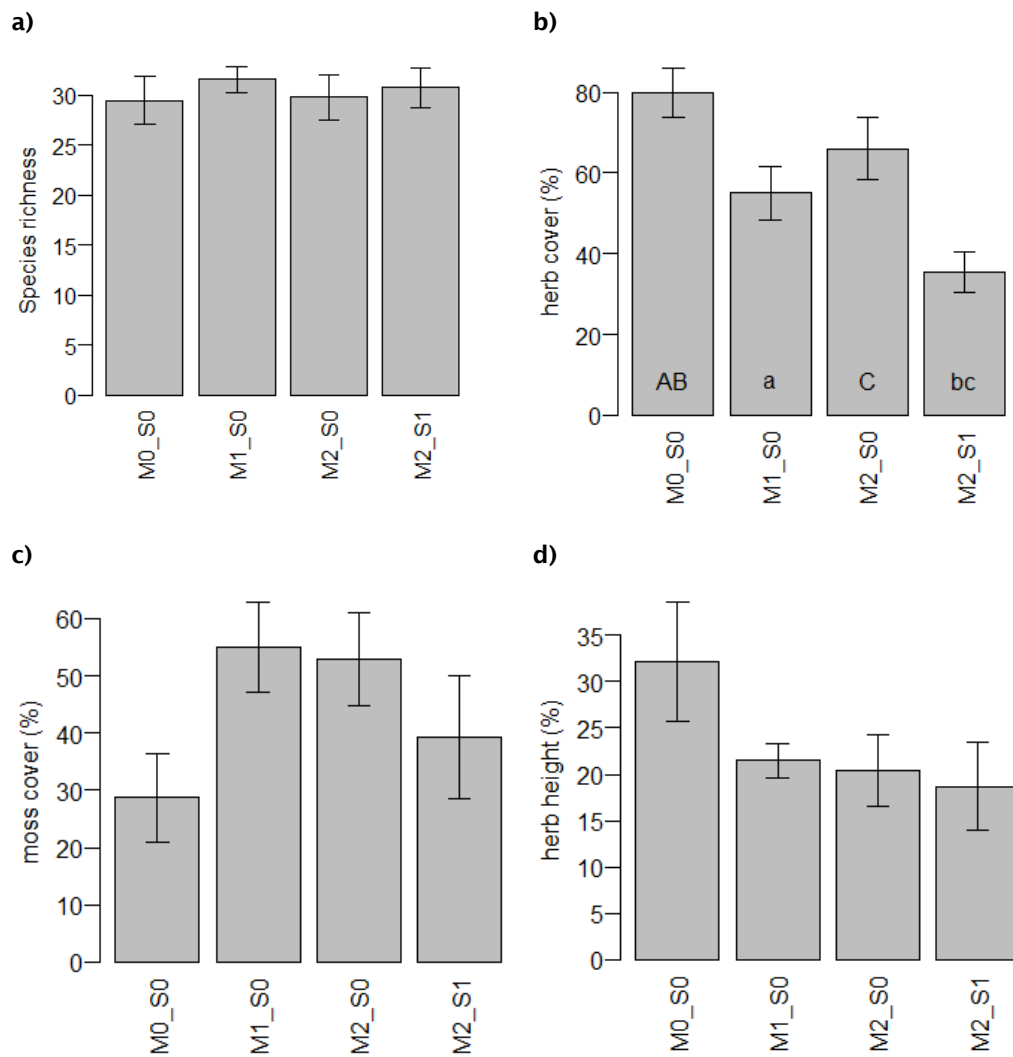


Figure 2-4. Species richness (i.e. number of species of vascular plants, mosses, and lichens) (a), herb cover (b), moss cover (c), and average height of herb layer (d) in plots with four different management types. Mean and standard errors of 10 plots are shown for each management type. As none of the response variables were related to the decalcification depth, the results of multiple comparison test of among the four management types, not adjusted for covariate (i.e. ANOVA), are shown with alphabet ($p < 0.05$). Groups with upper-case letters are significantly ($p < 0.05$) different from those with lower-case letters (e.g. 'A', and 'a').

2.3.4 Effect of management on plant species indicator values

Plot-mean Ellenberg values for light was not significantly related to the covariate decalcification depth ($p = 0.08$ with ANCOVA, Table 2.3). It was significantly higher for sod-cut plots (M2_S1) than others ($p < 0.001$ with ANOVA; Figure 2-5a). This indicates that the sod-cut plots have more species which are adapted to abundant light conditions. Note that all management types had high values for light availability, indicating light-rich conditions for all studies plots.

Plot-mean Ellenberg values for nutrient was not related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.3). It was not affected by management type neither ($p > 0.05$ with ANOVA; Figure 2-5b).

Plot-mean Ellenberg values for acidity was significantly related to the covariate decalcification depth ($p > 0.05$ with ANCOVA, Table 2.3). It was slightly influenced by management type ($p < 0.05$ with ANCOVA). Sod-cut & recently-mown plots (M2_S1) had a higher value than not-sod-cut & recently-mown plots (M2_S0) ($p < 0.05$ with multiple comparison test; Figure 2-5c), indicating more frequent occurrence of species adapted to base-rich conditions in M2_S1 plots.

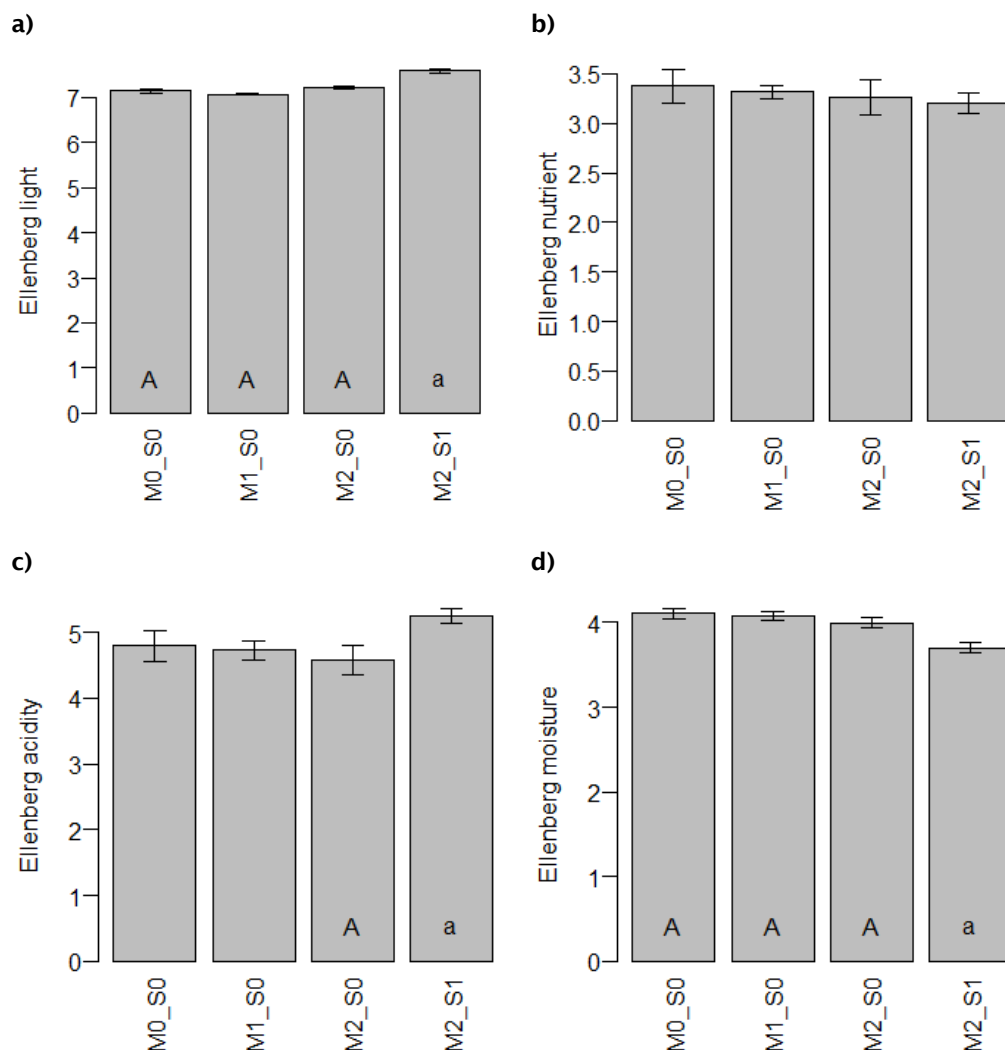


Figure 2-5. Plot-mean Ellenberg indicator values for light (a), nutrient (b), acidity (c), and moisture (d) in plots with four different management types. Mean and standard errors of 10 plots are shown for each management type. Results of multiple comparison test among the four management types were shown with alphabets. For Ellenberg value for acidity, which was significantly related to the decalcification depth, multiple comparison test was conducted after adjusted for covariate (i.e. ACNOVA). For the rest, multiple comparison test was done on not-adjusted response variable (i.e. ANOVA). Groups with upper-case letters are significantly ($p < 0.05$) different from those with lower-case letters (e.g. 'A', and 'a').

Plot-mean Ellenberg values for moisture was not related to the covariate decalcification depth ($p > 0.05$ with ANCOVA; Table 2.3). It was significantly different among management types ($p < 0.001$ with ANOVA; Figure 2-5d), being significantly lower (i.e. more species adapted to dry conditions) in sod-cut plots (M2_S1).

2.3.5 Effect of management on plant species composition

Never mown plots (M0_S0) had higher percentage of woody species than mown & not sod-cut plots (M1_S0 and M2_S0) (Figure 2-6). Sod-cut plots (M2_S1) had less total cumulative cover than other plots, and the proportions of woody species and annual species were higher than other plots (Figure 2-6). The majority of woody species in sod-cut plots (M2_S1) were *Hippophae rhamnoides* and *Rubus caesius*, whereas those in unmown plots (M0_S0) were more diverse. Relative high occurrence of annual species in M2_S1 plots were more visible when number of species, instead of cumulative cover, was looked at (results not shown).

Composition of ecological species groups was highly variable among plots even within a management type (Figure 6-3 **Error! Reference source not found.** in Appendix).

Nevertheless, there was a trend that sod-cut plots (M2_S0) had much higher cover of species typical for 'dry pioneer vegetation nutrient-poor calciumcarbonate-rich' and a lower cover of species typical for 'dry dune grassland nutrient-poor' and for 'mesophytic grassland moderately nutrient-rich' (Figure 2-7). The decrease of the latter two species groups were not evident when number of species, instead of cumulative cover, was looked at (results not shown).

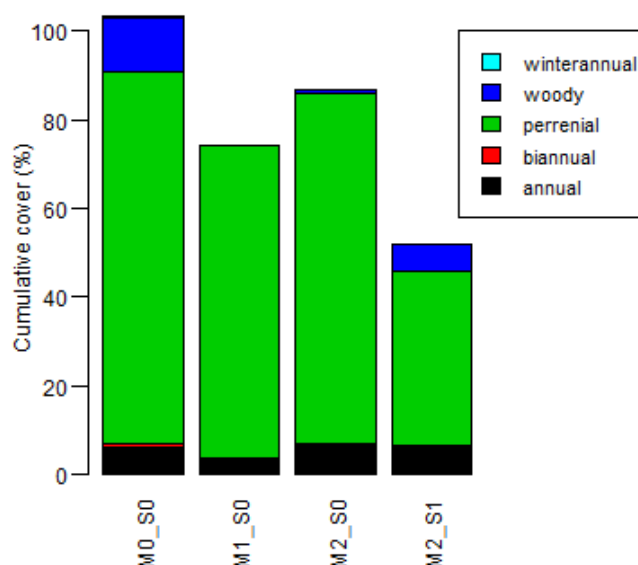
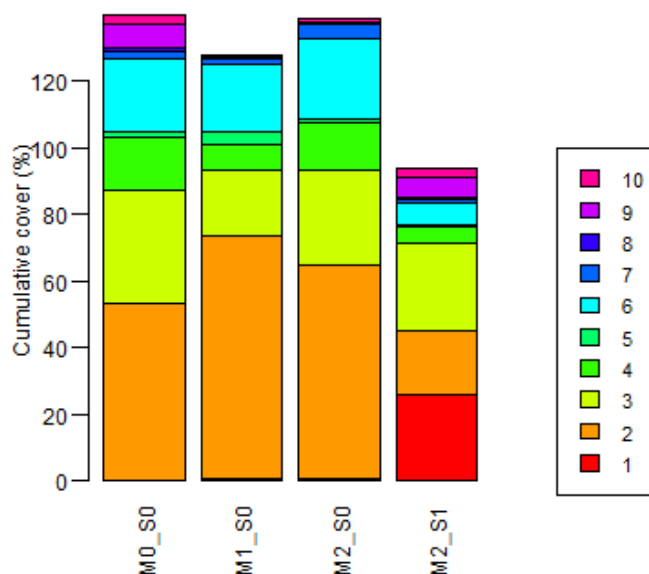


Figure 2-6. Cumulative cover of plant species, categorized into life span, for four management types. Cumulative cover was averaged for 10 plots within each management type.



1: dry pioneer vegetation nutrient-poor calciumcarbonate-rich	6: mesophylic grassland moderately nutrient-rich
2: dry dune grassland nutrient-poor	7: grassland nutrient-rich
3: dry dune grassland nutrient-poor base-rich	8: wet grassland nutrient-rich
4: dry dune grassland nutrient-poor base-poor	9: dry forest edge, forb, shrub & forest vegetation base-rich
5: heathgrassland & heathland	10: others

Figure 2-7. Cumulative cover of plant species, categorized into ecological species group, for four management types. Cumulative cover was averaged for 10 plots within each management type.

In CCA analysis, five explanatory variables (SOM pool, log-transformed decalcification depth, a dummy variable for sod-cutting, and two dummy variables for mowing type) explained only 22.7 % of the total variation in the species composition data, of which 66.5% was explained by the first (46.3%) and second (20.2%) CCA axis. Monte-Carlo permutation test indicated that the obtained model was significant ($p=0.002$).

The first CCA axis reflects presence of sod-cutting as well as recent mowing ('M2') (Figure 2-8 top). Sod-cut (M2_S1) plots were clearly ordinated on the positive side of this axis, whereas not sod-cut plots with contrasting mowing regimes (M0_S0, M1_S0, and M2_S0) were closely clumped on this axis. The second CCA axis is linked to low SOM content and decalcification depth (and therefore high pH). Plots were spread on this axis, although there was no clear distinction among different management types on this axis.

Several ecological species groups occupy a specific position in the ordination (Figure 2-8 bottom). Species categorized for 'dry dune grassland nutrient-poor base-poor' (green) are ordinated on left-bottom plane of the CCA diagram, which corresponds with deeply decalcified site conditions. Species belonging to 'dry pioneer vegetation nutrient-poor calciumcarbonate-rich' (red) were ordinated on right side of the CCA diagram, where all sod-cut plots locate. On the left-top corner of the CCA diagram which weakly corresponds to not-mown conditions, species categorized for 'dry forest edge, forb, shrub & forest vegetation base-rich' (purple) appear more often.

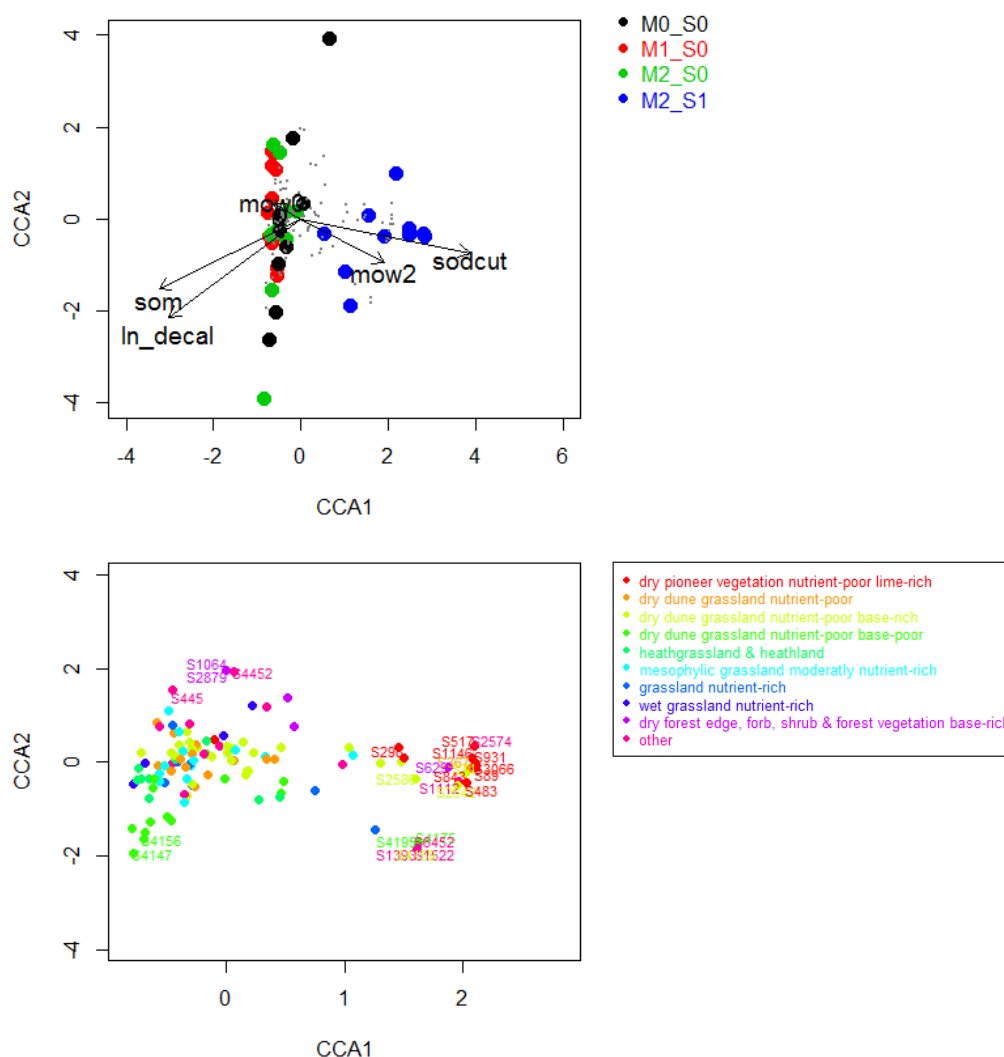


Figure 2-8. CCA-ordination diagram of 40 plots and 5 site factors (top) and plant species (bottom). The included site factors are SOM pool of 0-15 cm depth (kg/m²), log-transformed decalcification depth (cm), a dummy variable for sod-cutting, two dummy variables for mowing type (one for no mowing (M0) and the other for recent mowing (M2)). The colour of the species scores indicates ecological species group. For species which has larger scores than 1.5 on either axis 1 or axis 2, the species code is shown. See Table 6.2Error! Reference source not found. in Appendix for the description of the species code.

2.3.6 Interaction of decalcification depth and management effects

In order to examine if and how management effects interact with decalcification depth, multiple regression analysis was conducted. Here we discuss about the variables which were significantly or almost significantly ($p < 0.1$ with ANOVA) related to decalcification depth. See Table 6.3Error! Reference source not found. in Appendix for the detailed results of all regression analysis.

For SOM pool, there was significant interaction between management type and decalcification depth ($p < 0.05$ with ANCOVA with the interaction term). SOM pool hardly changed with increasing decalcification depth for sod-cut plots (M2_S0) (slope +0.07), whereas it increased with decalcification depth for other plots (slope +1.31, +1.13, and +0.41) for M0_S0, M1_S0, and M2_S0, respectively) (Figure 2-9a).

For soil pH_KCl of 0-5 cm depth, there was no significant interaction effect between management type and decalcification depth ($p > 0.05$ with ANCOVA with the interaction term). pH_KCl was strongly and negatively related to decalcification depth (regression coefficient $\beta = -0.46$, $p < 0.001$), and was higher at sod-cut plots (M2_S1) than others ($\beta = 0.73$, $p < 0.05$) (Figure 2-9b). Effects of mowing on pH_KCl were not evident ($p > 0.05$). For Plot-mean Ellenberg values for light, there was no significant interaction effect between management type and decalcification depth ($p > 0.05$ with ANCOVA with the interaction term). It was significantly higher in sod-cut plots (M2_S1) than others ($\beta = 0.38$, $p < 0.001$), but was almost significantly related to decalcification depth ($p = 0.082$) (Figure 2-9c).

For plot-mean Ellenberg values for acidity, the interaction effect between management type and decalcification depth was significant ($p < 0.001$ with ANCOVA with the interaction term). It did not change with decalcification depth for sod-cut plots (M2_S1) (slope 0.00), whereas it decreased with decalcification depth for the others (M0_S0, M1_S0, M2_S0) (Figure 2-9d).

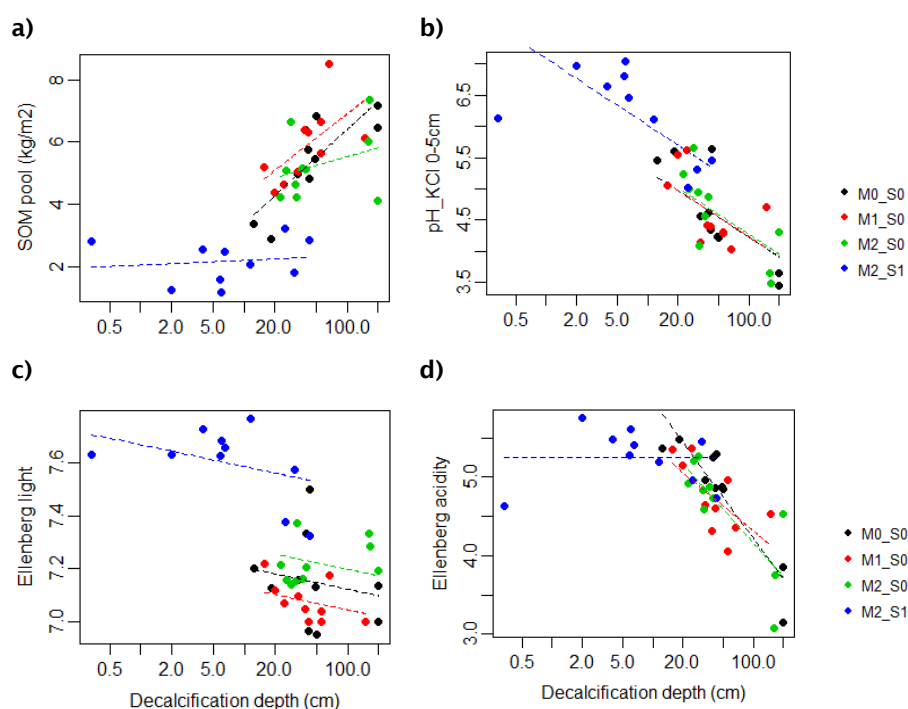


Figure 2-9. Relationships between decalcification depth and (a) SOM pool of 0-5 cm depth (b) soil pH_KCl of 0-5 cm depth, (c) plot-mean Ellenberg values for light, and (d) plot-mean Ellenberg values for acidity, for four management types. Regression models (see Table 6.3 *Error! Reference source not found.* in Appendix for details) for each management type are shown with broken lines.

2.3.7 Effect of mowing intensity and duration not mown

For the mown plots (i.e. management type 'M1_S0', 'M2_S0', and 'M2_S1'; $N=30$), the effects of mowing intensity and duration not mown was tested together with the effects of sod-cutting and decalcification depth.

Plot-mean Ellenberg value for moisture was significantly ($p < 0.05$) and positively related to mowing intensity (Figure 2-10b). This means that intensively mown plots have

higher occurrence of species adapted to wet condition. For plot-mean Ellenberg values for light, the effect of duration not mown was almost significant ($p=0.056$) (Figure 2-10c). This indicates that the longer a plot is now mown, the lower the chance of occurrence is for plant species which are adapted to abundant light condition. For the rest of the response variables, there was no significant effect of 'mowing intensity' nor 'duration not mown' (Error! Reference source not found. Table 6.4 in Appendix).

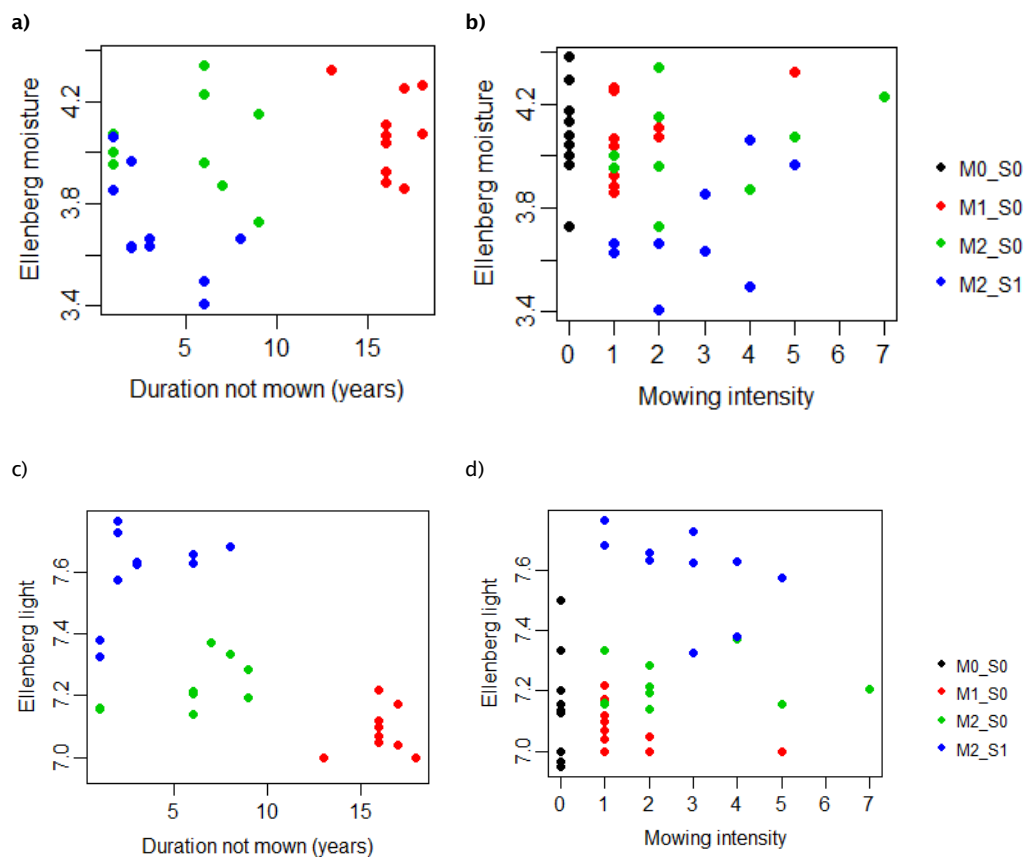


Figure 2-10. Relationship between plot-mean Ellenberg values for moisture (a,b) and light (c,d,) and duration not mown (left) and mowing intensity (i.e. total amount of mowing events during the period of 1995- 2014) (right). Note that never-mown plots (M0_S0) were not included in the regression analysis.

2.4 Discussion

Decalcification depth as a confounding factor to study management effects

It was revealed that there was a considerable bias in decalcification depth among different management types in this study. Sod-cut plots had significantly shallower decalcification depth than other management types. This pattern is because we selected the sod-cut sites within the OINS project of the year 2000-2001 only. The sod-cutting project aimed at reconstructing the artificial infiltration area in the Oostduinen. Oostduinen is for a greater part calcium carbonate rich (calcium carbonate rich top soils or only shallow decalcification), while the Middelduinen has also a large area of deeply decalcified soils. The plots of the other three management types without sod cutting were selected in both Oostduinen and as well Middelduinen, and therefore contain more sites with deeper decalcified soils. An extra possible explanation for the shallower decalcification depth in sod-cut plots is that removal of the top soils removes a part or the complete decalcified soil layer and therefore decreases the decalcification depth. At

the sod cut sites the depth of the removed top soil varied. In practice as much as soil was removed until SOM poor sand was exposed (several decimetres) (pers. comm. Marten Annema). Decalcification depth is an important factor in dune ecosystem, driving various processes in soil and vegetation. Thus, it is necessary to statistically control the effect of decalcification in order to examine the pure effects of management in dune ecosystems. Below we discuss about effects of sod-cutting and mowing on soil and vegetation, with explicit considerations of confounding effects of decalcification depth.

Effect of sod cutting on soil and vegetation

This study identified clear effects of sod-cutting on some soil characteristics of dry dune grasslands. Sod-cutting significantly reduced organic matter content of soil, both at 0-5 cm depth and 5-15 cm depth. Likewise, bulk density was significantly higher in sod-cut plots. Even 13 years after the sod-cutting event, the top soil layer (i.e. 0-5 cm depth) had similar characteristics to the sub-soil layer (i.e. 5-15 cm) in terms of SOM and bulk density, indicating a very slow soil development after the sod-cutting. Unknown is of the use of equipment for the sod cutting caused soil compaction and there also had an increasing effect on bulk density. Although SOM was strongly and positively related to decalcification depth, the effect of sod-cutting on reduction of SOM was significant even after accounting for the decalcification effect. Furthermore, significant interaction effect between decalcification depth and management types indicated that effect of sod-cutting in reducing SOM was especially large in deeply decalcified areas at an intermediate (13 years) time scale after the sod-cutting event. Note, however, that our sod-cut plots are restricted to moderately decalcified area (up to 43 cm depth). Therefore, it is uncertain to derive any conclusion from our analysis on the effect of sod-cutting at very deeply decalcified areas.

Effects of sod-cutting in improving pH were also evident. Although decalcification depth was a dominant factor determining soil pH, sod-cutting had an additional effect of increasing soil pH. In other words, given that decalcification depth is the same, a sod-cut plot would have a higher pH than a not-sod-cut plot. The magnitude of the positive effect of sod-cutting on pH was not different between deeply-decalcified and shallowly-decalcified area in our dataset. The positive effect of sod-cutting is probably due to decreased SOM content in sod-cut sites. This is in line with the observation in sandy soils that pH values at a low SOM content are higher than at a higher SOM content [among others: *Grootjans et al.*, 1997]). Additionally, less vegetation in sod-cut sites may be another explanation for their high pH: it leads to less acidifying effects of atmospheric deposition, as well as less CO₂ production by plant roots and soil fauna. Some of the vegetation variables were also influenced by sod-cutting. Vegetation structure had more visible changes by sod cutting. After sod was cut, herb cover significantly decreased and height of the herb layer became shorter (not significant, though), whereas moss cover increased (though not significant). Species composition also changed due to sod cutting. In general, sod-cut plots had more cover of annual plant species, more cover of species of base rich soils, more cover of pioneer species of nutrient-poor and base-rich conditions, and less cover of nutrient-poor dune grassland species. Sod-cut sites also had a higher cover of woody species and species of dry forest edge, forb, shrub and forest vegetation than mown site without sod-cutting. For this reason the sod cut sites were mown frequently by the manager in order to suppress development to shrub. Especially sod-cut sites in calcium carbonate-rich areas need mowing management afterwards (pers. comm. Marten Annema).

Furthermore, functional composition of plant species changed due to sod cutting too. Plot-mean Ellenberg values for acidity were much lower in sod-cut plots (i.e. more species adapted to base-rich conditions), even after confounding effect of decalcification depth was controlled. Plot-mean Ellenberg value for light was higher in sod-cut plots (i.e. more species adapted to abundant light condition). Higher availability of light can be caused by reduced above-ground biomass in sod-cut plots, as indicated by less and shorter herb layer. Plot-mean Ellenberg values for moisture were lower in sod-cut plots (i.e. more species adapted to dry conditions). The drier condition of sod-cut plots may be explained by reduced water retention in their SOM-poor soils and increased evapotranspiration from their relatively open soil surface. It should be noted that both Ellenberg value for light and Ellenberg value for moisture was hardly related to decalcification depth. Thus, sod-cutting itself, instead of the background soil conditions of the area, should have directly influenced these variables (i.e. light and moisture).

Despite a number of sod-cutting effects on vegetation structure and species composition, species richness was not higher in sod-cut plots compared to other management types. Knowing that the grasslands established on the sod-cut area are still early successional stage in terms of both soil and vegetation [succession from bare, SOM-poor sand soils takes 2-4 decades; *Aggenbach et al.*, 2013; *Fujita and Aggenbach*, 2015], it might take a longer time than 13 years until the species number reaches its potential maximum.

Effect of mowing on soil and vegetation

Mowing by choppering ('maaizuigcombi') affected soil and vegetation characteristics of dune grasslands to a much lesser extent than sod-cutting. Neither SOM content nor pH of top soil was different among never-mown, previously-mown, and recently-mown plots, whether or not the confounding effect of decalcification depth was corrected. Likewise, species richness did not differ among different mowing categories. There was, however, a slight influence of mowing on vegetation structure. Herb cover was significantly lower in previously-mown and recently-mown plots than never-mown plots. Although not statistically significant, there were trends that mown plots had higher moss cover and shorter herb layer. These changes in vegetation structure were not better explained when we used more detailed information about mowing practice for each location (i.e. mowing intensity and duration not mown). The small effect of mowing on vegetation structure is probably caused by the fact all management categories were grazed by cattle since 1993 or 2001, and grazing management was adjusted to create a low herb layer in autumn. Consequently mowing could have only a limited effect on the vegetation structure and light conditions. Another explanation is that mowing practice was carried out specifically at sites with encroachment of grasses or shrubs (*Salix repens*, *Hippophae rhamnoides*) (pers. comm. Marten Annema). The original state for mown and not mown sites could therefore differ, and the effect of mowing on vegetation structure there is probably larger than results of our study indicated. Moreover, our study does not have proper 'reference' plots which is not mown and has problem of grass or shrub encroachment. This hampers to find clear effects of mowing in our dataset. Furthermore, although not investigated, spatial differences in grazing pressure could have been a confounding factor.

Species composition changed due to mowing. Woody species were less abundant in previously-mown plots and recently-mown plots compared to never-mown plots. Also species typical for 'dry forest edge, forb, shrub & forest vegetation' had a higher cover in plots never mown. Mowing is therefore effective for reducing woody species. Plot-

mean Ellenberg value for light was slightly higher (though not significant) in recently-mown than never-mown plots, indicating that species adapted to abundant light conditions can survive better in mown plots. In line with this, 'duration not mown' was almost significantly related to plot-mean Ellenberg value for light, implying that consideration of mowing history in individual sites may help clarifying the mowing effect. Furthermore, there is a weak but significant effect of mowing intensity on Ellenberg value for moisture, implying that sites with more frequent mowing are wetter. This pattern, however, is probably linked to the fact that intensive mowing was applied in moist areas with water tables close to soil surface where plant productivity is higher than sites without influence of groundwater.

Despite these differences in species composition due to mowing, the ordination of species by CCA showed highly overlapped position of plots with different mowing regimes. This indicates that mowing had only minor influence in species composition in this system compared to other more dominant factors such as decalcification depth and sod-cutting. Moreover the explained variation of the CCA was low, indicating that other site factors that we did not incorporate in the model may play important roles in shaping the plant community. A possible factor for explaining biodiversity patterns on a plot scale (4 m²) is the spatial variation of calcium carbonate content and pH at a microscale, as was observed in the replica soil cores within the plots (results not shown). The small-scale spatial heterogeneity of soil characteristics is probably enhanced by activity of densely populated ground ants in the Middel- and Oostduinen. Because of time constraints more sophisticated analyses of confounding effects of soil properties on effects of mowing management were not conducted. Such analyses may reveal more subtle effects of soil factors. For the same reason the effects of management on individual plant species have not been analysed.

2.5 Conclusions and implications

This study found that sod-cutting has more drastic effects on soil and vegetation of dry dune grasslands than mowing. After 13 years, soils in sod-cut plots have lower SOM content in top (0-5 cm depth) and sub soil (5-15 cm depth), and the effect of sod-cutting on SOM reduction was stronger in deeply decalcified areas. Thus, our hypothesis 2 was supported for SOM. Moreover, sod-cutting increased soil pH, but our data provided no evidence that increase in pH was stronger in deeply decalcified areas. Thus, our hypothesis 1 was only partly supported. Sod-cutting also had consequences on vegetation. Sod-cutting led to less above-ground biomass due to lowered SOM and higher light availability, helping annual and pioneer species to establish. In addition, improved soil pH by sod-cutting allows survival of plant species adapted to base-rich condition, including typical base-rich grey dune pioneer species. However, species richness in sod-cut plots was not higher than in not managed plots, thus our hypothesis 3 was not supported. It may take longer time until species diversity is improved. It is important to realize that in this research we looked at the combined effects of sod cutting and mowing. From management practice it is known that encroachment of *Hippophae rhamnoides* after sod cutting is a threat for the development of calcium carbonate-rich dune grasslands, even in the case of grazing with cattle. When applying sod-cutting, a manager should be ready to carry out additional mowing afterwards, depending on the vegetation development.

