BTO 2020.024 | August 2020

BTO report

Effectiveness of measures to mitigate high nitrogen deposition in dry habitats

BTO

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Project number
402045.016 and 402045.107

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Client
BTO - Thematical research - Sources and environment

Quality Assurance
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Sent to
This report is distributed to BTO-participants and is public

Year of publishing
2020

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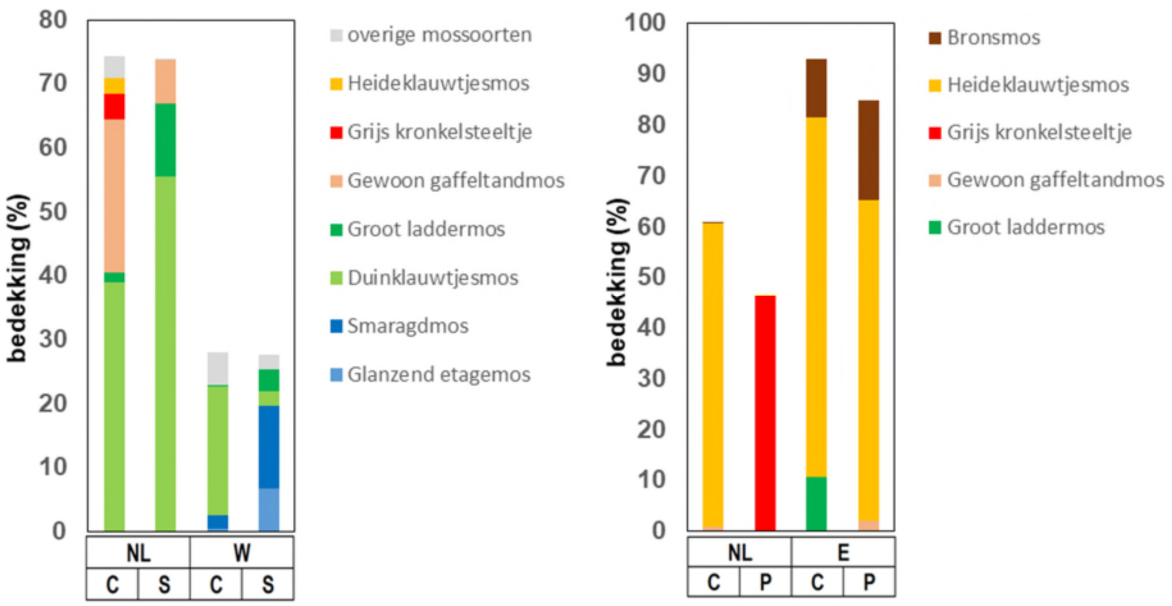
Keywords
nitrogen deposition, mitigation, dune grassland, heathland, ecological restoration

BTO *Management samenvatting*

Onderzoek naar effectiviteit van stikstofmitigerende maatregelen toont aan dat instuiving in duingraslanden werkt, maar plaggen van droge heiden niet

Auteurs: Drs. C.J.S. Aggenbach, Dr. Y. Fujita, MSc. A. Nanu, Prof. L. Jones, Dr. A.M. Kooijman,

Laagproductieve habitattypen binnenlandse zandgronden (H4030) en kustduinen (H2130) hebben al decennia te lijden van hoge stikstof (N)-depositie. Accumulatie van N in de bodem, N-uitspoeling naar het grondwater en verlies van kenmerkende plantensoorten zijn enkele effecten van deze hoge N-depositie. Om deze laagproductieve habitattypen te behouden en te herstellen worden N-mitigerende maatregelen toegepast. In dit BTO-onderzoek is van twee veel toegepaste N-mitigerende maatregelen de effectiviteit onderzocht: instuiving van kalkrijk zand op droge duingraslanden, en plaggen van droge heiden. Eerstgenoemde maatregel heeft geen gunstig effect op de N-beschikbaarheid, maar wel op de vegetatie. Bij plaggen van droge heiden wordt de netto N-mineralisatie sterk verlaagd en vrijwel alle aangevoerde N uit de lucht geaccumuleerd door micro-organismen, zodat op termijn bij opbouw van strooisel weer meer N-mineralisatie kan gaan optreden. Plaggen geeft geen herstel van droge heidevegetatie, maar leidde in het Nederlandse onderzoeksgebied tot ongewenste dominantie van de invasieve en N-minnende mossoort Grijs kronkelsteeltje.



Links het gemiddelde aandeel van mossoorten in duingraslandplots zonder (C) en met instuiving (S) van kalkrijk zand in Nederland (NL) en Wales (W). In Nederland is het aandeel van Duinklauwtjesmos hoger in plots met overstuiving, in Wales dat van Smaragdmos. Beide zijn basenminnende soorten.
Rechts: het gemiddelde aandeel van mossoorten in heideplots zonder (C) en met plaggen (P) in Nederland (NL) en Engeland (E). In Nederland leidt plaggen tot een dominantie van Grijs kronkelsteeltje, terwijl na plaggen in Engeland Heideklauwtjesmos en Bronsmos overheersen.

EINDCONCEPT

Belang: meer duidelijkheid over instandhouding schrale habitattypen bij hoge N-depositie

Een hoge atmosferische N-depositie is in Nederland een onopgelost milieuprobleem met sterk negatieve effecten op het voorkomen en de kwaliteit van nutriëntenarme habitattypen. In Nederland beoogt het Programma Aanpak Stikstof (PAS) bescherming van N-gevoelige habitattypen in Natura 2000-gebieden, door enerzijds geleidelijke vermindering van N-depositie, en anderzijds specifieke mitigerende maatregelen in en rond Natura 2000-gebieden te nemen voor behoud en herstel van habitattypen bij een hoge N-depositie. Dit zijn vaak 'reguliere' beheermaatregelen voor ecologisch herstel met beperkte wetenschappelijke onderbouwing voor hun mitigerende werking. De Nederlandse waterbedrijven hebben als natuurbeheerder en uitvoerder van PAS maatregelen behoefte aan meer zekerheid over de effectiviteit.

Aanpak: veldonderzoek in duin- en heidegebieden met hoge en lage N-depositie

Twee veel toegepaste mitigerende maatregelen zijn onderzocht op hun invloed op de N-huishouding en vegetatie: het stimuleren van instuiving van kalkrijk zand in droge duingraslanden en het plaggen van droge heiden. In vier gebieden (een duingebied met hoge N-depositie in Nederland (NL), een duingebied met een lage N-depositie in Wales (W), een heidegebied met een zeer hoge historische N-belasting in Nederland en een heidegebied met een minder hoge historische N-belasting in Engeland (E)) zijn plots geselecteerd met en zonder de maatregel. Daar zijn diverse bodemvariabelen onderzocht: afbraaksnelheid, N-huishouding (voorraden, mineralisatie, uitspoeling), productiviteit en soortensamenstelling van de vegetatie. De metingen zijn geanalyseerd op effecten van de maatregelen en N-depositie.

Resultaten: herstel vegetatie droog duingrasland door instuiving, geen herstel droge heide door plaggen

In duingraslanden leidt instuiving van kalkrijk zand niet tot een lagere voorraad organisch stofgehalte en N, maar verhoogt wel de bodem-pH (gunstig). Instuiving bevordert de afbraak van organische stof, maar de N-mineralisatie neemt niet toe (geen ongunstig effect). De soortenrijkdom verandert niet, maar de vegetatie herstelt wel door bevordering van basenminnende soorten.

In droge heiden zorgt plaggen voor een lagere voorraad van organische stof, totaal-N, ammonium, nitraat en fosfaat en voor een licht verhoogde pH. De netto N-mineralisatie en uitspoeling van N naar het grondwater dalen tot vrijwel nul, wat betekent dat de hoge N-aanvoer uit de lucht volledig wordt geaccumuleerd in de bodem. In ongeplagde heide treedt wel netto N-mineralisatie en -uitspoeling op. Plaggen leidt op een kortere termijn (12-20 jaar) tot een lagere beschikbaarheid van N, maar op langere termijn accumuleert veel N in de strooisellaag en neemt de N-mineralisatie toe. Plaggen zorgt niet voor toename van de soortenrijkdom, wel voor een hoge bedekking van Struikheide en leidt op de Nederlandse onderzoekslocatie tot dominantie van de N-minnende mossoort Grijs kronkelsteeltje (ongunstig effect). In het Engelse onderzoeksgebied worden de geplagde delen gedomineerd door Heideklauwtjesmos en Bronsmos (gunstig).

Beide mitigerende maatregelen hebben geen gunstig effect op de N-huishouding. In droge duingraslanden leidt instuiving van kalkrijk zand wel tot ecologisch herstel door mitigatie van verzuring, maar in droge heiden leidt plaggen niet tot herstel van de vegetatie.

Implementatie: verstuiving in duingebieden helpt, plaggen van heiden niet zinvol

Het bevorderen van kleinschalige verstuiving voor herstel van duingraslanden is een zinvolle maatregel. Het helpt door aanvoer van kalkrijk zand goed in duingebieden met oppervlakkige ontkalking. Deze maatregel maakt ook de versnelde verzuring door N-depositie ongedaan. De rol van de hoge N-depositie in het functioneren van microbiële gemeenschap in de N-huishouding vergt nader onderzoek. Plaggen van droge heiden is bij de huidige hoge N-depositie geen zinvolle herstelmaatregel. Behoud en hertel van dit habitattype vergt andere, te onderbouwen maatregelen en bovenal snellere vermindering van de N-depositie.

Rapport

Dit onderzoek is beschreven in het rapport *Effectiveness of measures to mitigate high nitrogen deposition in dry habitats* (BTO 2020.024.

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EINDCONCEPT

Preface

This study has been carried by KWR Water Cycle Research in cooperation with the Centre for Ecology and Hydrology (CEH, Environment Centre Wales) and the Institute for Biodiversity and Ecosystem Dynamics (IBED, University of Amsterdam). It was conducted in the joint research program of the Dutch drinking water companies, who manage large areas protected by the Habitat Directive. Currently they are adopting nature management to the strong adverse effects of a high atmospheric nitrogen deposition. Therefore an important question is to what extend measures for mitigating the adverse effects of nitrogen deposition are beneficial for ecological restoration. This publication reports the results of a descriptive field study on mitigating measures in sand dunes and in inland heathland areas. In order to gain more inside in the effects of a high nitrogen load this study was conducted in the Netherlands (high nitrogen load) and in UK ((relatively) low nitrogen load). With this study we intent to contribute to a better understanding of ecological effects of nitrogen deposition and to support policy on nature conservation and environmental pollution.

As is often the case in ecological field studies, the extensive field and lab work was only possible with the help of volunteers, employees of the drinking water companies, and colleagues. Jan Oome and Elke Seeber helped with installing the exclosures in Newborough and made many kilometers with heavy loads. In Luchterduinen Mark van Til (Waternet), Luc Geelen (Waternet), Rick (Waternet), Harrie van der Hagen (Dunea) assisted with installing exclosures and clipping biomass. Joost Tuithof (Brabant Water) and Jeffrey Ringroos helped with installing groundwater wells and digging out soil samples in Grootte Heide. Myrthe van Paridon and Bo van der Eerden (students Aeras Hogeschool) joined with biomass sampling and lab work. Alice Fitch (CEH) carried out GIS analyses. Sameh Kotb, Michael Roberts, David Fletcher, Nori Fitos and Lisanne van Willegen (all CEH) helped with field work in Newborough. Andree Nanu (master student IBED) did a major part of the laborious sampling work in the Dutch and UK study areas and subsequent lab work. Of great help were also her mother and father who speeded up the hot 2018 field campaign in UK. Moreover this provided a very pleasant Nanu-familiy experience. Martin de Haan assisted with lab work and Henk Krajenbrink (both KWR) with data analyses. Martin Hollingham provided nice housing and help with flat tires. Also, many thanks also to Matt and Jenny Swarbrick (Henbant Farm) for their great hospitality at the most convenient field work accommodation in Wales, and the support to overcome practical problems during the field campaigns Wales.

At last were happy to cooperate with the dune ecologists Laurence Jones (CEH) and Annemieke Kooijman (IBED) with a long track record in research on the effects of nitrogen deposition.

Camiel Aggenbach & Yuki Fujita

Contents

1 Introduction

1.1 Background

Drinking water companies are responsible for Natura 2000 habitats and other important nature types at their production sites. A high atmospheric nitrogen (N) load may, however, hamper these nature targets. High N-deposition is a severe and large scale environmental problem since the 1970's, and is still not solved. There is a lot of evidence for a strong adverse effect on a wide range of habitats (Bobbink et al. 2010; Bobbink & Hettelingh 2011). Moreover, a continuing high N-load will maintain high N-leaching rates to the groundwater (which is a source for drinking water). To cope with these environmental threats, the Dutch and Flemish governments aim for a gradual reduction of N-deposition so that N-emitting economical activities (agriculture, industry, traffic) have enough possibilities to grow. On top of this gradual reduction the governments pursue local measures to mitigate the adverse effects of high N-loads in Natura 2000 areas. The selection of measures (rewetting, soil disturbance, more vegetation management, etc.) are to a large extent based on expert analyses of habitat specific effects.

In the Netherlands, both policy lines (gradual reduction and local measures) were implemented in the ‘Programma Aanpak Stikstof’ (PAS; in English: Nitrogen Approach Program), which resulted in extensive measure packages for Natura 2000 areas. This programme started in 2015 and many measures have since been planned on a local scale and have partly been carried out. At the same time the state granted licenses for many new N-emitting activities. By this policy a major part of the 'economic growing space' was filled in. Although the program should lead to a gradual decline of N-deposition this was not conformed by monitoring data. Therefore concerns about the effectivity of the program for protecting sensitive habitats increased. In May 2019 the Dutch State Council (Raad van State) stated that the PAS was illegitimate and ruled that the PAS could no longer be used to grant N-emitting activities. However, they admitted that there still was a need of mitigating management in Natura 2000 areas, and therefore planned measures of the PAS will be carried out.

For drinking water companies the PAS led to a strong increase of nature management and restoration measures. Although the post-PAS policy on nature is not yet exactly known, intensive nature management will remain an important element in Dutch nature conservation. It is, however, questionable whether these activities are effective enough to mitigate the adverse effects of elevated N-load on nature targets and groundwater quality. Many of these measures can be regarded as 'regular' measures for ecological restoration of habitats which are degraded by combinations of pressures (desiccation, acidification, eutrophication, decrease in aeolian dynamics, changes in management etc.). Many measures selected for mitigating the adverse effect of a high N-load are not tested for the recovery potential of habitats which have already experienced a period of decades with a high N-load. Moreover, more fundamental insight into the effects on the nitrogen cycle is often lacking. For instance, in a recent review Jones et al. (2017) concluded that many local measures may improve habitat suitability for target plant species (e.g. light condition), but have often little effect on N-accumulation under the current high atmospheric loads. Extreme measures (sod cutting, intensive mowing) can substantially reduce N-accumulation, but these may result in undesired effects on other habitat components. A review study showed that ecosystems in recovery from high N load (i.e. those in which N addition is ceased or where N input has been reduced) respond rapidly in reducing soil NH_4 and NO_3 concentrations, but respond generally slow in terms of vegetation composition, below ground communities, and soil processes (Stevens, 2016). Possible barriers for the limited resilience are a continued critical load exceedance, lack of the seed bank or dispersion, and a lockup of the ecosystem in an alternative stable state (e.g. changed microbial community, high mineralization rate). This means that, even if gradual reduction of N-deposition is achieved by the government, the drinking water companies need to implement effective on-site measures in order to achieve nature targets in their water production area. At the same time they should carefully assess whether applied measures have no beneficial or even an adverse effect on habitats. Moreover, the choice of the measures should be adjusted to the actual N-deposition levels and changing climate, that are beyond control of the drinking water companies. To judge the effectiveness of local measures, it is essential to understand how they influence soil and vegetation processes that control N-pools and N-fluxes, and whether those effects are altered by external abiotic conditions, such as N-deposition and climate.

1.2 Research aim

The aim of this study was to gain insights into the (combined) effects of N-deposition, climate, and local measures in dry, nutrient poor habitats in coastal dunes and inland nature areas (H2130 Fixed coastal dunes with herbaceous vegetation; H4030 European dry heaths) in order to aid drinking water companies to choose effective measures to mitigate the adverse effects of high N-loads. To that aim, we first carried out field and lab measurements in dry habitats that differ in N-load by selecting a dune and heathland area in the Netherlands (high N-load) and a dune and heathland area in UK (low N-load). In the dune areas we assessed the effect of aeolian sand-deposition of calcareous sand in old dune grasslands. In the heathland area the effect of sod cutting was evaluated. In each area plots were selected without and with measure. For the high-N and low-N dune areas we also selected control sites with different microclimate (flat, south- and north-facing slopes) in order to gain more insight in climatic effects. For both heathland areas we selected only flat slopes. On each site we primarily focused on examining N-fluxes and N-pools in soil and vegetation, since two fluxes of N (i.e. N-availability for plants and N-leaching rate) are particularly important to determine the effectiveness of the measure and these fluxes are largely controlled by N-pool size and ecosystem processes. The field and lab results were interpreted statistically to examine the effects of N-deposition and microclimate.

Finally, we evaluated the effectiveness of the measures, under both high-N and low-N conditions, in terms of their contribution to target plant communities and reduction of N-leaching to groundwater. Our findings will be translated to recommendations for policy and nature management.