Mowing in grazed dune grasslands, on the other hands, had no visible effects on SOM nor soil pH. Thus our hypothesis 2 for mowing was not supported. Also, mowing had

only minor effects on vegetation variables. Compared to never-mown plots, mown plots had slightly lower herb cover, more moss cover, and less woody species. The mowing intensity and duration not mown did not clearly affect vegetation either. From this we conclude that in a dune area with seasonal grazing management mowing has no strong effect in the plant species composition of Grey dunes. However the effects on vegetation structure might affect the species composition of small terrestrial fauna, and possibly also affect soil fauna because of effects on micro-climate.

Summarizing, in order to conserve Grey Dunes, sod-cutting is an effective measure to initiate soil succession on a base rich soil and keep open vegetation structure, especially in moderately decalcified (0-4 dm) areas. However, one cannot expect a positive effect of sod-cutting on species diversity at an intermediate time scale. Also, it should be taken into consideration that species composition may drastically change after sod-cutting, as sod-cutting changes SOM content, soil acidity, light condition, and possibly moisture condition of the site. Mowing hardly changes SOM content and soil pH, even with the intensive mowing regime 'maaizuigcombi', yet it can promote open vegetation structure and suppress woody species. Since mowing is a rather simple measure and can be applied at a small spatial scale, it is a good option to intervene in unwished development of the vegetation (e.g. increased woody species, strong grass encroachment) and keep heterogeneous grassland types on a landscape level. In grazed dune areas it should be applied as an additional measure. Because mowing frequency does not have a clear effect on vegetation, there is little need for regular mowing at the same place in a grazed dune area. The best strategy will be incidental mowing.

3 Effects of mowing, sod-cutting, and shrub removal on grey dunes: meta-analysis

3.1 Introduction

To restore Grey Dune vegetation, measures like reintroduction of grazing, sod cutting, shrub removal, and mowing have been applied during the past two decades. These measures have been stimulated by a national program for ecological restoration (EGM/OBN). For the coming years, more intensive restoration measures such as mowing, sod cutting and shrub removal are planned, because of the implementation of large mitigation program for negative effects of atmospheric N-deposition (Programmatiese Aanpak Stikstof: PAS). These measures are mostly aiming at constraining encroachment of tall grasses and shrubs and promoting short, species-rich dune grasslands. Effectiveness of these measures to reach their nature conservation goals is still uncertain. There has been a number of studies that described the ecological effects of the restoration measures such as grazing, mowing and sod cutting in dune areas. Yet, despite the increasing number of studies and database available, few studies have attempted to aggregate these studies to clarify whether and to what degree these measures bring positive effects on grey dune conservation, and under which conditions the effects can be maximized. Such comprehensive studies are necessary to assess the effectiveness of restoration measures on a broad context and scale up the insights from local studies to implication for nature management on a regional level. To improve the knowledge on the efficiency of restoration measures in Grey Dunes, this study aims at evaluating effectiveness of three types of common restoration measures (mowing, sod cutting and shrub removal) on the natural values of Grey Dunes using existing monitoring dataset of Dutch dune ecosystems. Furthermore, based on the evaluation of the measures on the past, we will provide advice for the choice and design of restoration measures in grey dunes in future.

This study is restricted to the calciumcarbonate-rich coastal dunes of the Renodunal district. Data available from monitoring activities and previous studies of 10 different locations within 4 coastal dune nature conservation areas were used (243 plots). Each location has a different history of mowing, sod cutting, shrub removal, and their combinations. In most locations cattle grazing was a standard measure. Because the monitoring regime is not identical among the dataset and only certain conditions are met for all dataset, we decided to compare treated plots and untreated plots (i.e. control plots) 4-7 years after the start of the measures. See Method section for more details about the choice of data.

Mowing, sod cutting and shrub removal are mainly applied to improve light conditions, reduce nutrients and set back succession to reverse human induced eutrophication effects, such as loss of species, loss of habitat characteristic species, grass and shrub encroachment, loss of bare sand patches and invasion of exotic species [among others, *Houston*, 2008]). Therefore, we selected the following vegetation characteristics as

indicators of effectiveness of the measures: total vegetation cover, vegetation cover of plant functional groups (shrubs, herbs, mosses+lichens), species richness, species saturation (percentage of characteristic Grey Dune plant species found), and the abundances of a commonly encroaching grass species (*Calamagrostis epigejos*) and an invasive moss species (*Campylopus introflexus*). Note that different grass species can be responsible for encroachment in some of the study area (e.g. *E. maritime* in Infiltration area). For sake of simplicity, however, we use *Calamagrostis epigejos* only as an indicator species of grass encroachment. Based on the previous studies [e.g. Houston, 2008], we expect that if a restoration measure is effective the treated plots show the following vegetation characteristics compared to the control (i.e. not treated) plots:

- Lower total vegetation cover (=more bare sand), but not below 85%
- Increase of moss cover, decrease of the herb cover, decrease of shrub cover
- Increase of plant species richness
- Increase in the abundance plant species characteristic for Grey Dunes (i.e. a higher species saturation index);
- Decrease of the abundance of 'encroaching' tall grass *Calamagrostis epigejos* and the invasive moss species *Campylopus introflexus*

The research questions are:

- Do different restoration measures (mowing, sod cutting and shrub removal) have positive effects on the selected vegetation characteristics 4-7 years after the start of the measure?
- Are the effects of restoration measures (mowing/ sod cutting / shrub removal) similar between the studied locations?

Based on information of previous studies summarized by [Smits and Kooijman, 2012a; b] mowing (& grazing) is expected to have a long response time of on average >10 years, whilst sod cutting and shrub removal are already effective in, for example, reducing nutrients immediately or within a few years and eliminating shrubs after immediately. Therefore, after a period of 4-7 years, it is expected to observe a larger effect of sod cutting and shrub removal than of mowing.

3.2 Methods

3.2.1 Data selection

This study's evaluation was based on existing datasets of published and unpublished studies, including monitoring reports and management effect studies produced by Dune water companies (Dunea, PWN, Waternet, and Evides) and research institutes in the Netherlands. Additionally some of our own field data were included. In order to compile data for our meta-analysis, we selected a part of the dataset with the following criteria:

- The studied areas belong to the Renodunal flora district of the Netherlands. The Wadden Islands were excluded from the analysis because of their calciumcarbonate-poor, iron-poor soils and corresponding vegetation types.
- All study areas are within the habitat type 'Grey Dunes', i.e. 'fixed dunes with herbaceous vegetation' (code H2130).
- Locations were only selected if they had plots which were subject to mowing, sod cutting and/or shrub removal restorative measures, and had control plots to compare with the treated plots within these locations. Control plots are defined as

untreated plots that were monitored similarly to the treated plots in the same location.

- Preferably the dataset provide vegetation monitoring data from PQs (permanent plots, also called 'Permanent Quadrats').
- The selected locations had monitoring data from at least one data point several years after treatment, but preferably over multiple years after treatment and with a measurement before the treatment was applied ('0'-state)
- Locations were classified as calciumcarbonate-rich ('kalkrijk', code H2130-A), and calciumcarbonate-poor Grey Dune grasslands ('kalkarm', code H2130-B), so the effect of the soil base status could be included into our evaluation. Communities belonging to the 'Violion caninae' alliance ('heischraal', class 'Nardetea', code H2130-C) did not occur in our datasets.

3.2.2 Study areas

The selected data are from 10 locations within 4 major areas within the: National Park Zuid-Kennemerland (1), Amsterdamse Waterleidingduinen/ Amsterdam Water Supply Dunes (2), Voornes Duin (3), and Middelduinen (4) (Figure 3-1). Additionally, detailed maps of part of the locations at the Amsterdamse Waterleiding Duinen (Amsterdam Water Supply Dunes) and the locations at Voornes Duin can be found in in Appendix. (Figure 6-4, Figure 6-5, Figure 6-6, Figure 6-7, Figure 6-8, Figure 6-9). See Table 3.1 for the overview of the selected datasets.



Figure 3-1. Overview map of the studied areas and locations.

There are some location-dependent discontinuities in the study design, details of execution of the measures, and background characteristics of the soils. See following sections for the detailed information of each location. Some of the important differences can be noted:

- The locations Middelduinen 1 & 2 (Middelduinen), Palmveld + Zegveld (AWD) are different from the other locations because they are deeply decalcified (calciumcarbonate-poor top soil).

- Locations at Voorne (Panweg, Vogelpoel, Middelduinen 2) are additionally treated with grazing measures.
- In Middelduinen 2, treatment was started much more early (20-23 years) before the in this study analyzed year, than in the other locations that fall neatly within the 4-7 year range and the exact starting year is unknown. Also, this location has been treated in the analysis as ‘annual mowing’, while in fact the mowing frequency of the plots within this location is variable, and likely to be lower than once a year (classified as at least mowed 1-5 times in the past 10 years).
- In Middelduinen 2 the type of mowing that has been applied is different from that of other locations. Here vegetation has been ‘chopped off’ (Dutch: ‘chopperen’ or ‘maaizuigcombi’). This is a more drastic form of mowing than regular mowing. This type of mowing also removes the (a part of) the litter layer, and can even create locally bare soil.

3.2.2.1 NP Zuid-Kennemerland

Zuidervlak & Kraansvlak

The locations Zuidervlak and Kraansvlak were previously studied for the years 1991 (‘0’state, before measure), 1993 and 1998 by Kooijman *et al.* [2005] as part of their ‘EGM2’ (OBN) study on the effects of restorative measures in open dry dunes. In Kooijman *et al.* (2005), Zuidervlak is described as a calciferous location, that is grass-encroached by *Ammophila arenaria* and *Calamagrostis epigejos*. Kraansvlak is described as a shallowly decalcified location, grass-encroached by *C. epigejos*. The treatments that were compared for both locations were: mowing once, annual mowing, sod cutting and control, i.e. a grass encroached vegetation, where no measures had been applied (see also Table 3.1 for more information on the study design). Additional grazing measures were not mentioned in the report, but since the plots are not located within an enclosure (as is the case for the location Tilanuspad at AWD, which is also studied by Kooijman *et al.* (2005)), some form of grazing, at least by rabbits, is likely to be present.

For this study, only data of 1998 (7 years after the treatments started) were available to be analyzed.

3.2.2.2 Amsterdamse Waterleiding Duinen (AWD)

Rozenwaterveld & Infiltration Area

The effects of sod cutting at the locations Rozenwaterveld and Infiltration Area were previously studied by Van Til and Kooijman [2007] (1990-2006), and later on by Kuiters [2012] (1990-2010) (see Table 3.1 for monitoring years). Rozenwaterveld is described as a vegetation of Taraxaco-Galietum dry dune grassland, which is grass encroached by *C. epigejos* and also has a high cover of the dwarf shrub *Rosa pimpinellifolia*. The Infiltration area is described as Phleo-Tortuletum ruraliformis dry dune grassland, which is grass encroached by *Elytrigia maritima*. The vegetation types indicate calciumcarbonate-rich soils.

At both locations, plots where ‘shallow’ sod cutting had been applied were compared to control plots, i.e. grass encroached plots without treatment. Shallow sod cutting comprises only the first 5 cm of the top soil, and is an intermediate measure between mowing and ‘regular’ sod cutting (deeper than 5 cm). Apart from ‘sod cut’ and control plots, reference plots of the goal type Grey Dune vegetation, which was not grass-encroached, were available for comparison. However in this study, these were left out

of the data analysis, since reference plots were not used at any of the other study locations. No additional grazing measures were applied, until 2012. From 2012 onwards the locations were grazed by sheep, to compensate for a crash of the rabbit population (personal communications Mark van Til, March 2014).

In this study, data of 2008 (6 years after the treatment started) has been used to compare to the other locations. Additionally, time series data of 1990-2013 has been used to give an impression of the development of vegetation cover and species richness at these locations over time (Figure 6-11, Figure 6-12 in Appendix).

Palmveld + Zegveld

Mourik [2005] previously studied the effects of mowing at the locations Palmveld and Zegveld for the period 1990-2005. These locations have a history of former agricultural use as grazing areas for herded sheep, until mid-19th century. Palmveld and Zegveld are dry valleys, vegetated by closed dune grassland, which is dominated by the tall grasses *Calamagrostis epigejos* or *Agrostis* sp. Their sand soil is rich in humus, and local decalcification depths are described as 'deep' (i.e. a high decalcification depth, with calciumcarbonate-poor sand in the top soil). Treatment of the mowed plots at Palmveld and Zegveld started at the end of the eighties (estimated at 1987) and has been applied approximately once every 2-3 year, in summer. Mowed plots were compared to grass encroached plots without treatment. No additional grazing treatments were applied.

In this study, data of 1993 (6 years after the mowing measures started) has been used to compare to the other locations. Additionally, time series data of 1991-2005 has been used to give an impression of the development of vegetation cover and species richness at these locations over time (Figure 6-10 in Appendix).

Tilanuspad

Tilanuspad was also part of the 'EGM2' study of *Kooijman et al.* [2005] and has been previously studied for the years 1991 ('0'state, before measure), 1993 and 1998. Tilanuspad is described as a calciumcarbonate-rich location (low decalcification depth), with dry dune grasslands that are grass-encroached by *Elymus athericus*. This location lays within an enclosure that keeps out large grazers, and also rabbits. The treatments that were compared for both locations were: mowing once, annual mowing, sod cutting and control, i.e. a grass encroached vegetation, where no measures had been applied.

For this study, only data of 1998 (7 years after the treatments started) was available to be analysed.

3.2.2.3 Voornes Duin

Panweg and Vogelpoel

Panweg and Vogelpoel were previously studied by *Van der Heiden et al.* [2010] (2004-2008 data), and *Dijkstra* [2011] (2007-2010 data) (see Table 3.1 for monitoring years). Vegetation types at these locations were mixed, but the dry areas, that were used in this study, were described as dry nutrient poor, dune grasslands, encroached by tall grasses and shrubs. Soil sample measurements of *Van der Heiden et al.* [2010] showed a well buffered (low decalcification depth) situation for Panweg and Vogelpoel. For Panweg, plots where shrub removal, or a combination of shrub removal and mowing had been applied in 2005, were compared to 'untreated' grass & shrub

encroached controls. All studied plots at Panweg have been additionally grazed by Charolais cattle, seasonally (July-December), since 2006. Also, new shrub shoots were removed each winter.

For Vogelpoel, plots where shrub removal had been applied in 2007, were compared to untreated grass & shrub encroached controls. All studied plots at Vogelpoel have been additionally grazed year round by cattle (Schotse Hooglanders), since June 2008. In this study, data of 2011 (6 and 4 years after the restorative measures started, respectively for Panweg and Vogelpoel) has been used to compare to the other locations. Additionally, time series data of 2005-2011 (Panweg) and 2007-2011 (Vogelpoel), have been used to give an impression of the development of vegetation cover and species richness at these locations over time (Figure 6-13 and Figure 6-14 in Appendix).

3.2.2.4 Middelduinen

Middelduinen 1

Middelduinen 1 has been previously studied as one of the locations within the 'EGM2' research [Kooijman *et al.*, 2005], for the years 1991 ('0'state, before measure), 1993 and 1998. In Kooijman *et al.* [2005], Middelduinen 1 is described as a dry dune grassland, encroached by *Carex arenaria*. This location has an average decalcification depth of 90cm, and is has been grazed until 1972 (which makes it potentially rich in phosphates). In the past the area with the plots have never been fertilized (personal communication Marten Annema). After 1972, no grazing management was applied in the study plots. Reintroduction of grazing by cattle in the Middelduinen was excluded from the plots by a fence. Because of a strong decline of the rabbit population grazing pressure by rabbits was low.

The treatments that were compared for both locations were: mowing once, annual mowing, sod cutting and control, i.e. a grass encroached vegetation, where no measures had been applied.

For this study, similar to the other EGM2 locations, only data of 1998 (7 years after the treatments started) were available to be analyzed.

Middelduinen 2

Middelduinen 2 has been studied only recently, according to 2013/2014 vegetation data, on soil characteristics measured in 2014 in relation to restorative measures (Chapter 2).

At this location grass encroached plots on which a treatment of mowing (variable frequency), or a combination of sod cutting and mowing had been applied, were compared to grass-encroached control plots.). A different type of mowing is applied here than in all other locations: the vegetation has been 'chopped off' (Dutch: 'chopperen'). This is a more drastic form of mowing, which removes also (a part) of the litter layer. However is a more superficial treatment than sod cutting because it does not remove the mineral top soil. All plots were additionally grazed by cattle from early summer to (late) autumn.

The decalcification depth varied, but was not independent from treatment type: sod cut plots had a lower decalcification depth (~20 cm on average) than mowed plots (~40 cm on average for plots that had been mowed 1-5 times over the past 10 years) (Chapter 2). Thickness of the humus-rich mineral layer was on average 5-15cm.

For this study only monitoring data of 2013/2014 was suitable for use, which was approximately 20-23 (!) years after treatment originally started (starting year varied). Mowing plots were selected that were mowed 1-5 times within the past 10 years.

This data set is analysed more intensively in chapter 2. Here the effects of vegetation management on soil properties are also examined.

Table 3.1. Overview of selected datasets, per selected location. This table shows the location codes that are used in the results section. Also an overview is given for each location of the numbers of plots, treatment type, number of plots per treatment, the year the treatment was first applied, and the years that had available data for our study, and if there exist measurements of 'zero-state' (i.e. before the treatment was applied). NA= Not Applicable. PQ = permanent plot.

Area nr.	Area name	Location	Location Code	Number of sites	Plots in PQs	Plots (N)	Plot size (m)	Treatments (number of sites, plots)	Treatment year (start)	Nr. of years studied	Years	Zero?	Study
1	NP Zuid-Kennemerland	Zuidervlak	1_ZDVL	9	Yes	36	2x2	Control (2sites, 8p), Sod cutting (3sites, 12p), Mowing (3 sites, 12p), Mowing 1x (1site, 4p)	1991	1 (1998)	1991, 1993, 1998	yes, 1991	EGM2: Kooijman et al. (2005), OBN onderzoek
1	NP Zuid-Kennemerland	Kraansvlak	1_KRNSVL	9	Yes	36	2x2	Control (2sites, 8p), Sod cutting (3sites, 12p), Mowing (3 sites, 12p), Mowing 1x (1site, 4p)	1991	1 (1998)	1991, 1993, 1998	yes, 1991	EGM2: Kooijman et al. (2005), OBN onderzoek
2	Amsterdamse Waterleiding Duinen	Rozen-waterveld	2_RZNV	5 (plot clusters)	?	20	2.5x 2.5	Reference (5), Control (5), Sod Cutting (10)	2002	7	2002, 2003, 2004, 2006, 2008, 2013	Yes, 2002	Van Til & Kooijman (2007), Kuiters (2012)
2	Amsterdamse Waterleiding Duinen	Infiltration Area	2_INFIL	5 (plot clusters)	No	15	2.5x2.5	Reference (5), Control (5), Sod Cutting (5)	2002	7	2002, 2003, 2004, 2006, 2008, 2013	Yes, 2002	Van Til & Kooijman (2007), Kuiters (2012)
2	Amsterdamse Waterleiding Duinen	Palmveld+ Zegveld	2_PV+ZV	14	No	10	3x3 (2x2, 3x4, 5x5)	Mowing (10), Control (4)	end of 80s	12 (6)	1991-1996, 1998, 1999, 2001, 2005	No	Mourik (2005)
2	Amsterdamse Waterleiding Duinen	Tilanuspad	2_TILP	9	?	36	2x2	Control (2sites, 8p), Sod cutting (3sites, 12p), Mowing (3 sites, 12p), Mowing 1x (1site, 4p)	1991	1 (1998)	1991, 1993, 1998	yes, 1991	EGM2: Kooijman et al. (2005), OBN onderzoek
3	Voornes Duin	Panweg (3.1)	3_PANW	NA	?	12	3x3	Control (only grazed, 6p), Shrub removal (4p), shrub removal + mowing (2p). Additional: grazing (all plots)	2005	5	2005, 2006, 2007, 2008, 2011	yes, 2005	Van der Heijden (2010), Dijkstra (2011)

Area nr.	Area name	Location	Location Code	Number of sites	Plots in PQs	Plots (N)	Plot size (m)	Treatments (number of sites, plots)	Treatment year (start)	Nr. of years studied	Years	Zero?	Study
3	Voornes Duin	Vogelpoel (3.2)	3_VGPL	NA	?	12	3x3	Control (grazed only)(5p), Shrub removal (5p), Mowing (2p). Additional: grazing (all plots)	2007	3	<u>2007</u> , 2008, 2011	yes, 2007	Van der Heiden (2010), Dijkstra (2011)
4	Goeree: Middelduinen	Middel-duinen 1 (4.1)	4_MID1	9	Yes	36	2x2	Control (2sites, 8p), Sod cutting (3sites, 12p), Mowing (3 sites, 12p), Mowing 1x (1site, 4p)	1991	1 (1998)	<u>1991</u> , 1993, 1998	yes, 1991	EGM2: Kooijman et al. (2005), OBN onderzoek
4	Goeree: Middelduinen	Middel-duinen 2 (4.2)	4_MID2	NA	?	28	2x2	Control (9p), Mowing (10p), Sod cutting + Mowing (9p). Mowing frequency was variable for this location and often less than annually. Deviant mowing type: chopping (Dutch: 'chopperen'). Additional: grazing (all plots).	Variable, end of 80s	1 (2013/2014)	2013/2014	No	Chapter 2 of this study

3.2.3 Data analysis

Within locations, treated plots (i.e. plots where one or more restoration measures had been applied) were compared to control plots (CON) that had not been subject to any of these measures. The existing combinations of the restoration measures were: mowing, sod cutting, shrub removal, sod cutting+ mowing, and shrub removal + mowing. Since only a part of the dataset have data from multiple years, and measured years differed from a study to another, we used the data from a single year between 4 and 7 years after treatment application (T4, T5, T6 or T7) for comparison between control and treatment plots. For example when sod cutting had been applied in 2001, 2001 would be T1, 2002 would be T2 and so on. T6 had the best data availability across locations, but if T6 wasn't available T5, T7 or T4 was taken as an alternative.

For each location, average values and standard deviations of the following variables were calculated per treatment for the selected year:

- Vegetation cover: total vegetation cover, shrub cover, herb cover, moss cover
- Species Richness (i.e. the number of species of vascular plants and of mosses+lichens per plot)

Community composition: Saturation index. This is a measure for how well the measured vegetation community matches with the target community ('Grey Dunes'). The species typical for the target community (i.e. defined as species with a frequency of more than 20% in the reference relevée sets for Grey Dunes) are listed in

- Table 6.5 in Appendix.
- Abundances (expressed as cover percentage) of *Calamagrostis epigejos* (native invasive tall grass) and *Campylopus introflexus* (exotic invasive moss), as indicators for unwanted grass or moss encroachment.

Note that plot size is different among dataset, varying from 4m² to 12m².

To express the differences between control and treatment within each location, i.e. 'effect size', log response ratio's (RR). We used RR, instead of percentage change, because RR is approximately normally distributed and therefore statistical inferences such as confidence interval can be easily computed. Moreover, with RR, the positive and negative changes can be more symmetrically expressed (e.g. when treatment plot has a half and double value compared to the control plot, it is expressed as 50% and 200% in percentage change, whereas it is expressed as -0.7 and +0.7 in RR). RR was calculated according to the methods of Lajeunesse [2011], which were adapted from Hedges *et al.* [1999]:

$$RR = \ln(\bar{X}_T / \bar{X}_C)$$

where \bar{X}_T is the average of the treated plots and \bar{X}_C is the average of the control plots.

Furthermore, the variance of RR was calculated as:

$$\hat{\sigma}^2(RR) = \frac{(SD_C)^2}{N_C \bar{X}_C^2} + \frac{(SD_T)^2}{N_T \bar{X}_T^2}$$

where N_C and N_T is the number of control or treated plots, respectively.

The RR values reflect whether the treatment has a positive (RR>0), negative (RR<0), or neutral (RR=0) effect on the variable compared to the control. When a treatment plot has a value 10%, 50%, 150%, or 200% of the control plot, the RR value becomes -2.3, -0.7, 0.4, or 0.7, respectively.

To test if the positive or negative log Response Ratio values were significantly different from zero, i.e. if the effect of a treatment was significant, 95, 99 and 99,9 % confidence intervals of RR were computed by taking the square root of the RR variance, and by multiplying this to the z-standard score that corresponds with the CI:

$$CI = Z \cdot \sqrt{\hat{\sigma}^2(RR)}$$

where z is a constant factor (z=1.690 for 95% CI, z=2.326 for 99% CI, z=2.575 for 99.9% CI).

When 95% CI or 99% CI is above zero, we consider the effect as significantly (p<0.05 or p<0.01, respectively) positive, whereas when CI is below zero, we consider the effect as significantly negative.

For the abundance of *Calamagrostis epigejos* and *Campylopus introflexus*, RR was calculated only when these species were present in both control and treated plots. Since shrub cover values were missing for Zuidervlak, Kraansvlak, Tilanuspad, and Middelduinen 1, and zero for many of the plots in other areas, their response ratios were not calculated and thus excluded from the statistical analysis. Nevertheless, average and standard deviation of all variables for all treatments are shown in Appendix (Table 6-6Error! Reference source not found.). RR are also shown for all treatments in Table 6-7 Error! Reference source not found.of AppendixError! Reference source not found..

3.3 Results

3.3.1 Vegetation cover

Overall, the total vegetation cover was slightly more often reduced than increased in treated plots in comparison to control plots (12 out of the 21 RR values were negative), 4-7 years after treatment (Figure 3-2). The RR values for all treatments ranged between -1.10 (33 % of control) and 0.28 (132 % of control).

Mowing

The effect of mowing on the vegetation cover after 4-7 years, for both once mowed and yearly mowed plots, turns out to be modest, with RR values that never exceeded a ± 0.3 range (i.e. 74 - 135 % of control). The majority of the mowed plots had higher total cover than control: Zuidervlak (once mowed), Kraansvlak, Palmveld+Zegveld, Vogelpoel, Middelduinen 1, Middelduinen 2. Most of these positive effects (4 out of 7) were significant ($p < 0.05$). Only a few mowed plot had less total cover than control (Zuidervlak (mowed annually), Tilanuspad), of which the effect was significant only 1 location ($p < 0.05$).

The effect of yearly mowing (MOW) was stronger than the effect of mowing only once (MOW 1x) at Zuidervlak and Kraansvlak. However, at Tilanuspad the difference was very small, and remarkably, at Middelduinen 1, the effect of mowing once (MOW 1x) was stronger than the effect of yearly mowing (MOW).

Sod cutting

After 4-7 years, total cover was consistently lower in sod cutting (SOD) plots in comparison to controls, being significant ($p < 0.05$) in 4 out of the 6 locations where this treatment was studied. The magnitude of the negative effect was large in Zuidervlak ($RR = -0.67$, $p < 0.05$), Infiltration Area ($RR = -0.85$, $p < 0.05$) and Tilanuspad ($RR = -1.10$, $p < 0.05$), and moderate in Rozenwaterveld ($RR = -0.21$, $p < 0.05$).

At Middelduinen 2, the one location for which a combination of sod cutting and mowing (SOD+MOW) had been applied, total vegetation cover was significantly ($p < 0.05$) lower than the controls ($RR = -0.33$).

Shrub removal

Shrub removal (Panweg, Vogelpoel) had no significant ($p > 0.05$) effect on the total vegetation cover 4-7 years after treatment. It was the case even when combined with mowing (SHRUB+MOW: Panweg). RR values ranged between 0 and -0.2.

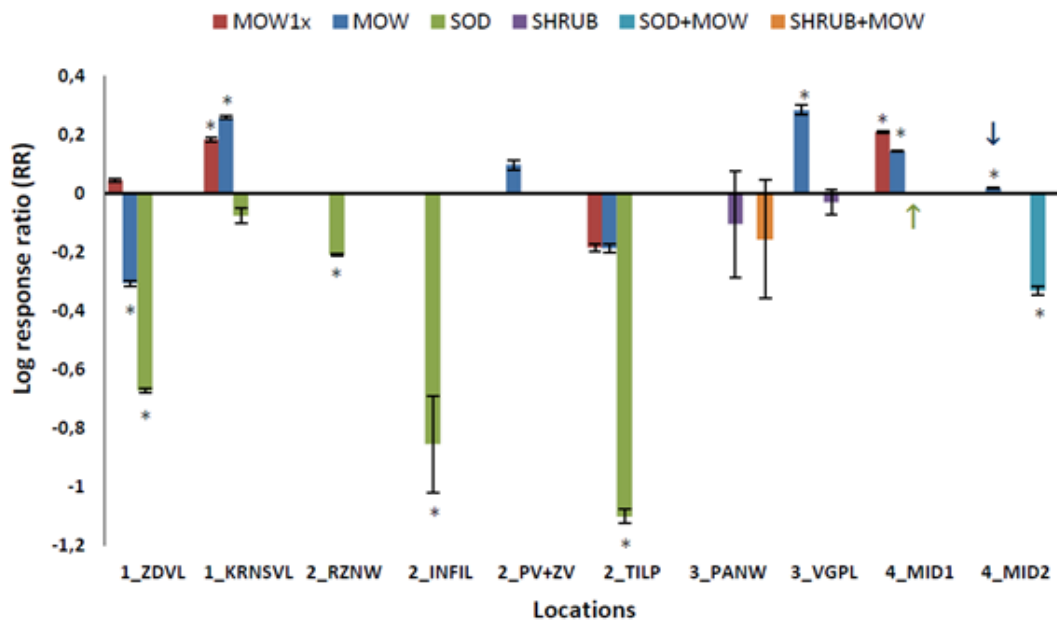


Figure 3-2. Log response ratio (RR) of the total vegetation cover 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

3.3.2 Herb and moss cover

In general, measures had much larger effects on the moss cover than on the herb cover (Figure 3-3, Figure 3-4). RR values vary between -2.50 and 5.27 for moss cover, and between -0.88 and 1.11 for herb cover. Furthermore, the positive effect of the all treatments (MOW1x, MOW, SOD) in Middelduinen1 on moss cover was remarkable.

Mowing

Herb cover responded positively to annual mowing (MOW) in 3 of the 7 study locations (Palmveld+Zegveld, n.s. and Vogelpoel, $p < 0.05$; Kraansvlak, n.s.), but had a negative effect in the other 4 (Zuidervlak, $p < 0.05$; Tilanuspad, $p < 0.05$, Middelduinen2, n.s.; Middelduinen2, n.s.). Mowing once (MOW1x) had either a slightly positive significant ($p < 0.05$) effect on herb cover (Kraansvlak $RR = 0.29$; Middelduinen 1, $RR = 0.20$), or little effect (Zuidervlak $RR = 0.03$, n.s.; Tilanuspad $RR = -0.03$).

Furthermore, annual mowing (MOW) had a positive effect on moss cover in 6 out of 7 locations, being significant in Zuidervlak ($RR = 1.99$), Kraansvlak ($RR = 0.60$), and Middelduinen 1 ($RR = 5.27$). The response of the moss cover to mowing once (MOW1x) were less consistent, with positive values for Zuidervlak ($RR = 0.56$) and Middelduinen 1 ($RR = 2.08$), and a negative value ($RR = -0.93$) for Tilanuspad, but neither of them being significant.

Sod cutting

Sod cutting had consistently a negative effect on herb layer, either sod-cutting alone or combined with mowing. In 7 locations examined, the negative effects were significant

($p < 0.05$) in 6 locations (Zuidervlak $RR = -0.71$, Kraansvlak $RR = -0.28$, Rozenwaterveld $RR = -0.61$, Tilanuspad $RR = -0.88$, Middelduinen 1 $RR = -0.13$, Middelduinen 2 $RR = -0.79$). The effect of sod-cutting on moss layer was not consistent among locations. It was negative in 3 out of 7 locations in which 2 was significant ($p < 0.05$) (Infiltration Area $RR = -1.60$, Tilanuspad $RR = -2.50$), whereas it was positive in 4 out of 7 locations in which 1 was significant (Middelduinen1 $RR = 4.91$).

Shrub removal

Shrub removal (either applied on itself (SHRUB), or combined with mowing (SHRUB+MOW)) had a positive effect on herb cover and a negative effect on moss cover in all 3 locations tested, but none of the effects were significant.

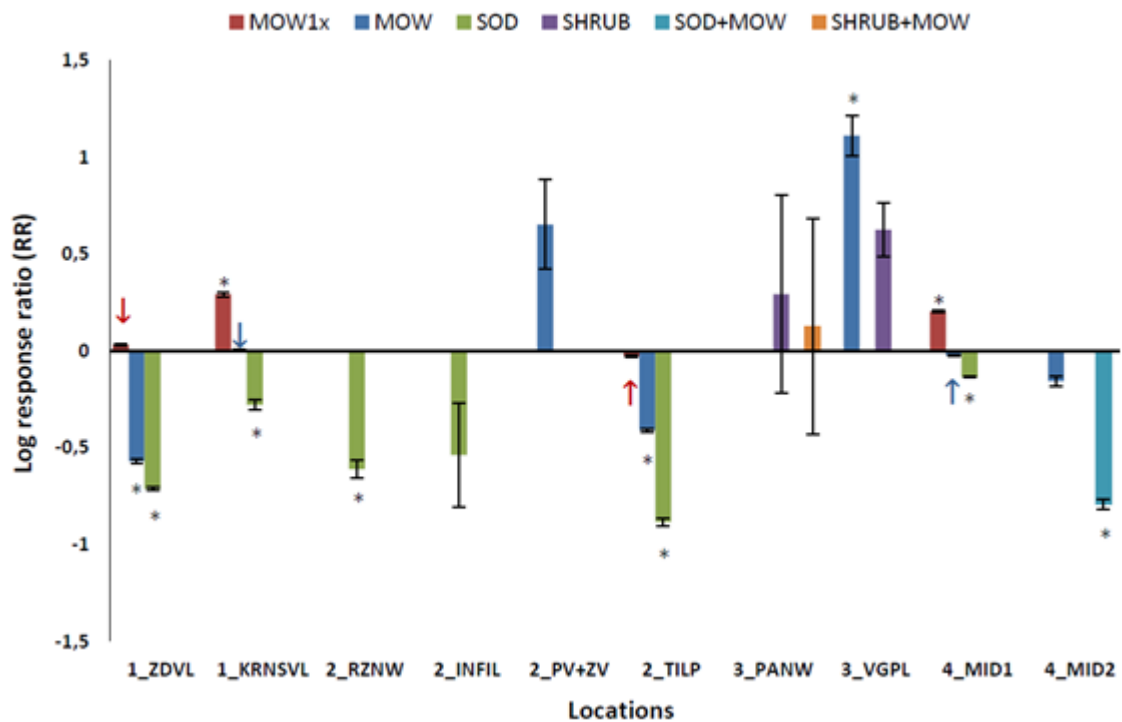


Figure 3-3. Log response ratio (RR) of herb cover, 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

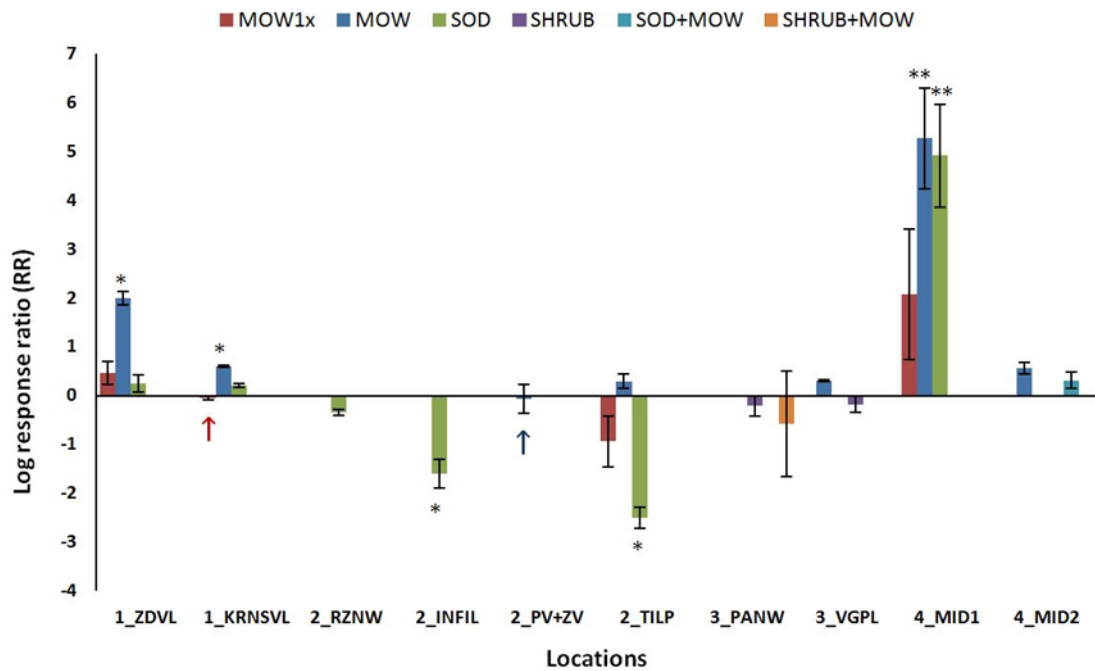


Figure 3-4. Log response ratio (RR) of moss cover, 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

3.3.3 Species richness

In general, species richness was generally higher in treated plots than in control plots, ranging from -0.09 to 0.72. For the few exceptions where species richness was lower, the negative effects were smaller than 0.1 (RR between 0 and -0.1) and not significant.

Mowing

Annual mowing consistently had a positive effect on species richness (RR's between -0.01 and 0.63, with an average of 0.30), except for Middelduinen 2, where RR was negative, but very close to zero (RR=-0.01) and not significant. All positive RR's were significant, except for the RR of Palmveld+Zegveld. Mowing once (MOW 1x) also had a positive effect in all locations, except at Zuidervlak (RR=-0.05, n.s.). However effect size was smaller than for annual mowing, and one positive RR value was not significant (Tilanuspad).

Sod cutting

The effects of sod cutting on species richness were positive in 4 out of 6 locations (RR's between -0.09 and 0.72), and only very slightly negative (RR between 0 and 0.1) for Tilanuspad (RR=-0.09, n.s.) and Infiltration area (RR=-0.05, n.s.). The effect of sod cutting on species richness seems to be similar to that of annual mowing, however average RR is lower (average RR =0.16), exceeding 0.2 only once, for Middelduinen 1 (RR=0.72). Also the positive RR's for Zuidervlak and Rozenwaterveld are not significant.

Shrub removal

Shrub removal also had a positive effect on species richness in the two locations where it was studied (Panweg: $RR=0.23$, Vogelpoel: $RR=0.08$), although none of them were significant ($p>0.05$). In the one location where shrub removal was combined with mowing (SHRUB+MOW), the effect size was negative, but small and not significant (Vogelpoel: $RR=-0.09$).

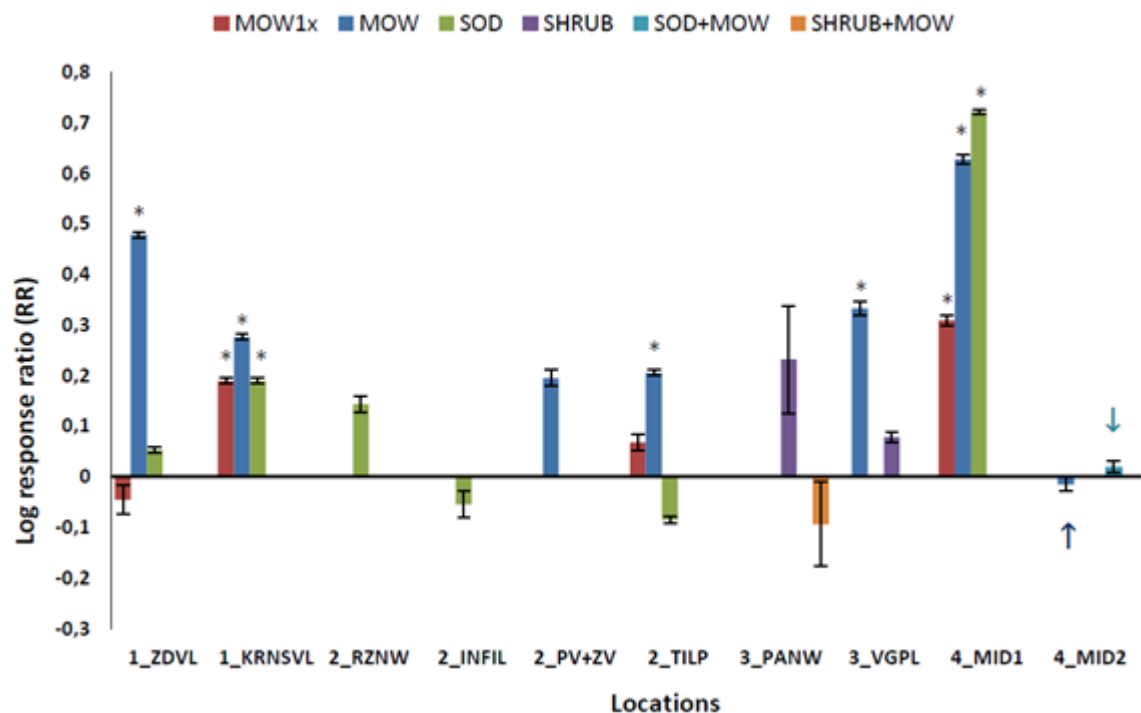


Figure 3-5. Log response ratio (RR) of species richness, 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

3.3.4 Species saturation

Overall the effects of restoration measures on species saturation were more often a positive than a negative after 4-7 years (13 out of 21 RR values were positive, of which 7 were significant). RR values varied from -0,27 to 0,45.

Mowing

Annual mowing (MOW) either had a significantly positive effect on species saturation, or no significant (+/-) effect. Out of the 7 locations where annual mowing was studied, 5 had positive and 2 had negative RR values.

Mowing once (MOW1x) had significant positive response ratio's at 3 out of 4 locations: Zuidervlak ($RR=0,45$), Kraansvlak ($RR=0,24$), and Middelduinen 1 ($RR=0,34$); but for Tilanuspad the RR value was significantly negative ($RR=-0,27$). It is remarkable that mowing once (MOW1x) seemed to have stronger +/- effects on species saturation than

annual mowing or sod cutting at the 3 locations: Zuidervlak, Tilanuspad and Middelduinen 1. This is different from the trends previously observed for other variables, and from what one would expect on the impact of the measure.

Sod cutting

The effect of sod cutting (SOD) varied from significantly positive (2 out of 6 locations), to a negative effect (1 out of 6 locations), or no significant (+/-) effect (3 out of 6 locations). Kraansvlak and Rozenwaterveld had significantly positive RR values (RR=0,31 and RR=0,35, respectively); Infiltration Area had a significantly negative RR value (RR=-0,23); and Zuidervlak, Tilanuspad, and Middelduinen1, had non-significant negative RR values.

The RR value of sod cutting combined with mowing (SOD+MOW) was negative, very close to zero (Middelduinen 2, RR=0,01) and not significant.

Shrub removal

Shrub removal (SHRUB) had positive response ratios for species saturation in the two locations where shrub removal was studied (Panweg, RR=0,26; Vogelpoel, RR=0,26), but these effects were not significant. At Panweg, the RR value of shrub removal combined with mowing (SHRUB+MOW) was negative (RR=-0,09) but not significant.

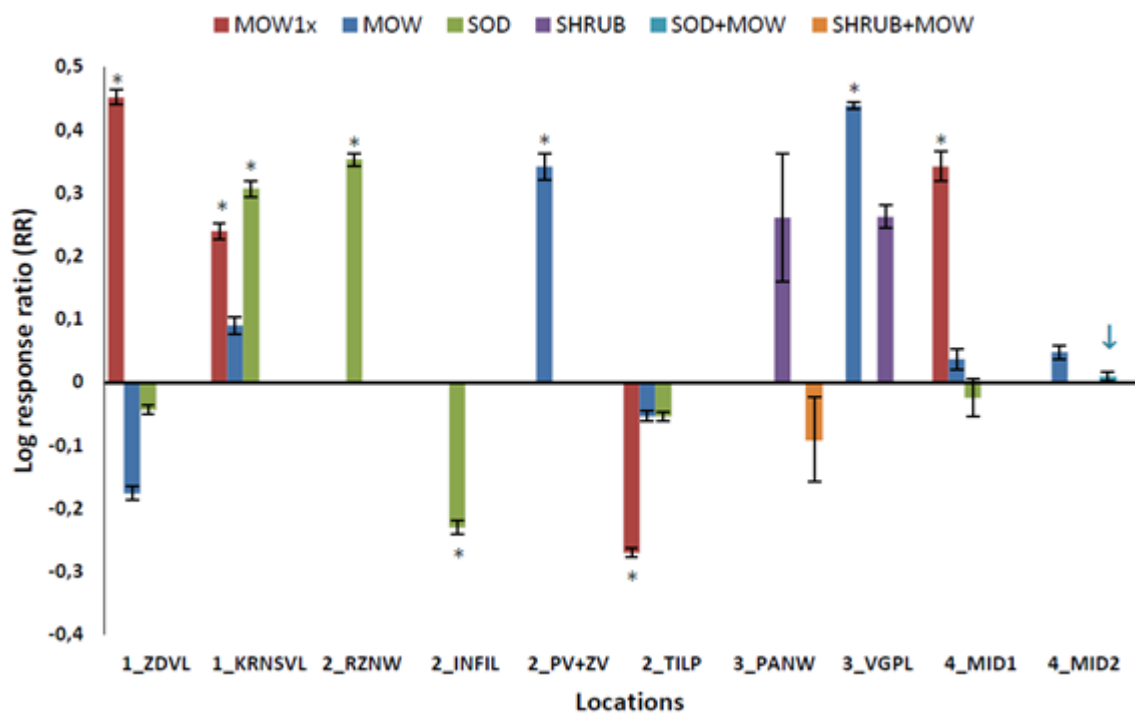


Figure 3-6. Log response ratio (RR) of species saturation (i.e. a measure for how well the measured vegetation community matches with the target community), 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

3.3.5 Development of *Calamagrostis epigejos*

In general, the effect of restoration measures on *C. epigejos* were either significantly negative (6 out of 19 RR values) or not significant (+/-)(13 out of 19 RR values).

Mowing

The effect of annual mowing (MOW) on the abundance of *C. epigejos* was either significantly negative (Zuidervlak; Palmveld+Zegveld), or not significant (+/-/close to zero for Kraansvlak, Tilanuspad, Vogelpoel, Middelduinen1 and Middelduinen 2). The effect of mowing once (MOW1x) could only be studied in 2 locations: Zuidervlak where the effect was significantly negative, and Kraansvlak where it was also negative but not significant.

Sod cutting

Like annual mowing, sod cutting (SOD) influenced the abundance of *C. epigejos* either negatively (Zuidervlak, Kraansvlak, Rozenwaterveld), or had no significant effect (Infiltration Area, Middelduinen 2).

Shrub removal

The effects of shrub removal (SHRUB) were positive but not significant in any of the two locations (Panweg, Vogelpoel). The effect of shrub removal in combination with mowing, as applied at Panweg, was negative but not significant.

3.3.6 Development of *Campylopus introflexus*

Since the invasive moss species *Campylopus introflexus* didn't occur in enough of the studied plots to get comparable averages for the studied locations, figures are not shown. The only locations where comparison between treatment and control plots was possible were Palmveld+Zegveld and Infiltration Area. In Palmveld+Zegveld average abundance of *C. introflexus* was significantly lower in annually mowed (MOW) plots than in controls (RR=-3,42, $p<0,001$). In Infiltration Area *C. introflexus* was significantly lower in sod-cut (SOD) plots than in controls (RR=-2.77, $p<0,001$).

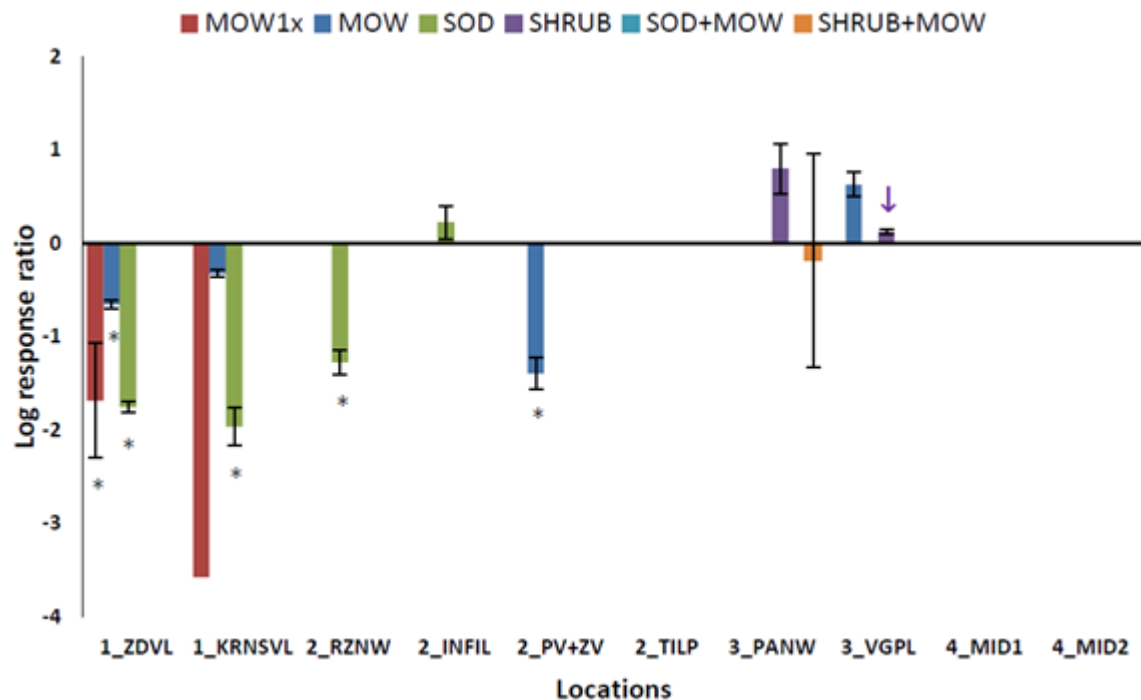


Figure 3-7. Log response ratio (RR) of abundance of *Calamagrostis epigejos*, 4-7 years after treatment. The error bars show the variances of RR. MOW1x= mowed once, MOW= mowed annually, SOD=sod cut, SHRUB= shrubs removed, SOD+MOW= combination of sod cutting and mowing, SHRUB+MOW= combination of shrub removal and mowing. A key to the location codes can be found in Table 3.1. For Kraansvlak, the standard deviation of MOW1x is not shown in an error bar, because it was extremely large (125.57) due to a very large standard deviation value of the control plot compared to their average value. When a bar is very short and difficult to visualize, an arrow of the same colour was added. When a treatment is not measured at a certain location, it shows as a gap instead of a bar on the x-axis. An asterisk (*) or a double asterisk (**) means that the RR was significantly different from zero, with a confidence interval of 95% or 99% respectively.

3.4 Discussion

The main goal of this study was to determine if mowing, sod cutting and shrub removal measures that were applied in degraded, grass and/or shrub encroached Grey Dunes, were generally effective in stimulating development of vegetation characteristics of the 'target-type' Grey Dune habitat, i.e. a low vegetation, without trees and little or no shrubs, consisting of a large variety of (short) grasses, mosses, lichens and herbs [Houston, 2008]. Expectations were that 4-7 years after the treatment was (first) applied total cover would have decreased, and relative moss cover would have increased in comparison to herbs and shrubs. Also, species richness would have become higher, with more characteristic Grey Dune species. Furthermore, abundance of tall grasses such as *C. epigejos* was expected to have decreased, in case they were a problem before application of the measure. Abundances of invasive moss *C. introflexus* may decrease after measures such as mowing, although the effects of measures were not always consistent.

Effects of mowing and sod cutting

As summarized in Table 3.2, mowing, sod cutting, and combined application of sod cutting and mowing had in general 'expected' effects on plant community assembly (i.e. species richness, species saturation, abundance of unwanted species) and therefore

considered effective after 4-7 years. This is in line with previous studies [Annema and Jansen, 1998; Kooijman *et al.*, 2005; Kuiters, 2012; Melis, 2014; Van Til and Kooijman, 2007]. In contrast, the effects of mowing and sod-cutting on vegetation structure (e.g. herb cover, moss cover) were not always consistent with the expectations. The responses of vegetation structure were in general variable among study areas, and the direction of responses was sometimes opposite for mowing and sod-cutting. This could be because the mowing and sod-cutting involve different mechanisms to influence plant community assembly. Mowing has moderate impact in improving light conditions for slow growing plant species, whereas sod-cutting completely re-set plant growth and soil development, strongly influencing soil base status, soil nutrient availability, and plant species composition.

Besides the general positive effects of mowing and sod-cutting on plant communities of grey dune, we observed large variations in effectiveness of these measures among different locations, and some locations showed weak or 'unwanted' responses 4-7 years after the treatment started. A possible explanation is that the conditions of control plot, on which our calculations of effect size (RR) are based, are different among locations and therefore cause a bias in evaluating the management effect. For example, the control plots of Middelduinen 2 have been grazed since the eighties while in Middelduinen 1 the control plots were encroached by grasses because of period without cattle grazing as well as a high N-deposition. This may explain the contrasting effects of mowing for these two datasets (i.e. much better effects of mowing in Middelduinen 1 than in Middelduinen 2). Furthermore, the actual mowing method applied can be different among locations and among times. Mowing has been applied for different practical management objectives. It has been used for removing above ground biomass in dune grasslands with strong grass encroachment (e.g. projects in the nighties). Recently (e.g. recent mowing in Middelduinen 2) it is often applied for preventing development towards shrub and not for counteracting grass encroachment. In the latter case the effects on vegetation structure is limited because the standing crop of the herb layer is already low. Moreover, mown sites in most study area tend to have fertile soil conditions (e.g. relatively wet sites, pastures in the past), This may have caused another bias in comparing mown and not-mown plots.

A slow response time of ecosystems to restoration measures can be another reasonable explanation for weak or unwanted effects of mowing and sod-cutting in some locations. Previous studies showed that after sod cutting, which is considered a more drastic measure than mowing, vegetation cover reduction and re-colonization by pioneer species is observed shortly after the measure is applied, but full establishment of a Grey Dune characteristic vegetation community takes much more time [Grootjans *et al.*, 2002; Kuiters, 2012; Smits and Kooijman, 2012a; b; Van Til and Kooijman, 2007]. The additional time series data for mown sites in Palmveld + Zegveld (Figure 6-10 **Error! Reference source not found.** in Appendix) and sod-cut sites in Rozenwaterveld and Infiltration Area (Figure 6-11 **Error! Reference source not found.** and Figure 6-12 **Error! Reference source not found.** in Appendix) further supports this explanation. These figures indicated that the temporal dynamics of total cover and species richness did not differ much between control and mowed plots, whereas they did differ between control and sod-cut plots. The recovery of vegetation cover in sod-cut plots takes place even after a decade, and species richness keeps changing in sod-cut sites (at least in Rozenwaterveld) after a decade too. In addition, impacts of the measures on soil (e.g. the soil base status) may also play an important role in determining the temporal dynamics of species richness. Sod-cutting is expected to have immediate effects on soil organic matter content and soil acidity, whereas mowing would have only indirect

effects on soil. Since top soil pH has a strong effect on species richness of dry dune grasslands [Aggenbach *et al.*, 2013], soil development and concomitant changes soil acidity in after sod-cutting will influence species richness. The effect of restoration measures on top soil pH and soil organic matter accumulation is analysed in chapter 2 for the dataset of Middelduinen 2.

Effects of shrub removal

Shrub removal (as such or in combination with mowing) did not show any significant responses for any of the variables 4-7 years after the treatment started. Possible explanations are again that the monitoring data were collected too shortly after treatment, and thus more research on the long run may provide significant results. This explanation, however, is not clearly supported by the time series data of Panweg and Vogelpoel area (Figure 6-13 **Error! Reference source not found.** and Figure 6-14 **Error! Reference source not found.** in Appendix). These figures show that species richness keeps increasing in shrub-removed plots, but it was also the case in control plots. Thus, the increase in species richness after shrub removal may merely due to the development of the vegetation by reintroduced grazing management in all plots of this area after a long period of no vegetation management, rather than due to the local treatment effect of shrub removal.

Although not statistically significant, it is worth mentioning that shrub removal induced reverse effects for restoration in some locations (e.g. reduced species richness and saturation index after shrub removal + mowing treatment, and increased *C. epigejos* abundance after shrub removal) (Table 3.2). This may be because shrub removal improved light conditions and therefore (at least for a certain time period) promoted growth of tall grasses like *C. epigejos*. In addition, shrub removal may increase nutrient availability by enhancing soil decomposition (due to higher litter input and increased radiation to soil), which may favour eutrophic grass species too. Our time series data for shrub removal is limited, spanning only to 6 years. More data on shrub-removed sites on a longer time scale will be needed in order to obtain a broader picture of the effects of shrub removal in Grey Dunes.

General

The effects of restoration measures could strongly depends on the background conditions of the area, such as decalcification depth, presence of grazing animals, hydrological conditions, and the 'degradedness' of the vegetation before the treatment took place. We could not quantitatively test these confounding factors in this study. Nevertheless, it is remarkable that we observed consistent effects for most of the measures despite the variety of background conditions of the study areas. To better understand the mechanisms of the effects and make suggestions for restoration in a broader context, it is necessary to explicitly include these confounding factors in future analysis. Moreover it is important to examine the long term effects of sod cutting and shrub removal.

Effects of rabbits

Another phenomena worth to mentioning is the development during 11 years in the control plots of the Infiltration area. Here a strong change in vegetation structure and species richness ocured. The herb cover decreased, while the moss cover increased. The number of vascular and moss species increased (Figure 6-11 and Figure 6-12 in Appendix 6.2). This development was caused by a strong recovery of the local rabbit population, what converted a rough vegetation into a short grassland (pers. comm. Mark van Til), and improved the light conditions. This event illustrates that an increase

of grazing pressure by rabbits can have a strong effect comparable to local management of the vegetation.

Table 3.2. Summary of the effects of restoration measures on grey dunes after 4-7 years per studied variable. Results for abundance of *C. introflexus* are not shown due to limited number of plots examined. '+' = significant results were all positive. '-' = significant results were all negative. '+-' = significant results were found to be both positive and negative. '+(-)' or '(+)-' = the majority of the significant results is positive or negative, respectively. 'n.s.' = none of the results were significant, but trend directions are still shown as '+' (positive) or '-' (negative). 'NA' = no results available because of lack of occurrence of *C. epigejos* in control and/or treated plots.

Measure	Total cover	Herb cover	Moss cover	Species richness	Saturation index	Abundance of <i>C. epigejos</i>
General expectation	-	-(+)	+	+	+	-
Mowing	+ (-)	+ -	+	+	+(-)	-
Sod cutting	-	-	-(+)	+	+(-)	-
Sod cutting + Mowing	-	-	+ n.s.	+ n.s.	+ n.s.	NA
Shrub removal	- n.s.	+ n.s.	- n.s.	+ n.s.	+ n.s.	+ n.s.
Shrub removal + Mowing	- n.s.	+ n.s.	- n.s.	- n.s.	- n.s.	- n.s.

3.5 Conclusions and implications

Sod cutting is a fast and effective measure to reduce vegetation cover, and in the majority of cases it increased plant species richness and occurrence of characteristic species for Grey Dunes. However, after sod cutting is applied, recovery of the target vegetation can take a relatively long time (longer than the 4-7 years studied here). Although not studied in this meta-analysis, the impacts of sod-cutting on soils (e.g. base status, organic matter and nutrient availability, acidity) can also be drastic and remain for a long term. Thus, in order to evaluate the effectiveness of sod-cutting, long-term effects of sod-cutting need to be carefully monitored.

Based on this study, a good alternative measure would be mowing, because mowing turns out to be often just as effective as sod cutting in reaching a decreased (= more open) vegetation cover and suppressing grass encroachment. Moreover, mowing shows more positive effects in the vegetation (species richness, saturation index) than sod cutting in this study at 4-7 years after treatment. Mowing frequency can be adapted to the local state of the grassland: frequent mowing (once in 1-3 year) for grasslands with strong grass and shrub encroachment, and less frequent when the vegetation develops fast to a low and relatively open herb layer, as suggested by [Oosterbaan *et al.*, 2008]. At locations with low shrub encroachment and strong litter accumulation 'chopperen' is good option.

In line with the above-mentioned implications, it is suggested that less deep forms of sod cutting ('shallow sod cutting', only 5 cm depth from top soil) is more suitable than deep sod cutting, as far as the effects on a short (<10 years) time scale are concerned. Such forms of sod cutting will allow shorter recovery time of the characteristic vegetation [Kooijman *et al.*, 2005; Kuiters, 2012] and soil bacteria [Beije *et al.*, 2011].

However, some studies have reported shallow sod cutting to be less sustainable than deep sod cutting on a longer term (>10 years), and the shallow sod cutting may even enhance encroachment of tall grass and/or shrub if seed banks of these species stay partially intact at the 'new' soil surface [Jansen *et al.*, 2012; Smits *et al.*, 2012]. Thus, the depth of the sod-cutting should be chosen carefully, by taking specific goal and conditions of the site into consideration.

Whether a Grey Dunes will successfully be restored after restoration measures seems to largely depend on specific conditions of the location. Therefore, it is important to understand the underlying processes which regulate the development of Grey Dunes and factors that influence the processes. Potential factors are decalcification depth, soil pH profile, amount of litter, and the depth of the humus profile. Depth of sod cutting can interact with these factors. Additionally the spatial scale of sod cutting may affect the colonization rates of soil biota and plant species, and it is therefore important to determine the success of the measures on a large spatial scale. Knowledge on these issues is urgently needed to properly design the restoration measures on a large scale in near future under the frame work of Programmatische Aanpak Stikstof.

Shrub removal effects cannot be expected to be fully measurable after 4-7 years and needs a longer monitoring time span to be adequately analyzed. Also, data on locations where shrub removal had been applied were scarce. Therefore, more research on this measure is recommended.

Other recommendations based on this study are:

- To combine the different positive effects caused by different restoration measures, a mosaic of measures may be best practice;
- Data on thickness of the litter and humus layer, calciumcarbonate- and pH-profile and nutrient availability in soil need to be collected more consistently in addition to vegetation surveys, in order to be able to better link this data in the future and make a more complete 'ecosystem-approach' evaluation of restoration measures. The same data need to be collected for target fauna communities. Now these variables are often monitored separately, which makes large-scale data comparison very difficult.
- The impact of restoration measures on invasive species, such as *Rosa rugosa*, *Prunus serotina* and *Campylopus introflexus* needs to be studied separately, with comparisons between control and treated plots which both have observed (and possibly equal) occurrence of this species. This can be a selection criterion for selecting plots from the existing monitoring data, or needs to be implemented in the design of future field studies.

4 Effects of drift sand from small-scale blowouts on soil and vegetation in Luchterduinen

4.1 Introduction

Blowouts form an important element of dunes which drive and maintain the dynamic development of dune ecosystems. In Dutch dune ecosystems, small-scale blowouts promote local disturbances of soils and therefore contribute to maintaining different successional stages of dunes and conserving high biodiversity of dune ecosystems. On top of that, drift sands originated from blowouts can also have a strong influence on adjacent vegetation, especially stabilized, closed grasslands on old soils. The influence of drift sands can extend on a large spatial scale, if sand is deposited in dune grasslands by long distance transport. In dune zones without or with shallow decalcification, blowouts usually contain calciumcarbonate-rich substrate. Therefore the sedimentation of calciumcarbonate-rich drift sand raises the soil base status and pH, especially in decalcified and acidified (i.e. more deeply decalcified) areas. This effect on soil base status may also have a positive effect on biodiversity of plant and fauna community.

However, little is known about such positive effects of blowouts and drift sands on the soil chemistry and vegetation of old dune grasslands. Most of the existing studies on blowouts aimed at understanding the geomorphological effects of large blowouts [Hugenholtz and Wolfe, 2009; Jungerius *et al.*, 1981; Pease and Gares, 2013] or geochemical effects of sand nourishments by blowouts [Stuyfzand *et al.*, 2012], whereas ecological studies on the effects of small-scale blowouts are scarce. In foredunes near the coast, several studies investigated the effects of aeolian activity on dune vegetation. For example, Ten Haaf [2007] monitored the vegetation development at the Kerf and found a transition of acidified dune grassland into calciumcarbonate rich dune grassland caused by sand deposition. A similar effect was reported for the Noorderpan [Ten Haaf, 2007]. Also, Ketner-Oostra [2006] found that lichen species were promoted in *Violo-Corynephretum* vegetation when deposition of base rich sand occurred. Arens *et al.* [2009a] give an overview of effects of aeolian activity in more details, including those on mycoflora and fauna. These positive effects of aeolian activity observed in coastal foredunes indicate that drift sand from small-scale blowouts will also have similar positive effects on dune ecosystems, yet it has never been clarified.

Despite our limited knowledge on the effects of blowouts, artificial creation of blowouts has often been discussed as an optional restoration measure in coastal dunes, and also has been applied in several dune areas. Moreover, activating secondary blowouts will be an important measure in coming years in order to improve the quality of Grey Dunes and to counteract negative effects of a high atmospheric N-deposition. For many coastal dune areas this is planned in the framework of 'Programmatistische Aanpak Stikstof' (PAS). To make an effective plan of activation of secondary blowouts, we need

better knowledge on ecological effects of drift sand as well as their spatial and temporal dynamics. Moreover, to properly evaluate the effectiveness and extent of the impact of the blowouts on dune grasslands, we also need more process-based knowledge on how blowouts affect the surrounding soil and vegetation. It is expected that the effects of drift sand differ depending on a number of factors, such as chemical composition of the sand in blowouts, magnitude of decalcification in the areas, base chemistry of the local top soils, and size of the blowout.

This study aims at understanding the effects of drift sand from small-scale blowouts on soil properties and vegetation in existing dry dune grasslands. For that aim, we conducted a field survey in 4 different blowouts in Luchterduinen differing in decalcification depth of the surrounding area. We examined: 1) the effects of drift sand on soil base chemistry and plant community in old grasslands adjacent to blowouts, and 2) the spatial distribution of these effects, in particular in relation to the prevailing wind direction. Furthermore, we examined if the magnitude of the effects of a blowhole is depending on the calcium carbonate content of the blowhole as well as the background calcium carbonate content (i.e. degree of decalcification in the background area). We selected blowouts which have been and still are active for several decades, so that we exclude as much as possible the effect of different life span of aeolian activities.

4.2 Methods

4.2.1 Sampling location

The field survey was conducted in four blowouts in the coastal dune area Luchterduinen, the Netherlands (Figure 4-1) (Photo 1). The blowouts have contrasting calcium carbonate richness, size, and levels of decalcification depth in the surrounding areas (Table 4.1). The aerial photos of 1979, 1990, 2001, 2006, and 2011 were analysed to ensure that all blowouts existed for more than 35 years (i.e. from 1979 to 2014) with a diameter of more than 20 m at any time slice, and were surrounded by grasslands during the past 35 years (Figure 4-2). Also, none of the blowouts was close to the coast (>2km) or other big blowouts in the direction of prevailing wind (>150m). In the field, we also checked that the surrounding areas of the selected blowholes were not on a steep slope and not disturbed by animals (particularly rabbits). The density of ants species which live in the soil and transport soil to the surface, was not a criterion. At each blowhole, we established two transects: one runs parallel to the prevailing wind direction (i.e. south-west), the other runs perpendicular to this (i.e. north-west to south-east) (Figure 4-2.). Since we are primarily interested in the effect of sand deposition on dune grasslands, we adjusted the exact direction of the transect in the field so as not to run across shrubs or woodlands. We stretched the transects up to the point where the influence of the blowout becomes not evident in terms of visible recent sand deposits in the soil profile (i.e. no fresh sand layer on a humus layer) and a normal pH-profile of the soil (i.e. no elevated pH-values in the top soil).



Figure 4-1. Locations of four blowouts (1, 3, 5, 9) in Luchterduinen, overlaid on the aerial photo of 2011.