This study will answer the following research question:

- Is it possible to achieve recovery of quality and functioning of H2130 and H4030 habitats under high stress of N-deposition with mitigating measure without strong negative side effects on habitat components?

More specific:

- What is the effect of high N-deposition on the quality of target vegetation and N-leaching in dry habitats?
- Is the measure blow-out creation, which promotes sedimentation of calcareous sand in old dune grasslands, effective in H2130 in order to achieve target vegetation and reduce N-leaching in this habitat?

- Is the measure sod cutting effective in H4030 in order to achieve target vegetation and reduce N-leaching in this habitat?

1.3 Hypothesis on effects of mitigating measures

When assessing the effects of measures which aim for mitigating adverse effects of high N-deposition, it is useful to have a general idea of the ecosystem effects of a high N-load. Based on research in different ecosystem types (Bobbink et al. 2010) we present in Figure 1 a scheme of the ecological effects of a high N-load. To this scheme we added the functioning of biological N_2-fixation, decomposition and N-leaching. The most important effects are:

- A higher availability of mineral N affects species composition directly via promoting fast-growing species and thereby outcompeting slow-growing species, and indirectly by suppressing biological N_2-fixation (favouring non-N_2-fixating plant species), increasing the shoot:root ratio (higher aboveground plant cover) and suppressing mycorrhizas (favouring non-mycorrhiza species). On a long-term also plant species can decrease or disappear by a strong physiological stress of a high N-deposition. A high NH_y-load can cause a high soil NH_4-concentration which is toxic for several plant species.
- Indirectly the high input of mineral N affects the N-mineralisation by changing biomass pool and properties. By enhancing the litter pool and its N-content N-mineralization will increase. A higher input of N can also change the nutrient stoichiometry from N- to P-limitation.
- On the long term a high N-deposition can increase the sensitivity of the ecosystem for disturbance (e.g. dying of species by diseases, drought stress). These disturbance events open the vegetation canopy and might lead to strong changes in vegetation (e.g. invasion of a species).
- In contrast to increasing disturbance, a high N-load can also decrease disturbance. For example it can lower aeolian dynamics in coastal dunes (Aggenbach et al. 2018). A high N-load promotes a dense vegetation layer with deep rooting plant species, and therefore makes coastal dunes less sensitive for secondary aeolian activity.
- A high load of atmospheric deposition of strong acids and NH_y-deposition contributes to strong soil acidification. This is a slow, long term process, and will also affect species composition.
- Because of an elevated atmospheric N-input and an increased N-mineralization N-leaching to the groundwater will increase.

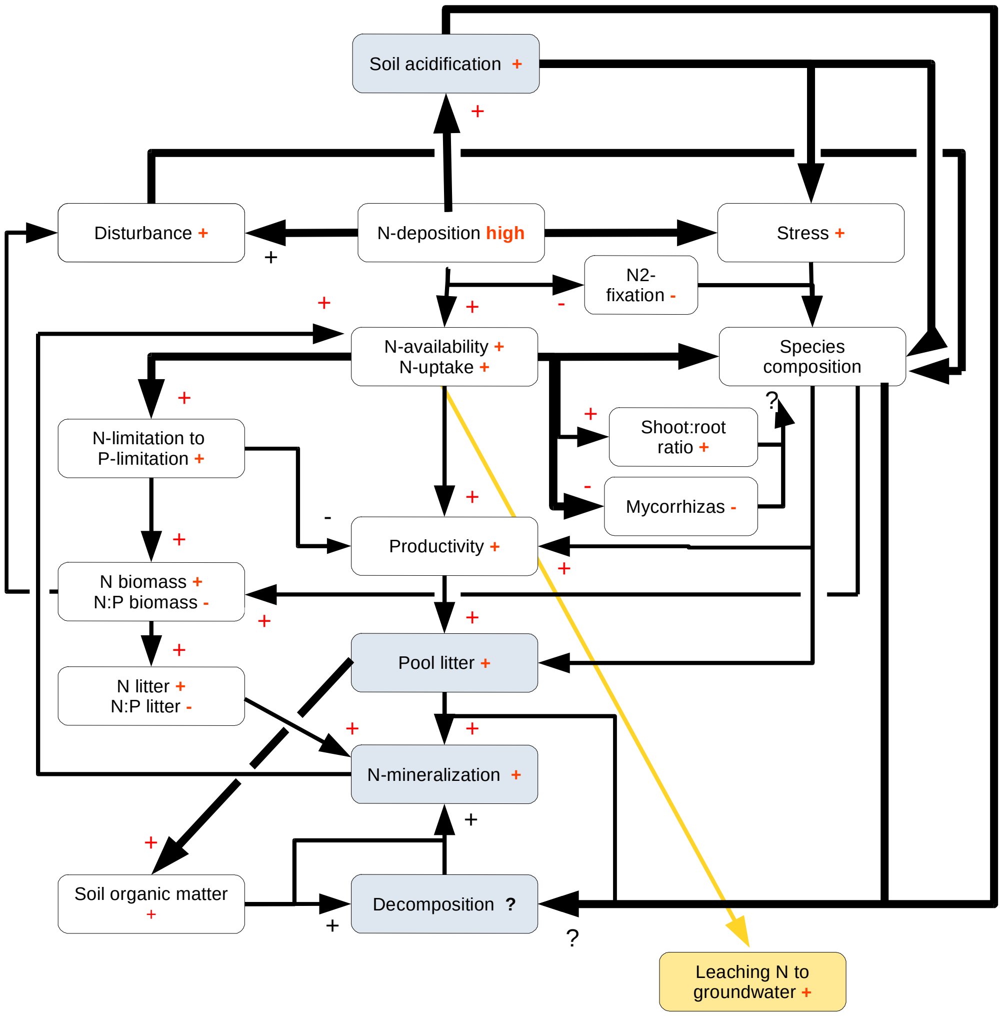


Figure 1: A general scheme of the ecosystems effects of a high atmospheric N-deposition on ecostems (modified after Bobbink et al. 2010). Thick lines indicate long-term and thinn lines for short-term effects.. Effects: + = increase; - = decrease; -- = strong decrease; ? = unknown.

For formulating hypothesis we added the effects of mitigating measures to the scheme in Figure 1. Below we present our expectation about effects of activating deposition of calcareous sand in old dry dune grasslands and sod cutting in dry heathlands.

Deposition of calcareous sand in old dry dune grasslands

We want to assess the ecosystem effects of deposition of calcareous sand in old dune grasslands. Many dune grasslands in the Netherlands are negatively affected by soil acidification and a high N-load. Major parts of these dune grasslands are old successional stages (80 year and more) which have a decalcified (top)soil. A low intensity of deposition of calcareous sand (< ca. 1-2 cm/y) from nearby blowouts increases topsoil pH and botanical quality of dry dune grasslands (Aggenbach et al. 2018). Enhancing of small-scale aeolian activity by activating blowouts is therefore a promising measure for restoring species rich dune grasslands. The old humus profile is preserved, which is necessary to have species rich vegetation, and at the same time the base status of the topsoil is improved.

In Figure 2 a scheme is presented for the expected effects of deposition of calcareous sand in old dune grasslands.

- Input of sand will cause stress for plants, mosses and lichens by burial with sand. Because the sand deposition is generally weak, this stress will not be very strong. Many dune grassland species can survive this weak stress. Only in years with a strong sand deposition, stress can be temporary high, and might cause major changes in vegetation by disturbance, and even rejuvenation of the vegetation.
- Sand deposition is expected to increase the topsoil pH because of input of calcium carbonate. This will counteract the acidification by N-deposition as long as sand deposition is proceeding, and even after sand deposition has stopped due to remained calcium carbonate pool. The increase of soil pH will have a strong effect on the species composition of the vegetation by favouring basiphilous and suppressing acidiphilous species. This is regarded as the main beneficial effect for the dune grassland vegetation.
- Input of sand will lower the soil organic matter content of the topsoil due to a dilution effect with mineral sand, and therefore might lower the decomposition and N-mineralization. On the other hand, by an increase of soil pH, decomposition might be enhanced as decomposing microbes generally prefer neutral to high pH. Depending on the balance of these two processes decomposition rate can either increase or decrease.
- Changes in plant species composition can affect productivity, nutrient contents and the content of other substances affecting decomposability of the above- and belowground biomass, and therefore the litter quality. These effects all influence decomposition and N-mineralization rates of the litter, but whether the combined effects are negative or positive is hard to predict. For this reason the net effect of sand deposition on N-mineralization and the N-availability for vegetation is uncertain.
- The effect on N-leaching to the groundwater is also unknown and depends on the balance of input by N-deposition + N_2-fixation + N-mineralization, and microbial retention by immobilisation + uptake by vegetation.

Sod cutting in dry heathlands

Sod cutting is a measure which has been applied on a large scale in dry heathlands to counteract encroachment with grasses (*Molinea caerulea* and *Deschampsia flexuosa*) and to restore typical heathland species. With removing greater a part of the litter layer on the mineral soil profile most of the accumulated N is also removed. However recent research indicated sod cutting has disadvantageous effects on soil chemistry (removing nutrients as P, Mg, Ca) and physical soil properties (too much drought stress), especially when after sod cutting a soil poor in organic matter is left (Beije et al. 2014). Nowadays sod cutting is applied only at a small scale and when the heathland has a high grass cover in the Netherlands, with a superficial sod cutting depth which leaves the horizon with fine humic particles. The measure is a part of regular nature management, which typically consists of grazing, removing trees, mowing, removing a part of the raw litter horizon (choppering) and burning. There is research which points to the importance of old litter layers for a high N-immobilisation and retaining other nutrients which naturally are present in low pools (e.g. P, Ca, Mg). Therefore some researchers indicate it is better to aim for old heathlands by grazing and removal of trees (cited in Beije et al. 2014). However, sod cutting could be necessary to create patches with an open vegetation structure for special lichen species and small fauna. It is unsure how effective sod cutting is to restore habitat quality.

In heathlands we expect the following effects of sod cutting (Figure 3):

- An important effect of sod cutting is strong disturbance by removing the old vegetation and topsoil where a major part of the biological activity (microbes, mesofauna) takes place. After sod cutting a new vegetation has to develop and gradually a new litter layer on the mineral soil profile is developing. Because of a temporary low vegetation cover typical heathland species may establish, but it also offers the chance for invasion of unwanted species.
- Sod cutting removes a greater part of the litter and soil organic material of the topsoil, which is the major source for decomposition and N-mineralization. Therefore we expect that the decomposition and N-mineralization will be lower than in the old heath land. N-availability will also get lower, but absolute levels are still high due to high atmospheric input. Heathlands are known for strong N-immobilisation (Bobbink et al. 2010), and we expect therefore that the ecosystem can still accumulate a major part of the N-deposition.
- N-leaching to the groundwater will decrease because of a lower N-mineralization and a high retention capacity for N. Because of the very low soil pH nitrification will be hampered (Dorland et al. 2003). Mineral N consist mainly of NH_4 which adsorbs well to the soil. There is hardly any easily leachable NO_3.
- With litter removal a major part of nutrient pools like P, Mg, Ca, K is removed. This lowers the availability of these minerals for vegetation and herbivorous fauna. With litter removal also the water holding capacity is lowered, and therefore drought stress for vegetation and soil fauna is much higher after sod cutting.
- After sod cutting the pH of the new topsoil might be slightly higher than the pH of the acidic litter (LHF-horizon) of old heathlands. We expect that the increase of soil pH will be of minor importance for the vegetation development, because it will be still low, and in the aluminium buffer range. The Al-concentration in pore water will stay high, which is a strong stress factor for heathland species sensitive for acidification (De Graaf et al. 2004).

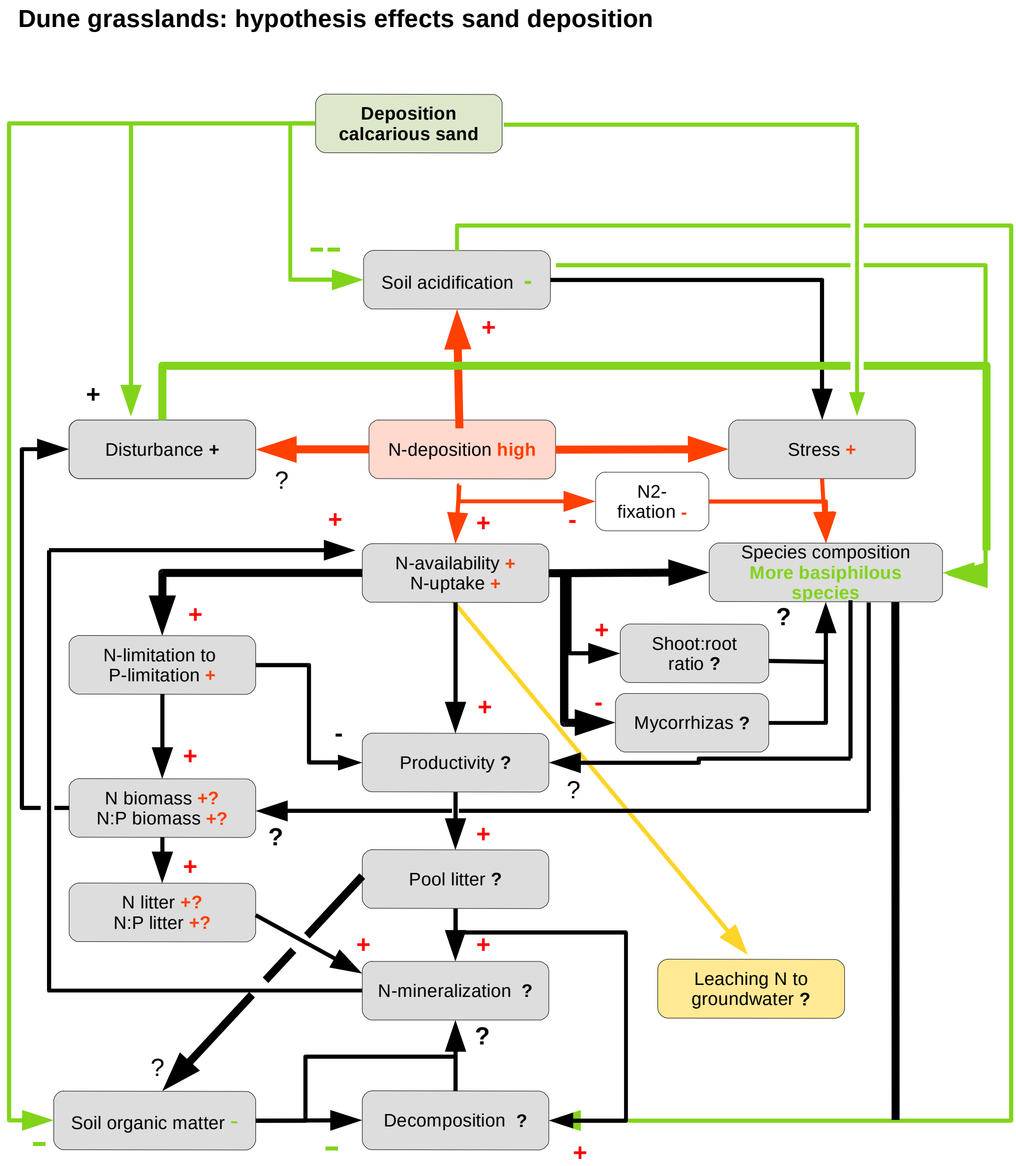


Figure 2: A hypothetical scheme of the ecosystems effects of of calcarious sand deposition in a old dune grassland with a high N-deposition. Thick lines indicate long-term and thinn lines for short-term effects. Colors: green = direct and strong effects of sand deposition on soil and vegetation; red = direct effects of N-deposition; black = indirect effects. Effects: + = increase; - = decrease; -- = strong decrease; ? = unknown.