Table 4.1. Characteristics of four sampling locations around a blowout

Blowout number	Dune type	Size of blowout	Calciumcarbonate-richness of blowout	Decalcification of surrounding area (cm below surface)
1	Inner dune	large	rich	30-60
3	Inner dune	medium	poor	40-80
5	Middle dune	small	rich	20-25
9	Middle dune	medium	rich	10-25

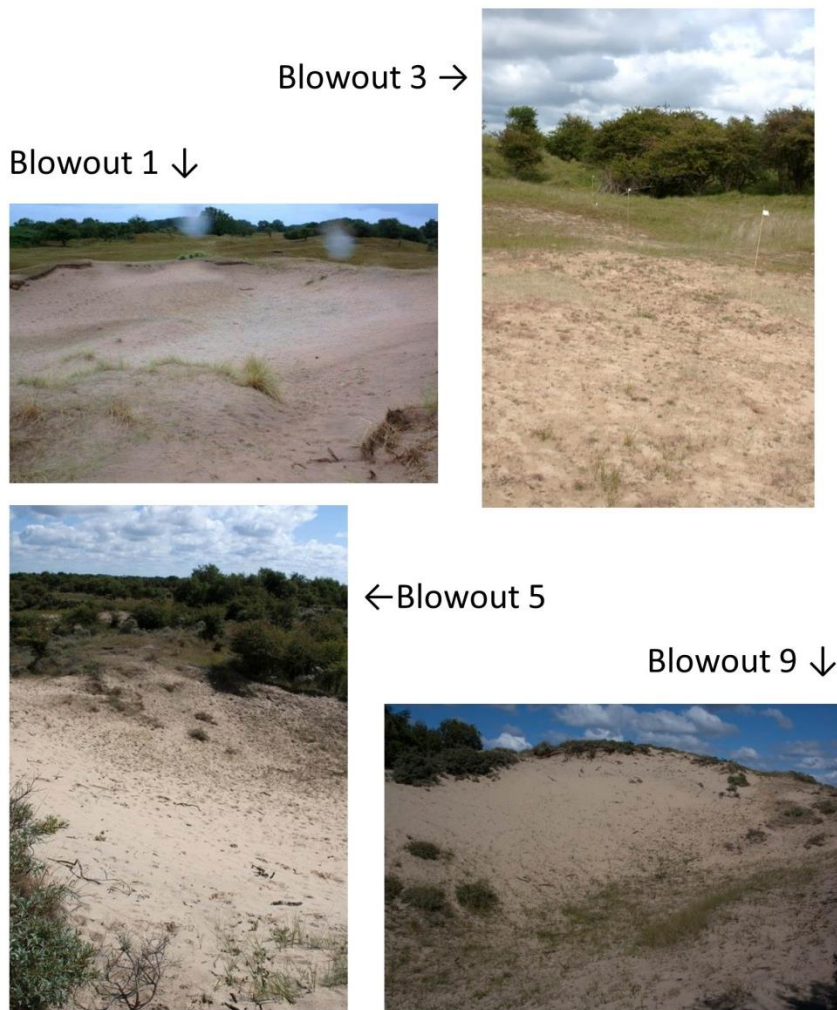
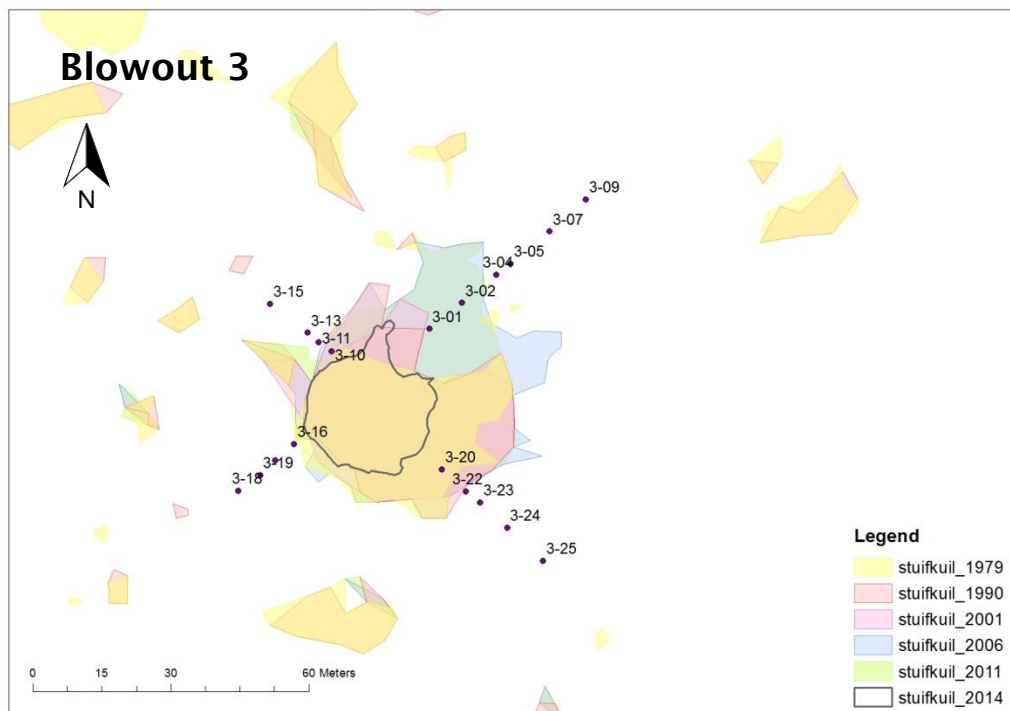
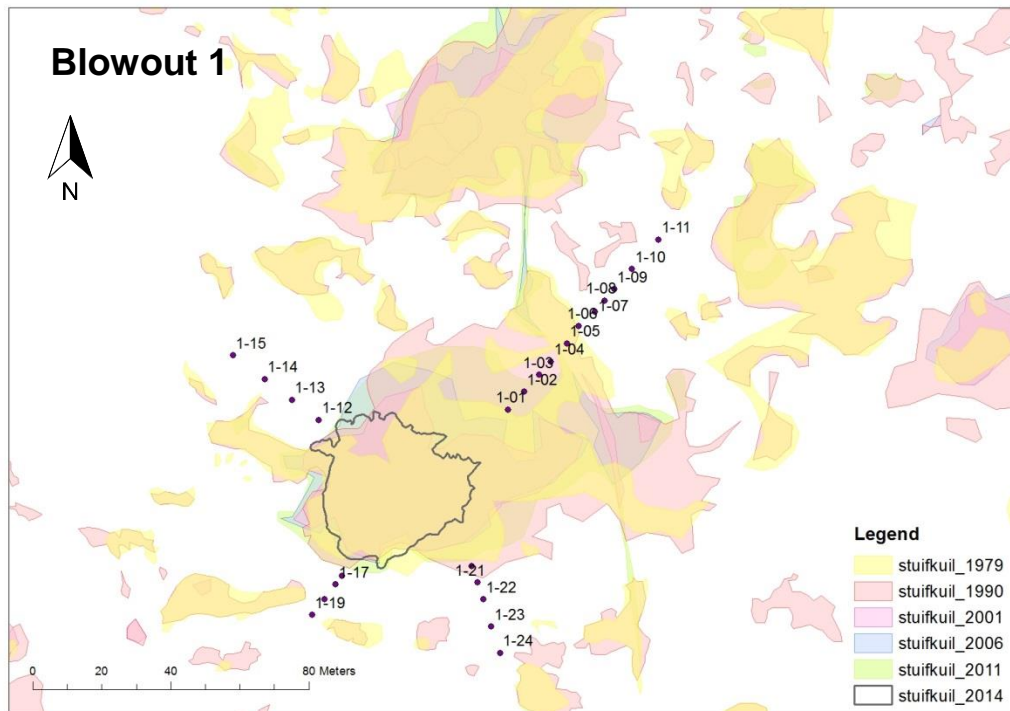


Photo 1: Investigated blowouts in the Luchterduinen. Pictures were taken in June-July 2014 in north-east direction where most of the sand is deposited. Top left: blowout 1, top right: blowout 3, below left: blowout 5, below right: blowout 9.



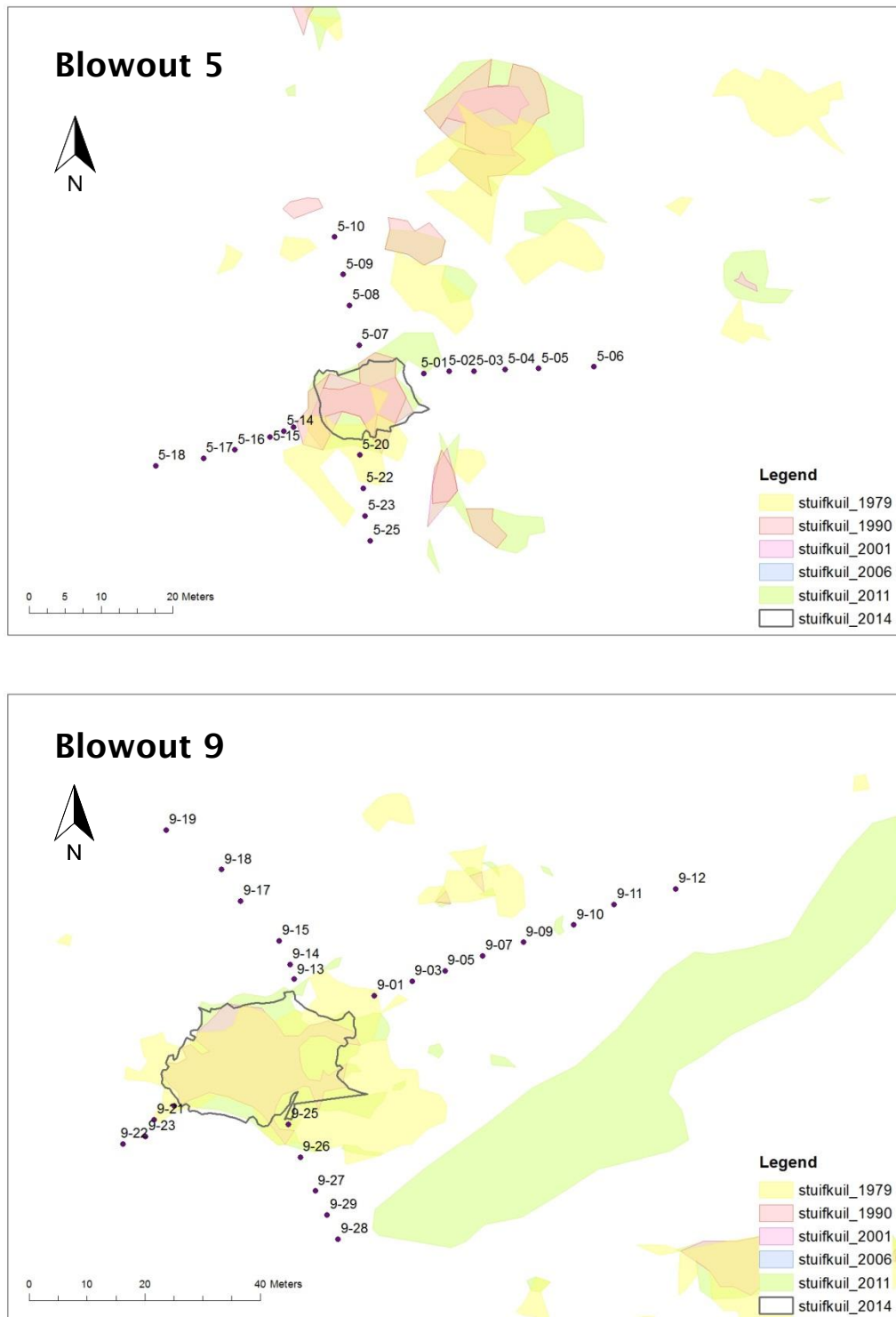


Figure 4-2. Spatial development of the four blowouts in the last ca. 40 years. The boundaries of patches with white sand (no or sparse vegetation) were detected on the aerial photos of 1979, 1990, 2001, 2006, and 2011. The extents of the deflation area of the blowouts at the sampling time of this study (2014), measured in the field with GPS, are also shown in black lines. Dots are the soil profile sampling points of this study, on SW-NE and NW-SE transect.

4.2.2 Soil sampling

Between May and July 2014, on each transect, we sampled soil profiles down to ca. 30cm depth with a 'humushapper' at the interval of ca. 3-10 m between sampling points (see Figure 4-3 **Error! Reference source not found.** for the layout of the sampling points). For each soil layer, we recorded the soil type (S: living moss, L: dead moss, F: fresh to slightly decomposed litter, C: organic-poor sand, AC sand with moderate amount of organic matter, Ah: organic-rich sand). We also estimated calcium carbonate richness by dropping 10% HCl solution. When dry, the soil was wetted with MilliQ (very mineral poor water). We distinguish three classes of calcium carbonate richness: K0: no fizzing, K1: weak fizzing visible or audible, K2: strong fizzing visible. With this method, decalcification depths up to 120 cm were obtained for each sub location by using both the hummushapper profile and as well using a Edelman soil auger. The decalcification depth was defined as the depth of the top of the first layer with class K1 or K2. Soil pH was measured *in situ* pH with a pH meter (Hanna HI99121). Depth of the pH measurements was adjusted to the humus and calcium carbonate profile.

On the north-east transect of each blowout, we selected four points for extra soil measurements. Here soil samples were taken down to 15cm depth, for each of 3 layers. The depths of the 3 layers were location-specific, determined by the soil horizons described above. For each soil layer, ca. 100g fresh soil was sampled and kept in fridge for chemical analysis in the lab. Another set of soil samples was taken for the same 3 layers with a metal ring (diameter 67.3mm) for bulk density estimate. In addition, within the deflation area of each blowout, soil samples were taken from 4 points (one in each quadrant; Figure 4-3) for the depth of 0-5cm, 10-15cm, 25-35cm, and 40-50cm. The 4 soil samples of each depth level were mixed and stored in fridge for chemical analysis in the lab. Similar 4 soil samples were taken with the metal ring (diameter 67.3mm) for bulk density estimate for the depth of 0-5cm, 10-15cm, 25-35cm, and 40-50cm.

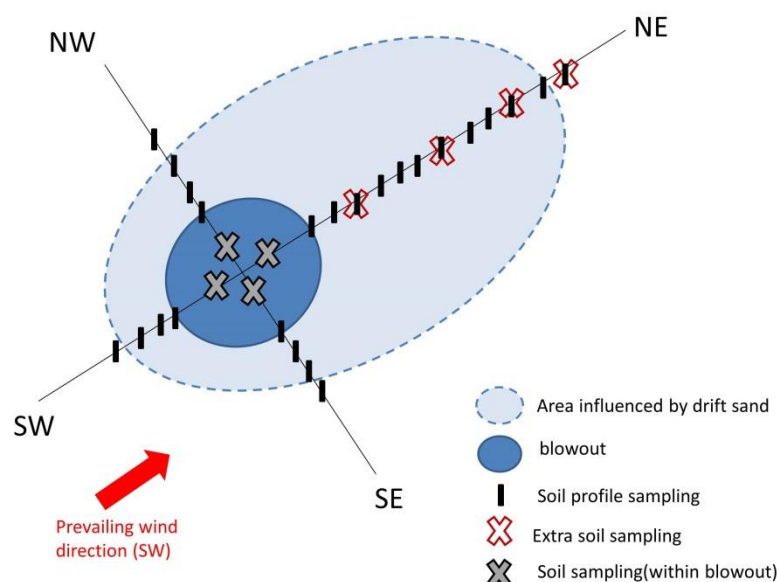


Figure 4-3. Layout of soil sampling points.

4.2.3 Soil analysis

The soil samples for bulk density estimates were weighed after drying at 65° C for 48 hours. The soil samples for chemical analysis were homogenized after removal of visible roots and living mosses were removed and sieved with a 2 mm sieve, and split into subsamples for further analysis. With sieving no shell fragments were removed. pH_KCl and pH_H₂O were measured with a pH meter (Hanna H199121) after mixing ca. 10g of the field moist soil with 25 ml 1M KCl solution and with 25 ml demineralized water, respectively, and shaking for two hours. Moisture content of soil was determined after drying at 105 ° C for 48 hours. Oven-dry soil sub-samples (48 h at 70 °C) were homogenized and ground in liquid N. C and N contents (%) were determined with a Carlo Erba NA1500 elemental analyser (Thermo Fisher Scientific). 200 mg of soil was digested with 4 mL HNO₃ (65%) and 1 mL H₂O₂ (30%) using a microwave labstation (Milestone srl) to measure total Al, Ca, Fe, K, Mg, Mn, Na, P, S, Si, Zn with ICP. Exchangeable cations were determined by extracting ca. 5.5 g of field moist soil with 200 ml 0.2M SrCl₂ solution and shaking for 2 hours. The extracts were filtered and a part of the extract was acidified with 65 % HNO₃ (in ratio of 1:300 in volume). Concentrations of NH₄ in the unacidified extract were determined colorimetrically with FSA, and concentrations of other cations (Al, Ca, Fe, K, Mg, Mn, Na, P, S, Si, Zn) in the acidified extract were determined with ICP. For the estimate of SOM content, soil was first dried at 65° C for 48 hours and sifted with a 2mm sieve, and then thoroughly ground in a mortar. 2.5g of the ground soil was heated in an oven at 105°C for 2 hours and at 550°C for 4 hours. After cooling in a desiccator, dry mass was again measured. soil organic matter content (SOM, %) content was then calculated according to *Stuyfzand et al.* [2012]:

$$\text{SOM} = 100 \times (\text{dry mass}_{105^\circ\text{C}} - \text{dry mass}_{550^\circ\text{C}}) / \text{dry mass}_{105^\circ\text{C}} - 0.07 \times L$$

where $\text{dry mass}_{X^\circ\text{C}}$ is dry weight at temperature X°C (g), L is the clay content (%).

The term with L is used for correction of release of strongly bound water at high temperatures.

Calciumcarbonate content was expressed as percentage of CaCO₃ (% dw). CaCO₃ was estimated as total Ca minus exchangeable Ca. We did not calculate dolomite content (MgCO₃) because in dune sands MgCO₃ is nearly absent [*Stuyfzand*, 1993]

Base saturation BS (meq/meq) was calculated as:

$$\text{BS} = (\text{Ca}_{\text{exch}} + \text{Mg}_{\text{exch}} + \text{Na}_{\text{exch}} + \text{K}_{\text{exch}}) / \text{CEC}_{\text{cal}}$$

where X_{exch} is exchangeable cation X (meq/kg), and CEC_{cal} is the cation exchange capacity calculated according to *Scheffer and Schachtschabel* [2002]:

$$\text{CEC}_{\text{cal}} = 5.6 \cdot L + 5.1 \cdot (\text{pH}_{\text{H}_2\text{O}} - 1.16) \cdot 0.5 \cdot \text{SOM}$$

When the value of BS was > 1, the value was converted to 1. Values above 1 are caused by dissolution of CaCO₃ by CO₂ in the SrCl₂-extract.

Also a proxy for base saturation (BC/SOM) was calculated by the ratio of the sum of exchangeable base cations (BC) divided by soil organic matter (SOM). This ratio avoids difficulties in estimates of CEC_{cal} in the calculation of BS.

4.2.4 Vegetation recording

In the beginning of June 2014 vegetation was recorded in the north-east transects for all blowouts. A plot of 1m² was established next to the soil profile sampling points, and abundance of vascular plants, mosses, and lichens was recorded with Londo scale.

4.2.5 Mapping boundaries

The boundaries of blowouts were mapped in the field using RTK-GPS (accuracy ± 0.02 - 0.03 m). In addition, we classified the soil profile sampling points into three categories of degree of influence by the blowout (i.e. "strongly influenced", "weakly influenced", or "hardly influenced"). A point was classified as "strongly influenced" if a calciumcarbonate-rich sand deposit on the top surface is evident in the calciumcarbonate profile, and/or the pH of the top layer(s) is distinctly higher (i.e. > 1 pH unit) than the layers underneath. A point was classified as "weakly influenced" if the pH of the top layer(s) is 0.3 to 1.0 pH unit higher than the layers underneath. Subsequently, we roughly drew the boundary of the zones with drift sand influence by connecting the three transition points (from strongly to weakly influenced point, and from weakly to hardly influenced point) on the transects. Size of each zone was calculated on GIS. Note that the end point of some transects is still weakly influenced, indicating that our estimates of weakly-influenced zones can be underestimated.

4.3 Results

4.3.1 Soil profiles on transects

The changes in soil characteristics (pH, calciumcarbonate content, and soil layer type) are shown for the two transects (i.e. SW-NE and NW-SE transects) of blowout 1 in relation to the distance from the blowout (Figure 4-4). Soil pH of bordering areas of the blowout was higher than background pH (Figure 4-4 top). The closer the point was to the blowout, the deeper in the soil profile the blowout had an influence on pH. The influence of the blowout on soil pH was strongest and reached farthest on the NE transect. Discrete calciumcarbonate-rich layers were present in the top of the soil profile at several spots around the blowout (Figure 4-4 middle), indicating strong deposition of drift sand in these areas in the recent past. Organic soil layers of several points close to the blowout were covered by relatively a thick humus-poor sand layer (Figure 4-4 bottom), implying strong deposition of sand near the deflation zone. Similar patterns were observed in soils around blowout 3 (Figure 4-5).

Blowout 5 (Figure 4-6) and blowout 9 (Figure 4-7) had a much shallower decalcification depth. Consequently, soil pH was much higher in these areas, yet the patterns of soil pH around the blowout were similar among all blowouts.

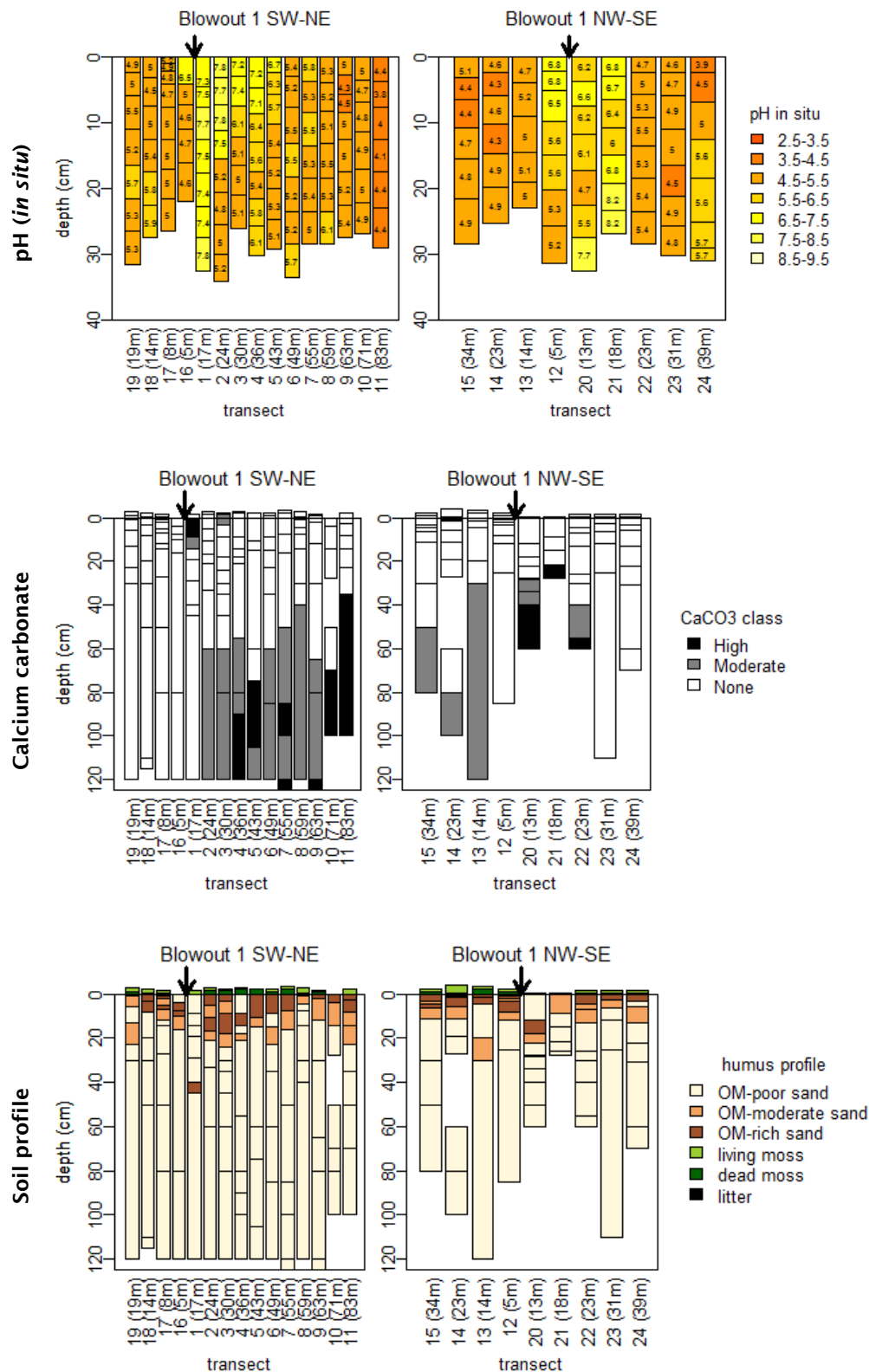


Figure 4-4. In-situ soil pH, calcium carbonate class (tested with HCl dropping), and soil types of soil profile sampling points on SW-NE transect (left) and NW-SE transect (right) of blowout 1. The position of blowout is shown with arrows. The distance between the blowout and the sampled site is shown in brackets.

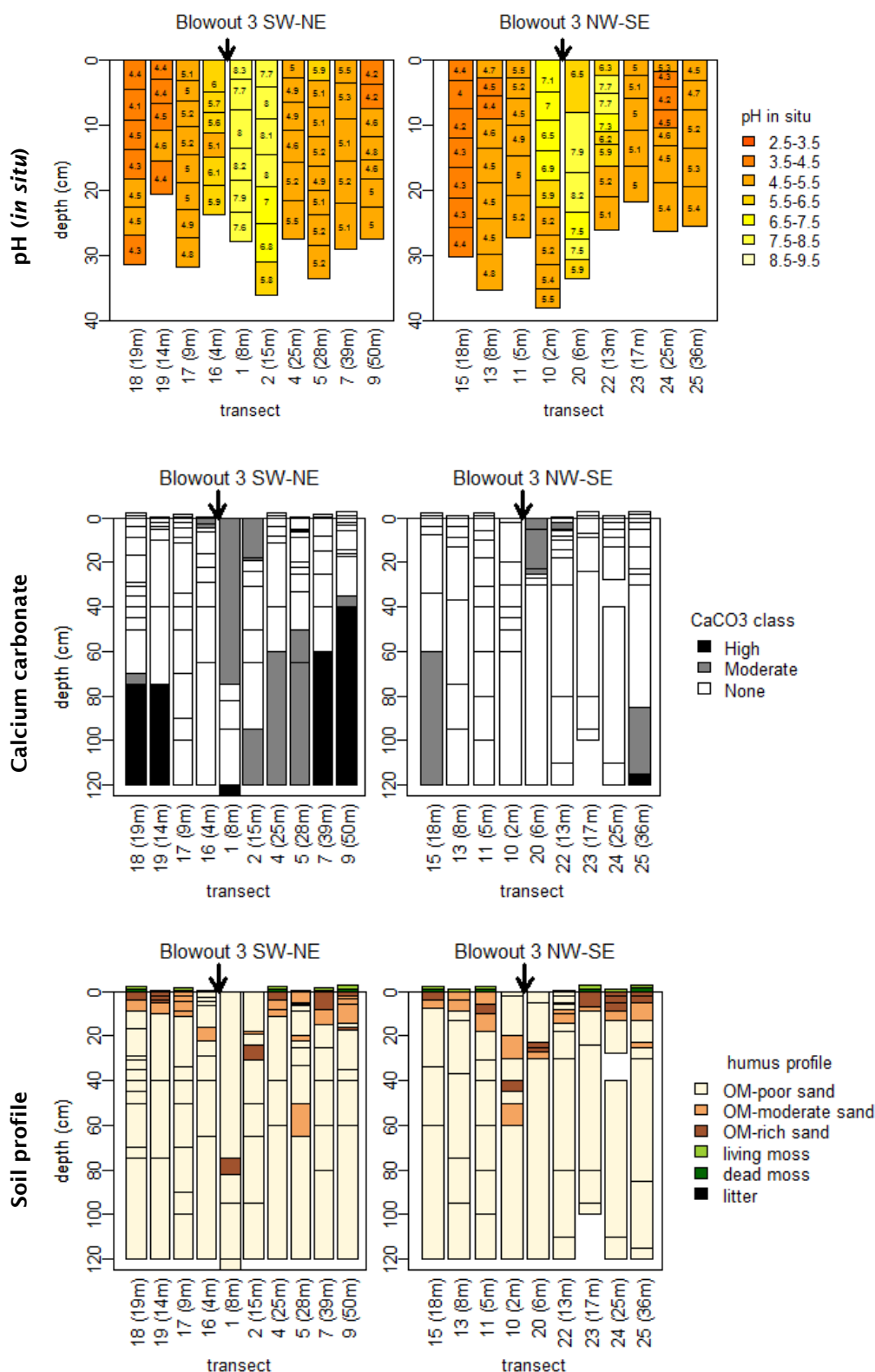


Figure 4-5. In-situ soil pH, calcium carbonate class (tested with HCl dropping), and soil types of soil profile sampling points on SW-NE transect (left) and NW-SE transect (right) of blowout 3. The position of blowout is shown with arrows. The distance between the blowout and the sampled site is shown in brackets.

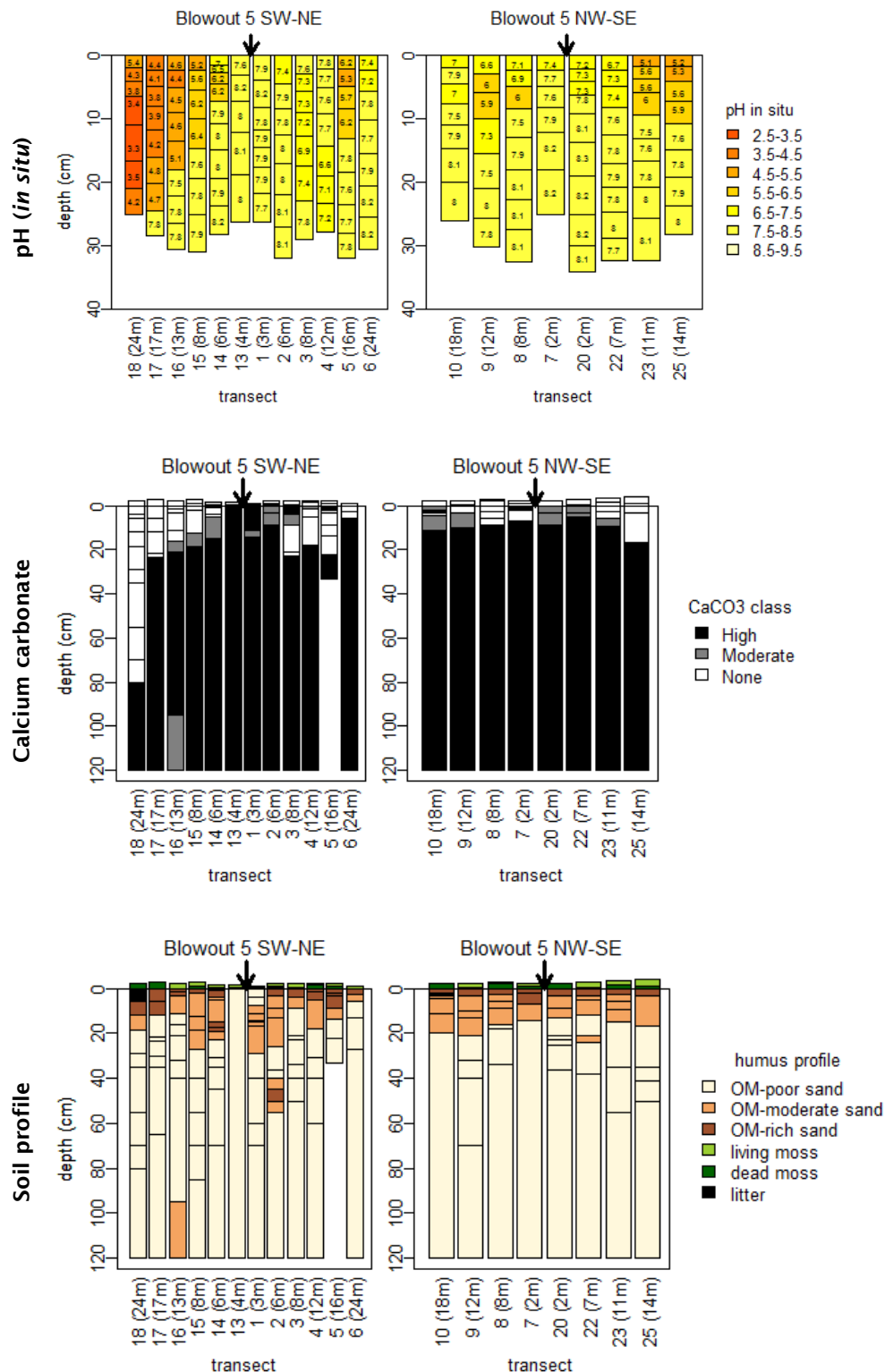


Figure 4-6. In-situ soil pH, calcium carbonate class (tested with HCl dropping), and soil types of soil profile sampling points on SW-NE transect (left) and NW-SE transect (right) of blowout 5. The position of blowout is shown with arrows. The distance between the blowout and the sampled site is shown in brackets.

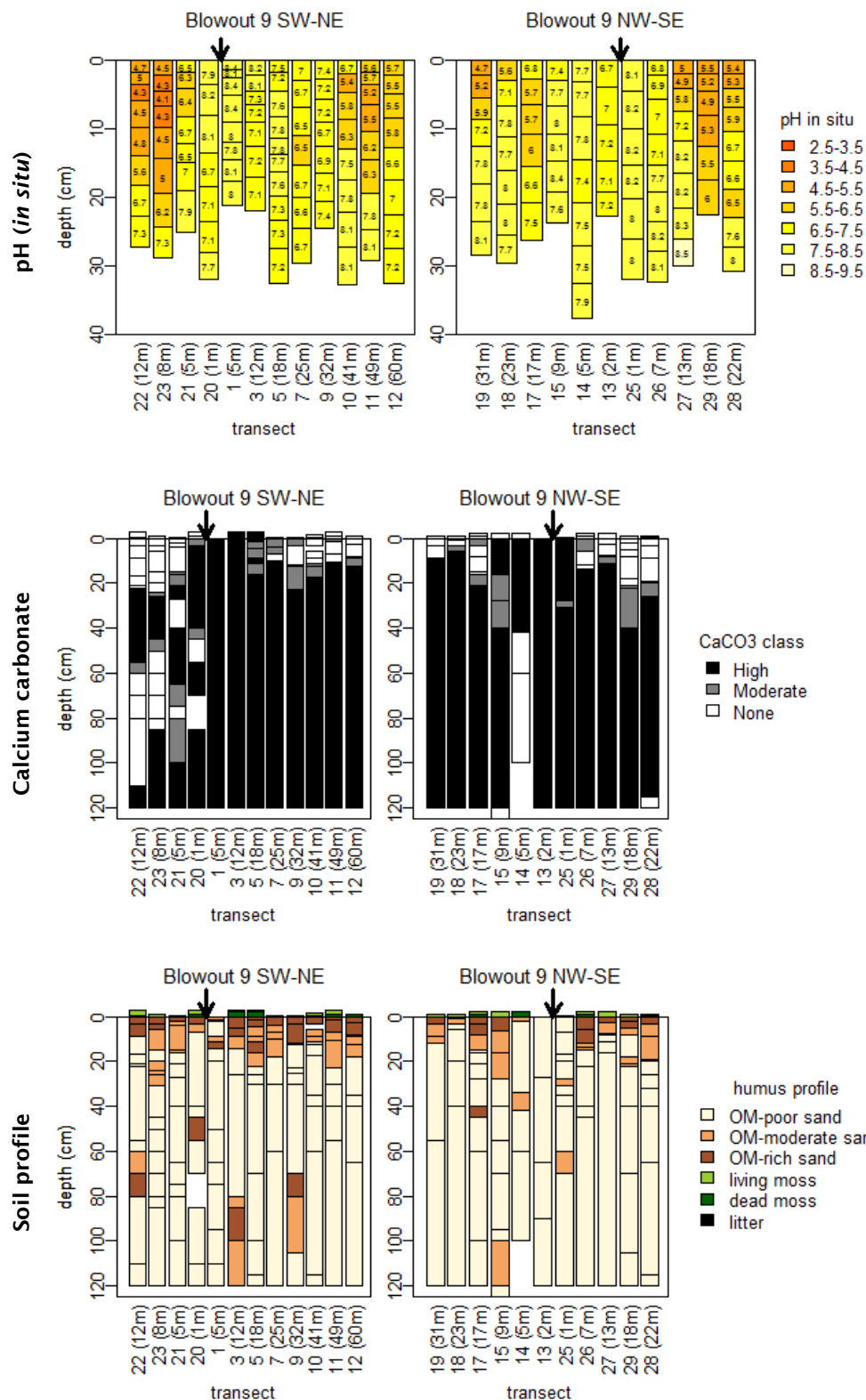


Figure 4-7. In-situ soil pH, calcium carbonate class (tested with HCl dropping), and soil types of soil profile sampling points on SW-NE transect (left) and NW-SE transect (right) of blowout 9. The position of blowout is shown with arrows. The distance between the blowout and the sampled site is shown in brackets.

4.3.2 Spatial extent of influence of drift sand

The boundary of the zones which are strongly and weakly influenced by the blowout is shown in Figure 4-8. The zones expanded most in North-East direction (i.e. opposite to the prevailing wind direction). The relative size of the strongly influenced zones (relative to the size of the deflation zone) was largest in blowout 5 (872 %), followed by blowout 9 (620 %), blowout 1 (390 %), and blowout 3 (308 %) (Table 4.2). When including the weakly influenced zones, the relative size was large in blowout 5 (989 %) and blowout 9 (1039 %), intermediate for blowout 1 (808 %), and smallest for blowout 3 (631 %) (Table 4.2).

Table 4.2. Summary of four blowouts and their influence.

Blowout number	Deflation zone	Strongly influenced zone		Weakly influenced zone	
	Size (m ²)	Size (m ²)	Percentage to size of deflation zone (%)	Size (m ²)	Percentage to size of deflation zone (%)
1	1363	5318	390	5694	418
3	585	1804	308	1889	323
5	117	1024	872	138	117
9	513	3180	620	2148	419

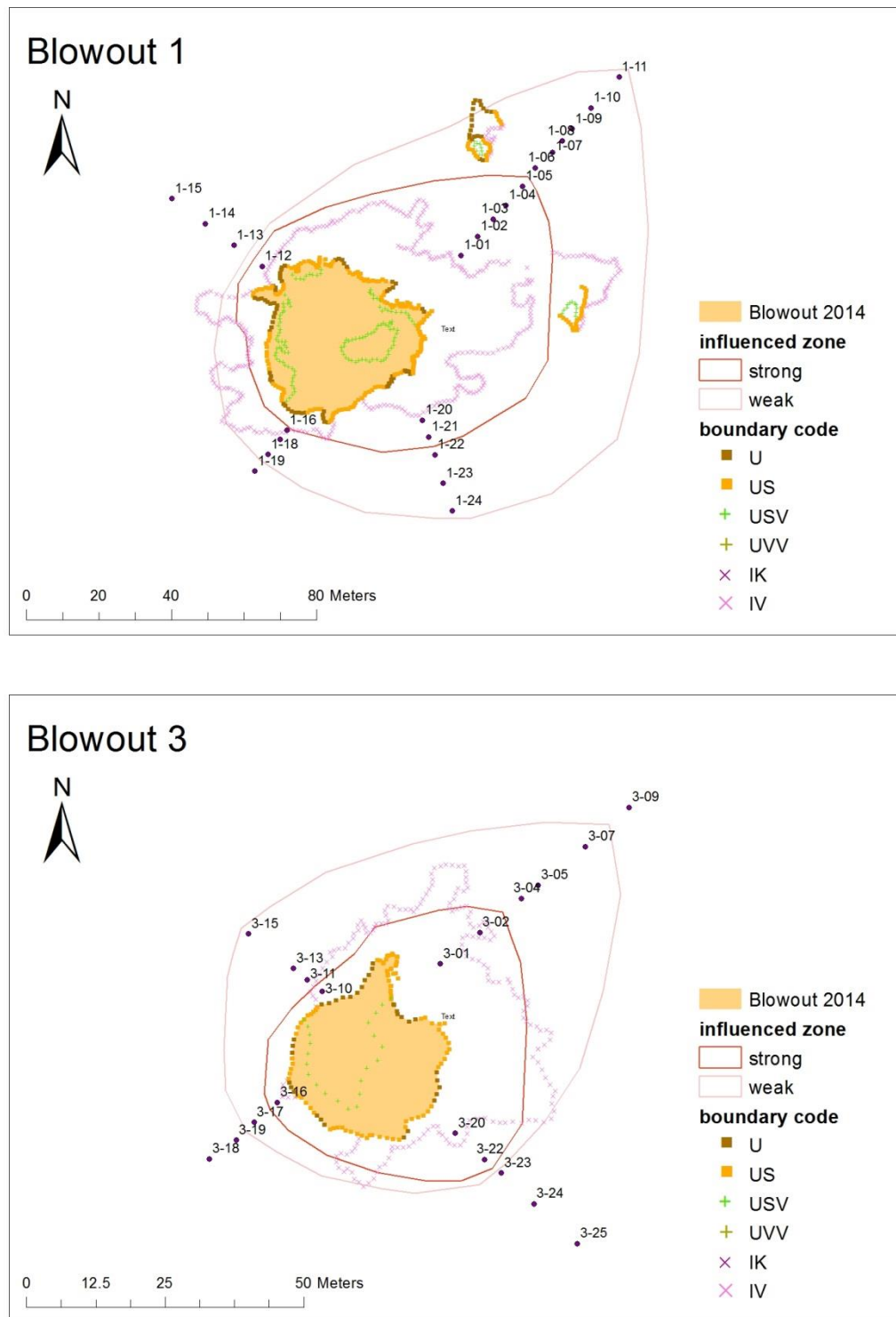


Figure 4-8. Zones which are strongly (red) and weakly (pink) influenced by blowouts. See section 4.2.5 how the boundaries were drawn. In addition, the boundaries observed in the field are also shown as follows. U: boundary of the deflation zone, US: boundary of deflation zone with steep edge, USV: boundary between not-vegetated and vegetated area within blowout, UVV: boundary between high vegetation cover (>10%) and scarce vegetation cover (<5%), IK: boundary between bare sand and scarce vegetation cover (<5%) within zone with strong sand deposition, IV: boundary between zone with strong sand deposition and vegetation with mosses.

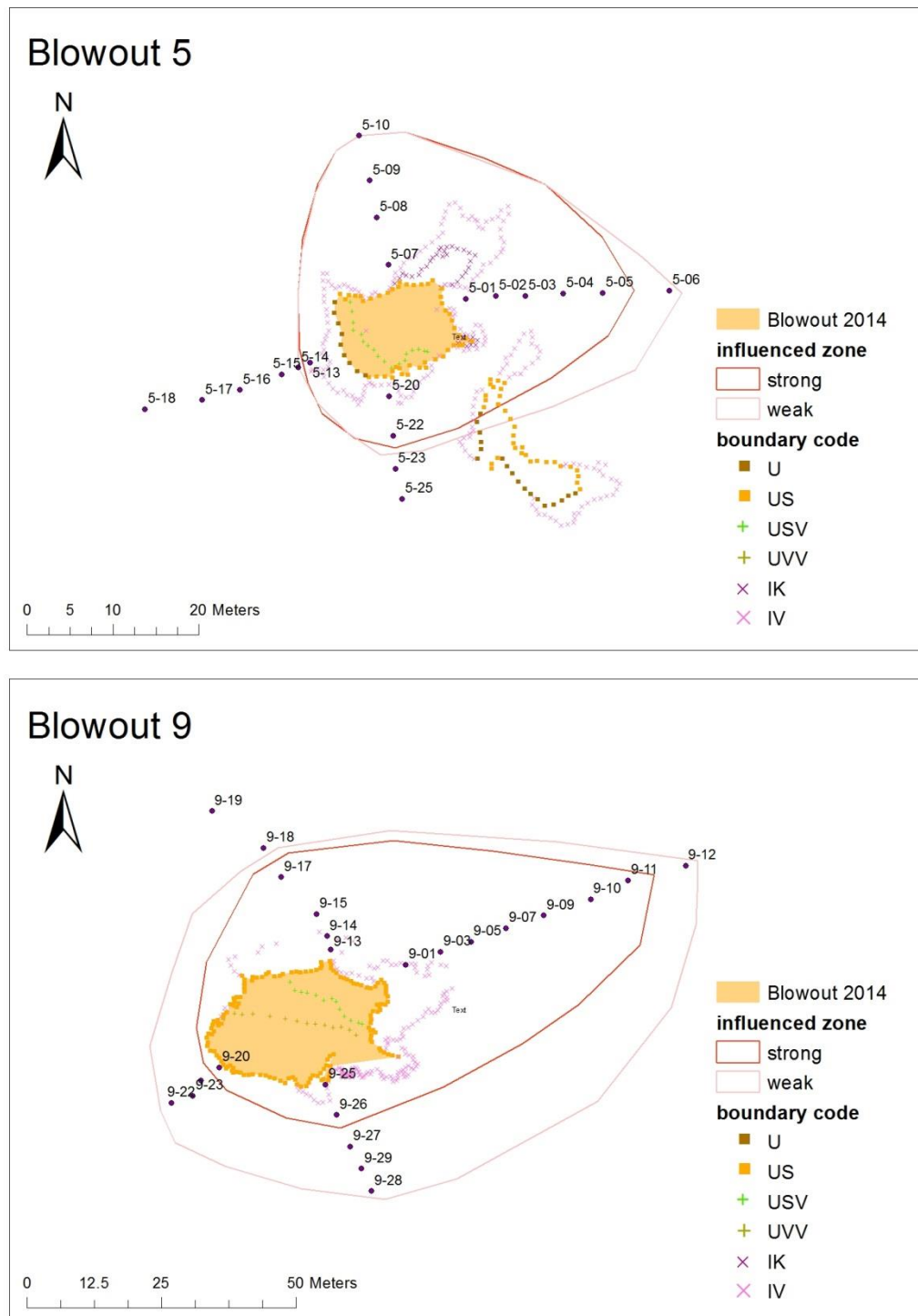


Figure 4-8: continuation.

4.3.3 Soil base chemistry

Using detailed measurement data of extra soil sampling points (i.e. 4 points on NE transect for each blowout), we explored geochemical factors that determined soil acidity. See Figures in Appendix (Figure 6-15Error! Reference source not found., Figure 6-16Error! Reference source not found., Figure 6-17Error! Reference source

not found., Figure 6-18Error! Reference source not found., Figure 6-19Error! Reference source not found., Figure 6-20Error! Reference source not found.) for the overview of actual values of chemical variables (calcium carbonate content, soil organic matter content, exchangeable base cations, and a proxy for base saturation) for each depth.

Soil pH was in general higher in blowout 5 and 9 than in blowout 1 and 3, and was strongly correlated with the proxy BC/SOM for base saturation (Figure 4-9 left; Pearson's correlation coefficient 0.96 for pH_KCl, 0.97 for pH_H₂O, $p < 0.001$ for both). A much higher pH in blowout 5 and blowout 9 should thus be explained by either of the two components of base saturation, i.e. base cations and CEC (the latter is approximated by SOM) (Figure 4-9 right). The range of SOM content was similar among the blowouts, whereas the content of exchangeable base cations was much lower in blowout 1 and 3 even on the top soil where calcium carbonate-rich drift sand is trapped. The higher exchangeable base cation content (and therefore a higher ratio of base cations to SOM) of the dune grassland in adjacent to blowout 5 and 9 can be explained by two factors: 1) they have higher calcium carbonate content within the blowout (carbonate concentrations in top soil layer were 191 meq/kg soil for blowout 1, 119 meq/kg soil for blowout 3, 370 meq/kg soil for blowout 5, and 496 meq/kg soil for blowout 9), and 2) they have higher background calcium carbonate-richness since they are located in superficially-decalcified middle dunes. The exchangeable cation pool on the top soil layer was approximately 2 to 3 times higher in blowout 5 and 9 compared to blowout 1 and 3, and this magnitude of difference is in accordance with the difference in carbonate concentrations in the deflation areas among the blowouts. This indicates that input of drift sand is a dominant factor in determining base richness of top soil layer. In other words, a higher input of calcium carbonate causes a higher base saturation of the top soil. Still, when SOM content is high ($> \text{ca. } 5\%$), a very high amount of exchangeable cations is needed to saturate the cation adsorption complex ($> \text{ca. } 150 \text{ meq/kg soil}$) (Figure 4-9 right). Even for calcium carbonate-rich blowout 5 and 9, calcium carbonate input by drift sand was not enough to maintain high base saturation in those SOM-rich surface soils, resulting in only moderately high pH (ca. 6-7).

Figure 4-9 and Figure 4-10 illustrate different pH-buffer mechanisms of soils. Strong buffering by CaCO₃ occurs in a part of the deeper soil layers of blowouts 5 and 9 (marked as group 1 in Figure 4-9), where carbonate content is higher than ca. 50 meq/kg. These soils have a high pH_KCl ($> \text{ca. } 7$) and a ratio of base cation to SOM of 2500-3700 meq/kg. Most of these soils have a low SOM content ($< 2.5\%$). Another two groups, consisting of top soils (group 2) and deeper soils (group 3), have an pH in the range of 5-7 and an intermediate ratio of base cations to SOM (1000-2500 meq/kg). These were present mainly in blowouts 5 and 9, and to a lesser extent in blowout 1. The deep soils (group 3) have a low SOM content and an intermediate carbonate content (40-100 meq/kg). In contrast, the top soils (group 2) are organic rich and they have a higher carbonate content (80-320 meq/kg) than group 3. Despite their high carbonate content, the base saturation of soils in group 2 is not very high and soil pH is buffered only moderately. Probably pH is buffered both by calcium carbonate and cation exchange for this group. Another possible explanation for the moderate pH-buffer of group 2 might be that the calcium carbonate is relatively young (i.e. recently deposited) and difficult to dissolve, and thus dissolution of calcium carbonate by acids is not (yet) enough to completely saturate the cation adsorption complex. The last group (group 4) consists of most soils of blowouts 1 and 3. These soils have a low pH (< 4.5), a low carbonate content ($< 50 \text{ meq/kg}$) and a low ratio of base cations to SOM (< 500). Here the pH is buffered mainly by Fe and Al.

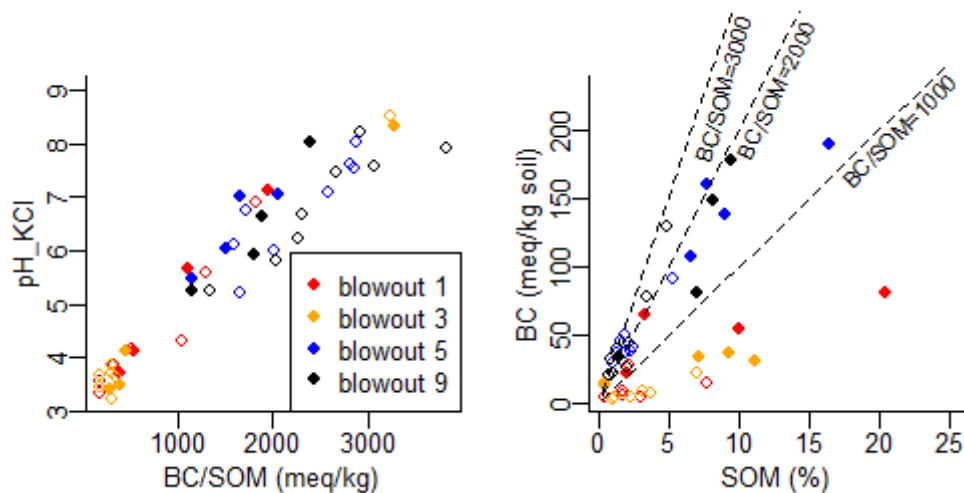


Figure 4-9. Left: Relationship between proxy for base saturation (i.e. sum of exchangeable base cations (BC) divided by soil organic matter (SOM)) and pH_{KCl} . Right: Relationship between soil organic matter content (SOM) and exchangeable base cations (BC). Dotted lines indicate where the BC/SOM equals to 1000, 2000, and 3000. For each blowout (which is presented with different colours), data is shown for 3 depths of 4 points on NE transect (i.e. $N=12$ for each blowout). Soils in deflation zone (i.e. transect 0) are not included in the figures. Filled circles are the top soil layer, whereas open circles are the second and third soil layers.

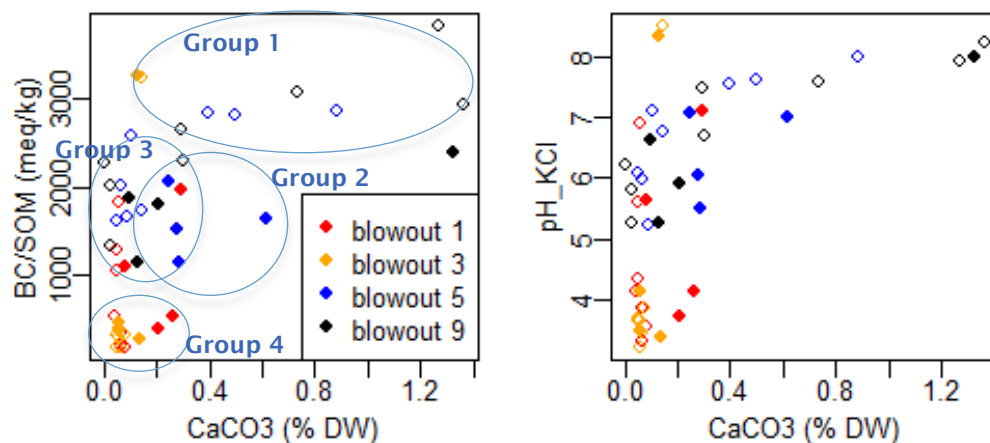


Figure 4-10. (Left) Relation between calcium carbonate content (CaCO_3) and proxy for base saturation (i.e. sum of exchangeable base cations (BC) divided by soil organic matter (SOM)). (Right) Relationship between calcium carbonate content and pH_{KCl} . For each blowout (which is presented with different colours), data is shown for 3 depths of 4 points on NE transect (i.e. $N=12$ for each blowout). Soils in deflation zone (i.e. transect 0) are not included in the figures. Filled circles are the top soil layer, whereas open circles are the second and third soil layers. Circles indicate groups of soils in which different pH-buffering mechanisms rule. See text for description of each group.

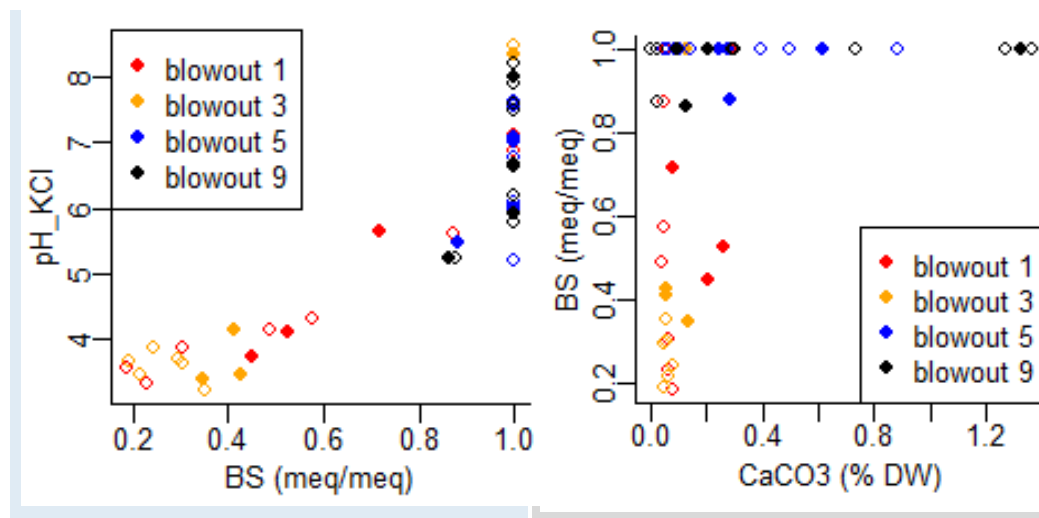


Figure 4-11. Left: Relationship between base saturation and pH_KCl. Right: Relation between calcium carbonate content (CaCO₃) and base saturation. For each blowout (which is presented with different colours), data is shown for 3 depths of 4 points on NE transect (i.e. N=12 for each blowout). Soils in deflation zone (i.e. transect 0) are not included in the figures. Filled circles are the top soil layer, whereas open circles are the second and third soil layers.

4.3.4 Vegetation

Most plots, except those next to the blowouts, had closed vegetation structure with cumulative cover (vascular+moss+shrub layer) of 100 % or more (Figure 4-12). In blowouts 3, 5 and 9 there exists a distinct shift from moss-poor vegetation to moss-rich vegetation along the transect. For blowout 1 the moss cover increases gradually with increasing distance from the deflation zone. Species richness was highest at the intermediate distance from the blowout, and lower at places closer to and farther from the blowout (Figure 4-13).

There was a slight trend in blowout 1 and 3 that species typical for calciumcarbonate-rich conditions (group 2 and 7 in Figure 4-13) decreased as the distance from the blowout increased, and species typical for calciumcarbonate-poor sites (group 3 in Figure 4-13) were more numerous at intermediate distance from the blowout. In blowout 5 species of 'dry dune grassland nutrient poor and calcium carbonate rich' (group 2) have an optimum at intermediate distance.

The plot-mean Ellenberg values for acidity also indicate the change in species composition in terms of their tolerance to soil acidity (Figure 4-14). Although the range of the Ellenberg values of the occurring species were not different among plots, the median values decreased as the distance from the blowout increased, especially in blowout 1 and blowout 3.

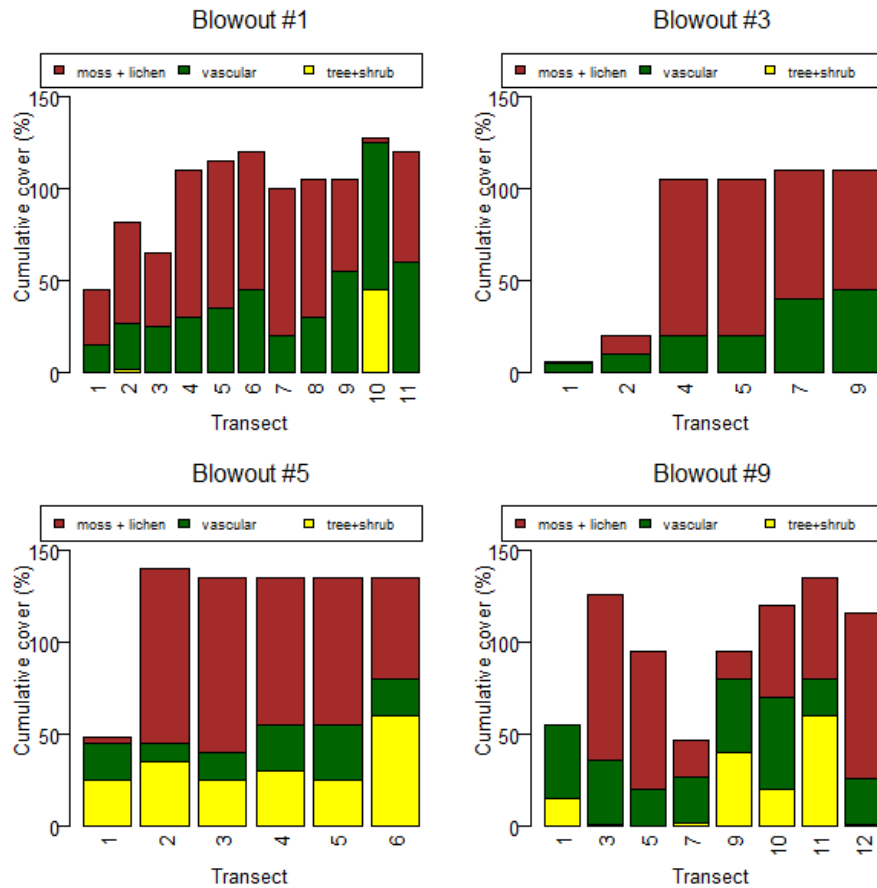


Figure 4-12. Cumulative cover of plants, categorized into functional groups (mosses and lichens, vascular plants, and trees and shrubs), of each plot on NE transects.

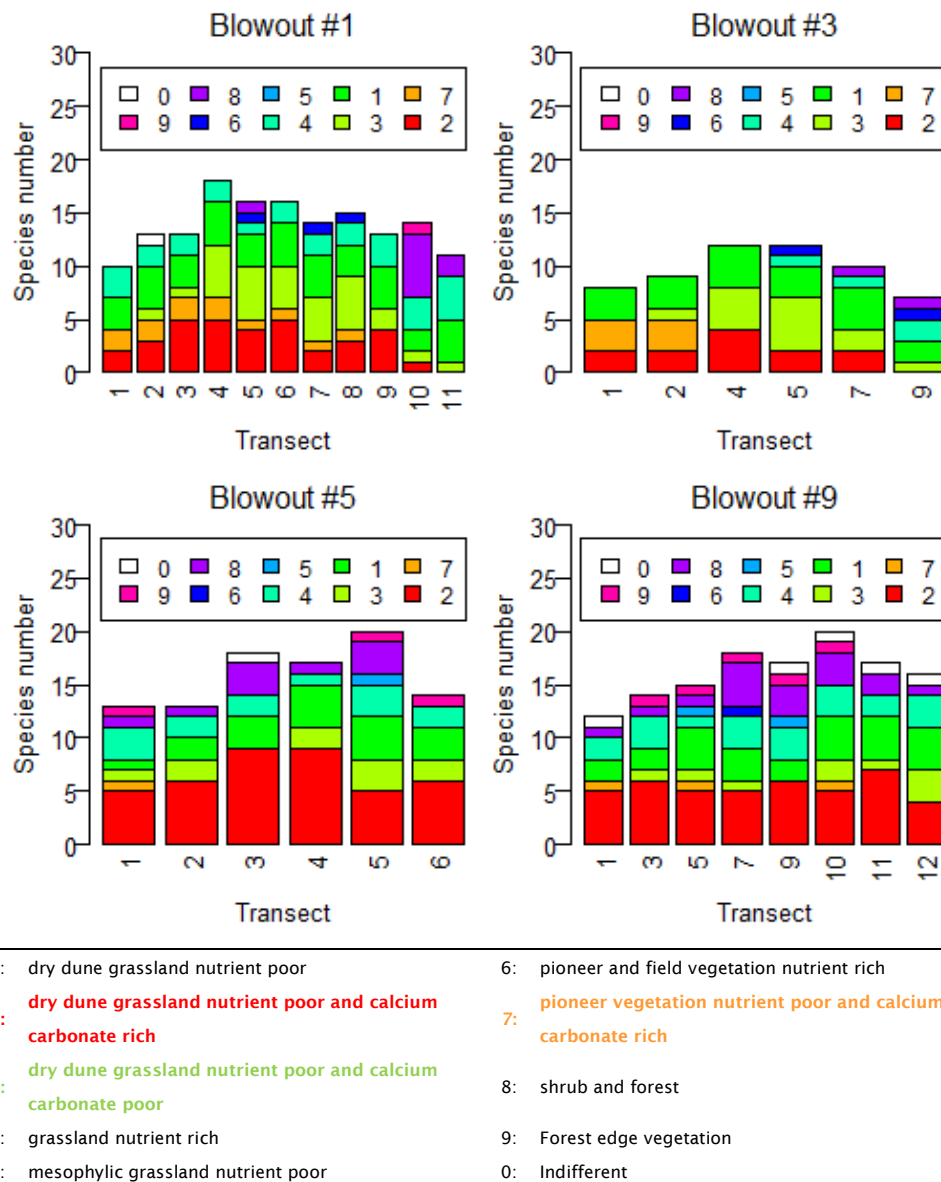


Figure 4-13. Number of species of each plot on NE transects. Species were categorized into ecological species groups. Group 2 (red) and 7 (orange) are species typical for calciumcarbonate-rich sites, whereas group 3 (light green) is species typical for calciumcarbonate-poor sites. Cumulative cover of species are shown in Figure 6-21 in Appendix.

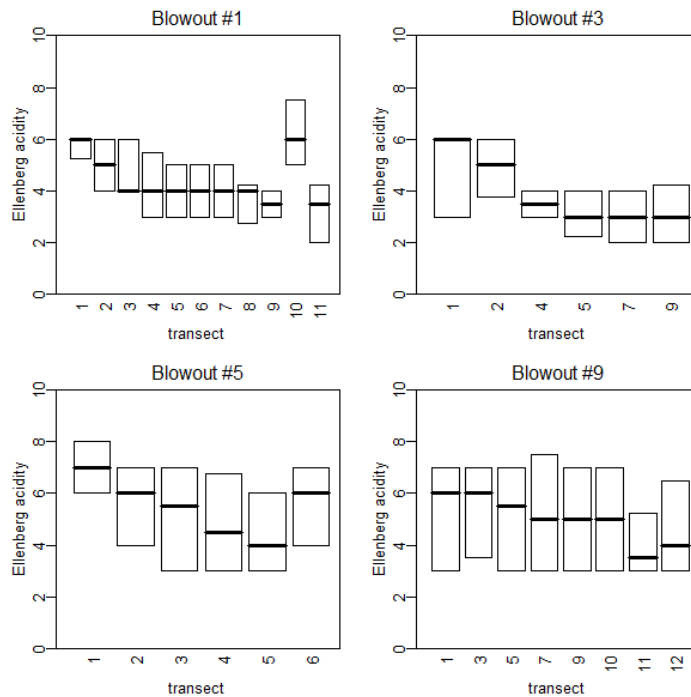


Figure 4-14. Plot-mean Ellenberg acidity values of the occurring species. Median values are shown with bold lines. 25th and 75th percentiles are also shown as boxes. A higher Ellenberg acidity value means that the species is adapted to a higher pH range.

4.4 Discussion

Blowouts in Luchterduinen had a large influence on soil pH of surrounding Grey Dune vegetation. As expected from the prevailing wind direction (SW) in the Netherlands, the influence was strongest in the NE direction: top soil pH was maintained higher than the background pH for the longest distance in NE direction compared to SW, SE, and NW directions (Figure 4-15). At the NE site the effect on soil pH extends for several tens of meters. The pH at SW side (and mostly at NW side too) was remarkably steep. Here pH effects are restricted to a zone of 5 to 20 m.

On average, a blowout influenced soil pH of an area 8.7 times larger than the size of the deflation zone. The relative size of the influenced zone (i.e. relative to the size of blowout) was different among blowouts: it was much larger for those in 'calciumcarbonate rich' middle dunes (989 % for blowout 5 and 1039 % for blowout 9) than those in more deeply decalcified inner dunes (808 % for blowout 1 and 631 % for blowout 3) (Figure 4-16). This difference is even more evident for the strongly influenced zone.

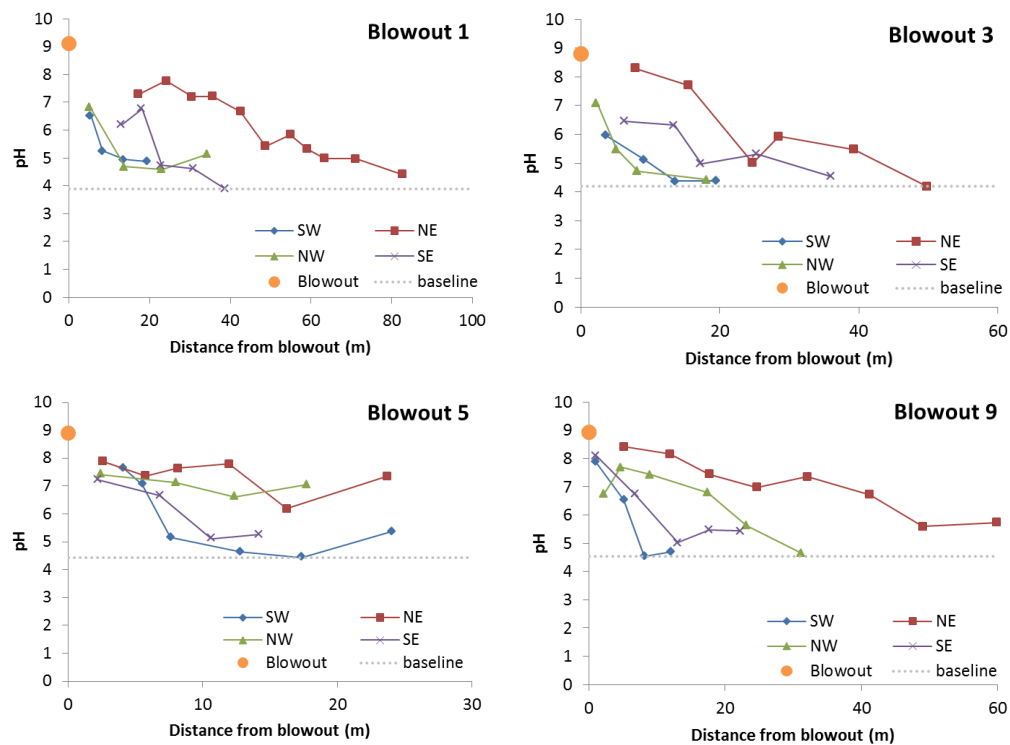


Figure 4-15. In-situ pH of the top soil layer in relation to the distance between the sampling point and the boundary of blowout. Values are separately shown for the soil profile sampling points of South-West transect (SW), North-East transect (NE), North-west transect (NW), and South-East transect (SE). $\text{pH}_{\text{H}_2\text{O}}$ value of the top soil (0-5cm depth) within the blowhole is also shown. See Figure 4-4 to Figure 4-7 for the pH values of other depths. Baseline pH values, approximated as the lowest pH value of the transect, are shown in dotted lines.

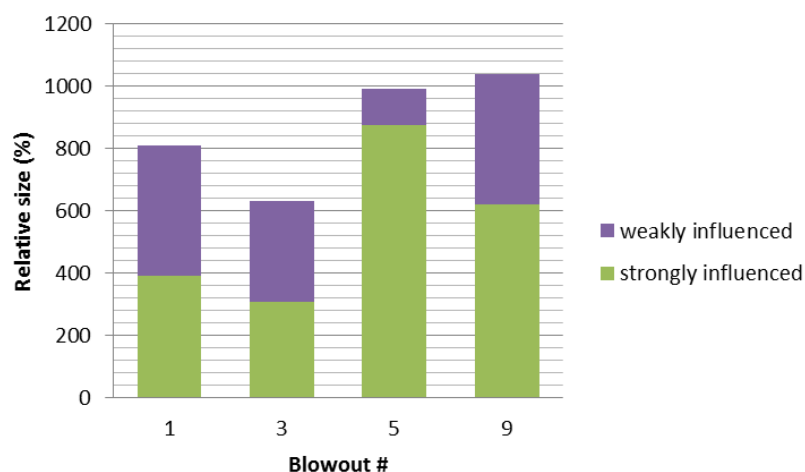


Figure 4-16. Relative size of influenced zones by blowouts, expressed as percentage of the size of the influenced zone over the size of the blowout. Influenced zones were split into strongly influenced zones and weakly influenced zones. See Figure 4-8 for the spatial distribution of the zones.

The difference in relative size of influence can be attributed to the geochemistry of the sand in the deflation zone. Blowout 5 and 9 has more calciumcarbonate-rich sand than blowout 1 and 3, as seen in difference in carbonate concentrations within blowouts.

The higher calcium carbonate content of the drift sand in blowout 5 and 9 resulted in a higher base cation pool in the top soil of the adjacent dune grasslands, which contributed to higher base saturation and therefore maintenance of high soil pH. In addition, blowout 5 and 9 are closer to the coast and therefore wind force could be higher, which possibly account for a larger spatial influence of these blowouts. The influence of drift sand on the soil base status diminishes with increasing distance from the deflation zone, due to decreased input of drift sand as well as increased amount of soil organic matter. Soil organic matter contributes to a large part of CEC (as seen in the equation in section 4.2.3) and therefore largely interfere with the base chemistry of the soil. To increase the base saturation and pH in an organic-rich top soil, a larger amount of calcium carbonate input is needed than for a SOM poor soil. Thus, whether top soil pH can be improved by deposition of drift sand depends on multiple factors, such as geometry of the blowout (size, direction), chemistry of the drift sand, and local heterogeneity of soil organic matter content. This suggests that different considerations need to be taken in middle dunes and inner dunes when designing secondary blowouts in the context of nature management.

Blowouts also affect vegetation of the surrounding area. The effects on dune grassland vegetation were most likely caused by the change in soil acidity, as demonstrated by an increase in acid-intolerant species and species adapted to calciumcarbonate-rich areas nearby blowouts. Interestingly, the effects of blowout on plant species composition were more visible in inner dunes (blowout 1 and 3) than in middle dunes (blowout 5 and 9), despite that the effects of drift sand on top soil pH was stronger in blowouts 5 and 9. An explanation for this pattern is that the soils around blowouts 5 and 9 are only shallowly decalcified and therefore even SOM-rich top soils can be buffered to maintain rather high pH. Therefore, over the whole range of their transects, species typical for calcium carbonate-rich dune grasslands, such as *Taraxaco-Galietum*, occur more commonly than at the other blowouts. In the deeply decalcified inner dunes, the background pH was lower than in middle dunes. Therefore even a slight improvement of soil pH by drift sand resulted in significant change in habitat conditions for plants. In this study we examined the effects of blowouts with a long-lasting aeolian activity (> 35 years). Many secondary blowouts are active for a shorter period. Therefore this study quantifies an upper limit for the effect of blowouts on the soil and vegetation of adjacent dune grasslands. Also the area where calcium carbonate and pH profiles are influenced by drift sand will probably be smaller in blowouts with a shorter aeolian lifespan compared with those estimated in this study. However, strong storms, which occur infrequently and irregularly, account for mayor part of sand transport from secondary blowouts. Therefore sand deposition may not linearly be correlated with aeolian lifespan.

4.5 Conclusions and implications

This study reveals that blowouts have significant effects on base chemistry of soils (most notably pH) and vegetation of the surrounding area. A blowout influences an area ca. 9 times larger than its own size, and the influence reaches the farthest in the North-East direction. The magnitude of the influence on soil pH depends on the quantity of drift sand (i.e. distance and direction from the blowout) and geochemistry of the drift sand (i.e. calcium carbonate content), base status of the background soil substrate, as well as soil organic matter content of the soil.

The concomitant effect of blowouts on adjacent old dune grasslands was also evident. Species adapted to base-rich conditions have chance to occur on spots near blowouts. This contributes to species richness on a landscape level, especially in deeply decalcified areas where a slight improvement in soil acidity may bring a prominent change in habitat conditions for plants.

Creation of secondary blowouts can be considered as an effective management option for dune grassland conservation, especially when the blowout contains outcropping calcium carbonate-rich sands and when the surrounding area is deeply decalcified. Also in areas with shallow decalcification depth, blowouts help to maintain high pH in SOM-rich top soils. The expected positive effects of blowouts are improved top soil base status in the nearby areas (especially on NE direction) and increased species richness on a landscape level. It should be noted that soil pH of stabilized grasslands with high SOM accumulation may be less easily improved by drift sand because of their high CEC. To better evaluate the effectiveness of drift sand on dune grasslands, more detailed measurements of soil chemistry are needed, with more combinations of different types of blowouts (size, quality, aeolian lifespan), and different decalcifications levels of the background area. Besides this research should also focus on the sustainability of positive effects after aeolian activity ceased. Also, for a better understanding of the buffering mechanism, it would be useful to quantify the calcium carbonate input from blowouts in adjacent grasslands. Furthermore, spatial analysis of aerial photos of longer time series is needed to understand long-term dynamics of blowouts in different dune landscapes and factors influencing the dynamics.