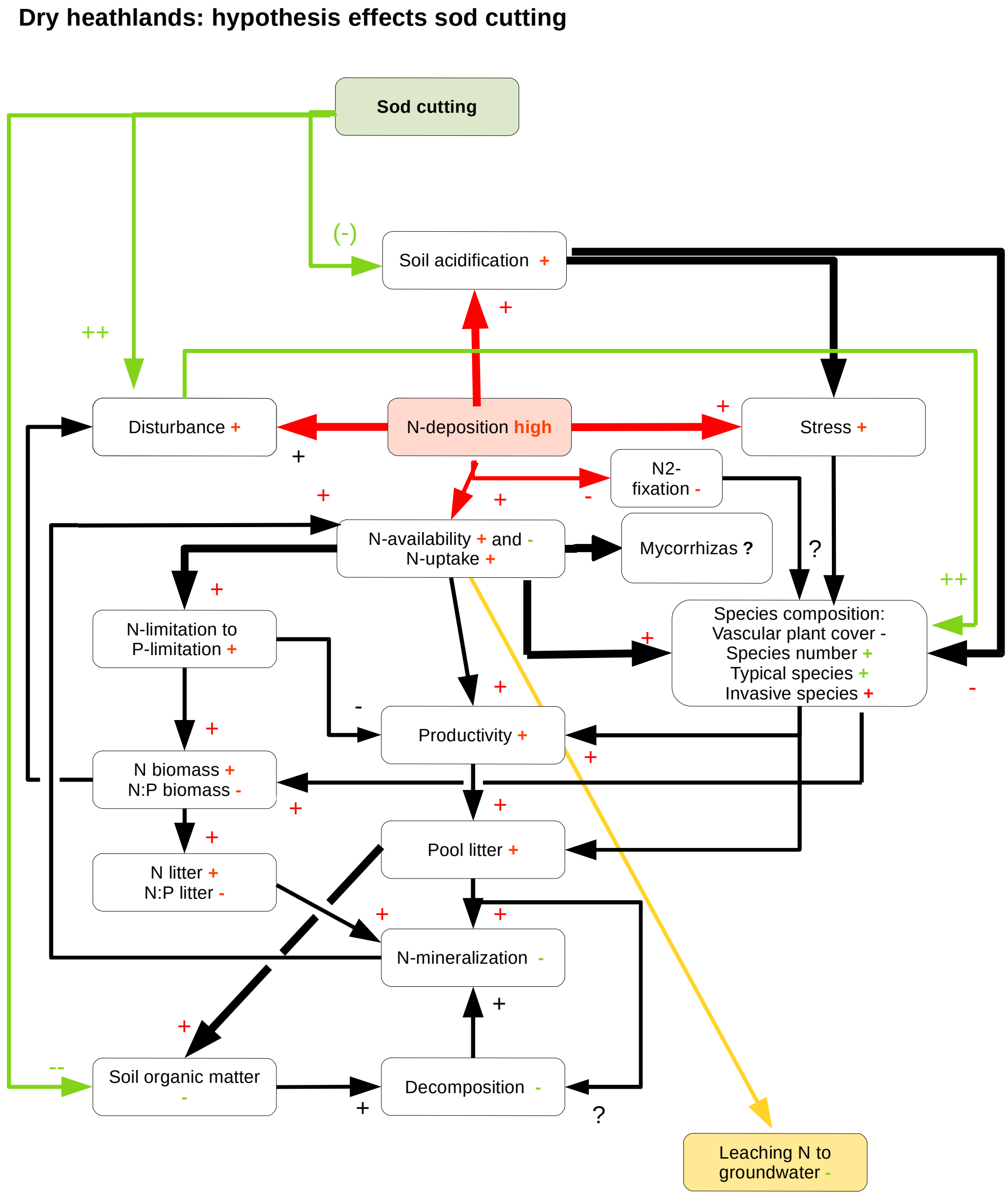


Figure 3: A hypothetical scheme of the ecosystems effects of sod cutting in dry heathlands with a high N-deposition. Thick lines indicate long-term and thinn lines for short-term effects. Colors: green = direct and strong effects of sand deposition on soil and vegetation; red = direct effects of N-deposition; black = indirect effects. Effects: + = increase; - = decrease; -- = strong decrease ? unknown.

2 Methods

2.1 Research sites

For this study, we selected a coastal dry dune grassland area and a dry heathland area both in the United Kingdom (UK) and in the Netherlands (NL) (Figure 4). The selected coastal dry dune grasslands were situated in Luchterduinen (LD) in NL (52.31 N, 4.52 E) and Newborough Warren (NB) on the island Anglesey in Northwest Wales, UK (53.14 N, 4.36 W). The selected dry heathlands were Groote Heide (GH) in NL (49.43 N, 8.44 E) and Little Budworth Common (LB) in Cheshire, England, UK (53.19 N, 2.62 W). Except for LB these areas are assigned as Special Area of Conservation (SAC) under the Habitats Directive 92/43/EEC and are located in the Atlantic biogeographical region.`

Each area has different grazing schemes. The dune grasslands of LD are grazed by Fallow deer, whereas those of NB are grazed by cattle and ponies. The heathlands of GH are grazed extensively by cattle, whereas those of LB are not grazed at all. All areas are also grazed by rabbits.

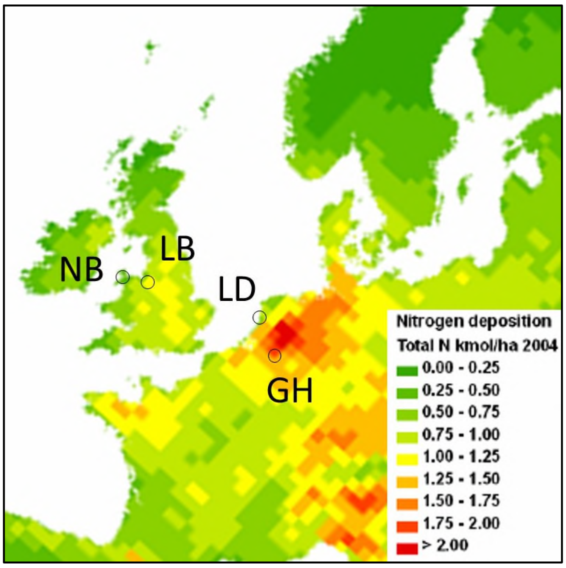


Figure 4: The four selected study sites in the Netherlands and United Kingdom. As background the modelled total N-deposition per EMEP grid square in 2004. Study sites: dune area Luchterduinen ('LD') in NL, dune area Newborough Warren ('NB') in Wales (UK), heathland area Groote Heide ('GH') in NL, heathland areas Little Budworth ('LB') in England (UK).

2.2 Atmospheric N-deposition levels of study sites

Our assumption was that atmospheric N-deposition levels were much higher at the selected areas in NL than those in UK (Figure 4). To test our assumption, we have checked local atmospheric N-deposition levels of LD, NB, GH, and LB derived from national transport and deposition models.

2.2.1 Dutch sites: Luchterduinen (LD) and Groote Heide (GH)

For the period 1981 until 2015 modelled NO_x and NH_y deposition levels of the OPS-model were used by averaging model cells with plots. The total N-values of 2015 were compared with the more accurate Aerius 2016L model. Results of both models were similar with 19.8 and 16.7 kg N/ha/y in GH for respectively the OPS and Aerius model. For LD these values were respectively 16.5 and 17.8 kg N/ha/y. Model results of the OPS model from 1981 and later are corrected for an underestimation of NH_3-deposition. Slightly higher results of the Aerius model probably can be explained by a recent correction for the NH_y input from the sea by volatilization of N from dead algae at high pH (Kooijman et al. 2017).

For 1950 and 1970 modelled average national values of total N-deposition were downscaled to both areas based on the values of 1981, 1991, 2001, 2011 and 2015. For GH the scaling factor is 1.05 and for LD 0.69. The modelled N-deposition before 1981 is not corrected for an underestimation of NH_3-deposition.

2.2.2 UK sites: Newborough (NB) and Little Budworth Common (LB)

For the period 1800-2010 wet NH_y, dry NH_y, wet NO_x and dry NO_x deposition were calculated with the national model and downscaled to the local deposition by the method listed in Tipping et al. (2017). Values of the model cells with the plots were used. Deposition values were calculated with the roughness factor of the vegetation type ‘moorland’.

2.3 Climatic conditions of study sites

Climatic conditions of dune grasslands are generally similar between UK and the Netherlands (Figure 5). The annual precipitation rates are around 805 mm in LD and 850 mm in NB, and annual mean temperatures are 9.7 ˚C in LD and 10.2 ˚C in NB during 1931– 2014, with some variation within seasonal patterns (Aggenbach et al. 2017). The ratio of precipitation to potential evapotranspiration in summer, which indicates the aridity, is slightly lower in LD than NB (i.e. LD experiences more drought stress in summer than NB).

The climatic conditions of heathland plots are also similar between UK and the Netherlands (Figure 6). The annual precipitation rates are around 760 mm for GH, 810 mm for LB. The annual mean temperatures are around 9.5 ˚C for GH and 9.5 ˚C for LB. LB has a smaller seasonal fluctuation of the temperature.

2.4 Weather conditions during the field study in 2018 and 2019

Measurements were carried out during 2018 and 2019. In NW-Europe the summer of 2018 was very hot and had very low precipitation. Therefore the vegetation in all our study sites experienced strong drought stress indicated by dying of aboveground vegetation in dune grass in early in the growing season, and desiccation of *Calluna vulgaris* in the heathland. Signs of drought stress were most evident in the two Dutch study areas. For the plots of the NL dune area we calculated the cumulative actual transpiration for a reference productive grassland (Figure 7) based on the recorded soil profiles and measured soil moisture properties (Aggenbach et al. 2020). In the 2018 summer the vegetation had more than two months drought stress, much longer than the drought stress periods in 2019. This was the case irrespective of the position of the plots on flat, north and south facing slopes.

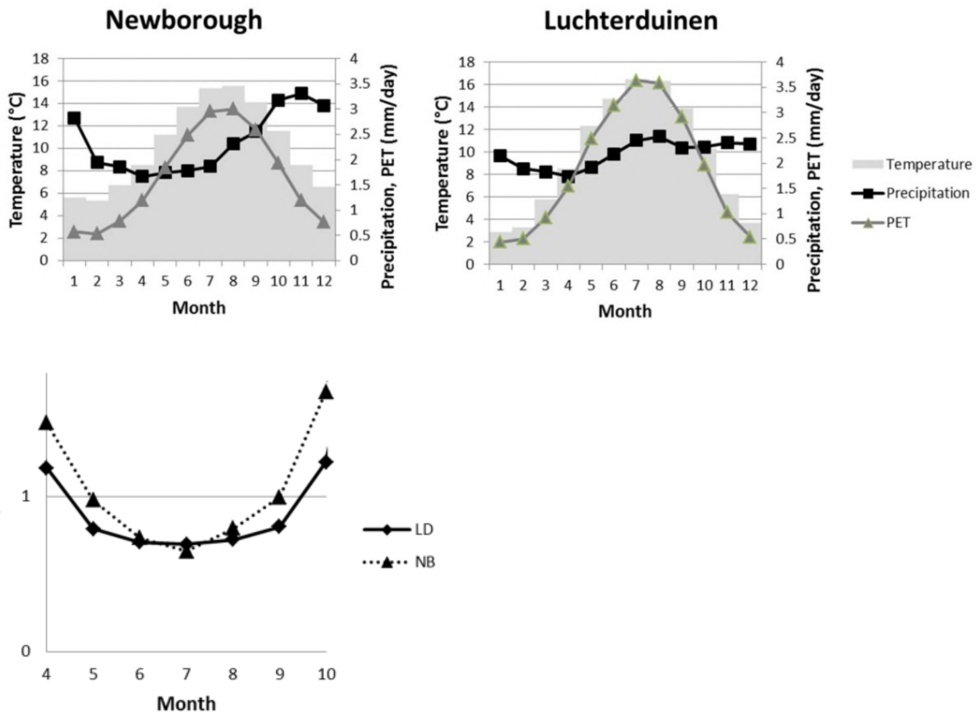


Figure 5. Monthly average of temperature, precipitation, and potential evapotranspiration (above) and the ratio of rainfall to potential evapotransporation from April to October (below) between 1931 and 2014. The weahter data of NB is taken from the weather station nearby RAF Valley. The weather data of LD is taken from Valkenburg weather station.

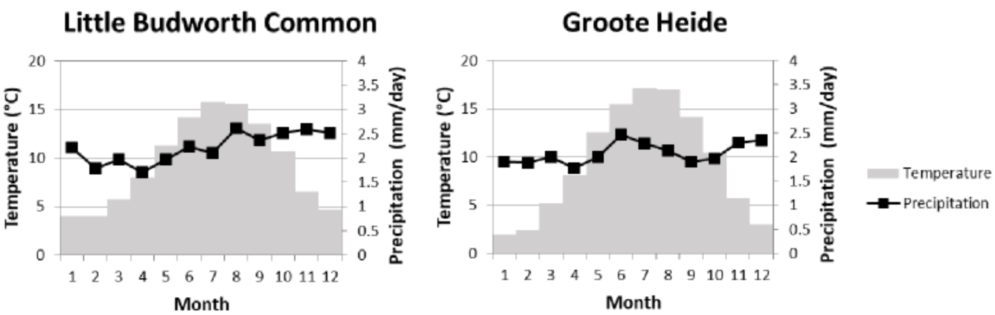


Figure 6. Monthy average weather data of GH and LB between 1931 and 2014. For GH, data is of Maastricht weather station (http://www.klimadiagramme.de/Europa/maastricht.html). For LB, data is of Manchester weather station (http://www.klimadiagramme.de/Europa/manchester.html).

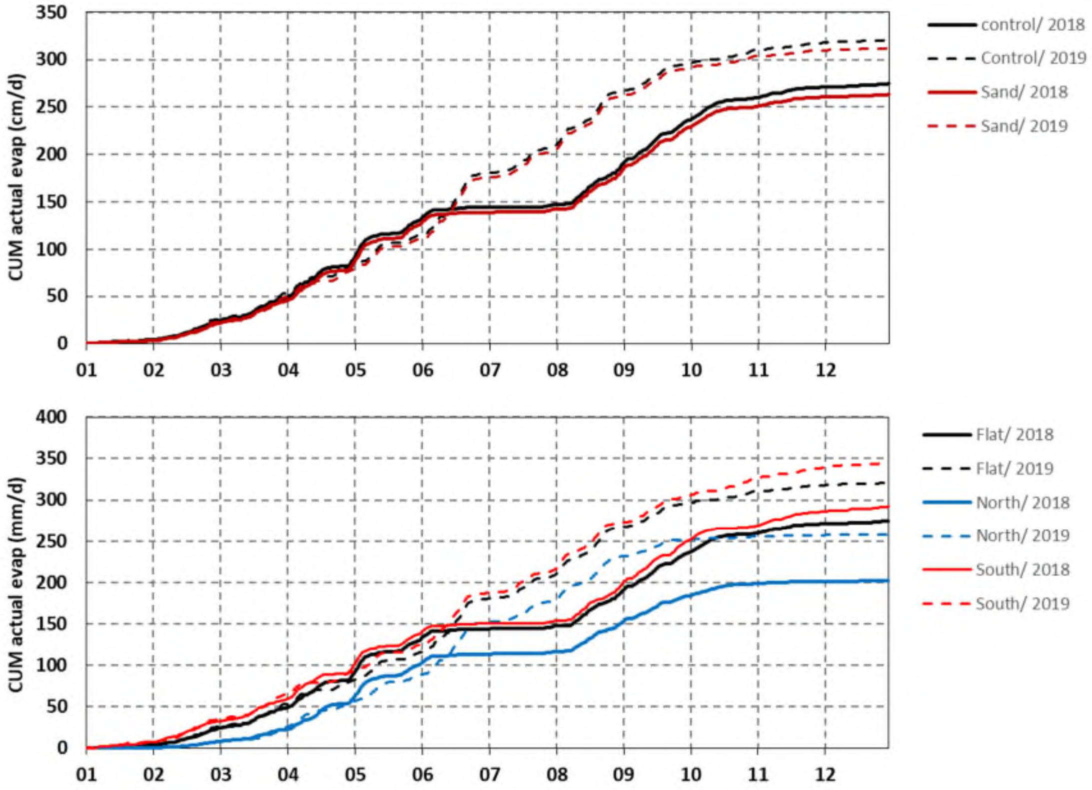


Figure 7: Cumulative actual transpiration in the dune area Luchterduinen calculated for the plots based on soil profile, measured water retention characteristics and soil profiles. Transpiration is calculated for a productive grassland. Above: average of flat plots without (Control) and sand depisition (Sand). Below: average of plots without sand deposition at flat, noth and south slopes (see for methods Aggenbach et al. 2020)..

2.5 Dry grassland sites

The analysis is limited to old successional stages because these are the dominant succession stage in the selected dune areas and also in many other dune areas. In LD, we choose to focus on superficially and deeper decalcified, dune grasslands only, because the effect of deposition of calcareous sand is expected more prominent on these soils than in soils with calcite in the top layer (Aggenbach et al. 2018). Here the site selection included acidic and as well calcareous dune grasslands varying in decalcification depth (Attachment IV.3), which often had a pH depth profile with low pH in the topsoil and higher pH in the subsoil (Attachment IV.1). In NB, we selected calcareous dune grasslands on soils with were mostly not decalcified. Acidic dune grasslands hardly occur there. Only a few selected sites in NB had shallow decalcification(Attachment IV.3), and pH was overall high and showed not much stratification for depth (Attachment IV.1).

We selected old dune grasslands on flat surfaces in NB and LD, both without (‘Control’) and with (‘Sand’) the influence of deposition of calcareous sand from a nearby blowout. In addition, to assess impacts of microclimate, we selected dune grasslands without influence of sand deposition on north-facing slope (i.e. wetter conditions) and south-facing slopes (i.e. drier conditions). The locations on old dune soils were pre-selected using aerial photograph sequences (see Aggenbach et al. 2017). The final decision of the locations was made in the field in February 2018. For LD soil age of the plots was > 80 years, and for NB soil age ranged from 34 to 53 years for most plots and was >160 y for three plots with treatment ‘measure’. See Table 1 for number of established plots for each category. Although we primarily aimed at having the same number of replicas for each combination of variables, practical constraints in the field (e.g. absence of suitable locations) prevented us from doing so. See Attachment I.1 and I.2 for the exact locations of each plot.

2.6 Dry heathland sites

For GH information about sod cutting areas and age was kindly provided by Rob van der Burg of de Bosgroepen Zuid (email communication). Plots with sod cutting were located in two areas which were sod cut in autumn 2005/spring 2006. Here time span between sod cutting and recording of the plots was 12 years. For LB sod cut areas were derived from an aerial photographs sequences (1945 Geoinformation group, 2000+ 2005 Infoterra Ltd. & Bluesky, 2010+2016 Bluesky). Three control plots were selected with a soil older than at least >73 years, and 9 sod cut sites with an age of 18 to 20 years.