5 References

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6 Appendices

6.1 Appendices of chapter 2

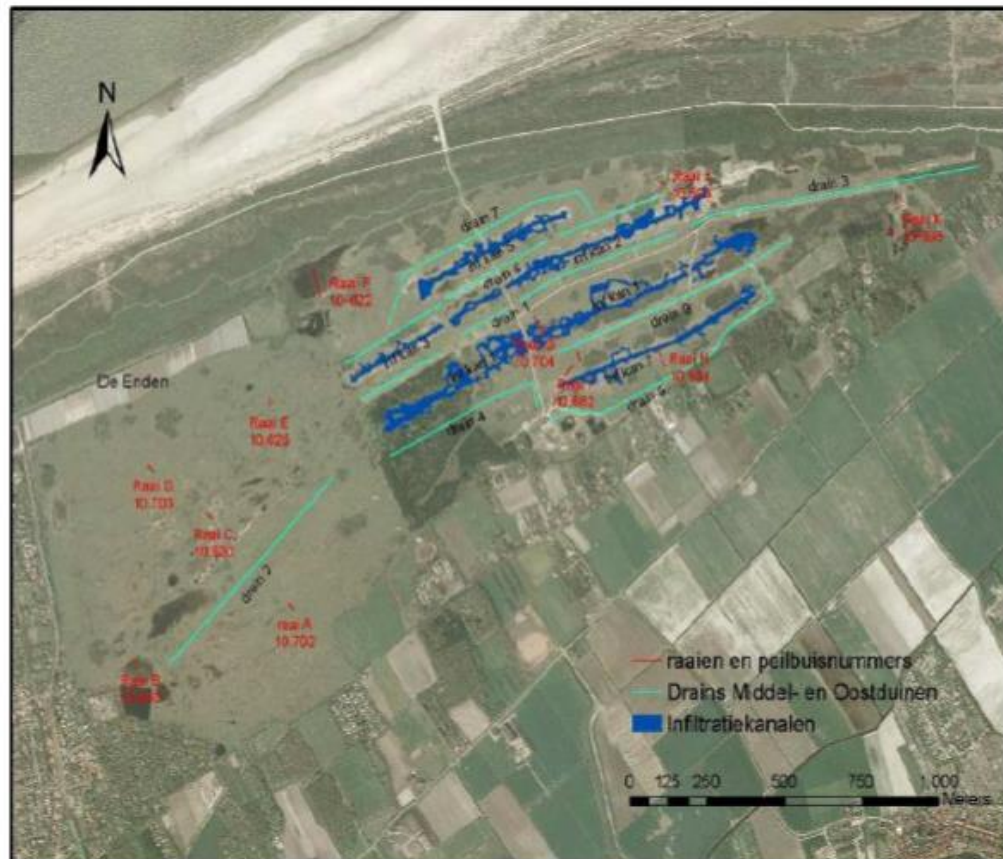


Figure 6-1. Aerial photograph of the "Middel- and Oostduinen" nature reserve on the island of Goeree-Overflakkee, province of Zuid-Holland, the Netherlands. Blue indicates the location of infiltration channels, and green lines indicate the location of water drains

Table 6.1 Pearson's correlation coefficients with log-transformed decalcification depth. N=40.

Variable	Correlation coefficient
BD_0_5	-0.56
BD_5_15	-0.32
pH_H2O_0_5	-0.66
pH_H2O_1_15	-0.69
pH_KCl_0_5	-0.82
pH_KCl_5_15	-0.79
SOMpool_0_15	0.70
SOM%_0_5	0.73
SOM%_5_15	0.57
sp richness	-0.11
herb cover	0.37
moss cover	-0.09
herb height	0.21
Ellenberg light	-0.64
Ellenberg moisture	0.47
Ellenberg acidity	-0.63
Ellenberg nutrient	-0.08

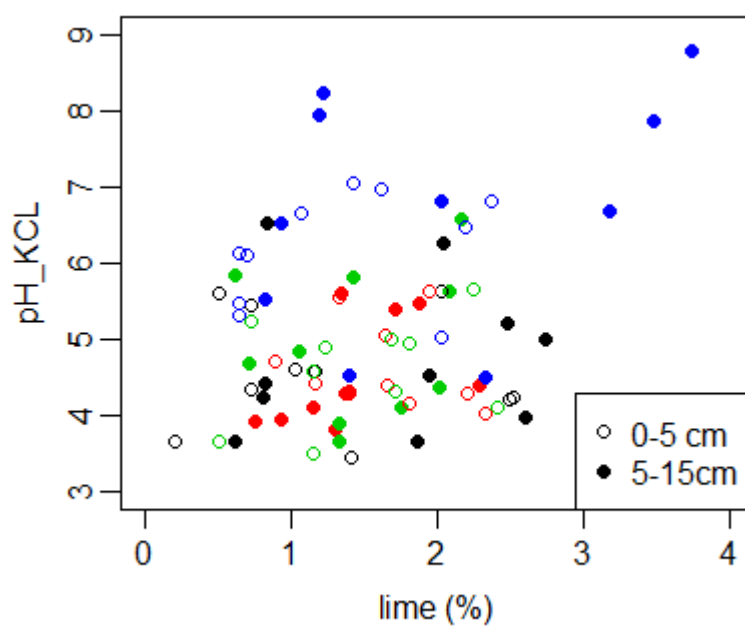


Figure 6-2. Relationship between calciumcarbonate content and pH_KCl. Data are shown for soils of 0-5 cm depth (open circles) and 5-15 cm depth (closed circles). Colour represents different management types; black: M0_S0, red: M1_S0, green: M2_S0, blue: M2_S2.

a)

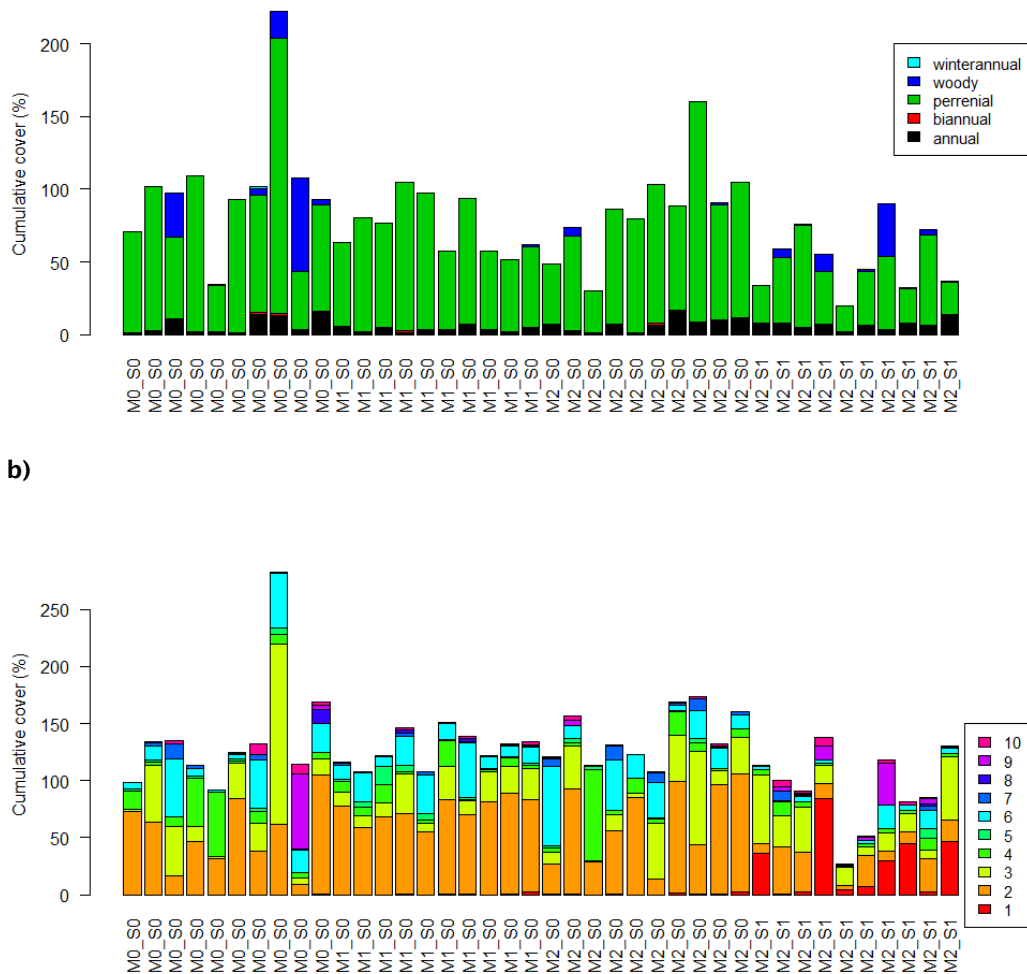


Figure 6-3. Cumulative cover of plant species, categorized into life span (a) and into ecological species group (b), for four management types. Data is shown for 10 plots for each management type. For the description of the codes of ecological species group, see figure legend of Figure 2-7.

Table 6.2. List of recorded plant species.

spnr	spname	spnr	spname
S4	Achillea millefolium	S1175	Sedum acre
S19	Agrostis capillaris	S1199	Danthonia decumbens
S21	Aira praecox	S1204	Silene nutans
S35	Allium vineale	S1248	Stellaria graminea
S50	Ammophila arenaria	S1261	Taraxacum sectie Erythrosperma
S66	Anthoxanthum odoratum	S1268	Teesdalia nudicaulis
S71	Anthyllis vulneraria	S1283	Thymus pulegioides
S89	Arenaria serpyllifolia	S1296	Trifolium arvense
S96	Arrhenatherum elatius	S1298	Trifolium campestre
S153	Briza media	S1299	Trifolium dubium
S174	Calamagrostis epigejos	S1305	Trifolium pratense
S215	Carex arenaria	S1306	Trifolium repens
S218	Carex caryophylla	S1307	Trifolium scabrum

S235	<i>Carex hirta</i>	S1308	<i>Trifolium striatum</i>
S292	<i>Cerastium arvense</i>	S1312	<i>Trisetum flavescens</i>
S296	<i>Cerastium fontanum</i> s. <i>vulgare</i>	S1347	<i>Veronica arvensis</i>
S298	<i>Cerastium semidecandrum</i>	S1355	<i>Veronica officinalis</i>
S350	<i>Convolvulus arvensis</i>	S1368	<i>Vicia sativa</i> s. <i>nigra</i> + s. <i>segetalis</i>
S367	<i>Corynephorus canescens</i>	S1369	<i>Vicia cracca</i>
S369	<i>Crataegus monogyna</i>	S1371	<i>Vicia lathyroides</i>
S372	<i>Crepis capillaris</i>	S1380	<i>Viola canina</i>
S390	<i>Dactylis glomerata</i>	S1393	<i>Vulpia myuros</i>
S445	<i>Elytrigia atherica</i>	S1474	<i>Festuca filiformis</i>
S462	<i>Equisetum arvense</i>	S1522	<i>Sagina apetala</i> s.s.
S483	<i>Erophila verna</i>	S1643	<i>Rosa canina</i> s.l.
S485	<i>Eryngium campestre</i>	S1766	<i>Centaurea jacea</i>
S517	<i>Festuca arenaria</i>	S1917	<i>Erodium cicutarium</i>
S520	<i>Festuca rubra</i>	S2290	<i>Jacobaea vulgaris</i>
S557	<i>Galium verum</i>	S2337	<i>Bromus hordeaceus</i>
S571	<i>Geranium molle</i>	S2434	<i>Ononis repens</i>
S604	<i>Helictotrichon pubescens</i>	S2462	<i>Elytrigia maritima</i>
S621	<i>Hieracium pilosella</i>	S2561	<i>Brachythecium albicans</i>
S625	<i>Hieracium umbellatum</i>	S2567	<i>Brachythecium rutabulum</i>
S629	<i>Hippophae rhamnoides</i>	S2574	<i>Bryum species</i>
S631	<i>Holcus lanatus</i>	S2586	<i>Bryum capillare</i>
S649	<i>Hypericum perforatum</i>	S2642	<i>Ceratodon purpureus</i>
S654	<i>Hypochaeris radicata</i>	S2679	<i>Dicranum scoparium</i>
S669	<i>Jasione montana</i>	S2775	<i>Homalothecium lutescens</i>
S693	<i>Koeleria macrantha</i>	S2788	<i>Hypnum cupressiforme</i> + <i>jutlandicum</i>
S725	<i>Leontodon autumnalis</i>	S2879	<i>Plagiomnium undulatum</i>
S727	<i>Leontodon saxatilis</i>	S2907	<i>Pleurozium schreberi</i>
S745	<i>Linaria vulgaris</i>	S2925	<i>Polytrichum juniperinum</i> v. <i>juniperinum</i>
S756	<i>Lolium perenne</i>	S2942	<i>Pseudoscleropodium purum</i>
S761	<i>Lotus corniculatus</i> + L. 'Sativus'	S2971	<i>Rhynchostegium megapolitanum</i>
S766	<i>Luzula campestris</i>	S2976	<i>Rhytidiadelphus squarrosus</i>
S843	<i>Myosotis ramosissima</i>	S3066	<i>Syntrichia ruralis</i> sl
S897	<i>Ornithopus perpusillus</i>	S3142	<i>Plagiomnium affine</i>
S931	<i>Phleum arenarium</i>	S4147	<i>Cladonia ramulosa</i>
S932	<i>Phleum pratense</i>	S4156	<i>Cladonia ciliata</i>
S946	<i>Plantago lanceolata</i>	S4159	<i>Cladonia humilis</i>
S958	<i>Poa pratensis</i>	S4169	<i>Cladonia foliacea</i>
S963	<i>Polygala vulgaris</i>	S4170	<i>Cladonia furcata</i>
S1010	<i>Potentilla reptans</i>	S4173	<i>Cladonia glauca</i>
S1045	<i>Ranunculus bulbosus</i>	S4175	<i>Cladonia grayi</i>
S1064	<i>Rhamnus cathartica</i>	S4183	<i>Cladonia portentosa</i>
S1066	<i>Rhinanthus angustifolius</i>	S4186	<i>Cladonia rangiformis</i>
S1089	<i>Rubus caesius</i>	S4189	<i>Cladonia scabriuscula</i>
S1093	<i>Rumex acetosa</i>	S4195	<i>Cladonia subulata</i>
S1094	<i>Rumex acetosella</i>	S4452	<i>Peltigera species</i>
S1112	<i>Sagina procumbens</i>	S5305	<i>Elytrigia repens</i>
S1124	<i>Salix repens</i>	S5401	<i>Euphrasia tetraquetra</i>
S1146	<i>Saxifraga tridactylites</i>	S6452	<i>Rubus species</i>

Table 6.3. Results of multivariate regression analysis of various response variables against 4 management types and log-transformed decalcification depth (cm). N=40. Tested response variables are SOM pool of 0-15 cm depth (kg/m²), soil pH_KCl of 0-5 cm depth, number of plant species (vascular plants + mosses + lichens), plot-mean Ellenberg values for light, nutrient, moisture, and acidity, cover of herbs (%), cover of mosses (%), and average height of herbs (cm). When interaction terms of management type and decalcification depth was significant ($p < 0.05$) with ANCOVA, the interaction terms were included in the regression model. Regression coefficient values and their p -values for each explanatory variables are shown. Adjusted R^2 values and their p values of the regression model are shown as well.

	SOM		pH_KCl		sp richness		Ell_light		Ell_nutrient	
	β	p	β	p	β	p	β	p	β	p
M1_S0	1.36	ns	0.01	ns	-5.49	ns	-0.08	ns	-2.15	<0.05
M2_S0	3.27	ns	0.05	ns	5.75	ns	0.08	ns	-0.69	ns
M2_S1	1.69	ns	0.73	<0.05	-19.44	<0.05	0.38	<0.001	-2.25	<0.001
log(decal)	1.31	<0.001	-0.46	<0.001	-4.10	ns (0.066)	-0.04	ns	-0.48	<0.01
M1_S0* log(decal)	-0.19	ns			1.89	ns			0.55	<0.05
M2_S0* log(decal)	-0.90	ns			-1.29	ns			0.16	ns
M2_S1* log(decal)	-1.25	<0.01			6.67	<0.05			0.60	<0.001
R^2_{adj}	0.74		0.71		0.17		0.74		0.26	
p	<0.001		<0.001		ns (0.07)		<0.001		<0.05	

	Ell_moistur e		Ell_acidity		herb cover		moss cover		herb height	
	β	p	β	p	β	p	β	p	β	p
M1_S0	-0.88	<0.05	-1.28	ns	-137.06	<0.01	25.45	<0.05	-10.42	ns
M2_S0	-0.14	ns	-0.68	ns	21.76	ns	24.60	ns	-11.97	ns
M2_S1	-1.04	<0.001	-2.47	<0.001	-101.98	<0.001	-0.57	ns	-9.85	ns
log(decal)	-0.11	ns	-0.76	<0.001	-11.12	ns	-5.75	ns	1.90	ns
M1_S0* log(decal)	0.22	<0.05	0.30	ns	29.84	<0.01				
M2_S0* log(decal)	0.01	ns	0.13	ns	-8.81	ns				
M2_S1* log(decal)	0.21	<0.01	0.76	<0.001	18.77	<0.05				
R^2_{adj}	0.51		0.61		0.57		0.09		0.05	
p	<0.001		<0.001		<0.001		ns		ns	

Table 6.4. Results of multivariate regression analysis of various response variables against mowing intensity, duration not mown, sod-cutting, and log-transformed decalcification depth (cm). Only mown sites were used (i.e. 'M1_S0, M2_S0 and M2_S1, N=30). See caption of for description of the response variables.

	SOM		pH_KCl		sp richness		Ell_light		Ell_nutrient	
	β	p	β	p	β	p	β	p	β	p
Mowing intensity	0.06	ns	-0.09	ns	0.76	ns	-0.02	ns	0.04	ns
Duration not mown	0.06	ns	-0.01	ns	0.00	ns	-0.01	ns	0.00	ns
Sod-cutting	-2.44	<0.001	0.78	<0.05	-0.23	ns	0.34	<0.001	-0.10	ns
log(decal)	0.28	ns	-0.40	<0.001	0.08	ns	-0.03	ns	0.01	ns
R^2_{adj}	0.72		0.72		-0.11		0.79		-0.11	
p	<0.001		<0.001		ns		<0.001		ns	

	Ell_moisture		Ell_acidity		herb cover		moss cover		herb height	
	β	p	β	p	β	p	β	p	β	p
Mowing intensity	0.05	<0.05	-0.01	ns	1.69	ns	-1.63	ns	1.08	ns
Duration not mown	0.01	ns	-0.01	ns	-1.00	ns	0.07	ns	0.21	ns
Sod-cutting	-0.22	<0.05	0.16	ns	-27.96	<0.05	-26.59	ns	5.86	ns
log(decal)	0.05	ns	-0.21	<0.05	2.96	ns	-7.12	ns	3.83	ns
R^2_{adj}	0.49		0.28		0.25		-0.01		0.00	
p	<0.001		<0.05		P<0.05		ns		ns	

6.2 Appendices of chapter 3

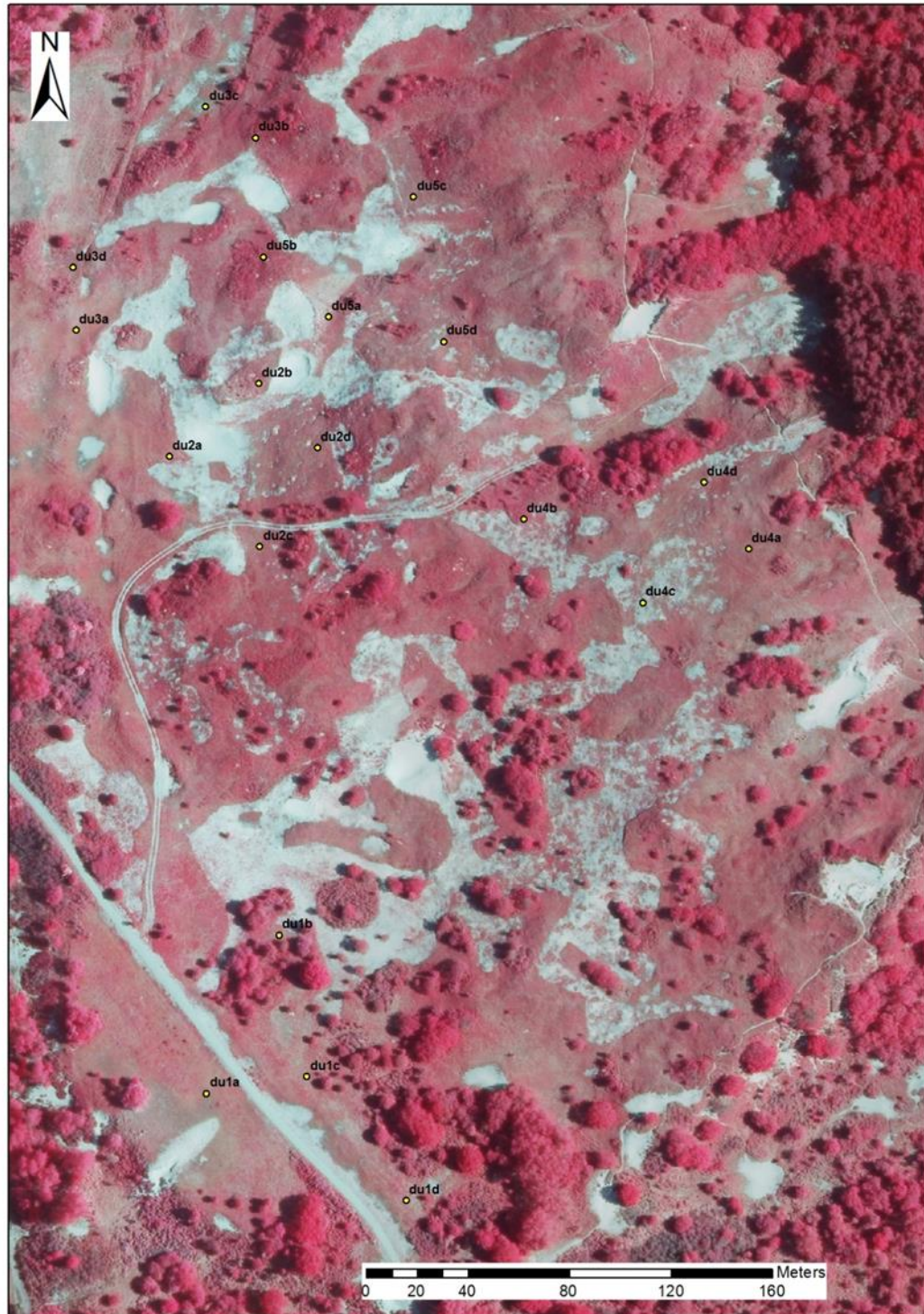


Figure 6-4. Map of Rozenwattveld with the location of plots, at the Amsterdam Water Supply Dunes (AWD).

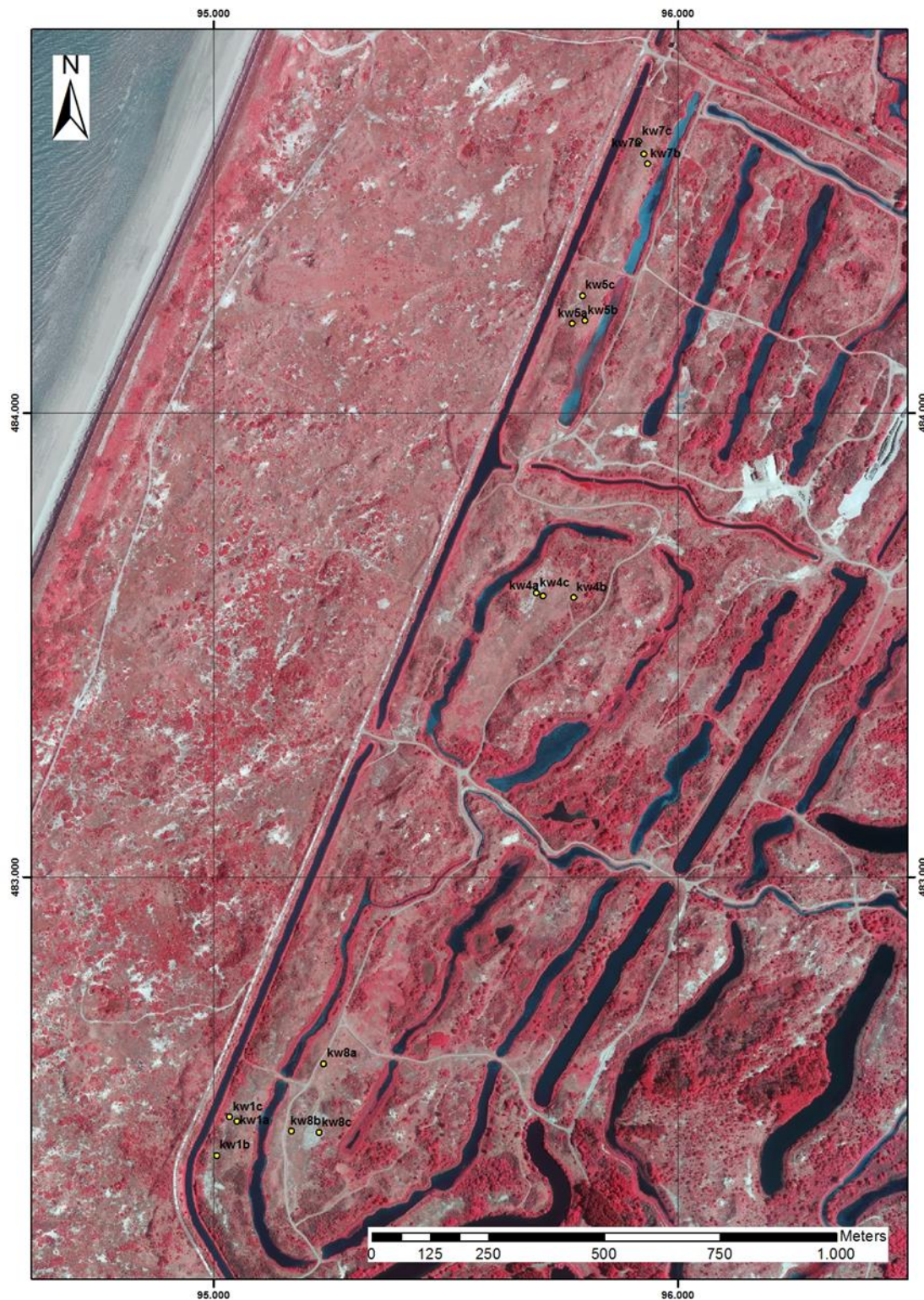


Figure 6-5. Map of the Infiltration Area with the location of plots, at the Amsterdam Water Supply Dunes (AWD).

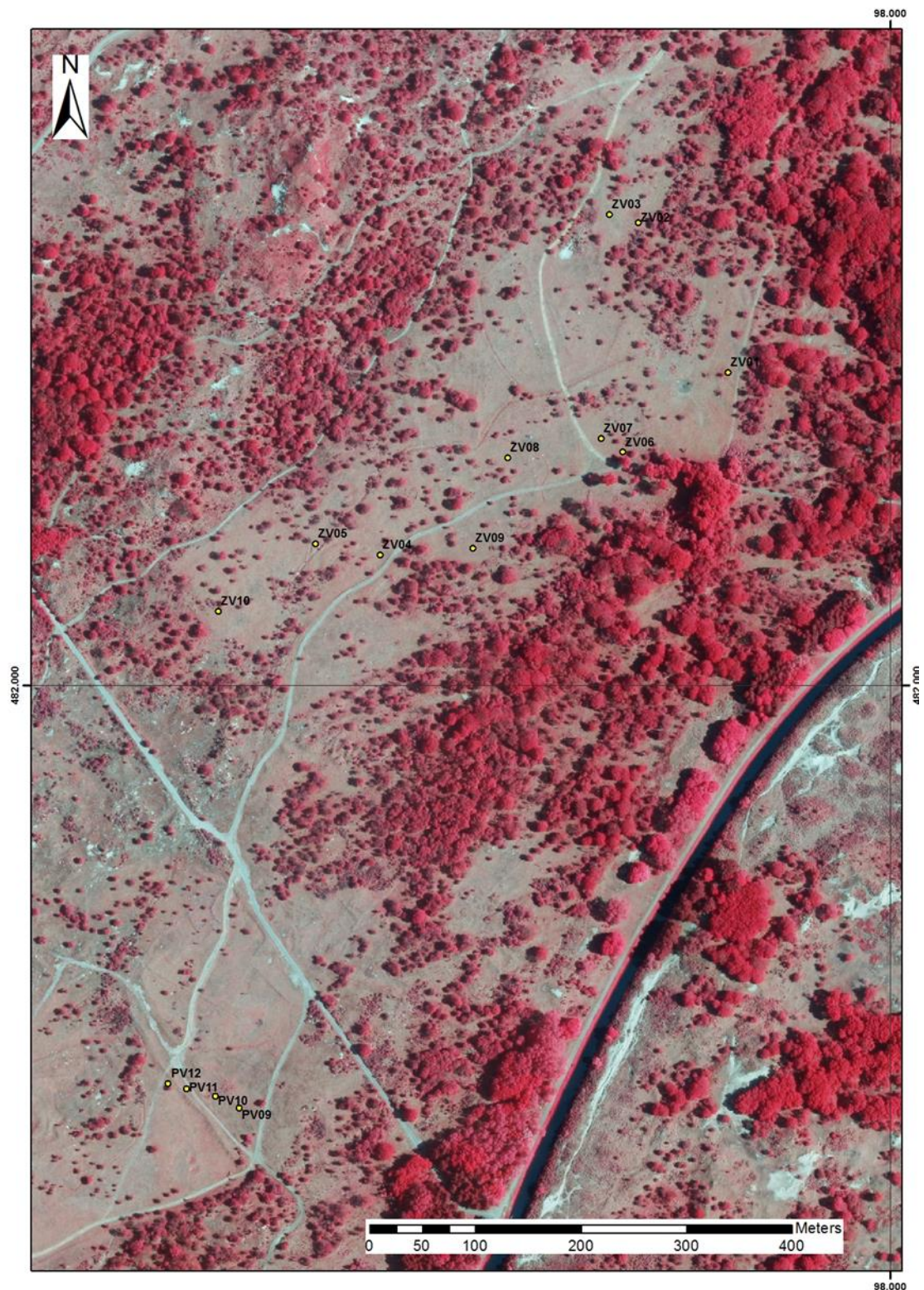


Figure 6-6. Map of Palmveld & Zegveld with the location of plots, at the Amsterdam Water Supply Dunes (AWD).

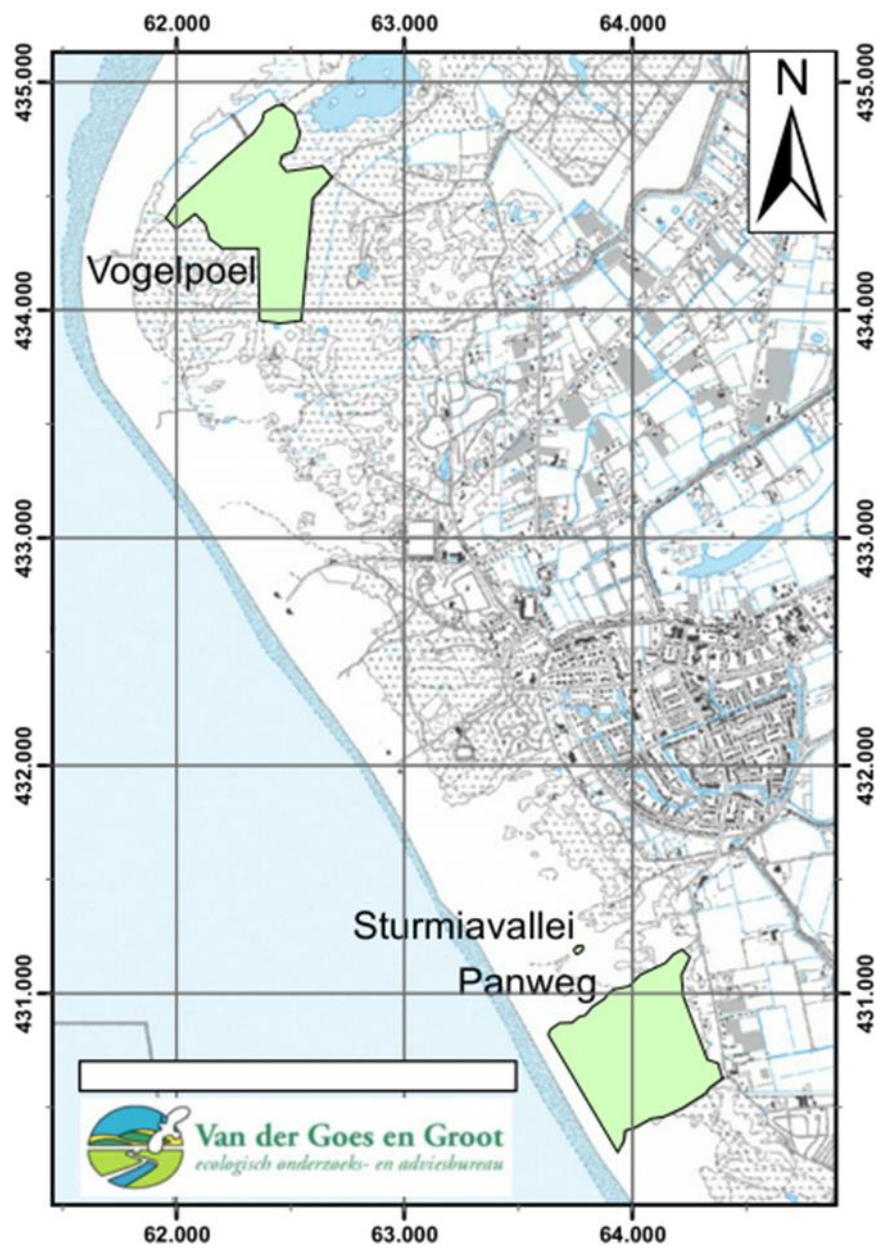


Figure 6-7. Overview map of Panweg and Vogelpoel at Voornes Duin



Figure 6-8. Map of Panweg with the locations of the monitored plots at Voornes Duin.