Table 1. Overview of research sites. On each plot, vegetation was recorded and bulk density was measured. The colors of circles indicates which extra variables were measured on the plot. Red (●): Soil chemistry and N-mineralization, green (●): Plant productivity and peak standing crop, brown (●): Root samples, black (●): Soil microbial biomass and respiration.

Country	Vegetation type	Location	grazing	Management	Number of plots		
					flat	north slope	south slope
NL	Dune grassland	Luchterduinen (LD)	Fallow deer	Control (age >80 y)	5●●●●	3●	3●
				measure (sand deposition) (age >80 y)	7●●●●		
	Heathland	Groote Heide (GH)	ext. cattle	Control (age: centuries)	6●		
				measure (sod cut) (age: 12 y)	6●		
UK	Dune grassland	Newborough Warren (NB)	pony and cattle	Control (age 53 y)	6●●●●	3●	3●
				measure (sand deposition) (6 plots age 34-53 y; 3 plots age >160 y)	6●●●● + 3●		
	Heathland	Little Budworth Common (LB)	No grazing	Control (age > 73 y)	3●		
				measure (sod cut) (age 18-20 y)	9●		

2.7 Field sampling and recording

2.7.1 Measurement design

In each plot, soil and vegetation samples were taken and vegetation and soil profile were recorded. Between dune grassland and heathland plots there are some differences in plot design. In dune grassland plots soil profiles were recorded and soil profiles for root cores were collected at 3 subplots (Figure 8). Soil samples for bulk density and chemical analyses were collected around the sampling subsite where the soil sample for mineralization measurement was taken. Besides 3 subplots for sampling aboveground vascular plant standing crop, also 3 subplots in exclosures for measuring aboveground vascular plant production were present. In the heathland plots we described 1 soil profile in a dig hole and 3 replica soil samples were collected around this hole (Figure 9). At heathland plots only aboveground vascular plant biomass was sampled for standing crop measurements (no exclosures installed). Productivity measurements were not possible because this involves in shrub dominated vegetation a time-consuming effort which was exceeding the project budget.

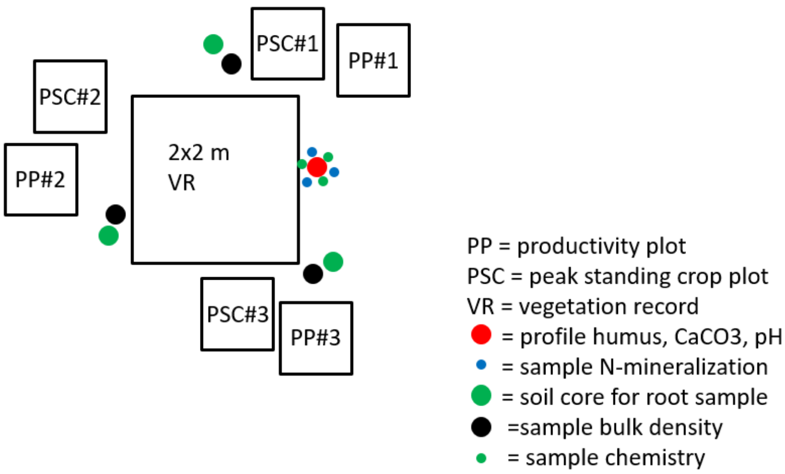


Figure 8. Configuration of soil and vegetation sampling in dune grasslands. Note that productivity, peak standing crop, N-mineralization sample, and soil chemistry sample were not taken in all plots. See Table 1 for the sampling program.

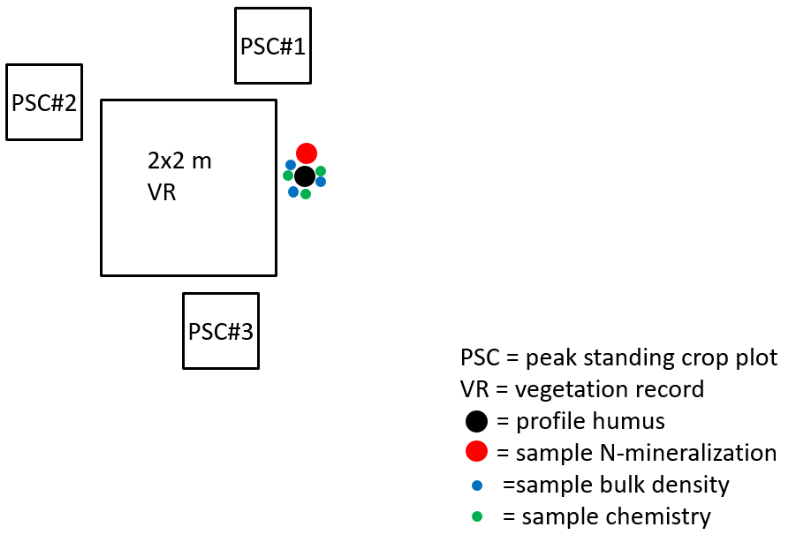


Figure 9. Configuration of soil and vegetation sampling in dry heathlands. See Table 1 for the sampling program.

2.7.2 Description humus profile, $CaCO_3$ profile, and in-situ pH profile

Soil profiles were recorded at 3 points per site. Upper soils till ca. 30 cm depth were taken with a ‘humushapper’, a rectangular device that cuts out a ca. 3x10 cm broad core up to a depth of ± 30 cm. Deeper soils profile until maximum 120 cm depth were taken with an Edelman auger in order to assess the decalcification depth. Deeper soil profiles were taken only in dune areas when the soil was deeply decalcified.

For each soil horizon, we recorded the humus profile type until ca. 30 cm depth according to Van Delft (2004) with some modifications. Additionally, we recorded the thickness of the living moss layer (S), and horizons with dead moss (Sd). For graphical presentation purpose, the soil horizons were further grouped into five categories: living moss, dead moss, fresh to slightly decomposed litter (L+F), strongly decomposed litter (H), organic-rich sand (Ah), sand with moderate amount of organic matter (AC), sand which accumulated organic matter (Bh; only in a podzol profile), and organic-poor mineral layer of sand (C).

Calcium carbonate profiles were recorded at least till 30 cm depth, and maximum till 120 cm depth, by identifying calcium carbonate presence using a 10% hydrochloric acid test. We distinguish four classes: C0: no visible nor audible fizzing, C1: no visible fizzling, audible fizzling, C2: weak fizzling visible , C3: strong fizzling. Calcium carbonate profile was recorded only for dune grasslands, because heathland soils were completely decalcified.

In dune areas soil pH was measured in situ pH with a pH meter (Hanna H199121). When dry, the soil was wetted with MilliQ (very mineral poor water) in order to have pore water at positions for measurement. Depth of the pH measurements was done at regular intervals of 2.5, 5.0, 7.5, 10, 15, 20, 25, 30 cm below the top of the mineral profile (Figure 10).

2.7.3 Soil sampling

Three types of soil samples were taken at each plot: bulk density samples (for all plots), chemistry samples (for a selection of plots), and N-mineralization samples (for a selection of plots). The bulk density samples and chemistry samples were taken for the topsoil (0-5 cm) and subsoil (10-15 cm); the N-mineralization samples were taken for the topsoil (0-5 cm) only. In coastal dunes litter (L) and horizons with dead moss (Sd) were omitted from the topsoil samples. Thick litter and dead moss layers do not occur in the dune grasslands. In the heathlands we took the soil samples in *Calluna* patches in order to have soils with a clear litter layer, because the litter layer is very important for nutrient turnover in heathlands. The fresh litter (H) was excluded; only fermented and strongly decomposed litter (F+H) was included in the topsoil samples.

Soil samples for bulk density analysis were taken with Kopecky rings at 0-5 and 10-15 cm depth at three points per plot. Diameter of the rings is 6.7 cm and volume is 176.3 ml. Three replicas were pooled in one plastic bag, making the total sample volume 529.0 ml.

Soil samples for chemical analysis were taken at the dune sites with a 'humushapper' at 0-5 and 10-15 cm depth at three points per plot (Figure 10). When it was too hard to take soil cores with the 'humushapper' (which was the case in heathlands), samples were taken with Kopecky rings at the same depths. Tree replicas were pooled in one plastic bag. The samples were stored at 4°C.

Soil samples for the N-mineralization experiment were taken in PVC rings of 11 cm inner diameter and 7 cm height. Soils were filled until the height of 5 cm, making the volume of a soil sample approximately 475.2 ml. After clipping the aboveground vegetation, the rings were covered with a cap at the bottom and top. Rings were transported with the soil surface upward, and stored at 4°C until the incubation experiment started.

2.7.4 Vegetation recording

At each plot a representative square of 2 x 2 m was selected to record vegetation structure and species composition. Vegetation records were made in June 2018+2019 for LD, and in August 2018 for GH, August 2018+2019 for NB and August 2018 LB. Cover (%) of bare soil, litter, vascular plants, moss and lichens, and shrubs were recorded. Heights of low layer and high layer (when present) of the vascular plants were measured. Vascular plants, mosses, and lichens were identified and their abundance was recorded in percentage. Because of the extreme dry spring and summer in 2018, the vascular plant biomass produced in the growing season was partly dried out. Cover of this recently dried out biomass was included in the species cover. In the heathland plots the percentage of dried out, brown *Calluna* leaves relative to all leaves was recorded as measure for actual drought stress.

Figure 10. Top: Taking chemistry soil samples from a soil core in the humushapper. Bottom: measuring the depth profile for in-situ pH was a soil electrode.

2.7.5 Vegetation sampling

At all dune grassland sites (18 in LD and 21 NB), before the growing season (February 2018, February 2019), three cages were installed per plot in order to prevent grazing by cattle, horses, deer, sheep and rabbits and to estimate the productivity of aboveground vascular plant biomass during the major part for the growing season for vascular plants without the influence of grazers.

The size of cages was 50x50x50 cm in NB, and a diameter of 100 cm and height of 60 cm in LD (Figure 11). Before installation, the vegetation structure was recorded and aboveground biomass was removed. All aboveground vascular plant biomass was removed by clipping, except for rosettes (mostly *Hieracium pilosella).* Rosettes were not clipped because the rosette plants might have a low ability to regrow. In some of the dune plots *Hieracium pilosella* had a high cover and makes up most of the biomass.

In both 2018 and 2019, plant biomass was harvested at the peak of the growing season (in the beginning of July in LD, end of August in NB), to estimate peak standing crop and annual productivity of vascular plants. The annual productivity samples were taken inside each of the three cages, in a 25x25 cm^2 square, which represent the condition within the cage. The peak standing crop samples were taken outside the cages, paired to each of the annual productivity samples, in a 25x25 cm^2 square, which represent the condition outside the cage.

In a small selection of the dune plots, outside the cages, the living parts of moss and lichens were also sampled in the same square as the peak standing crop samples. The average height and cover of the mosses were recorded as well. The sites where moss was sampled were LD-N03, LD-N05, LD-N07, LD-N11, LD-N16, LD-N17 in LD and NB-04, NB-14, NB-21 in NB (all flat plots).

For flat dune plots, soil cores of root biomass were sampled with a 'humushapper' three times outside the cages, in the same square as the peak standing crop samples. The 'humushapper' samples a soil surface of ca. 3x10 cm square. This surface is small compare to the heterogeneity of root density in the soil. However, we applied this 'quick & dirty' sampling method due to budget limitations in order to get insight in the biomass and nutrient pools in roots. When possible a soil core of 30 cm depth was taken. In some cases it was not possible to sample this depth due to the dry conditions, but most roots were included in the samples nevertheless, because these are concentrated in the topsoil. The size of the harvested soil core was recorded, in order to calculate the surface and volume of the soil core. The harvested roots were either sieved in the field or in the lab to remove sand (when sand was dry), or washed in water (when sand was moist).

In the heathlands sites only peak standing crop was sampled in 1x1 m^2 plots. Each site had 3 replica's. The plots were located in *Calluna* patches, so open patches were omitted. We used bigger plots here than in the dune grasslands, because of the larger size of *Calluna* plants compare to dune grassland plants.

Figure 11. Exclosure cages installed at a site in NB (picture taken early June 2018), and LD (picture taken early July 2018).

2.7.6 Moss monitoring for N-deposition level

The total nitrogen content of pleurocarp mosses is known to be a good bio-indicator for the recent atmospheric N-deposition level and can be used as a cheap proxy with a high spatial resolution. For this reason N-content is monitored in NW-Europe in the ICP Vegetation program. The Netherlands only joined in 2005, but afterwards policy showed no interest anymore for such monitoring. According to the ICP Vegetation protocol (https://icpvegetation.ceh.ac.uk/sites/default/files/ MossmonitoringMANUAL-2015-17.07.14.pdf; Harmsen et al. 2014) we sampled moss in 6 locations in LD and 5 locations in NB representing spatial clusters in an area of 50 m x 50 m of 5 to 10 subsites. Sampling was conducted in the beginning of July 2019 in LD and in the end of August 2019 in NB.

We selected species which are validated in the ICP Vegetation monitoring. For each area we selected the best indictor moss species which was common: on LD *Hypnum cupressiforme var. lacunosum* and in NB *Pseudoscleropodium purum*. The subsamples were mixed to make a composite sample per location. Moss cushions that are sandy and/or occupied by ants were avoided. In order to minimize interception effects of tree canopy, mosses were sampled further than 3 m away from tree canopy. Disposable plastic, non-talcum gloves were used when picking up the moss.

The moss samples were kept in the fridge until further processing. The samples were carefully cleaned by removing dead material and attached litter. The green and green-brown shoots from the last three years growth were included. Brown parts were not included, even if the green parts only represent the last two to three years of growth. The cleaned samples dried at 40 °C for at least 48 hours, and then weighed. After pre-processing the moss samples they were milled, and N-total was measured.

2.7.7 N-measurements in groundwater

To estimate N-leaching, NO_x and NH_4 concentrations in shallow groundwater were measured in LD, NB, and GH.

The sampling in LD was a part of the bigger sampling campaign (Stuyfzand et al. 2019, DPWE project decalcification in coastal dunes) in which 28 sampling wells of 28 mm diameter were installed in February - March 2018 by Waternet. The filter was placed ca. 1-2 m below the groundwater level in winter. Of 28 wells, 6 wells were located near the plots of this study. These plots were 2 control plots (LD_05 and LD_09) and 4 sand-deposited plots (LD_01, LD_02, LD_03, LD_07). Groundwater was sampled in July 2018. From each well, ca. 100 ml groundwater was sampled after filtering with 0.45 μm filter. The samples were analysed for HCO_3, pH-lab, Cl, SO_4, NO_3, NO_2, NH_4, DOC, all cations, tracer elements, Br, S-total and P-total by external labs (Aqualab Zuid, Bureau Veritas Minerals).

For NB, shallow groundwater wells were installed adjacent to 3 plots: 2 control plots (NB_07, NB_10) and 1 sand-deposited plot (NB_13) in February 2018. The filter bottom was respectively at 3.40, 3.10 and 3.24 m below soil level and the filter length was 0.7 m. The water samples (taken in August 2018) were analysed for pH, EC, Cl, Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, Zn, inorganic and organic dissolved C, N-NH_4, N-NO_x, and P-PO_4. It turned out that the samples were strongly reduced and therefore cannot be used for the further analysis (all NO_3 was denitrified).

For GH, shallow groundwater wells were installed in adjacent to 4 plots: 2 control plots (GH_07, GH-09) and 2 sod-cut plots (GH_02, GH_03) in April 2018. The filter bottom was respectively at 2.68, 3.17, 4.22 and 3.13 m below soil level and the filter length was 0.7 m. The water samples (taken in December 2019) were analysed for pH, EC, Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, Zn, inorganic dissolved C, N-NH_4, N-NO_x, DIN, total dissolved N, and P-PO_4.

To convert N-concentrations in groundwater (in mg N/L) to annual N-leaching rate per square meter (mg N/m^2/year), we used empirical relationships between annual precipitation and recharge under different types of vegetation, derived from field observation of Dutch coastal ecosystems (Stuyfzand 2016). Annual recharge (R_N, mm/year) can be computed as:

$$R_N = p \ln(P) - c$$

where P is the annual precipitation on open field (mm/year), p and c are the vegetation-type-specific constants. p and c values were 730 and 4360 for poor grassland vegetation, 720 and 4370 for heath vegetation (Stuyfzand 2016). The annual precipitation was set as 582 mm, the value measured at De Bilt weather station in 2018.

With another rough assumption that N-concentrations in leachate remain stable all through the year, we estimated the annual N-leaching rate (mg N/m^2/year) by multiplying the annual recharge with the dissolved N-concentrations in the shallow groundwater sampled in summer.

2.8 Soil lab analysis

Three types of soil samples (i.e. bulk density samples, chemistry samples, N-mineralization samples) were analysed in the lab. An overview of lab procedures is given in Attachment II.

2.8.1 Soil bulk density samples

Soil bulk density samples were dried at 50 °C for at least 48 hours and then weighed. Soil bulk density (g/cm^3) was calculated as: soil dry weight (g) / soil volume (cm^3).