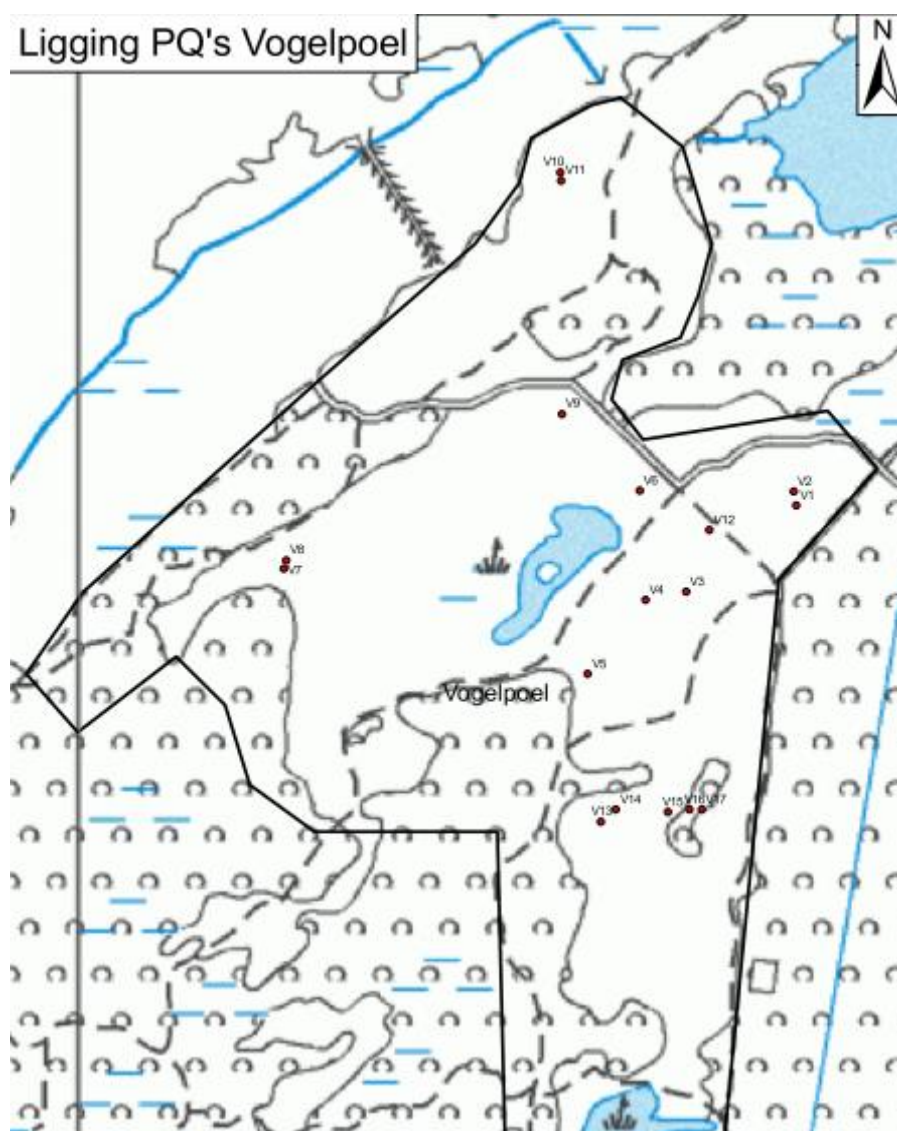


Figure 6-9. Map of Vogelpoel with the locations of the monitored plots at Voornes Duin.

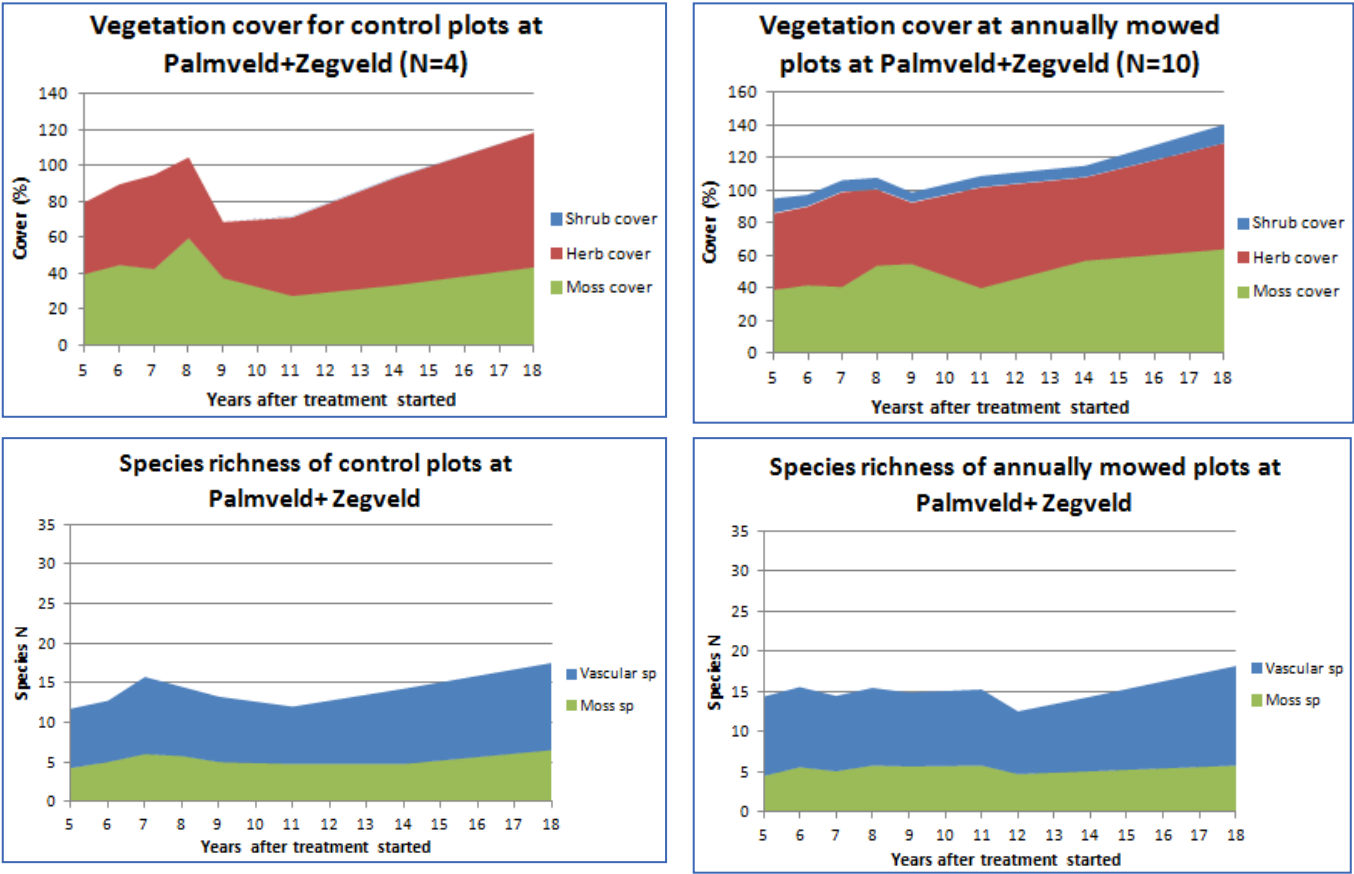


Figure 6-10. Vegetation cover (top) and species richness (bottom) after mowing of Palmveld + Zegveld, averaged per monitoring year. Graphed for (left) control and (right) mowed plots at Palmveld + Zegveld, at the Amsterdam Water Supply Dunes (AWD).

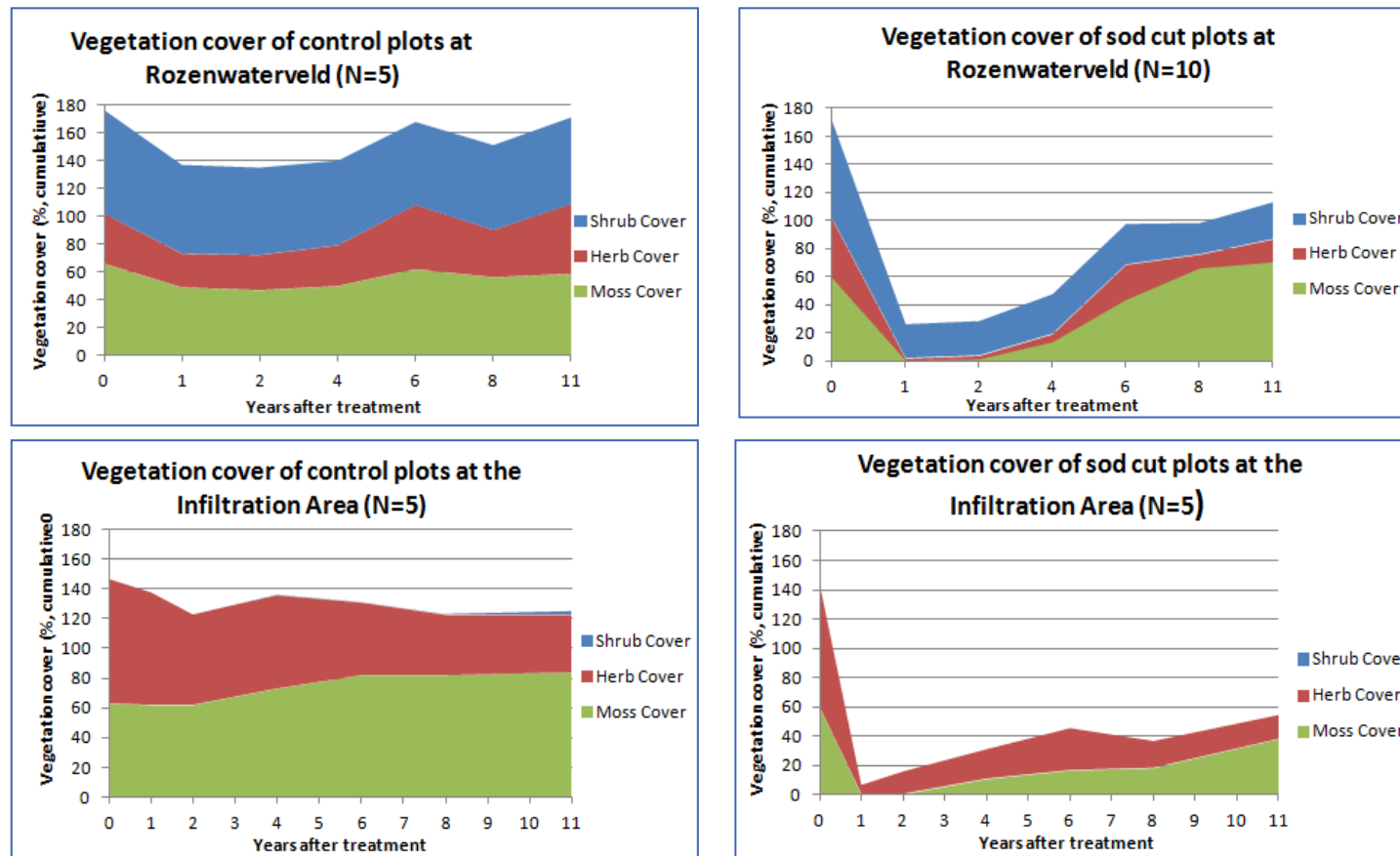


Figure 6-11. Vegetation cover after sod cutting at Rozenwaternveld (top) and Infiltration Area (bottom), both in the Amsterdam Water Supply Dunes (AWD), averaged per monitoring year. Data are shown for control plots (left) and sod cut plots (right).

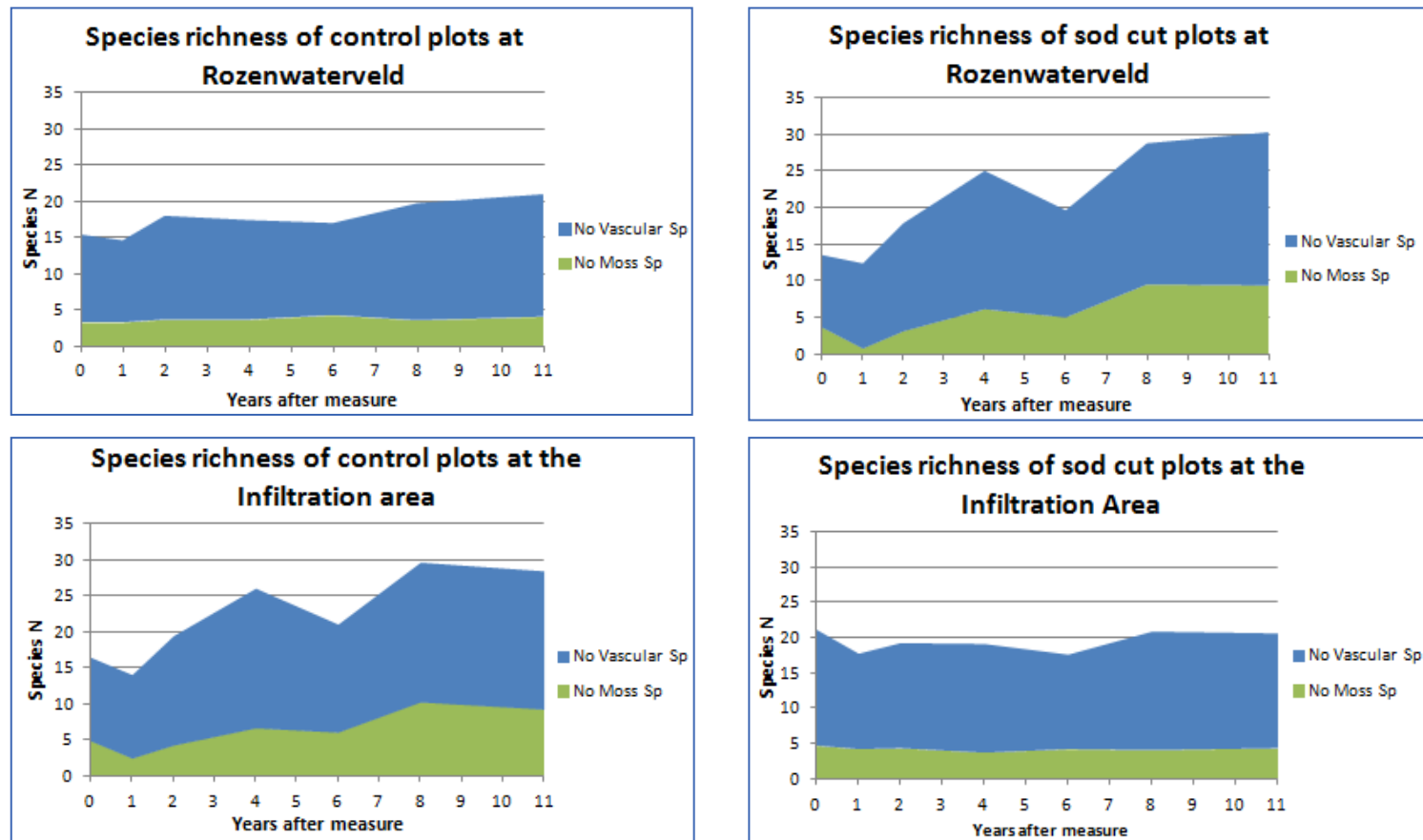


Figure 6-12. Species richness after sod cutting at Rozenwaterveld (top) and Infiltration Area (bottom), both in the Amsterdam Water Supply Dunes (AWD), averaged per monitoring year. Data are shown for control plots (left) and sod cut plots (right).

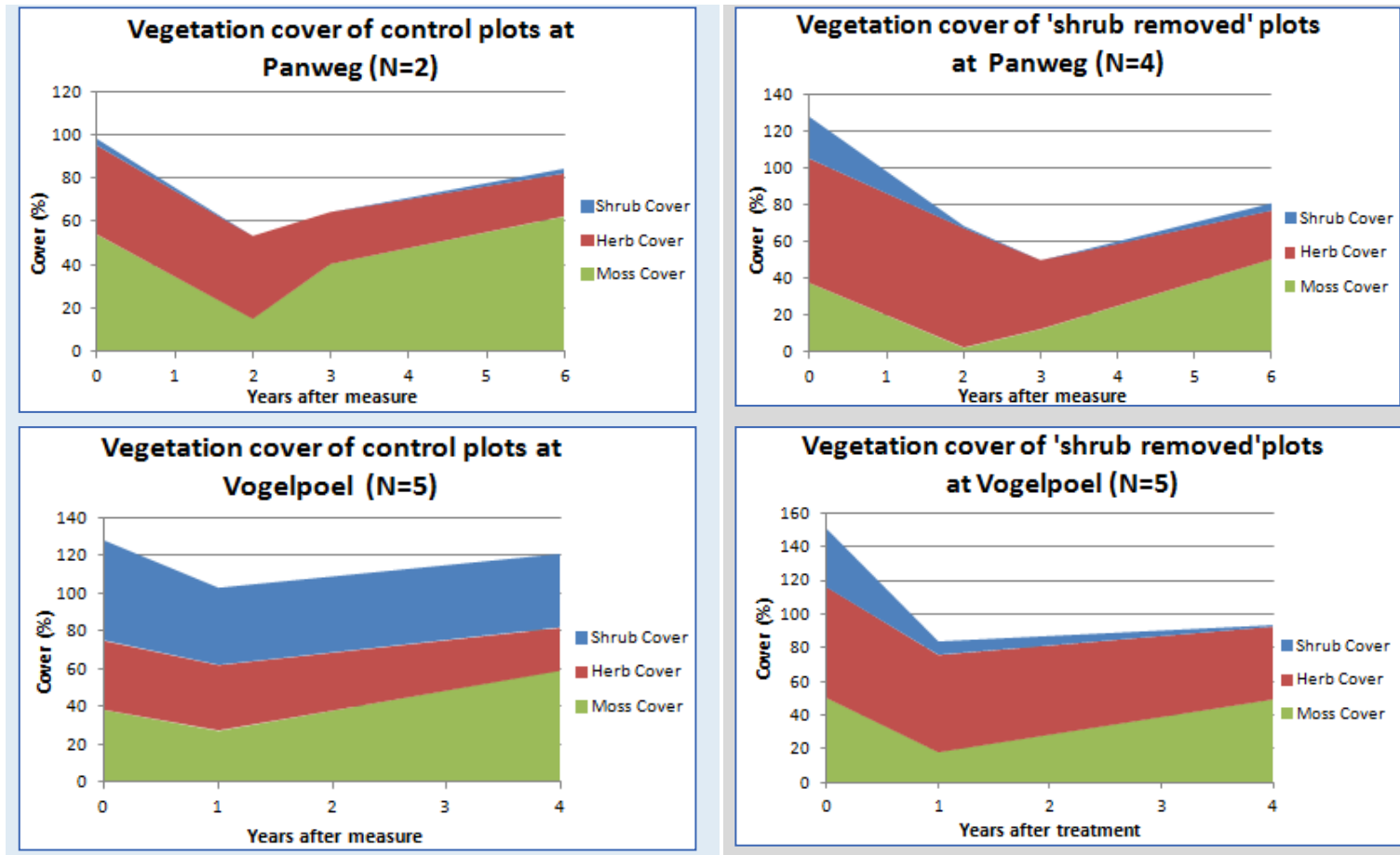


Figure 6-13. Vegetation cover after shrub removal at Panweg (top) and Vogelpoel (bottom), both in Voornes Duin, averaged per monitoring year. Data are shown for control plots (left) and shrub-removed plots (right).

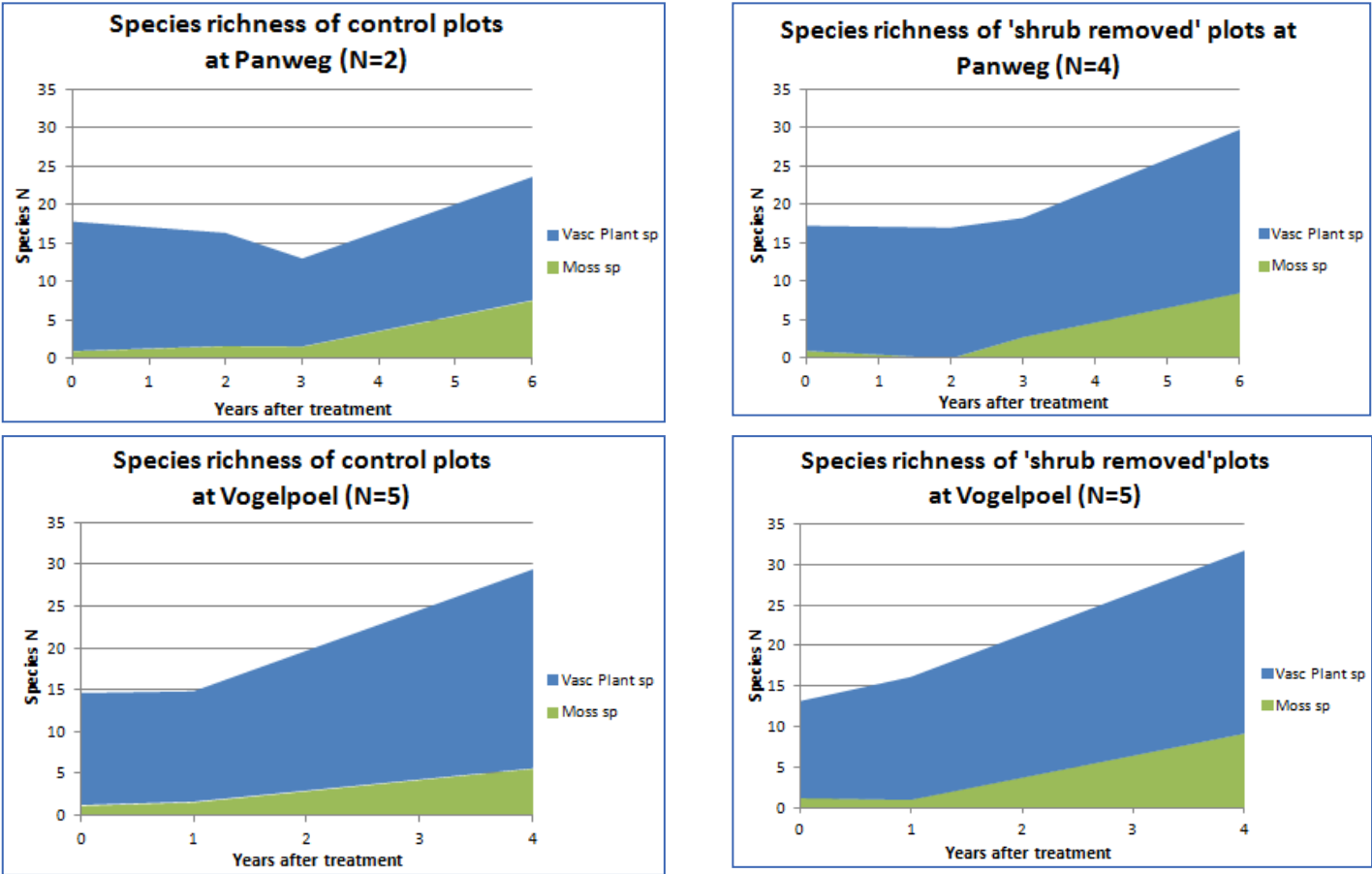


Figure 6-14. Species richness after shrub removal at Panweg (top) and Vogelpoel (bottom), both in Voornes Duin, averaged per monitoring year. Data are shown for control plots (left) and shrub-removed plots (right).

Table 6.5. List of species typical for Grey Dunes, used for calculation of saturation index [Aggenbach unpublished].

Species	funct gr.	ecological species group
<i>Achillea millefolium</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Agrostis canina</i>	kruid	wet duneslack vegetation nutrient-poor base-poor
<i>Agrostis capillaris</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Agrostis gigantea</i>	kruid	dry forest edge and forb vegetation base-rich
<i>Agrostis stolonifera</i>	kruid	wet grassland nutrient-rich
<i>Agrostis vinealis</i>	kruid	dry dune grassland nutrient-poor base-poor
<i>Aira praecox</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Allium vineale</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Ammophila arenaria</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Aneura pinguis</i>	mos	wet pioneer vegetation nutrient-poor base-rich
<i>Anthoxanthum odoratum</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Anthyllis vulneraria</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Arenaria serpyllifolia</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Arrhenatherum elatius</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Barbula convoluta</i>	mos	dry pioneer vegetation nutrient-poor lime-rich
<i>Betula pendula</i>	boom	shrub and forest
<i>Betula pubescens</i>	boom	shrub and forest
<i>Blackstonia perfoliata</i> s. <i>serotina</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Bolboschoenus maritimus</i>	kruid	salt grassland
<i>Brachythecium albicans</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Brachythecium mildeanum</i>	mos	wet grassland nutrient-rich
<i>Brachythecium rutabulum</i>	mos	grassland nutrient-rich
<i>Briza media</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Bromus hordeaceus</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Bryum capillare</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Bryum pseudotriquetrum</i>	mos	wet duneslack vegetation nutrient-poor base-rich
<i>Bryum rubens</i> s.s.	mos	unknown
<i>Bryum</i> species	mos	unknown
<i>Calamagrostis epigejos</i>	kruid	grassland nutrient-rich
<i>Calliergonella cuspidata</i>	mos	wet duneslack vegetation nutrient-poor base-rich
<i>Campylopus introflexus</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Cardamine pratensis</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Carex arenaria</i>	kruid	dry dune grassland nutrient-poor
<i>Carex caryophyllea</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Carex disticha</i>	kruid	wet marsh vegetation nutrient-rich
<i>Carex flacca</i>	kruid	wet duneslack vegetation nutrient-poor base-rich
<i>Carex hirta</i>	kruid	wet grassland nutrient-rich
<i>Carex nigra</i>	kruid	wet duneslack vegetation nutrient-poor base-poor
<i>Carex nigra</i> x <i>trinervis</i>	kruid	wet duneslack vegetation nutrient-poor base-poor
<i>Carex oederi</i> s. <i>oederi</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Carex panicea</i>	kruid	wet duneslack vegetation nutrient-poor base-rich

Species	funct gr.	ecological species group
<i>Carex trinervis</i>	kruid	wet duneslack vegetation nutrient-poor base-poor
<i>Centaurea jacea</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Centaureum erythraea</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Centaureum littorale</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Centunculus minimus</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Cerastium arvense</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Cerastium fontanum</i>	kruid	grassland nutrient-rich
<i>Cerastium fontanum s. vulgare</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Cerastium semidecandrum</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Cerastium species</i>	kruid	unknown
<i>Ceratodon purpureus</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Cirsium arvense</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Cirsium palustre</i>	kruid	wet grassland nutrient-rich
<i>Cirsium vulgare</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Cladina ciliata</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladina portentosa</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladonia ciliata</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia foliacea</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladonia furcata</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladonia glauca</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia grayi</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia humilis</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladonia portentosa</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia ramulosa</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia rangiformis</i>	korstmos	dry dune grassland nutrient-poor base-rich
<i>Cladonia rei</i>	korstmos	heathgrasslands nutrient-poor weakly-buffered
<i>Cladonia scabriuscula</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Cladonia subulata</i>	korstmos	dry dune grassland nutrient-poor base-poor
<i>Convolvulus arvensis</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Convolvulus sepium</i>	kruid	wet forb vegetation nutrient-rich
<i>Cornus sanguinea</i>	kruid	shrub and forest base-rich
<i>Corynephorus canescens</i>	kruid	dry dune grassland nutrient-poor
<i>Crataegus monogyna</i>	struik	shrub and forest base-rich
<i>Crepis capillaris</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Cynosurus cristatus</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Dactylis glomerata</i>	kruid	grassland nutrient-rich
<i>Dactylorhiza majalis s. praetermissa</i>	kruid	wet duneslack vegetation nutrient-poor base-rich
<i>Dactylorhiza species</i>	kruid	unknown
<i>Danthonia decumbens</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Dicranum scoparium</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Drepanocladus aduncus</i>	mos	wet duneslack vegetation nutrient-poor base-rich
<i>Drepanocladus polygamus</i>	mos	wet duneslack vegetation nutrient-poor base-rich
<i>Eleocharis palustris</i>	kruid	wet pioneer vegetation nutrient-rich

Species	funct gr.	ecological species group
<i>Eleocharis quinqueflora</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Elytrigia atherica</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Elytrigia maritima</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Elytrigia repens</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Epilobium hirsutum</i>	kruid	wet forb vegetation nutrient-rich
<i>Epilobium montanum</i>	kruid	shrub and forest base-rich
<i>Epilobium parviflorum</i>	kruid	wet pioneer vegetation nutrient-rich
<i>Epilobium tetragonum</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Epipactis palustris</i>	kruid	wet duneslack vegetation nutrient-poor base-rich
<i>Equisetum arvense</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Equisetum palustre</i>	kruid	wet grassland nutrient-rich
<i>Equisetum x moorei</i>	kruid	dry forest edge and forb vegetation base-rich
<i>Erodium cicutarium</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Erodium cicutarium s. dunense</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Erodium lebelii</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Erophila verna</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Eryngium campestre</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Euonymus europaeus</i>	kruid	shrub and forest base-rich
<i>Eupatorium cannabinum</i>	kruid	wet forb vegetation nutrient-rich
<i>Euphrasia stricta</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Euphrasia tetraquetra</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Eurhynchium praelongum</i>	mos	shrub and forest base-rich
<i>Fallopia convolvulus</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Festuca arenaria</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Festuca arundinacea</i>	kruid	wet grassland nutrient-rich
<i>Festuca filiformis</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Festuca rubra</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Fragaria vesca</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Galium aparine</i>	kruid	dry forest edge and forb vegetation base-rich
<i>Galium mollugo</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Galium palustre</i>	kruid	wet marsh vegetation nutrient-rich
<i>Galium saxatile</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Galium uliginosum</i>	kruid	wet grassland nutrient-rich
<i>Galium verum</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Gentianella campestris</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Geranium molle</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Glechoma hederacea</i>	kruid	shrub and forest base-rich
<i>Gnaphalium luteo-album</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Helictotrichon pubescens</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Hieracium pilosella</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Hieracium umbellatum</i>	kruid	dry dune grassland nutrient-poor
<i>Hippophae rhamnoides</i>	kruid	shrub and forest base-rich
<i>Holcus lanatus</i>	kruid	mesophytic grassland moderately nutrient-rich

Species	funct gr.	ecological species group
<i>Holcus mollis</i>	kruid	shrub and forest base-poor
<i>Homalothecium lutescens</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Hydrocotyle vulgaris</i>	kruid	wet duneslack vegetation nutrient-poor
<i>Hypericum perforatum</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Hypnum cupressiforme</i> + <i>jutlandicum</i>	mos	dry dune grassland nutrient-poor
<i>Hypnum cupressiforme</i> s.l. species	mos	dry dune grassland nutrient-poor
<i>Hypnum cupressiforme</i> v. <i>lacunosum</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Hypochaeris radicata</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Isolepis setacea</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Jacobaea vulgaris</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Jasione montana</i>	kruid	dry dune grassland nutrient-poor base-poor
<i>Juncus alpinoarticulatus</i> s. <i>atricapillus</i>	kruid	wet duneslack vegetation nutrient-poor base-rich
<i>Juncus articulatus</i>	kruid	wet pioneer vegetation nutrient-rich
<i>Juncus bufonius</i>	kruid	wet pioneer vegetation nutrient-rich wet pioneer vegetation nutrient-poor weakly buffered
<i>Juncus bulbosus</i>	kruid	
<i>Juncus conglomeratus</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Juncus conglomeratus</i> x <i>effusus</i>	kruid	wet grassland nutrient-rich
<i>Juncus effusus</i>	kruid	wet grassland nutrient-rich
<i>Juncus inflexus</i>	kruid	wet grassland nutrient-rich
<i>Juncus maritimus</i>	kruid	salt grassland
<i>Juncus subnodulosus</i>	kruid	wet marsh vegetation nutrient-rich
<i>Kindbergia praelonga</i>	mos	shrub and forest base-rich
<i>Koeleria macrantha</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Leontodon autumnalis</i>	kruid	wet grassland nutrient-rich
<i>Leontodon saxatilis</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Ligustrum vulgare</i>	kruid	shrub and forest base-rich
<i>Linaria vulgaris</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Linum catharticum</i>	kruid	wet duneslack vegetation nutrient-poor base-rich wet pioneer vegetation nutrient-poor weakly buffered
<i>Littorella uniflora</i>	kruid	
<i>Lolium perenne</i>	kruid	grassland nutrient-rich
<i>Lonicera periclymenum</i>	kruid	shrub and forest base-poor
<i>Lotus corniculatus</i> + L. 'Sativus'	kruid	dry dune grassland nutrient-poor base-rich
<i>Lotus pedunculatus</i>	kruid	wet grassland nutrient-rich
<i>Luzula campestris</i>	kruid	dry dune grassland nutrient-poor
<i>Lycopus europaeus</i>	kruid	wet marsh vegetation nutrient-rich
<i>Lythrum salicaria</i>	kruid	wet marsh vegetation nutrient-rich
<i>Medicago lupulina</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Mentha aquatica</i>	kruid	wet marsh vegetation nutrient-rich
<i>Moehringia trinervia</i>	kruid	shrub and forest base-rich
<i>Myosotis laxa</i> s. <i>cespitosa</i>	kruid	wet marsh vegetation nutrient-rich
<i>Myosotis ramosissima</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Odontites vernus</i> s. <i>serotinus</i>	kruid	salt grassland

Species	funct gr.	ecological species group
<i>Ononis repens</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Ophioglossum vulgatum</i>	kruid	wet duneslack vegetation nutrient-poor base-rich
<i>Ornithopus perpusillus</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Parentucellia viscosa</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Pellia endiviifolia</i>	mos	wet duneslack vegetation nutrient-poor base-rich
<i>Pellia epiphylla</i>	mos	shrub and forest base-rich
<i>Peltigera</i> species	korstmos	unknown
<i>Phleum arenarium</i>	kruid	dry pioneer vegetation nutrient-poor lime-rich
<i>Phleum pratense</i>	kruid	dry dune grassland nutrient-poor
<i>Phragmites australis</i>	kruid	wet marsh vegetation nutrient-rich
<i>Picris hieracioides</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Plagiomnium affine</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Plagiomnium medium</i>	mos	mesophytic grassland moderately nutrient-rich
<i>Plagiomnium undulatum</i>	mos	shrub and forest base-rich
<i>Plantago coronopus</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Plantago lanceolata</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Plantago major</i> s. <i>major</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Pleurozium schreberi</i>	mos	heathland nutrient-poor acid
<i>Poa pratensis</i>	kruid	dry dune grassland nutrient-poor
<i>Poa trivialis</i>	kruid	grassland nutrient-rich
<i>Pohlia nutans</i>	mos	shrub and forest base-poor
<i>Polygala vulgaris</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Polygonum aviculare</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Polytrichum commune</i>	mos	wet duneslack vegetation nutrient-poor base-poor
<i>Polytrichum formosum</i>	mos	shrub and forest base-poor
<i>Polytrichum juniperinum</i>	mos	dry dune grassland nutrient-poor base-rich
<i>Polytrichum juniperinum</i> v. <i>juniperinum</i>	mos	dry dune grassland nutrient-poor base-poor
<i>Potentilla anglica</i>	kruid	wet grassland nutrient-rich
<i>Potentilla anserina</i>	kruid	wet grassland nutrient-rich
<i>Potentilla erecta</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Potentilla reptans</i>	kruid	wet grassland nutrient-rich
<i>Prunella vulgaris</i>	kruid	wet grassland nutrient-rich
<i>Prunus serotina</i>	kruid	shrub and forest base-poor
<i>Pseudoscleropodium purum</i>	mos	dry dune grassland nutrient-poor
<i>Pulicaria dysenterica</i>	kruid	wet grassland nutrient-rich
<i>Quercus robur</i>	boom	shrub and forest
<i>Radiola linoides</i>	kruid	wet pioneer vegetation nutrient-poor base-rich
<i>Ranunculus acris</i>	kruid	grassland nutrient-rich
<i>Ranunculus bulbosus</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Ranunculus flammula</i>	kruid	wet duneslack vegetation nutrient-poor
<i>Ranunculus repens</i>	kruid	grassland nutrient-rich
<i>Rhamnus cathartica</i>	struik	shrub and forest base-rich
<i>Rhamnus frangula</i>	struik	shrub and forest base-poor

Species	funct gr.	ecological species group
Rhinanthus angustifolius	kruid	wet grassland nutrient-rich
Rhynchosstegium confertum	mos	shrub and forest base-rich
Rhynchosstegium megapolitanum	mos	dry dune grassland nutrient-poor base-rich
Rhytidiadelphus squarrosus	mos	mesophytic grassland moderately nutrient-rich
Riccardia chamedryfolia	mos	wet duneslack vegetation nutrient-poor base-rich wet pioneer vegetation nutrient-poor weakly buffered
Riccardia incurvata	mos	
Rosa canina s.l.	struik	shrub and forest base-rich
Rosa pimpinellifolia	kruid	dry dune grassland nutrient-poor base-rich
Rubus caesius	kruid	droge zomen en ruigten basenrijk
Rubus nemoralis f. laciniatus	struik	shrub and forest base-poor
Rubus plicatus	struik	shrub and forest base-poor
Rubus scissus	struik	shrub and forest base-poor
Rubus species	struik	unknown
Rubus ulmifolius	struik	shrub and forest base-rich
Rumex acetosa	kruid	grassland nutrient-rich
Rumex acetosella	kruid	dry dune grassland nutrient-poor base-rich
Rumex crispus	kruid	wet grassland nutrient-rich
Rumex obtusifolius	kruid	dry forest edge and forb vegetation base-rich
Sagina apetala s.s.	kruid	pioneer vegetation
Sagina nodosa	kruid	wet pioneer vegetation nutrient-poor base-rich
Sagina procumbens	kruid	pioneer vegetation
Salix alba	boom	shrub and forest base-rich
Salix cinerea	struik	shrub and forest base-rich
Salix purpurea	boom	shrub and forest base-rich
Salix repens	kruid	indifferent
Salix species	struik	shrub and forest
Samolus valerandi	kruid	wet pioneer vegetation nutrient-poor base-rich
Satureja acinos	kruid	dry dune grassland nutrient-poor base-rich
Saxifraga tridactylites	kruid	dry pioneer vegetation nutrient-poor lime-rich
Schoenoplectus tabernaemontani	kruid	wet marsh vegetation nutrient-rich
Schoenus nigricans	kruid	wet duneslack vegetation nutrient-poor base-rich
Sedum acre	kruid	dry pioneer vegetation nutrient-poor lime-rich
Sedum album	kruid	dry pioneer vegetation nutrient-poor lime-rich
Senecio species	kruid	unknown
Senecio sylvaticus	kruid	dry pioneer and field vegetation nutrient rich
Silene nutans	kruid	dry dune grassland nutrient-poor base-rich
Stellaria graminea	kruid	mesophytic grassland moderately nutrient-rich
Stellaria uliginosa	kruid	wet grassland nutrient-rich
Syntrichia ruralis sl	mos	dry pioneer vegetation nutrient-poor lime-rich
Taraxacum laevigatum	kruid	dry dune grassland nutrient-poor base-rich
Taraxacum sectie Erythrosperma	kruid	dry dune grassland nutrient-poor base-rich
Taraxacum sectie Hamata	kruid	wet grassland nutrient-rich
Taraxacum sectie Ruderalia	kruid	mesophytic grassland moderately nutrient-rich

Species	funct gr.	ecological species group
<i>Teesdalia nudicaulis</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Teucrium scorodonia</i>	kruid	shrub and forest base-poor
<i>Thymus pulegioides</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Tortula ruralis</i>	mos	dry pioneer vegetation nutrient-poor lime-rich
<i>Tortula ruralis</i> v. <i>arenicola</i>	mos	dry pioneer vegetation nutrient-poor lime-rich
<i>Trifolium arvense</i>	kruid	dry dune grassland nutrient-poor
<i>Trifolium campestre</i>	kruid	dry dune grassland nutrient-poor
<i>Trifolium dubium</i>	kruid	dry dune grassland nutrient-poor
<i>Trifolium fragiferum</i>	kruid	wet grassland nutrient-rich
<i>Trifolium pratense</i>	kruid	grassland nutrient-rich
<i>Trifolium repens</i>	kruid	grassland nutrient-rich
<i>Trifolium scabrum</i>	kruid	dry dune grassland nutrient-poor
<i>Trifolium striatum</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Triglochin palustris</i>	kruid	wet grassland nutrient-rich
<i>Trisetum flavescens</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Tussilago farfara</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Urtica dioica</i>	kruid	moist forb vegetation nutrient-rich
<i>Veronica arvensis</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Veronica officinalis</i>	kruid	heathgrasslands nutrient-poor weakly-buffered wet pioneer vegetation nutrient-poor weakly buffered
<i>Veronica serpyllifolia</i>	kruid	unknown
<i>Vicia cracca</i>	kruid	mesophytic grassland moderately nutrient-rich
<i>Vicia lathyroides</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Vicia sativa</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Vicia sativa</i> s. <i>nigra</i> + s. <i>segetalis</i>	kruid	dry pioneer and field vegetation nutrient rich
<i>Viola canina</i>	kruid	heathgrasslands nutrient-poor weakly-buffered
<i>Viola curtisii</i>	kruid	dry dune grassland nutrient-poor base-rich
<i>Viola hirta</i>	kruid	shrub and forest base-rich
<i>Vulpia myuros</i>	kruid	unknown

Table 6.6. Calculated averages and standard deviations of total cover, shrub cover, herb cover, and moss cover per location, for each treatment Years after treatment: VAR= year variable and different from other locations, >10 years. NA= Non-Available data. Average cover values are based on cover percentages that were estimated in the field.