2.8.2 Soil chemistry samples

Soil chemistry samples were sieved and homogenized by hands until a uniform colour was reached. Living plant materials were removed as much as possible. Five subsamples were split from the homogenized samples for the following analyses: gravimetric moisture content (ca. 15 g fresh weight), dissolved nutrient concentrations (ca. 6 g fresh weight), pH_H2O (ca. 10 g fresh weight), pH_KCl (ca. 10 g fresh weight), soil respiration (ca. 15 g fresh soil), microbial biomass (ca. 6 g fresh weight), and soil organic matter, C, N and $CaCO_3$ content (the rest).

2.8.2.1 Gravimetric moisture content

The subsamples of gravimetric moisture content were weighted immediately after splitting to determine the fresh weight. Dry mass was measured after drying at 105°C for at least 24 hours. Gravimetric soil moisture content was then calculated as: (g wet mass – g dry mass)/g dry mass.

2.8.2.2 Dissolved nutrient concentration

The subsamples of dissolved nitrogen concentrations were extracted with K_2SO_4. After adding 75 ml 0.05M K_2SO_4 solution, the soils were shaken for 2 hours at 120 rpm and filtered with 0.2 µm filters. Concentrations of NH_4, NO_3, NO_2, PO_4, and total dissolved nitrogen in the extract were measured with autoanalyzer (Skalar). DON (dissolved organic nitrogen) was calculated as total dissolved nitrogen minus NH_4, NO_3, and NO_2.

2.8.2.3 Soil pH

The subsamples of pH_H2O were extracted with 25ml demineralized water and shaken for 2 hours at 120 rpm. The extracts were left for one night, and then shaken once again for 30 minutes. Identically, the subsamples of pH_KCl were extracted with 25 ml 1M KCl. The pH in the extracts was measured using a pH electrode (Hanna H199121).

2.8.2.4 Soil organic matter, organic C, organic N, and, $CaCO_3$ content

Dried soil was machine-ground. A subset of the ground soils was analysed by the sediment lab of VU for soil organic matter content (loss on ignition (LOI) at between 105 and 550 °C), and for calcite content (loss on ignition between 600 and 1000 °C) by TGA. Also the loss on ignition between 105 and 330 °C was measured. The ratio of

$LOI_{105\text{-}330\ oC}$ to $LOI_{105\text{-}550\ oC}$ was calculated as proxy for how easy the soil organic matter can burn.

Another subset of the ground soils was analyzed for organic C and organic N-content by combustion with CNS analyzer, also by the sediment lab of VU. Prior to this analysis, soils were acidified to remove carbonates.

2.8.2.5 Automated CO_2 Respiration Analysis

Soil respiration was measured with Respicond VI (Nordgren Innovations AB, Sweden). Respicond measures the CO_2 flux by capturing CO_2 in KOH. This results in a decrease of the conductance in the hydroxide solution, which was measured with platinum electrodes in each incubation vessel (Figure 12).

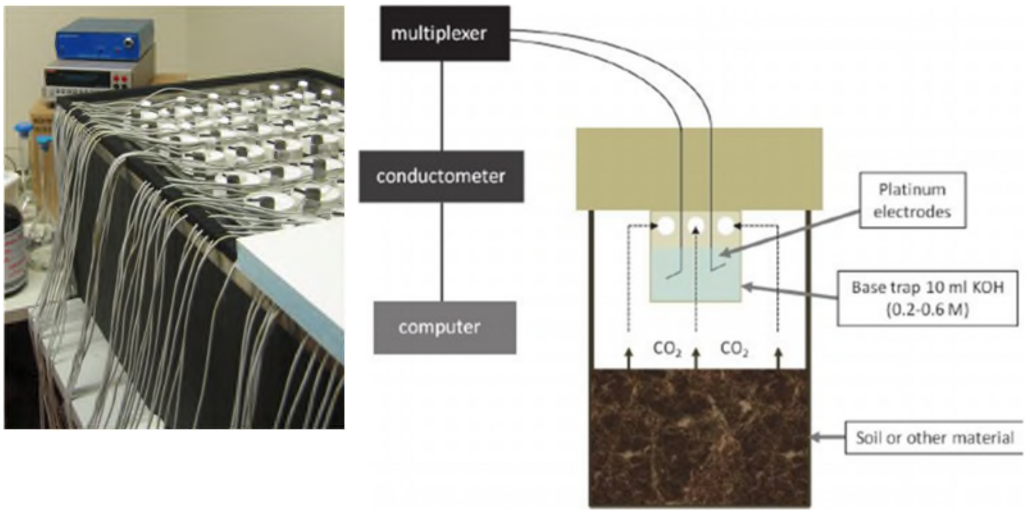


Figure 12. Left. Example of Respicond V installation (http://www.respicond.com). Right: Individual Respicond measurement cell (Kainiemi, V., 2014)

Prior to the incubation period, a small amount of water was added to each soil to make sure that the soil was not too dry to hamper microbial activities. We calculated the amount of water to add for each soil in a way that the water filled pore space became approximately 40% (See section 'N-mineralization experiment' 2.8.3 for the calculation method). Since RESPICOND is a closed system, the soil moisture content was, in theory, kept constant during the entire incubation period.

The RESPICOND experiment was run at 20 ˚C for 5 weeks, the period between 21 June 2018 and 9 August 2018. We also measured 2 blank samples. To check if the moisture was maintained throughout the experiment period, soil moisture was measured in the end of the experiment by weighing and drying the fresh samples in the 70˚C oven and weighed again. The weighting of the moist incubation rings revealed a median value of 36 % for the water filled pore space. There were 4 outliers (NB17 27 %, GH12 24 %, GH07 22 %, LB03 50%.

The raw data obtained from the Respicond (as mg CO_2 accumulated per sample tube) were first corrected for the measurement errors and outliners. A value was corrected when it exceeded the median by more than 200%, and the standard deviation by more than threefold. We observed daily fluctuation in CO_2 accumulation in all sample tubes including blanks, which should be caused by external factors, not by soil activity. To remove the confounding daily fluctuation, the CO_2 accumulation values of soil samples were corrected by subtracting average CO_2 values of blanks.

CO_2 accumulation rates in the first 24 hours were rather irregular, since the soil was not stabilized yet. Furthermore, there were several moments when small abrupt changes in CO_2 accumulation were observed. These abrupt changes were caused by external factors, such as replacing KOH solution. Therefore, we calculated CO_2 accumulation rates (mg CO_2/h) in several time periods which do not include irregular or changing CO_2 accumulation (i.e. 7.8 – 17.8h, 21.8 – 258.8h, 268.8 – 513.8h, 529.8 – 683.8h, and 694.8 – 912.8h). The accumulation rates were obtained by fitting a linear regression model for each time period. Subsequently, CO_2 accumulation rates for the period of 38 days, the period that the N-mineralization experiment was run, were calculated by summing up CO_2 accumulation rates of five periods (0-19h. 19-263h, 263-520h, 520-690h, and 690-912h). Finally, soil respiration rates for 38 days were calculated by dividing the CO_2 accumulation rates with gram soil (i.e. mg CO_2/kg soil/38 days).

To evaluate the decomposition rate, C turnover rate (g C-CO_2 respired/g soil total C/38 days) was calculated by dividing the soil respiration rates by soil total C content.

2.8.2.6 Microbial biomass

Soil microbial C, N, and P, can be estimated from the difference in extractable concentrations of C, N, P between fresh and fumigated soils. We used the chloroform fumigation method (Brookes et al. 1985). In this procedure, soils were fumigated with chloroform and then extracted with 0.05 mol/L K_2SO_4 solution. C, N, and P concentration of the fumigated soils in the K_2SO_4 extracts were compared with those of non-fumigated soils as described in section 2.8.2.2.

Approximately 6 g of fresh soil was weighted and stored in a glass bottle. The glass bottles were placed in a desiccator. To saturate the desiccator with chloroform, one large glass jar with approximately 2-3 cm chloroform and 4 carborundum boiling stones was placed under the desiccator’s plateau. In order to prevent the chloroform from being absorbed into the pump oil, a cold finger was placed in liquid N_2 in the tubing between the desiccator and the pump so that it could condense in the finger. The space in the desiccator was then vacuumed 3 times at intervals of about 2 hours and left in the chloroform atmosphere for 24 hours. After cleaning the desiccator, the soil samples were vacuumed 3 times in the desiccator. This was to make sure that all chloroform was removed from the soils, as chloroform residuals may interfere with measurements of carbon.

75 ml 0.05 mol/L K_2SO_4 solution was added to the fumigated samples. Three blanks were also prepared. The samples were shaken for 2 hours at 120 rpm and refrigerated until the next day when filtering took place. The extracts were filtered with 0.2 µm filters. The filtered extracts were split into plastic tubes, 15 ml for the TOC analysis and ca. 50 ml for nutrient analysis, and immediately frozen for a couple of months until analyses.

Total dissolved N and PO_4 in the extract was measured with the auto-analyzer, and total organic C was determined with the Elementar TOC system. The same measurement was conducted on the N-mineralization samples after the incubation period. For these samples, the extracts were not frozen but kept in a fridge, and analysed for C, N, P concentrations within a week.

Microbial C content (g microbial C / g dry soil) was calculated by subtracting the concentration of total organic C extracted from the chemistry soil (see section 2.8.2.2) from that in the paired fumigated soil. Microbial N-content (g microbial N / g dry soil) was calculated identically using the concentrations of total dissolved N in the extracts. To evaluate soil quality, microbial fraction (g microbial C / g soil total C) and microbial C:N ratios were calculated.

2.8.3 N-mineralization experiment

Soil samples for the N-mineralization experiment were first adjusted for the water content, since most of the soils were very dry (due to the extremely dry weather conditions of the 2018 summer) and the drought stress could hamper microbial activity. Because moisture conditions for soil microbes can be better reflected by the fraction of soil pore space filled with water, rather than the gravimetric moisture content, we aimed at achieving water filled pore space (WFPS) of 40% for all soils. The soil pore space was estimated using the following empirical relationship of soil bulk density and soil pore space, obtained from 44 dune soils in the Netherlands (Fujita et al. , 2018).

$$SPP = 0.96 - 0.36 * BD$$

where *SPP* is the soil pore space (cm^3/cm^3), *BD* is the bulk density (g/cm^3). Note that this empirical relationship was derived from relatively organic-poor soils, ranging approximately between 0.8 and 1.6 g/cm^3 in bulk density. Thus, the estimates of soil pore space for some of our organic-rich samples, especially the topsoil of heathlands, were unreliable, possibly causing large errors in the water adjustment.

The volumetric water content of the fresh soil was calculated as follows:

$$VWC = GWC * BD / WD$$

where *VWC* is the volumetric water content (cm^3 water/cm^3 soil), *GWC* is the gravimetric water content (g water/g dry soil), and *WD* is the density of water (g water / cm^3 water = 1).

Subsequently, in order to achieve the WFPS of 40%, the amount of water to add for each soil sample was calculated as:

$$W = (0.4 * SPP - VWC) * V$$

where *W* is the amount of water to add (cm^3), *V* is the volume of the soil samples (475.2 cm^3).

Since most soils were very dry and hydrophobic, the calculated amount of water could not be added at once. In those cases, water was added again after a few days. Note that, for a few soils, it was not possible to add all the calculated amount of water. See Attachment III for the actual water content in each soil during the experiment. The soils were stored in a fridge until the start of the N-mineralization experiment.

The soils were incubated for 38 days (29 June – 6 August 2018) at 20 °C (Figure 13). The lids of the samples were kept open. To keep the humidity in the incubator high, a bucket of water was left in the incubator. Twice during the incubation period, the weight of the soils was checked, and the amount of evaporated water was replenished with demineralized water. Although the inside of the incubator was dark, germination

of plants was observed in some soil samples. The germinated plants were clipped and left on the soil surface.
At the end of the incubation period, the soils were sieved and homogenized. Ca. 6 g (fresh weight) of soil was extracted with 75 ml 0.05M K_2SO_4 solution, shaken for 2 hours at 120 rpm, and then filtered with a 0.2 µm filter. Concentrations of NH_4, NO_3, NO_2, total dissolved N, and PO_4 in the extract were measured with the Skalar auto-analyzer. The concentrations of the nutrients were converted to the unit of mg N/gDW soil.

The rates of net N-mineralization were calculated as follows:

$$Nmin = (NH_4\_after + NO_3\_after + NO_2\_after - NH_3\_before - NO_3\_before - NO_2\_before) / D$$

where *Nmin* is the N-mineralization rate (mg N/kg soil/38 day); *NH_4_after, NO_3_after*, and *NO2_after* are the concentrations of NH_4, NO_3, and NO_2, respectively, at the end of the incubation period (mg N/kg soil); *NH_4_before, NO_3_before*, and *NO_2_before* are the concentrations of NH_4, NO_3, and NO_2, respectively, at the start of the incubation period (mg N/kg soil); *D* period of incubation in days. The N-concentrations measured with the chemistry samples (see section 2.8.2.2) were considered to be equivalent to the N-concentrations at the start of the incubation period.

Since N-mineralization rate per area, instead of per gram soil, is more relevant for growth of plants, N-mineralization rate from the topsoil of 1 m^2 was calculated as:

$$Nmin\_area = Nmin / BD * 1000 * topd$$

where *Nmin_area* is the N-mineralization rate per area (mg N/m^2/38 day), *BD* is the bulk density (g/cm^3 = kg /dm3), 1000 is to convert dm3 to m3, *topd* is the depth of the sop soil (m). We set *topd* as 0.1 m, because the top 10cm soils contain most of the organic matter.

Furthermore, to evaluate the mineralization rate of N, N-turnover rates (g N/g total C/38d) were calculated by dividing N-mineralization rate *Nmin* by soil total C.
In addition, P mineralization rates were computed based on P-PO_4 concentrations in the soil extracts, using the same calculations as N-mineralization rate. Note that geochemical processes of P, such as adsorption/ desorption, are not taken in account here. Therefore, the P mineralization rates are possibly underestimated or overestimated.

2.9 Vegetation lab analysis

2.9.1 Plant productivity

The peak standing crop samples, productivity samples were dried at 65 °C for 48 hours and weighed. The moss samples were sorted on sieves to remove sand and litter. When the moss contained lots of sand which is difficult to remove, they were washed with water. The sorted moss biomass was dried at 65 °C for 48 hours and weighed. The root samples were dried at 65 °C for 24 hours, and sieved and cleaned with hands to remove sand. The cleaned roots were dried again at 65 °C and weighed. The mass of the plant biomass samples was calculated in the unit of g biomass/m^2.

Figure 13. N-mineralization samples in the incubator. This picture was taken halfway through the experiment and some vegetation regrowth can be seen on the surface.

2.9.2 Plant nutrient concentrations

Annual productivity samples, the peak standing crop samples, and root samples of flat dunes of 2019 (N=24 each) and moss monitoring samples (N=11) were analysed for element concentration. Dried biomass samples of 3 subplots were chopped into small pieces and mixed, and then machine-ground. The ground samples were digested with H2SO4/H2)2/Se, and then determined for concentrations of total N and total P with SFA-Nt/Pt. In addition, only for the annual productivity samples, concentrations of K were determined with F-AES. The analyses were dune by Chemical Biological Soil Laboratory of WUR. For mosses also moss standard M3 used in the ICP Vegetation program was analysed. Two measurements (6.7 and 6.9 g N/kg DW) fitted well with the value of the standard (N-total = 6.81 ± 0.52 g N/kg DW).

Because we collected two different moss species (*H. cuppresiforme* in LD and *P. purum* in NB) for measuring the total N-content, and N-content in mosses is besides N-deposition also dependent on the species, we scaled the N-content of the NB samples to the content of *Hypnum cuppresiforme* according to Harmsens et al. (2014).

2.10 Data analysis

For each plot, average Ellenberg values for acidity, nutrient availability, and moisture were calculated. The average values were computed as unweighted average, as well as weighted average (i.e. weighing by cover of each species).

Number and cover of plant species associated with N-fixers were calculated for each plot. Plant species in Family *Fabaceae* and *Hippophae rhamnoides* were regarded as species associated with N-fixers.

For assessing the functional properties of the plant species composition cover weighted average values of several species traits were calculated. The following species traits were used:

- maximum canopy height and minimum canopy height derived from the LEDA database (Kleyer et al. 2008);
- specific leaf area derived from the LEDA database (Kleyer et al. 2008);

- shoot life span (value between 1 for 1 year and 2 for 2 or more years), number of clonal offspring (categories <1, 1, 2-10, 10+ offspring represented by values 0.5, 1, 6, and 15), clonal spread (< 0 cm = 0.1; 1-25 cm = 0.5; >25 cm -= 1), and root resprout (presence of freely dispersible clonal organs: 1 = present, 0 = absent) derived from the CLO-PLA database (Klimešová & De Bello 2009).

To examine the effect of management (control/managed) and area (LD/NB) for coastal dunes, GH/LB for heathlands), 2-way ANOVA was conducted. For dunes, plots on slopes were excluded from the analysis to avoid confounding effects of slopes. Prior to the analyses, a number of soil variables and plant variables were transformed to correct for right-skewed distribution. The equality of the variance was tested with Levene's test, and the normality of the residual values was tested with Shapiro-Wilk test at the significance level of p=0.05.