Area Nr.	Location code	Treatment code	Number of plots	Years after treatment	Monitoring year	Total cover	Shrub cover	Herb cover	Moss cover	Total number of species	N. of vascular species	N. of moss species	N. of redlist species	Saturation index	<i>C.epihejos</i> abundance	<i>C.introflexus</i> abundance
1	ZDVL	CON	8	7	1998	97.3±18.2	NA	94.8±17	2.4±2.4	17±3	16.1±2.7	0.9±0.6	2.5±0.8	0.97±0.13	16.88±7.99	NA
1	ZDVL	MOW1x	4	7	1998	101.6±7.5	NA	97.8±8.8	3.9±2.6	16.3±5.2	15.3±4.6	1±0.8	3.3±0.5	1.52±0.3	3.13±4.79	NA
1	ZDVL	MOW	12	7	1998	71.6±17.5	NA	53.7±16.8	17.9±9.7	27.4±3.4	24.3±3.1	3.2±1.2	1.8±1.4	0.81±0.25	8.75±3.39	NA
1	ZDVL	SOD	12	7	1998	49.7±9.6	NA	46.5±10.3	3.1±2.7	17.9±3	16.4±2.8	1.5±0.9	1.3±0.8	0.93±0.22	2.92±1.78	NA
1	KRNSVL	CON	8	7	1998	91.9±17.6	NA	59.1±10.3	32.8±12.2	11.4±2.1	9.4±2.1	2±0.8	0.3±0.5	0.83±0.25	19.38±10.16	NA
1	KRNSVL	MOW1x	4	7	1998	110.4±10.1	NA	79.1±13.5	31.3±9.4	13.8±1.3	11.8±1.3	2±0	NA	1.05±0.06	0.54±12.14	NA
1	KRNSVL	MOW	12	7	1998	119±12.6	NA	59.1±7.4	59.8±15.7	15±1.7	13.8±1.4	1.3±0.5	0±0.4	0.91±0.15	14±0.75	NA
1	KRNSVL	SOD	12	7	1998	85.1±41.9	NA	44.8±23.4	40.3±24.6	13.8±1.8	10.3±1.5	3.4±1	NA	1.12±0.14	2.71±3.86	0.54±1.44
2	RZNV	CON	5	6	2008	99.8±0.4	60±15.8	46±5.5	62±27.7	17±4.4	12.8±4.2	4.2±1.1	0.4±0.9	1.17±0.24	30±12.25	NA
2	RZNV	SOD	10	6	2008	81±16.9	28.8±6.9	25±16.5	43.8±19	19.6±3	14.6±3	5±1.7	0.5±0.5	1.67±0.21	8.38±8.39	5.25±12.59
2	INFIL	CON	5	6	2008	95.4±6.2	0.2±0.4	49±24.1	82±10.4	18.8±3.9	15±4.1	6±0.9	NA	1.75±0.33	9.2±8.65	NA
2	INFIL	SOD	5	6	2008	40.6±36.8	NA	28.6±30	16.6±20.2	17.8±5.4	13.4±4.5	4.3±1.7	0.6±0.4	1.39±0.19	11.5±0.89	NA
2	PV+ZV	CON	4	6	1993	82.5±20.6	NA	25±23.8	45±46.5	12.8±2.5	7.8±1.5	5±3.7	NA	0.84±0.16	60±14.14	25.5±34.65
2	PV+ZV	MOW	10	6	1993	90.9±11.9	7±12.5	48±10.3	42±22.5	15.5±3.8	9.9±4.4	5.6±1.7	NA	1.19±0.42	14.86±18.52	0.83±0.29
2	TILP	CON	8	7	1998	79±22.8	NA	59.6±9	19.4±20.4	14.3±2.8	12.8±2.4	1.5±0.8	NA	1.19±0.22	4.38±6.78	NA
2	TILP	MOW1x	4	7	1998	65.6±7.8	NA	58±5.6	7.6±9.4	15.3±3.3	14.5±3.3	0.8±0.5	NA	0.91±0.1	NA	NA
2	TILP	MOW	12	7	1998	65.5±16.7	NA	39.5±11.1	26±9.7	17.5±2.2	12.8±2.5	4.8±1.7	NA	1.12±0.23	0±0.19	NA
2	TILP	SOD	12	7	1998	26.3±10.8	NA	24.7±11.1	1.6±1.5	13.1±1.6	11.4±1.5	1.7±0.8	NA	1.12±0.2	NA	NA
3	PANW	CON	6	6	2011	67.2±36.9	2.2±28	19.8±24.2	62.4±44.2	23.6±11.5	16±10.6	7.6±2.9	1.2±1	1.3±0.65	1.8±1.67	NA
3	PANW	SHRUB	4	6	2011	60.5±43.9	4±7.3	26.5±27.2	50.5±34.4	29.8±15.3	21.3±10.6	8.5±4.8	1.5±1	1.69±0.83	4±2.83	1±2

Area Nr.	Location code	Treatment code	Number of plots	Years after treatment	Monitoring year	Total cover	Shrub cover	Herb cover	Moss cover	Total number of species	N. of vascular species	N. of moss species	N. of redlist species	Saturation index	<i>C.epihejos</i> abundance	<i>C.introflexus</i> abundance
3	PANW	SHRUB+MOW	2	6	2011	57.5±31.8	0.5±0.7	22.5±17.7	35±49.5	21.5±6.4	18±11.3	3.5±4.9	1.5±2.1	1.19±0.27	1.5±2.12	NA
3	VGPL	CON	5	4	2011	73±20.5	73±33.6	23±14.8	59±14.3	29.4±3.8	23.8±5.9	5.6±3	1.4±0.9	1.25±0.2	3.2±1.1	NA
3	VGPL	MOW	2	4	2011	97±2.8	97±0	70±14.1	80±14.1	41±5.7	32±7.1	9±1.4	3.5±0.7	1.94±0.09	6±2.83	NA
3	VGPL	SHRUB	5	4	2011	70.8±26.3	70.8±2.2	43±22.8	49.2±43.7	31.8±5.8	22.6±3	9.2±5	2.4±1.1	1.62±0.42	3.6±0.55	NA
4	MID1	CON	8	7	1998	67.2±6.8	NA	67.1±6.7	0.1±0.2	5.9±1	5.8±0.7	0.1±0.4	NA	0.84±0.29	NA	NA
4	MID1	MOW1x	4	7	1998	82.8±9.1	NA	82.3±9.3	0.5±0.6	8±1.4	7.3±1.3	0.8±1	NA	1.19±0.23	NA	0.13±0.5
4	MID1	MOW	12	7	1998	77.6±10.8	NA	65.5±6.3	12.1±7.9	11±2.8	7.8±2.7	3.2±1.2	NA	0.87±0.1	0±3.89	0.25±0.31
4	MID1	SOD	12	7	1998	67.2±7.1	NA	58.7±7.3	8.5±6.6	12.1±1.6	7.4±1	4.7±1	NA	0.82±0.36	NA	0.92±1.92
4	MID2	CON	9	VAR	2013/2014	97.3±2.2	NA	79.3±21.3	28.6±25.8	30.2±7.7	4.8±1.6	25.4±8.7	0.9±1.1	2.29±0.43	NA	NA
4	MID2	MOW	9	VAR	2013/2014	99.1±0.8	NA	67.8±25.2	49.8±25.3	29.8±7.6	4.4±2.5	25.3±9.9	0.3±0.5	2.4±0.58	0.33±0.71	NA
4	MID2	SOD+MOW	10	VAR	2013/2014	69.9±26.7	NA	36±15.2	39.1±34.3	30.8±6.3	5.4±2.3	25.4±5.6	1±0.7	2.31±0.44	0.4±0.52	NA

Table 6.7. Calculated log response ratios with variances. Years after treatment: VAR= year variable and different from other locations, >10 years. NA= Non-Available data. Average cover values are based on cover percentages that were estimated in the field.

Area Nr.	Location code	Treatment code	Number of plots	Years after treatment	Monitoring year	Total cover	Shrub cover	Herb cover	Moss cover	Total number of species	N. of vascular species	N. of moss species	N. of redlist species	Saturation index	<i>C.epihejos</i> abundance	<i>C.introflexus</i> abundance
1	ZDVL	MOW1x	12	7	1998	0.04±0.01	NA	0.03±0.01	0.46±0.23	-0.05±0.03	-0.06±0.03	0.13±0.23	0.29±0.02	0.45±0.01	-1.69±0.61	NA
1	ZDVL	MOW	4	7	1998	-0.31±0.01	NA	-0.57±0.01	1.99±0.14	0.48±0.01	0.41±0	1.29±0.08	-0.36±0.07	-0.18±0.01	-0.66±0.04	NA
1	ZDVL	SOD	12	7	1998	-0.67±0.01	NA	-0.71±0.01	0.25±0.18	0.05±0.01	0.02±0.01	0.54±0.1	-0.63±0.04	-0.04±0.01	-1.76±0.06	NA
1	KRNSVL	MOW1x	12	7	1998	0.18±0.01	NA	0.29±0.01	-0.05±0.04	0.19±0.01	0.23±0.01	0±0.02	1.2±0.43	0.24±0.01	3.58±125.57	NA
1	KRNSVL	MOW	4	7	1998	0.26±0.01	NA	0±0.01	0.6±0.02	0.28±0.01	0.38±0.01	-0.47±0.03	NA	0.09±0.01	-0.32±0.03	NA
1	KRNSVL	SOD	12	7	1998	-0.08±0.02	NA	-0.28±0.03	0.21±0.05	0.19±0.01	0.1±0.01	0.54±0.02	NA	0.31±0.01	-1.97±0.2	NA
2	RZNV	SOD	10	6	2008	-0.21±0	-0.74±0.02	-0.61±0.05	-0.35±0.06	0.14±0.02	0.13±0.03	0.17±0.02	0.22±1.11	0.35±0.01	-1.28±0.13	NA
2	INFIL	SOD	5	6	2008	-0.85±0.16	NA	-0.54±0.27	-1.6±0.3	-0.05±0.03	-0.11±0.04	-0.34±0.04	0.45±0.1	-0.23±0.01	0.22±0.18	NA
2	PV+ZV	MOW	10	6	1993	0.1±0.02	NA	0.65±0.23	-0.07±0.3	0.2±0.02	0.24±0.03	0.11±0.14	NA	0.34±0.02	-1.4±0.17	-3.42±0.47
2	TILP	MOW1x	12	7	1998	-0.19±0.01	NA	-0.03±0.01	-0.93±0.52	0.07±0.02	0.13±0.02	-0.69±0.14	NA	-0.27±0.01	NA	NA
2	TILP	MOW	4	7	1998	-0.19±0.02	NA	-0.41±0.01	0.29±0.15	0.21±0.01	0±0.01	1.15±0.04	NA	-0.05±0.01	NA	NA
2	TILP	SOD	12	7	1998	-1.1±0.02	NA	-0.88±0.02	-2.5±0.21	-0.09±0.01	-0.11±0.01	0.11±0.05	NA	-0.05±0.01	NA	NA
3	PANW	SHRUB	4	6	2011	-0.11±0.18	0.6±27.75	0.29±0.51	-0.21±0.2	0.23±0.11	0.28±0.14	0.11±0.1	0.22±0.24	0.26±0.1	0.8±0.27	NA
3	PANW	SHRUB+MOW	2	6	2011	-0.16±0.2	1.48±27.91	0.13±0.56	-0.58±1.08	-0.09±0.08	0.12±0.27	-0.78±1.02	0.22±1.13	-0.09±0.07	-0.18±1.14	NA
3	VGPL	MOW	2	4	2011	0.28±0.02	0.28±0.04	1.11±0.1	0.3±0.03	0.33±0.01	0.3±0.04	0.47±0.07	0.92±0.1	0.44±0.01	0.63±0.13	NA
3	VGPL	SHRUB	5	4	2011	-0.03±0.04	-0.03±0.04	0.63±0.14	-0.18±0.17	0.08±0.01	-0.05±0.02	0.5±0.12	0.54±0.13	0.26±0.02	0.12±0.03	NA
4	MID1	MOW1x	12	7	1998	0.21±0	NA	0.2±0	2.08±1.33	0.31±0.01	0.23±0.01	1.79±1.41	NA	0.34±0.02	NA	NA
4	MID1	MOW	4	7	1998	0.14±0	NA	-0.02±0	5.27±1.03	0.63±0.01	0.31±0.01	3.23±1.01	NA	0.04±0.02	NA	NA
4	MID1	SOD	12	7	1998	0±0	NA	-0.13±0	4.91±1.05	0.72±0.01	0.25±0	3.62±1	NA	-0.03±0.03	NA	NA
4	MID2	MOW	9	VAR	VAR	0.02±0	NA	-0.16±0.02	0.56±0.12	-0.01±0.01	-0.07±0.05	0±0.03	-0.98±0.41	0.05±0.01	NA	NA
4	MID2	SOD+MOW	10	VAR	VAR	-0.33±0.01	NA	-0.79±0.03	0.31±0.17	0.02±0.01	0.12±0.03	0±0.02	0.12±0.2	0.01±0.01	NA	NA

6.3 Appendices of chapter 4

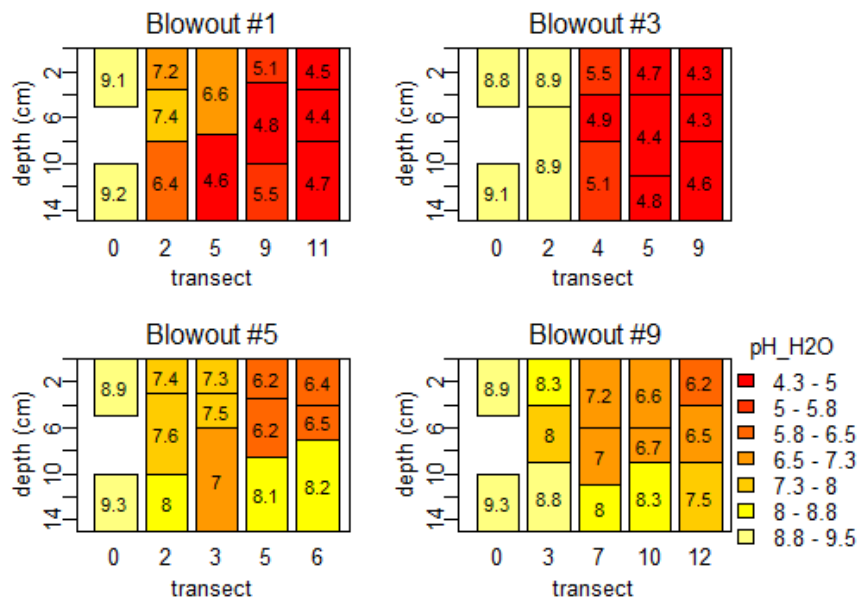


Figure 6-15. pH_{H_2O} values of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. pH_{H_2O} values within blowout (indicated as transect "0") are also shown for the depth 0-5cm and 10-15cm.

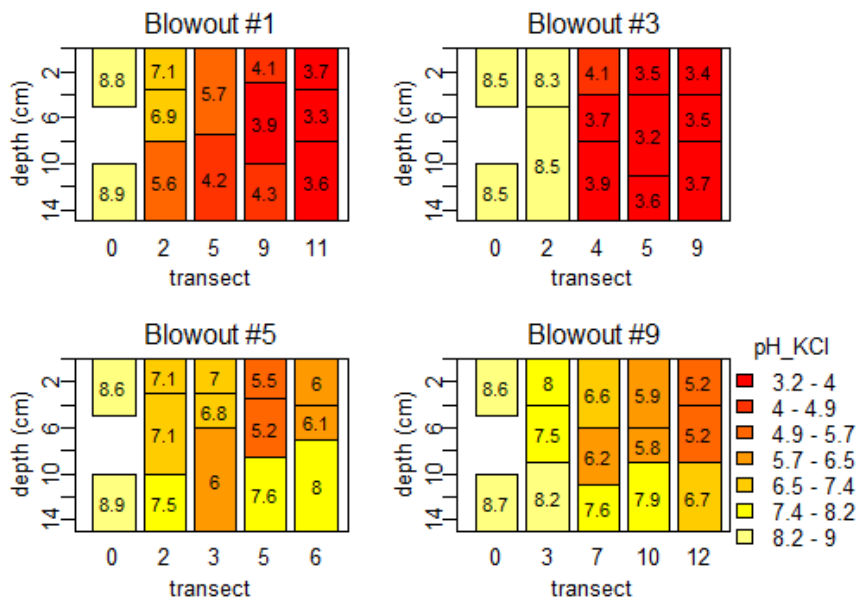


Figure 6-16. pH_{KCl} values of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. pH_{KCl} values within blowout (indicated as transect "0") are also shown for the depth 0-5cm and 10-15cm.

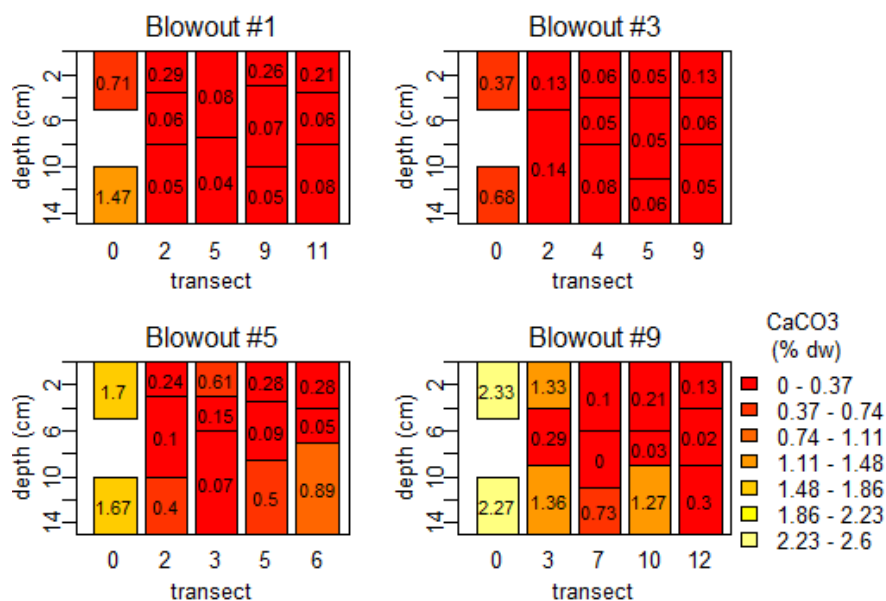


Figure 6-17. Calcium carbonate content (CaCO_3 % dry weight) of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. Carbonate content within blowout (indicated as transect "0") are also shown for the depth 0-5cm and 10-15cm.

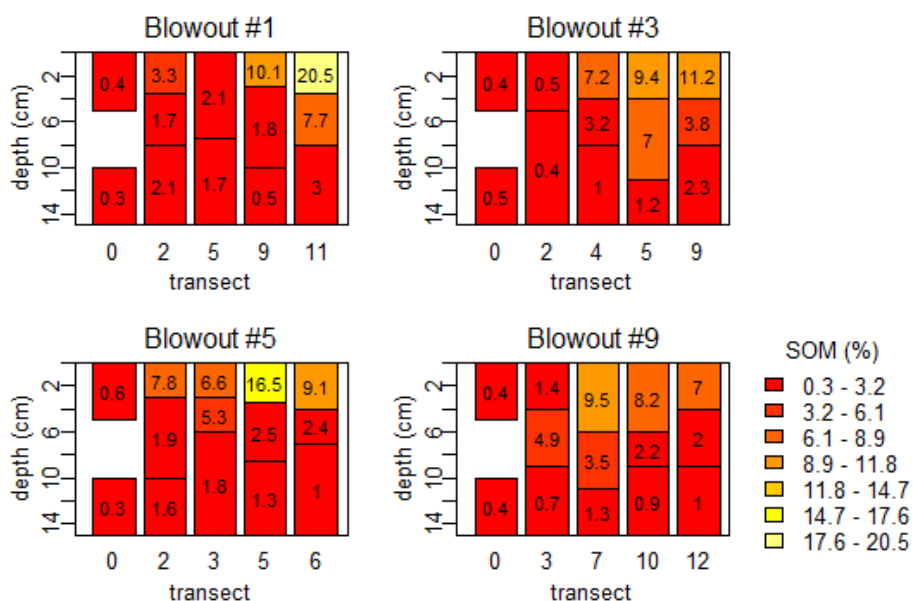


Figure 6-18. Soil organic matter content (%) of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. Soil organic matter content within blowout (indicated as transect "0") are also shown for the depth 0-5cm and 10-15cm.

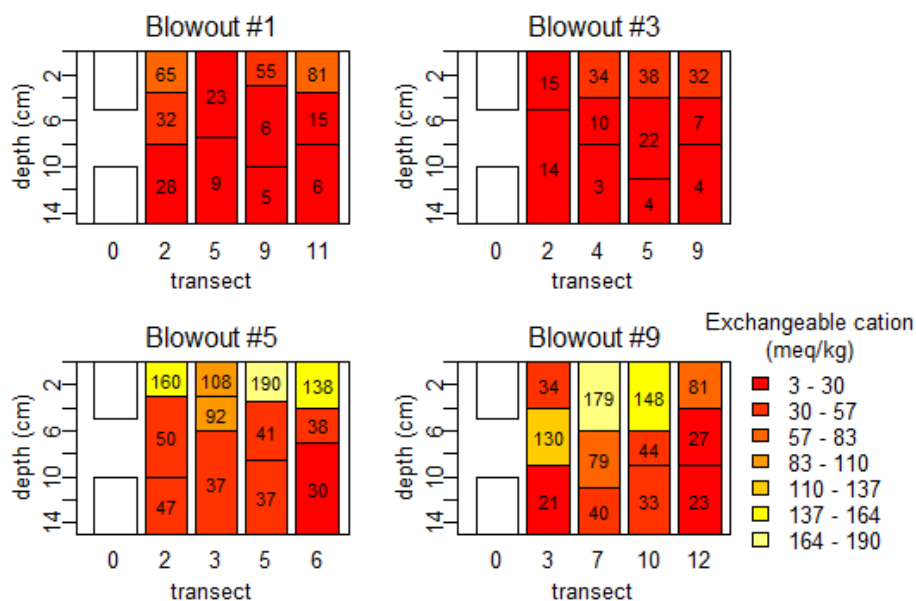


Figure 6-19. Total amount of exchangeable base cation (meq/kg soil) of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. Soils within blowouts (i.e. transect 0) have no values calculated.

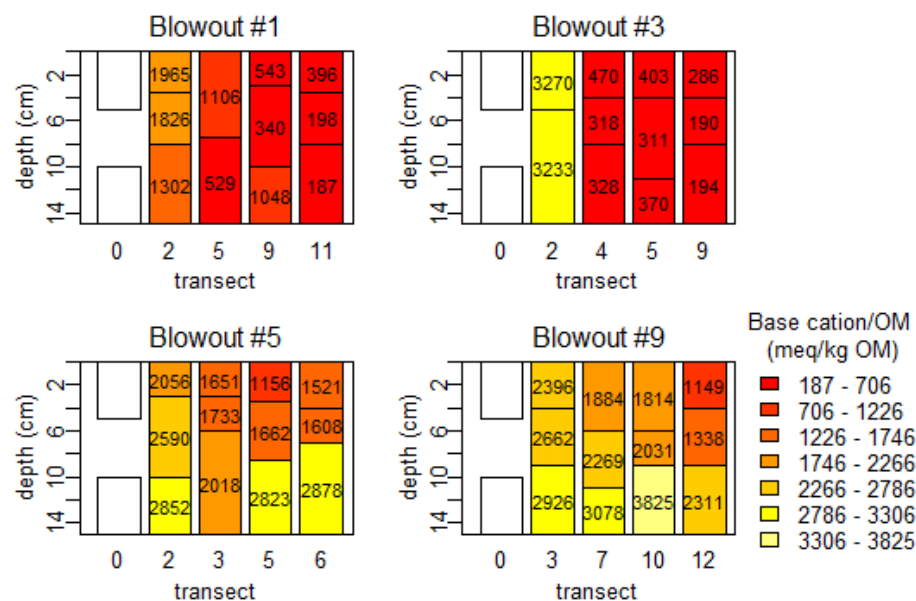


Figure 6-20. Proxy for base saturation (BC/SOM) of four extra soil sampling points on NE transect, for the three soil layers of 0-15cm depth. The proxy was calculated as total amount of exchangeable base cation (BC) divided by soil organic matter (SOM). Soils within blowouts (i.e. transect 0) have no values calculated.

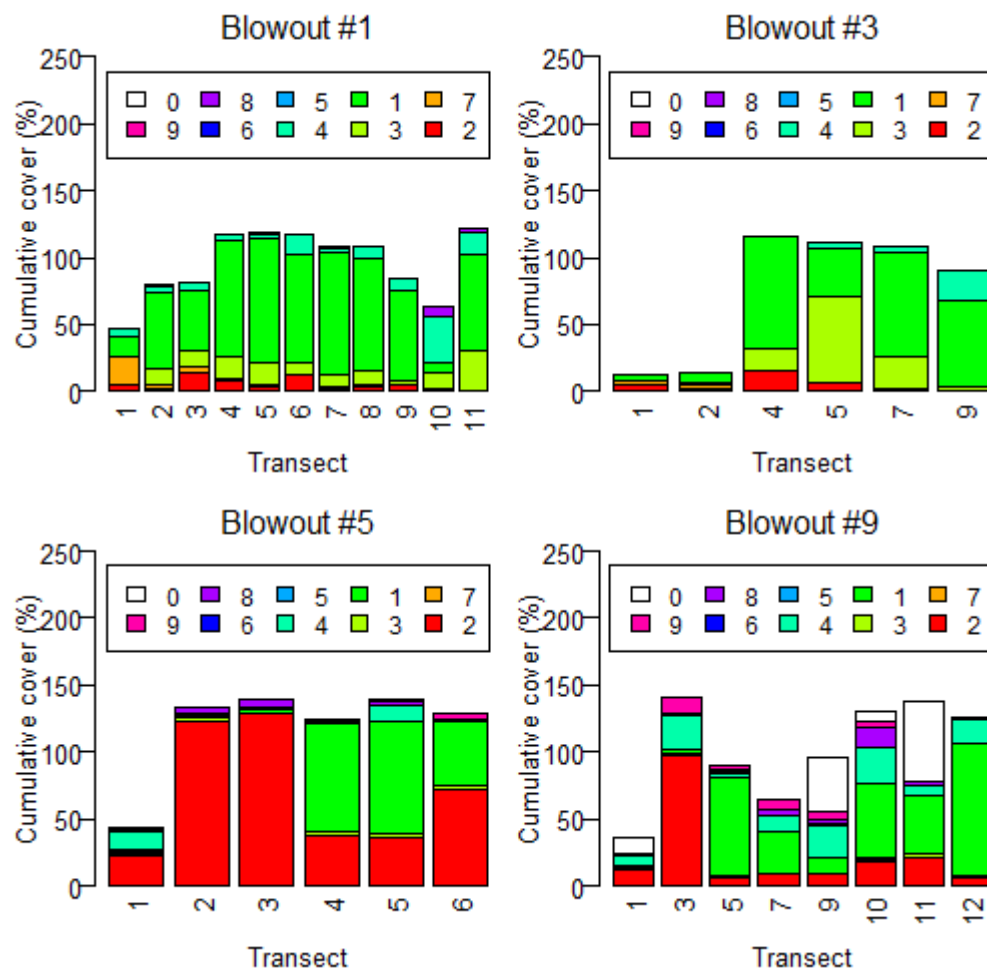


Figure 6-21. Cumulative cover of species of each plot on NE transects. See Figure 4-13 for the description of species group.

	%	%	-	-	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	µmol/g soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mmol/kg soil	mg/kg soil	mg/kg OM	mg/kg soil	mg/kg soil		
	SOM	LIME	pH_KCl	pH_H2O	Al_ex	Ca_ex	Fe_ex	K_ex	Mg_ex	Mn_ex	Na_ex	S_ex	Si_ex	Zn_ex	NH4_ex	des_Al	des_Ca	des_Fe	des_K	des_Mg	des_Mn	des_Na	des_P	des_Si	des_Zn	Carbonate	BS	cat_tot	cat_ex	
SOM	1.00	-0.37	-0.61	-0.62	0.18	0.57	0.18	0.67	0.89	0.62	0.74	0.77	0.29	0.75	0.60	0.47	-0.25	0.46	0.62	0.16	0.31	0.15	0.88	0.75	0.48	0.46	-0.46	0.40	0.64	-0.26
LIME	-0.37	1.00	0.48	0.48	-0.18	0.16	-0.14	0.05	0.09	0.12	-0.01	0.17	-0.02	0.08	-0.05	-0.18	0.46	0.00	-0.15	0.10	0.05	0.00	-0.29	-0.03	-0.11	-0.23	0.45	-0.42	0.16	0.45
pH_KCl	-0.61	0.48	1.00	0.99	-0.64	0.50	-0.63	0.18	-0.08	0.30	-0.29	0.24	0.19	-0.45	-0.15	-0.19	0.82	-0.05	-0.12	0.36	0.24	-0.19	-0.42	-0.23	-0.26	-0.16	0.88	-0.12	0.42	0.83
pH_H2O	-0.62	0.48	0.99	1.00	-0.61	0.46	-0.62	0.16	-0.10	0.26	-0.32	0.19	0.17	-0.45	-0.22	-0.21	0.80	-0.06	-0.15	0.33	0.22	-0.19	-0.42	-0.24	-0.30	-0.19	0.87	-0.10	0.39	0.81
Al_ex	0.18	-0.18	-0.64	-0.61	1.00	-0.57	0.83	-0.21	-0.11	-0.39	0.31	-0.32	-0.10	0.34	-0.08	0.14	-0.58	0.02	-0.18	-0.45	-0.40	0.25	-0.07	0.08	0.43	-0.21	-0.49	-0.61	-0.51	-0.60
Ca_ex	0.57	0.16	0.50	0.46	-0.57	1.00	-0.53	0.70	0.75	0.84	0.28	0.87	0.29	0.26	0.39	0.30	0.81	0.48	0.65	0.71	0.72	-0.13	0.68	0.60	0.09	0.51	0.56	0.52	0.99	0.81
Fe_ex	0.18	-0.14	-0.63	-0.62	0.83	-0.53	1.00	-0.19	-0.11	-0.41	0.30	-0.28	-0.10	0.19	0.09	0.05	-0.59	-0.08	-0.22	-0.45	-0.44	0.15	-0.04	0.02	0.47	-0.23	-0.49	-0.64	-0.48	-0.61
K_ex	0.67	0.05	0.18	0.16	-0.21	0.70	-0.19	1.00	0.73	0.68	0.50	0.76	0.28	0.37	0.36	0.46	0.55	0.56	0.67	0.54	0.67	0.03	0.74	0.69	0.33	0.53	0.37	0.15	0.74	0.55
Mg_ex	0.89	0.09	-0.08	-0.10	-0.11	0.75	-0.11	0.73	1.00	0.81	0.64	0.81	0.32	0.73	0.52	0.51	0.40	0.64	0.72	0.52	0.61	0.03	0.85	0.81	0.47	0.57	0.11	-0.03	0.81	0.40
Mn_ex	0.62	0.12	0.30	0.26	-0.39	0.84	-0.41	0.68	0.81	1.00	0.37	0.78	0.28	0.50	0.44	0.40	0.61	0.54	0.66	0.74	0.88	-0.15	0.72	0.62	0.22	0.57	0.42	0.31	0.87	0.63
Na_ex	0.74	-0.01	-0.29	-0.32	0.31	0.28	0.30	0.50	0.64	0.37	1.00	0.54	0.42	0.52	0.25	0.69	-0.03	0.64	0.44	0.34	0.35	0.15	0.61	0.61	0.75	0.28	-0.09	-0.32	0.35	0.01
S_ex	0.77	0.17	0.24	0.19	-0.32	0.87	-0.28	0.76	0.81	0.78	0.54	1.00	0.39	0.42	0.48	0.54	0.66	0.64	0.75	0.67	0.70	0.01	0.80	0.79	0.33	0.52	0.40	0.23	0.90	0.66
Si_ex	0.29	-0.02	0.19	0.17	-0.10	0.29	-0.10	0.28	0.32	0.28	0.42	0.39	1.00	0.08	0.01	0.46	0.21	0.44	0.43	0.47	0.37	-0.02	0.30	0.28	0.43	0.08	0.17	0.12	0.3	