For coastal dunes, effects of slopes were examined with 2-way ANOVA, with slope (flat/south-facing slope/north-facing slope) and area (LD/NB) as explanatory variables. Here plots with ‘measure’ were excluded from the analysis. Prior to the analyses, a number of soil variables and plant variables were transformed to correct for right-skewed distribution. The equality of the variance was tested with Levene's test, and the normality of the residual values was tested with Shapiro-Wilk test at the significance level of p=0.05. The difference among slopes was tested with multiple comparison test (Turkey HSD).

Variables which were measured in 2018 and 2019 were tested with 3-way linear mix model in order to test the effect of time. Plots was added as random factor because of the dependency of measurements in 2019 on those of 2018. Prior to the analyses of variables were transformed to correct for right-skewed distribution. The analyses were conducted for effects of management (control/managed), area (LD/NB) for dunes and year (2018/2019) with only flat plots, for effects of slope (flat/south-facing slope/north-facing slope), area (LD/NB) for dunes and year (2018/2019) for only control plots. The equality of the variance was tested with Levene test, and the normality of the residual values was tested with Shapiro-Wilk test at the significance level of p=0.05.

To explore the major axes of variations of soil variables, PCA (Principal Component Analysis) was conducted. Here flat dunes plots with complete soil measurements (N=24) were used. We choose 9 bulk variables of topsoil (0-5 cm depth) to include in the model: Bulk density (g/cm3), soil organic matter content (%), soil organic C content (kg C/m^2), soil organic N-content (kg C/m^2), soil C:N ratio, soil pH_KCl, $CaCO_3$ content (%), concentrations of N-NH_4, N-NO_x, and P-PO_4 concentration (mg N/kg dry soil and mg P/kg dry soil). Soil organic matter, Soil organic C, soil organic N, N_NH_4, and N-NO_x (after adding 0.1) were log-transformed prior to the analysis.

To explore the variations and similarities of species compositions among plots, ordination methods were applied. First, the plots were ordinated based on abundance (as cover %) of occurring plant species, using Detrended Correspondence Analysis (DCA). Prior to the analysis, the cover was log-transformed after adding 1.

DCA extracts the major variations purely based on the species composition, but what we were particularly interested in is the variation which are influenced by the two environmental factors: namely, N-deposition and management. Therefore, we also conducted a so-called ‘constrained ordination’ analysis, which extracts the variations in species composition which are related to the two environmental binary factors. For this, we applied Canonical Correspondence Analysis (CCA). Significance of the model was tested with permutation test, for the whole model, and for each of the environmental factors separately.

All analysis was conducted using the programming language R ver. 3.5.1. The ordination analyses were conducting using the R package 'vegan 2.5.4'

2.11 Calculation of C- and N-pools and fluxes

The N and C pools and fluxes were calculated from the measurements in 2018 for flat dune plots and heathland plots. The following C and N pools were quantified for soil organic matter, microbial biomass, aboveground plant biomass standing crop, root biomass. For N also pool dissolved particles, the pool of extractible mineral N was calculated. External fluxes for C and N were calculate for aboveground biomass consumed by grazers. This flux was calculated from the differences in productivity and standing crop. External N fluxes were also calculated for atmospheric deposition and N-leaching. Because we could nor measure N leaching in the UK dune area, we used a measurement from Jones et al. (2004) in calcareous dune grassland of another Wales dune area with a low N-deposition. There were no measurements of N-leaching in the UK heathland area. Calculates internal fluxes consisted of aboveground vascular plant production, net mineralization and immobilization in microbial biomass. For the heathland plots not all mentioned pools and fluxes could be quantified because of less intensive measurements compare to the dune plots. Input of N by biological N2-fixation and by large grazers were not calculated because of a lack of measurements. Denitrification was also not quantified. Storage in roots and mosses was not calculated because root and moss productivity was not measured. The same was the case for storage in new soil organic matter.

For some calculations we had to make assumptions and extrapolations. Plant biomass was measured as dry weight. For calculation of C-pools in plant biomass we assumed a C-content 50% DW. N- and C-mineralization were extrapolated from the 38 d incubation experiment to 90 days. N and C storage in microbial biomass was calculated for the 38 d incubation period. Note that the microbial immobilization rate is possibly overestimated, as we measured it in the incubation pots in where plant growth was suppressed strongly (and therefore low competition for mineral N by plants). Also C- and N-mineralization can be overestimated because this was measured during incubation with optimal moist conditions, while under field conditions microbial activity during spring and summer is hampered by strong drought stress. For this reason we extrapolated mineralization only for a period of 90 d. C and N pools in plant biomass were calculated by multiplying biomass per surface unit with the C and N content. Pools in mosses were calculated as follow. Standing crop of moss biomass was only measured in a part the dune plots. From this measurements we related moss biomass to moss cover (moss biomass = $32.9\ e^{0.025\ \mathrm{cover}}$; $r^2 = 0.43$). With this relation moss biomass for each plot was calculated from the recorded moss cover. The N-content of mosses was not measured in the normal plots but measured in several larger 50x50 m plots in the NL (6 plots) and UK dune (5 plots) area. We calculated for each dune area an average value of the moss N-content for calculation of the moss N-pool on plot level.

For presentation of the results pools and fluxes calculated on plot level were averaged for the combination of area management category (for dune areas control and sand deposition and for heathland areas control and sod cut).

3 N-deposition levels

For coastal dunes and heathlands the historical patterns during 1950 to 2010/ 2015 were compared for areas with low (lowN) and high N-deposition (highN).

3.1 Coastal dune areas

During 1950 until recently (2010 in NB and 2015 in LD), total N- deposition was much lower in the low N-area (Newborough; NB) than in the high N-area (Luchterduinen; LD) and had a little peak around 1990 (figure 9; Table 2). During the deposition peak in the Netherlands N-deposition in LD was ca. 3 times higher than in NB. Thus the high N-area was exposed for several decades to a high N-load. In the high N-area deposition peaked above the critical load (CL) of habitat H2130 Fixed dunes with herbaceous vegetation (`grey dunes`) for a long period (ca. 1960 until 2015). The current deposition here is at the CL level of the calcareous variant of this habitat, but still above the CL of the more sensitive acidic variant (both variants occur here). In the low N-area N-deposition was always below the CL of the calcareous variant of Grey dunes (no acidic variant here). In LD, the contribution of NH_y was ca. 50 % of the total N-deposition. In NB this was also the case until 1970's (Figure 15), but between 1970 and 1990 the contribution of NH_y deposition increased considerably due to a decrease of NO_x and an increase of NH_y deposition. Both areas have an increase of the NH_y/NO_x ratio, with the strongest increase in NB (Figure 16). However, in a location of the MAN monitoring program for air NH_3-concentration, values increased strongly in 2018 with 50% of the average value between the period 2005-2017 (https://man.rivm.nl/gebied/ kennemerland; plot De Zilk).[1]

3.2 Heathland areas

Although the low N-area (Little Budworth Common; LB) in England was selected as a low N-reference site, the N-deposition during the last decade was similar to the high N-area (Groote Heide; GH) (Figure 14). However for the historical N-loading the areas still differ strongly. Hostorical loading was much higher in the high N-area because of a high peak (max. 45 kg N/ha/y) during the 1970’s and 1990’s. In the low N-area N-deposition peaked later and at a lower level (80’s until now). In both areas the CL of habitat H4030 European dry heathlands was exceeded for several decades, with a longer and stronger exceedance in the high N-area. The NO_x deposition declined in both areas (Figure 15). In GH the NH_y deposition also declined, while in LB it increased threefold. Because of these trends in LB the NH_y/NO_x ratio increased strongly to a very high level, while in GH it showed no clear trend based on modelled values (Figure 16). However monitoring of air NH_3-concentration in the MAN monitoring program revealed a strong increase of ca. 50% between 2017 and 2018 for NH_y deposition (https://man.rivm.nl/gebied/ leenderbos_groote_heide_en_de_plateaux)(see footnote 1)

[1] For explanation for this strong increase are several reasons. Due to the long dry and hot periods in 2018 more NH_4 could vapour from dunged agricultural fields, and at the same time less wet NH_y was deposited because of a low precipitation. This caused elevated NH_3-concentration in the air (35% in NL between 2017 and 2018). Provisory calculations indicate that NH_y deposition was elevated ca. 10% (https://www.rivm.nl/nieuws/ammoniakmetingen-in-2018). A recent evaluation of NH3 concentrations and emissions in NL trends during 2005-2016 revealed NH_3 concentrations increased due to a decline of NO_x and SO_x concentration resulting in less conversion to aerosols (salts) and probably also because of an increase of NH_y-emission which is underestimated in the emission registration (Mara et al. 2019).

3.3 Discussion N-deposition patterns for high and low deposition areas

As described above, for the dune areas, the pattern of historical N-deposition clearly differs for high N and low N-areas. This means that the low N-area is an excellent reference for low N-deposition. For the heathland areas the pattern is less clear, because the low N-area did have a considerable high N-load from the 1980's until now with a long exceedance of the critical load, but recently total N-deposition became similar for both areas. The average N-deposition during the last 20 and 30 years was however slightly higher in the high N-area (Table 2). This is important as a recent study (Payne et al. 2019) showed that for heathlands the long term (20-30 y) cumulative N-load better explains the vegetation compositional variability than the short time (1-3y) cumulative N-load. Because for a 20 to 40 year window cumulative N-load in the low N-area was considerable lower than the high N-area (Table 2), the low N-area can still serve a relative low N-reference. There are however a two confounding factors. In the low N-area the sod cutting was done longer ago (18-20 years) than in the high N-area (15 years), and therefore the new soil after sod cutting experienced more cumulative N-deposition (Figure 14 graph right). Secondly, the NH_y/NO_x ratio in N-deposition increased to much higher values in the low N-area than in the high N-area. Research (Van den Berg 2016) showed that a high value for this ratio has adverse ecological effects on typical heathland plant species of habitat on acidic soils. For the control sites in the heathland area (without sod cutting) the situation is different, because these sites had in the past in the high N-area much more N-deposition. On average for a 40 year period here the total N-deposition was 1.5 times higher than in low N-area (Table 2).

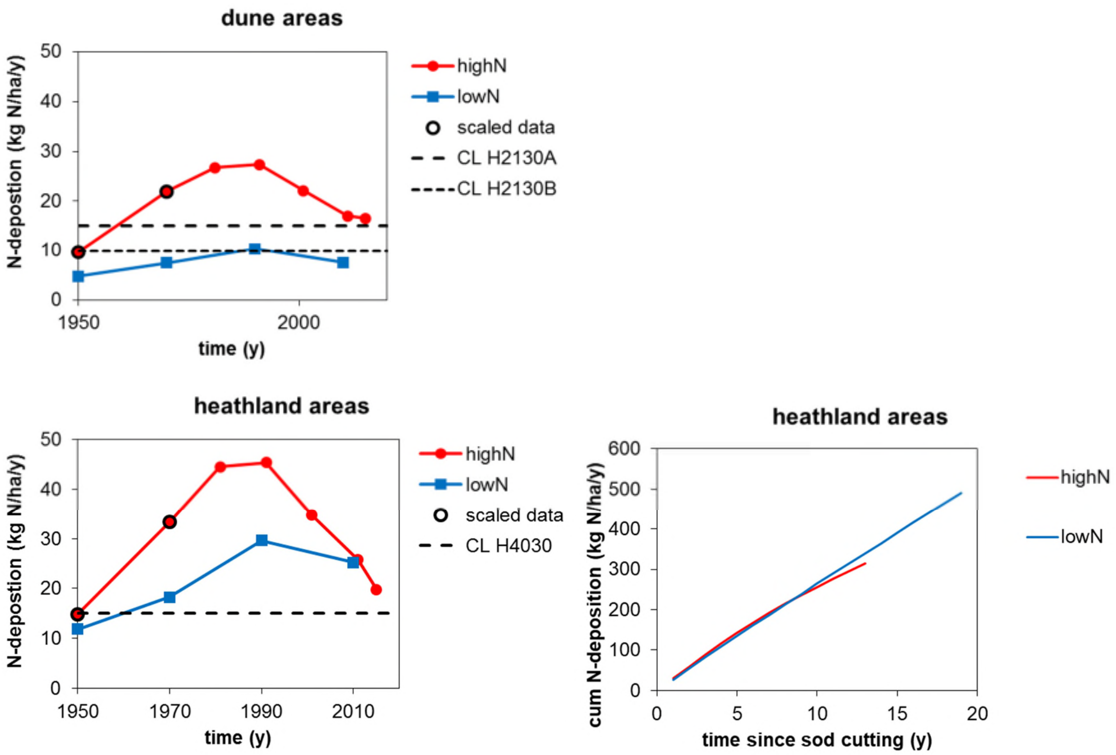


Figure 14. Trends of total N-deposition at the four study areas. Luchterduinen (dune) and Groote Heide (heathland) were selected for high N-deposition (highN), and Newborough (dune) and Little Budworth Common (heathland) were selected for low N-deposition (lowN). Critical loads of habitats are also indicated. H2130 = Fixed dunes with herbaceous vegetation (`grey dunes`), H2130A = calcareous variant, H2130B = acidic variant. Left graphs show trend of yeearly N-deposition and the right graph the cummulative N-deposition since sod cutting for the heathland areas.

Concerning for habitat quality is the long term increasing trend of the NH_y/NO_x ratio in the UK areas. Although in the NL areas such a strong increasing trend was not shown in the modelled profiles, recently (2017-2018) local measurements indicate NH_y deposition increased and therefore also the NH_y/NO_x ratio. This is in line with the increasing national trend of air NH_3 concentration (Mara et al. 2019).

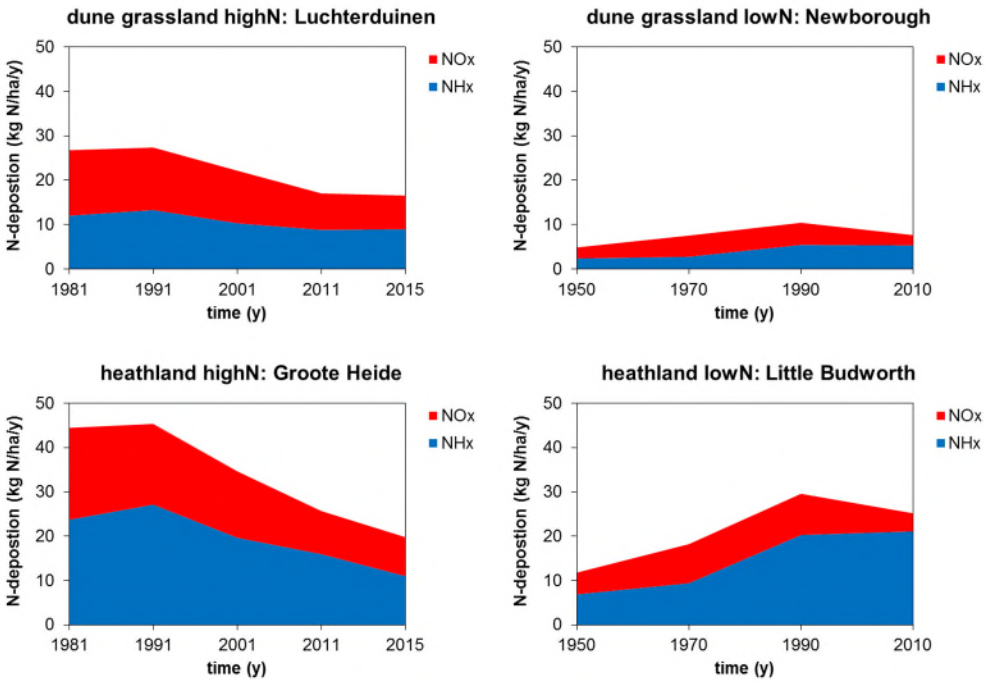


Figure 15. Trends of NH_y and NO_x deposition (stacked) at the four study areas. Luchterduinen (dune) and Groote Heide (heathland) were selected for high N-deposition (highN), and Newborough (dune) and Little Budworth Common (heathland) were selected for low N-deposition (lowN).

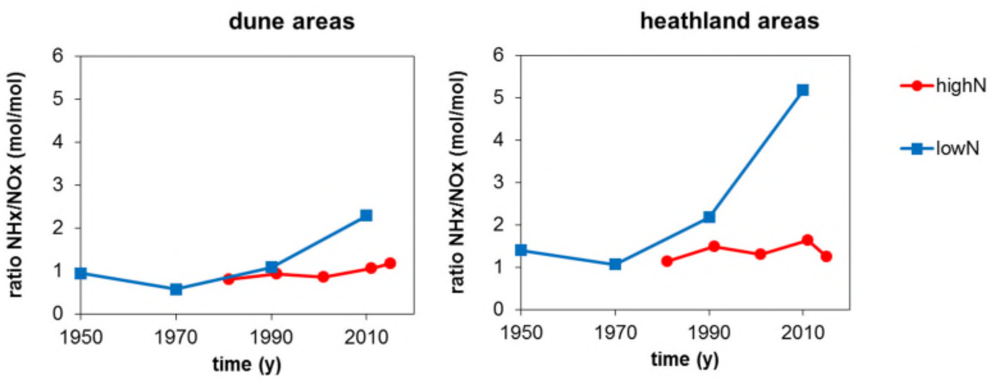


Figure 16. Trends of the ratio NH_y/NO_x (mol/mol) at the four study areas. Luchterduinen (dune) and Groote Heide (heathland) were selected for high N-deposition (highN), and Newborough (dune) and Little Budworth Common (heathland) were selected for low N-deposition (lowN).

Table 2: Average total N-deposition for the last 10, 20, 30 and 40 years for the study areas. Luchterduinen (dune) and Groote Heide (heathland) were selected for high N-deposition (highN), and Newborough (dune) and Little Budworth Common (heathland) were selected for low N-deposition (lowN).

Area	N load	average total N-depostion			
		10 y: 2009-2018	20 y: 1999-2018	30 y: 1989-2018	40 y: 1979-2018
NL: Luchterduinen (LD)	Nhigh	16.9	18.9	21.2	22.6
UK: Newborough (NB)	Nlow	7.6	8.1	8.7	8.9
NL: Groote Heide (GH)	Nhigh	22.7	27.6	32.5	35.5
UK: Little Budworth (LB)	Nlow	25.2	25.9	26.9	26.6

4 Effects of measure (sand deposition) on dune grasslands

Results of all ANOVA analyses related to this section are summarized in Attachment VII.1 and VII.4.

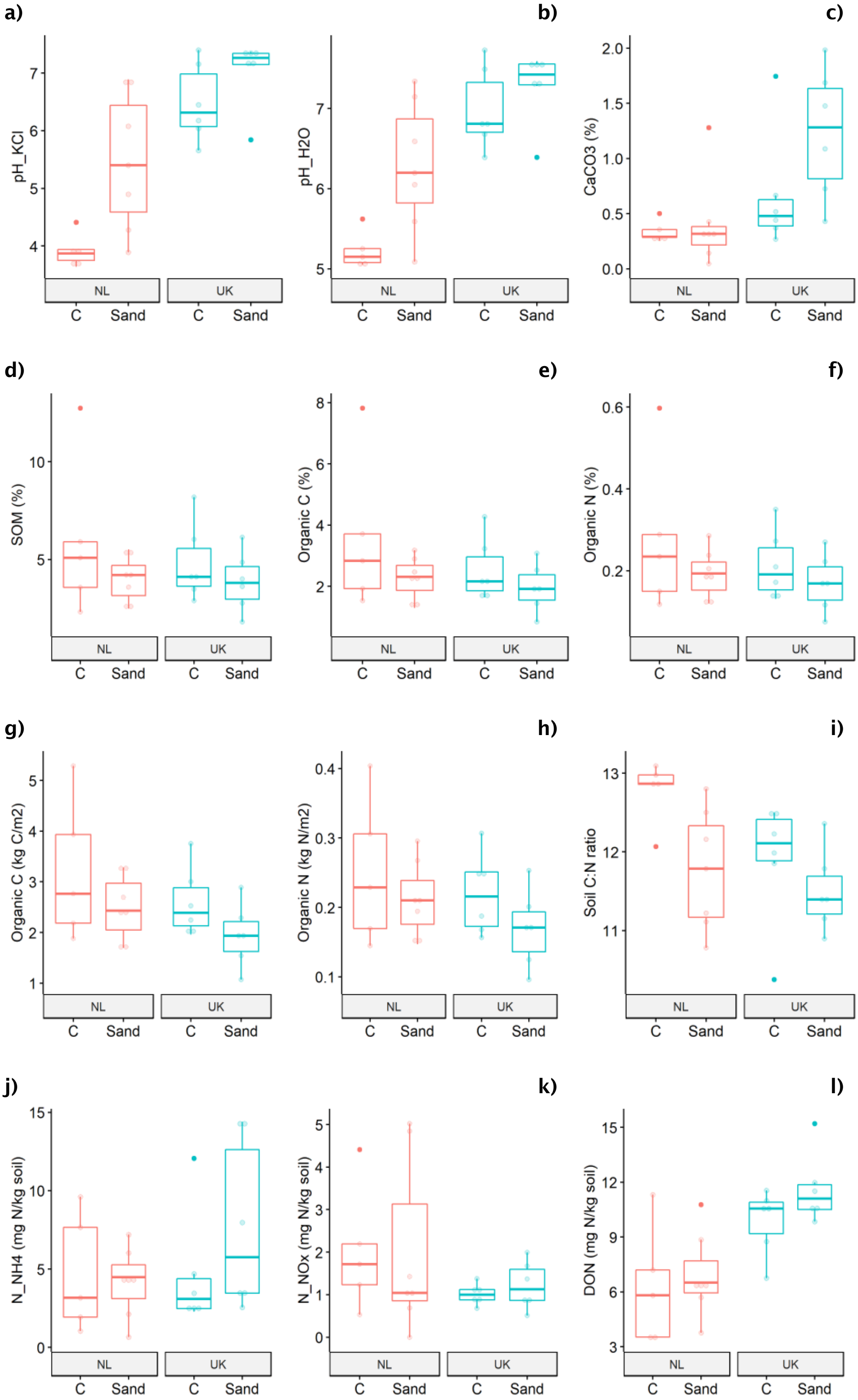
4.1 Effects of sand deposition on soil bulk parameters of topsoil

Sand deposition from blowouts had large effects on pH of the dune topsoil of 0 – 5 cm depth ($p<0.001$ with ANOVA for both pH_H2O and pH_KCl; Figure 17 a & b). Soil pH was lower for NL than for UK ($p<0.01$) because the soil of the dune grasslands in NL was deeper decalcified. This is in line with the higher calcium carbonate concentrations in UK than NL ($p<0.01$) (Figure 17c). Note that there was a large variation in pH within sand-deposited plots (and even within control plots) (Attachment V), possibly due to different degrees of exposure to sand deposition.

Content (in percentage of total soil) of soil organic matter, soil organic C and N-contents were all indifferent between areas ($p>0.1$) and management types ($p>0.1$), although they all tended to be slightly lower in sand-deposited plots than control plots (Figure 17 d - f). When soil organic C content was expressed per area (i.e. kg C/m^2), it was almost significantly ($p = 0.06$) lower for sand-deposited plots than control plots. (Figure 17 g & h). C content expressed per area (i.e. kg C/m^2) showed no difference for management,

Soil C:N ratio was significantly lower ($p<0.05$) in sand-deposited plots than control plots (Figure 17i), indicating that sand-deposited plots had relatively N-rich soil organic matter. Soil C:N ratio was slightly higher (although not significantly; $p=0.08$) for NL than UK, irrespective of higher atmospheric N-deposition levels in NL.

Concentrations of dissolved inorganic nutrients were indifferent between areas and management, in terms of $N\text{-}NH_4$, $N\text{-}NO_x$, total dissolved inorganic N (DON), and $P\text{-}PO_4$ ($p>0.1$ for all) (Figure 17 j - m). Dissolved organic N-concentrations were significantly higher for UK than NL ($p<0.001$).


a)
pH_KCl
b)
pH_H2O
c)
CaCO3 (%)
d)
SOM (%)
e)
Organic C (%)
f)
Organic N (%)
g)
Organic C (kg C/m2)
h)
Organic N (kg N/m2)
i)
Soil C:N ratio
j)
N_NH4 (mg N/kg soil)
k)
N_NOx (mg N/kg soil)
l)
DON (mg N/kg soil)
NL
UK
C
Sand

m)

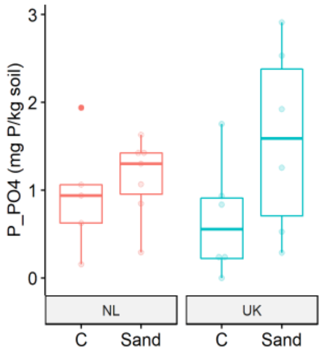


Figure 17. Median and quantiles (25th and 75th) of **soil bulk variables of flat dune topsoil** (0 – 5 cm depth). Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK'). Points depict the values of each replica. Open point are non-outliers and cloesd points outlayers. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 6 for UK_Sand (N = 24 in total).

In order to have a more integrated insight of effects of management on soil bulk properties and their variation within areas and treatments, ordination analysis (PCA) was conducted. The first and second axis explained 43.8 % and 26.1 % of the total variance, respectively. The first axis mainly reflected the variation in organic matter content of the soil (positively related to soil organic matter content, soil C, soil N and negatively related to bulk density), whereas the second axis reflected soil acidity (with high pH and $CaCO_3$ content on positive axis scores) (Figure 18). Further, N-NH_4 and P_PO_4 content were positively related to the second axis, and negatively with soil C:N ratio (i.e. relatively N-rich organic matter). The 4 main categories of our plots, differing in area and management, were more or less separated along the second axis of the PCA plane, with large overlap between the categories. The gradients of organic matter content were similar among the categories. In general, Dutch plots were located on the bottom of the plane, indicating lower soil pH due to a low $CaCO_3$-content, and a low soil C:N ratio. For UK plots the opposite was the case. For both NL and UK area, sand-deposited sites tended to locate higher on the plane (i.e. less acid).

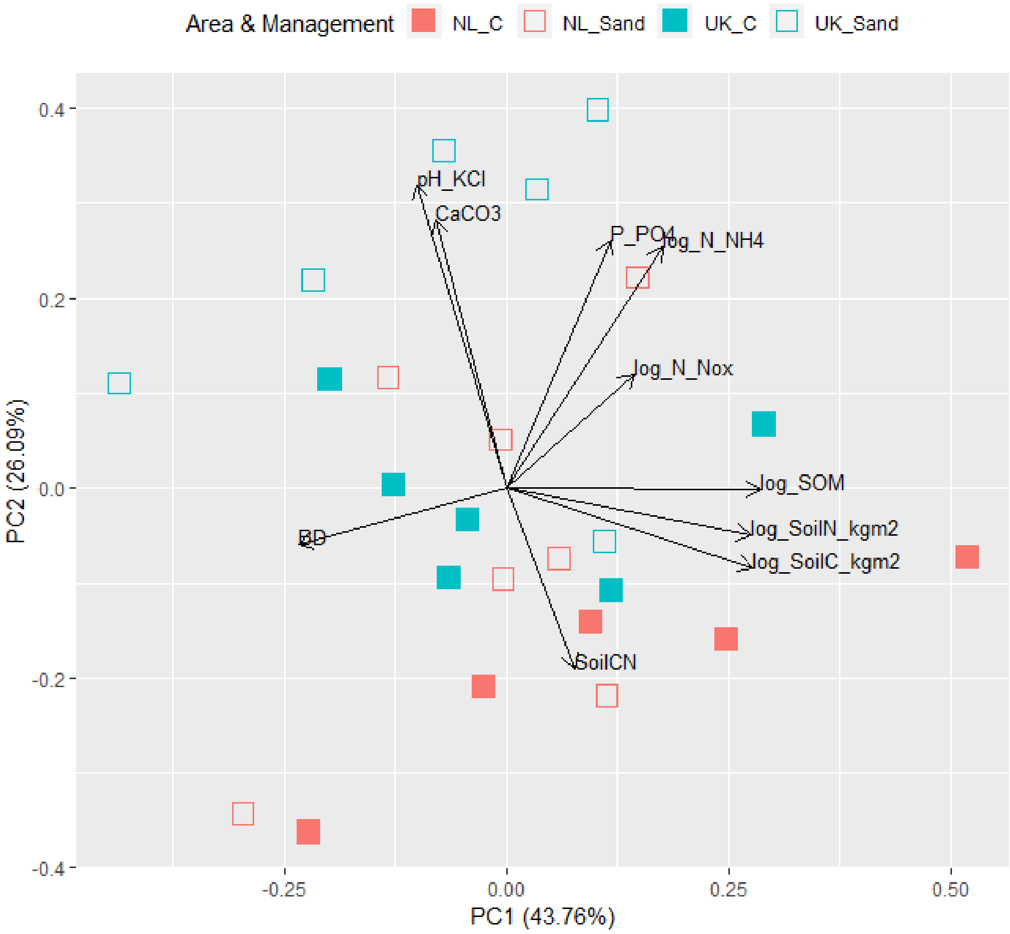


Figure 18. PCA diagram of flat dunes plots (N=24), based on 9 **soil bulk variables of topsoil** (0-5 cm depth): Bulk density (g/cm3), soil organic matter content (%), soil organic C content (kg C/m^2), soil organic N-content (kg C/m^2), soil C:N ratio, soil pH_KCl, $CaCO_3$ content (%), concentrations of N-NH_4, N-NO_x, and P-PO_4 concentration (mg N/kg dry soil and mg P/kg dry soil). Soil organic matter, Soil organic C, soil organic N, N_NH_4, and N-NO_x (after adding 0.1) were log-transformed prior to the analysis. Arrows depict loadings of these 9 soil variables.

4.2 Effects of sand deposition on soil bulk parameters of subsoil

For the subsoil (10 – 15 cm depth), there were no significant effects of management on any of the soil bulk parameters ($p>0.1$). Several parameters were significantly different between areas: pH_KCl and pH_H2O were higher in UK than in NL ($p<0.01$ and $p<0.001$, respectively; Figure 19 d & e); $CaCO_3$ content was higher in UK than in NL ($p<0.001$; Figure 19f); N_NH_4, dissolved inorganic N (DON), dissolved organic N, and P_PO_4 were higher in UK than in NL (respectively $p<0.01$, $p<0.05$, $p<0.05$, and $p<0.05$; Figure 19 g - i).

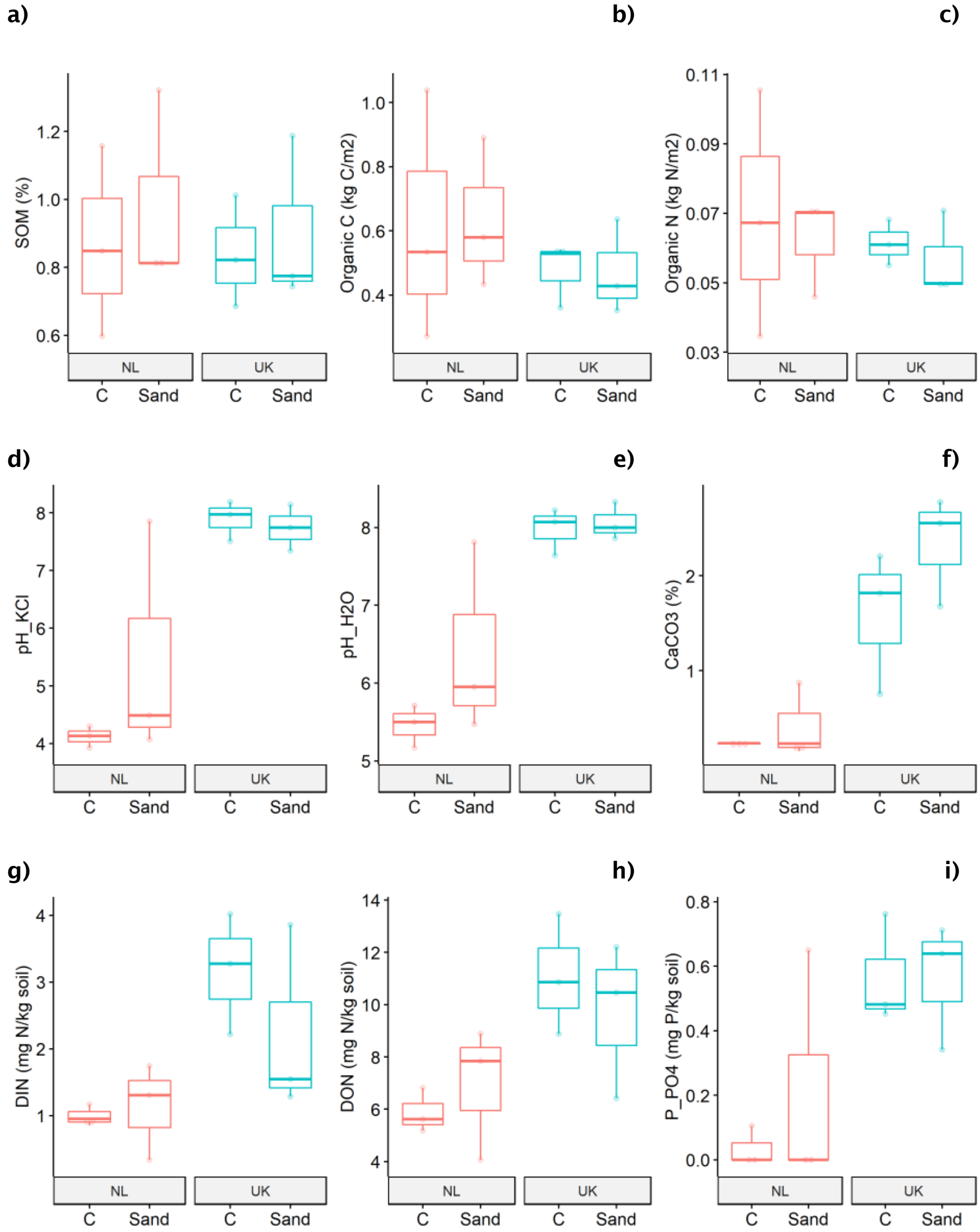


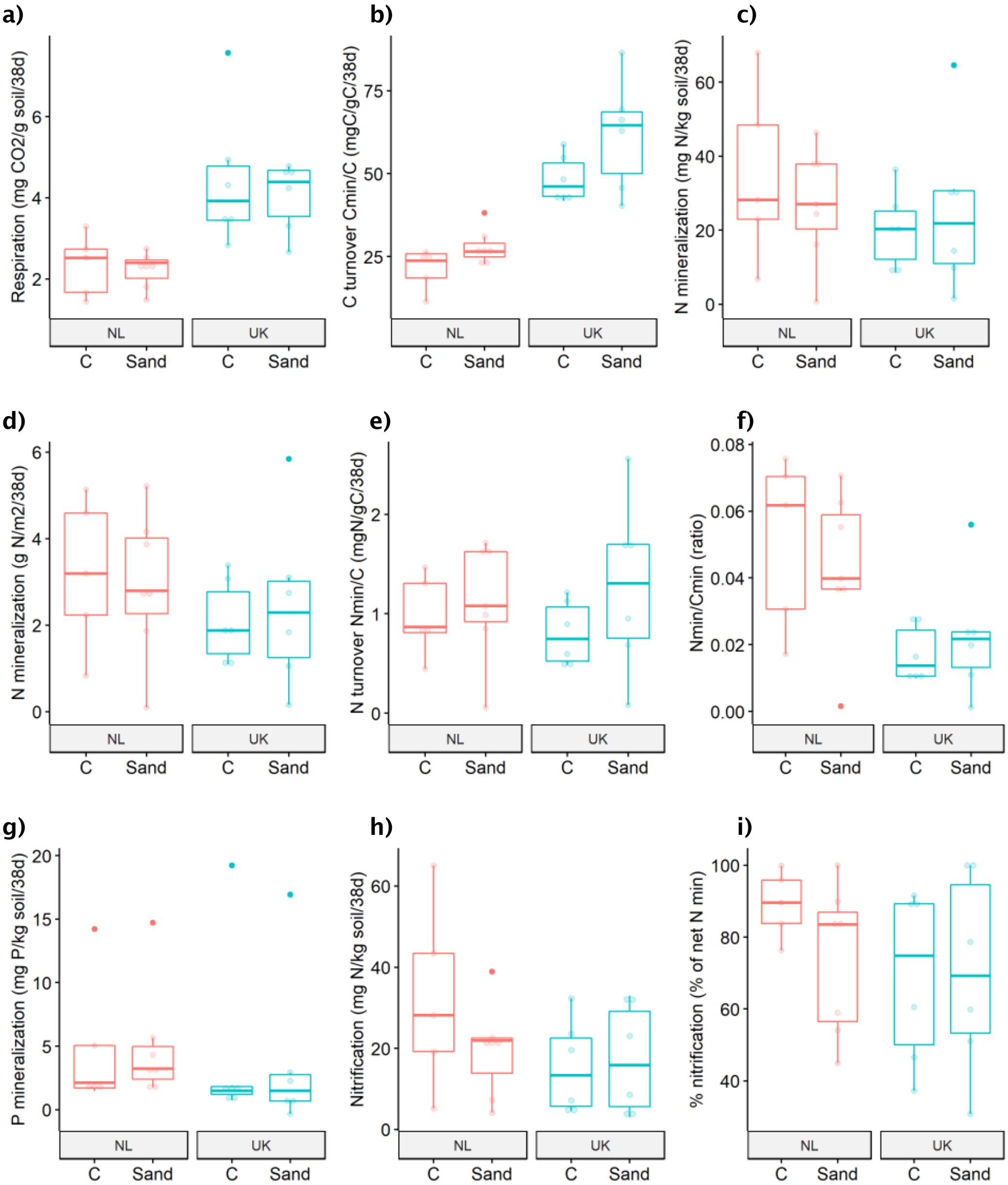
Figure 19. Median and quantiles (25th and 75th) of **soil bulk variables of flat dune subsoil** (10 – 15 cm depth) Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 3 (N = 12 in total).

4.3 Effects of sand deposition on microbial properties and activities of topsoil

Soil respiration rates per gram soil were higher for UK than NL ($p<0.001$; Figure 20a). Turnover rate of carbon (i.e. soil respiration rates divided by soil total C) was significantly higher for UK than NL ($p<0.001$) and higher for managed plots than control plots ($p<0.05$; Figure 20b).

N-mineralization rates were not significantly different between areas nor management, either when N-mineralization is expressed as rate per gram soil ($P>0.1$; Figure 20c) or as rate per square meter ($p>0.1$; Figure 20d). Turnover rates of N (i.e. N-mineralization rates divided by soil total C) were also indifferent between areas and management ($p>0.1$; Figure 20e), which was in contrast to the pattern found for C turnover rate. The ratio between N-mineralization and C mineralization (Nmin/Cmin) was significantly higher for NL than UK ($p<0.01$; Figure 20f). This means that turnover of N is relatively faster (compared to C turnover) in NL.

P mineralization rate, nitrification rate (estimated from the increase in NO_x during the incubation), percentage of nitrification (i.e. percentage of nitrification over net N-mineralization), and ratio between N-NO_x and N-NH_4 were not significantly different between areas nor management (Figure 20 g - j).



j)

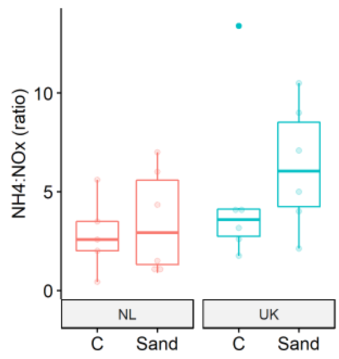
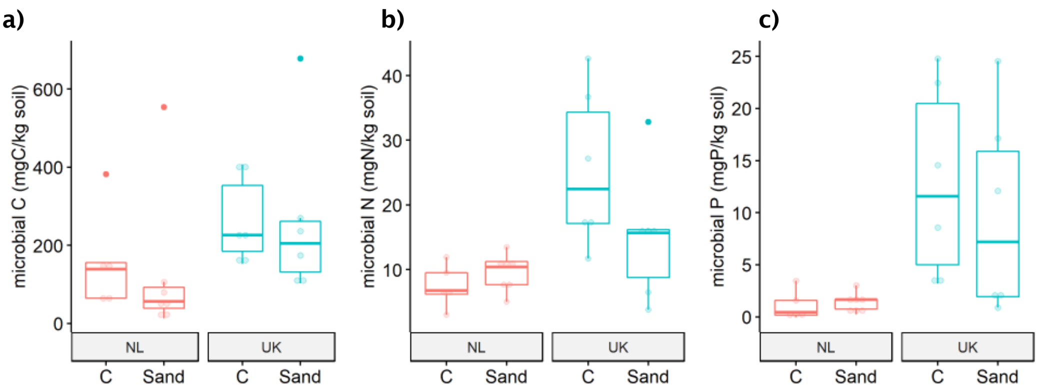


Figure 20. Median and quantiles (25[th] and 75[th]) of **soil variables** related to **microbial activities** of **flat dune topsoil** (0 - 5 cm). Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). % nitrification is the percentage of nitrification over net N-mineralization. NO_x:NH_4 is the ratio of N-NH_4 and N-NO_x. Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 6 for UK_Sand (N = 24 in total). For NH_4:NO_x, 1 plot of NL_Sand was omitted because the denominator (i.e. NO_x concentration) was zero.

Microbial C, N, and P-contents were higher for UK than for NL ($p<0.01$ for all; Figure 21 a - c). Also, when microbial biomass C is expressed as the fraction of soil total C, it was significantly higher for UK than NL ($p<0.001$; Figure 21d). There was no significant effect of management on microbial C, N, P, or fraction ($p>0.1$; Figure 21 a - d). Microbial N:C ratio was indifferent between areas and management ($p>0.1$ for both; Figure 21 e), whereas microbial C:P ratio and N:P ratio were higher in NL ($p<0.05$ and $p<0.01$ respectively; Figure 21f). Microbial N:P ratio in NL soils was higher than global average of microbial N:P ratio (ca. 6.9; Cleveland & Liptzin 2007). These patterns might reflect prevailing P-limitation in NL dune soils, and as well difference in microbial community structure.

During the incubation period, microbes generally increased in terms of C, N, P-content (Figure 21 g - l). Microbial N increased significantly more in UK soils than in NL soils ($p<0.01$) and therefore soil C:N ratio became significantly lower in UK ($p<0.01$). Higher microbial immobilization of N in UK soils are in line with relatively lower N-mineralization rates of those soils (see the paragraph above).



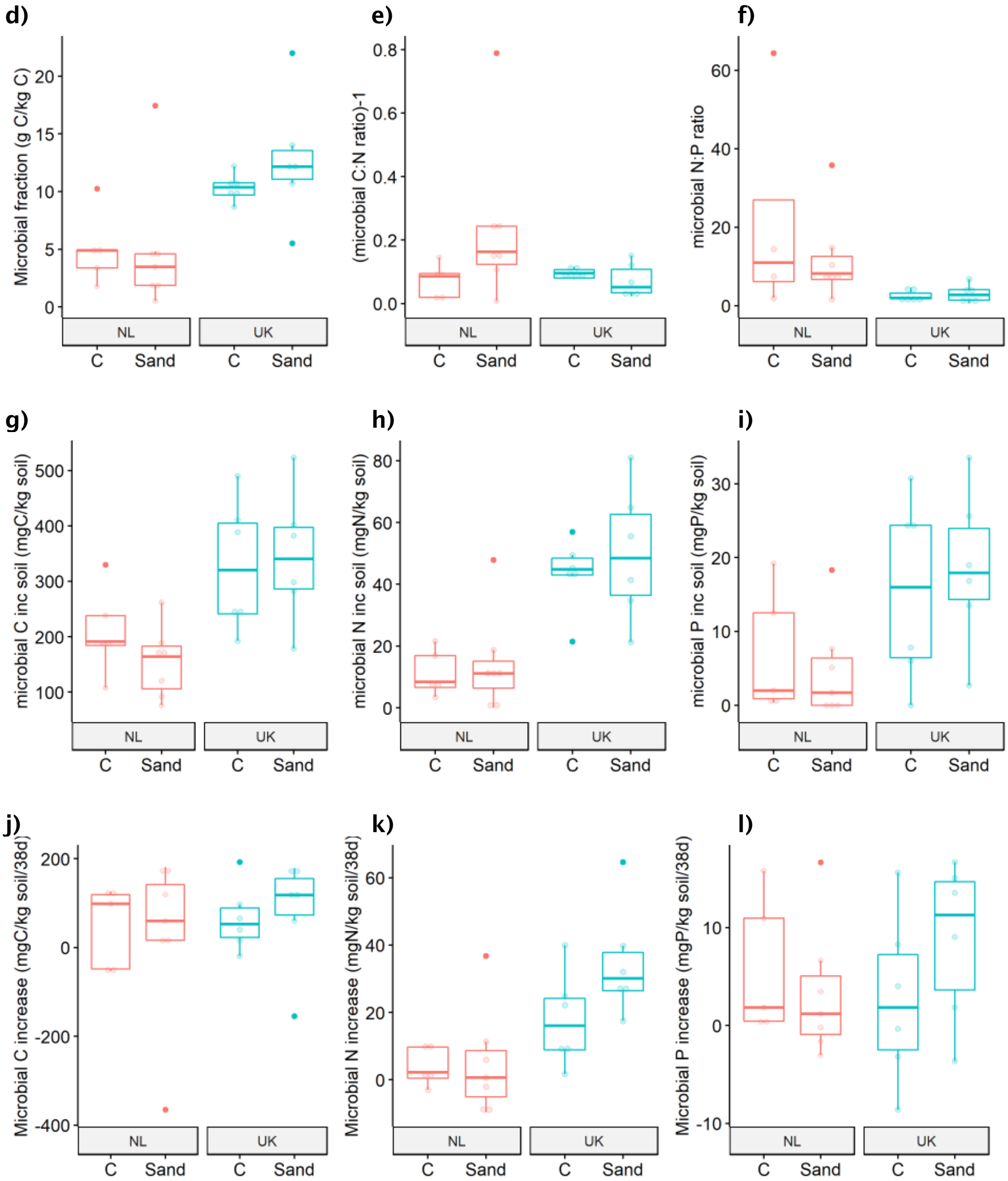


Figure 21. Median and quantiles (25th and 75th) of **soil microbial** stoichiometry of **flat dune topsoil** (0 - 5 cm). Figures a – f show the microbial element concentrations of soils before the incubation experiment, figures g – i show that of soils after the incubation experiment, and figures j – l show the changes in the elenent concentrations during 38 days of the incubation experiment (i.e. positive values mean increase). Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 6 for UK_Sand (N = 24 in total).

There was positive correlation between C turnover rate and pH_KCl (Spearman's correlation coefficient rho = 0.81, p<0.001; Figure 22 left-top) as well as between C turnover rate and microbial fraction (rho = 0.54, p<0.01; Figure 22 right-top). Multivariate regression of C turnover rates with pH_KCl and microbial fraction showed that only pH_KCl, but not microbial fraction, influenced C turnover rates (p<0.001 and p>0.1 for regression coefficients of pH_KCl and microbial fraction, respectively). This indicated that soil acidity is the primary factor which regulates C turnover (with a low pH acidity hampering C turnover).

Mineralization processes of C and N in soil are largely coupled. However, as shown in the previous section, the ratio of N-mineralization over C mineralization was lower for UK than NL. In theory, deviation of ratios between N-mineralization and C mineralization can be caused by difference in soil C:N ratio, microbial C:N ratio, or microbial yield efficiency (Manzoni and Porporato 2009). With our dataset, however, the ratio of N-mineralization:C mineralization was not related to soil C:N ratio (Figure 22 left-bottom) nor microbial C:N ratio (Figure 22 right-bottom).

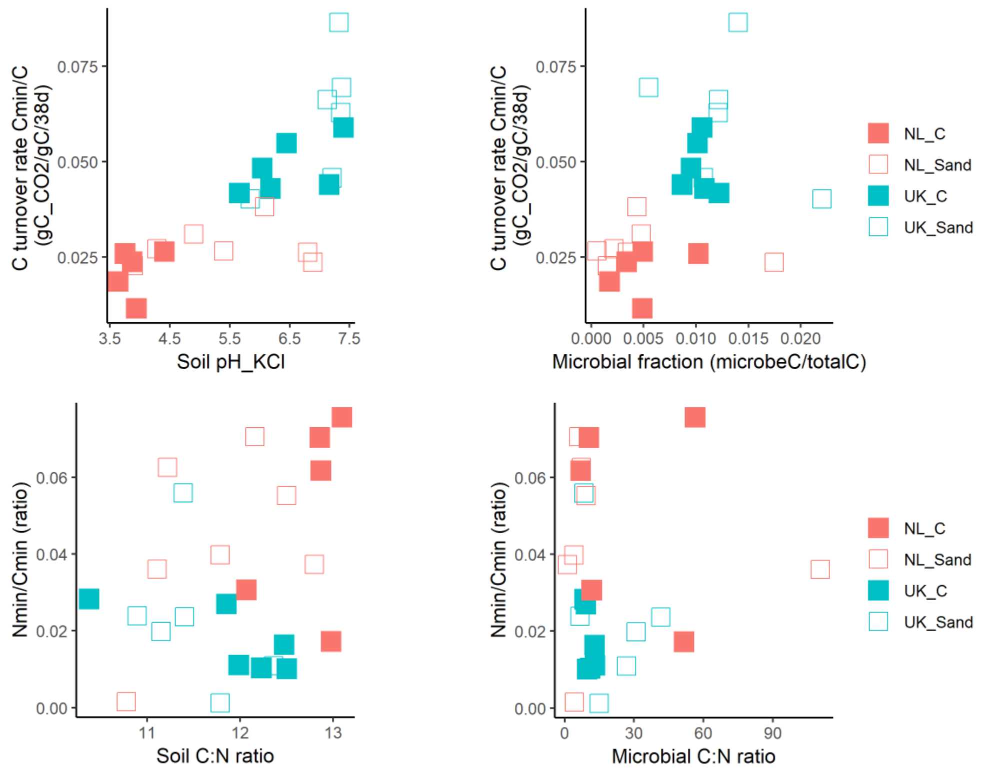


Figure 22. Relationship between **soil pH_KCl and C turnover rate** (C mineralization rates divided by soil total C) (lef-top) and between microbial **fraction and C turnover rate** (right-top), between soil **C:N ratio and ratio of N-mineralization over C mineralization** (left-bottom), and between **microbial C:N ratio and ratio of N-mineralization over C mineralization** (right-top) of flat dune **topsoil** (0 - 5 cm) of Luchterdinen ('NL') and Newborough Warren ('UK') (N=24).

Root biomass was in quantity the most important source for mineralization of fresh organic material (see section 4.7). Therefore we look at the relationship of the N- and P-mineralization with the quality of the root biomass (Figure 23). For mineralization we used the ratio of N- or P-mineralization to C-mineralization (Nmin/Cmin and Pmin/Cmin), and the ratio of N or P mineralization to root biomass in 2018 (Nmin/root biomass and Pmin/root biomass). As variables for root biomass quality we used N-content, P-content and N:P-ratio.

For Nmin/Cmin there was no significant relationship with root biomass N-content. There is a weak relation with P-content (regression: r_{adj}^2 = 0.16; p= 0.031) and with root biomass N:P ratio (regression: r_{adj}^2 = 0.26; p = 0.007). With lower P-content and higher N:P ratio of the root biomass N-mineralization tends to be higher, which is the case for most plots in NL. This implies that differences between NL and UK for root nutrient stoichiometry are only caused by difference in P-content, and this may effect N-turnover. For Pmin/Cmin there are no clear relations of with N-content, P-content and

N:P ratio of root biomass. There is a tendency for higher P mineralization in NL than in UK, but this is independent from root N- and P-content.

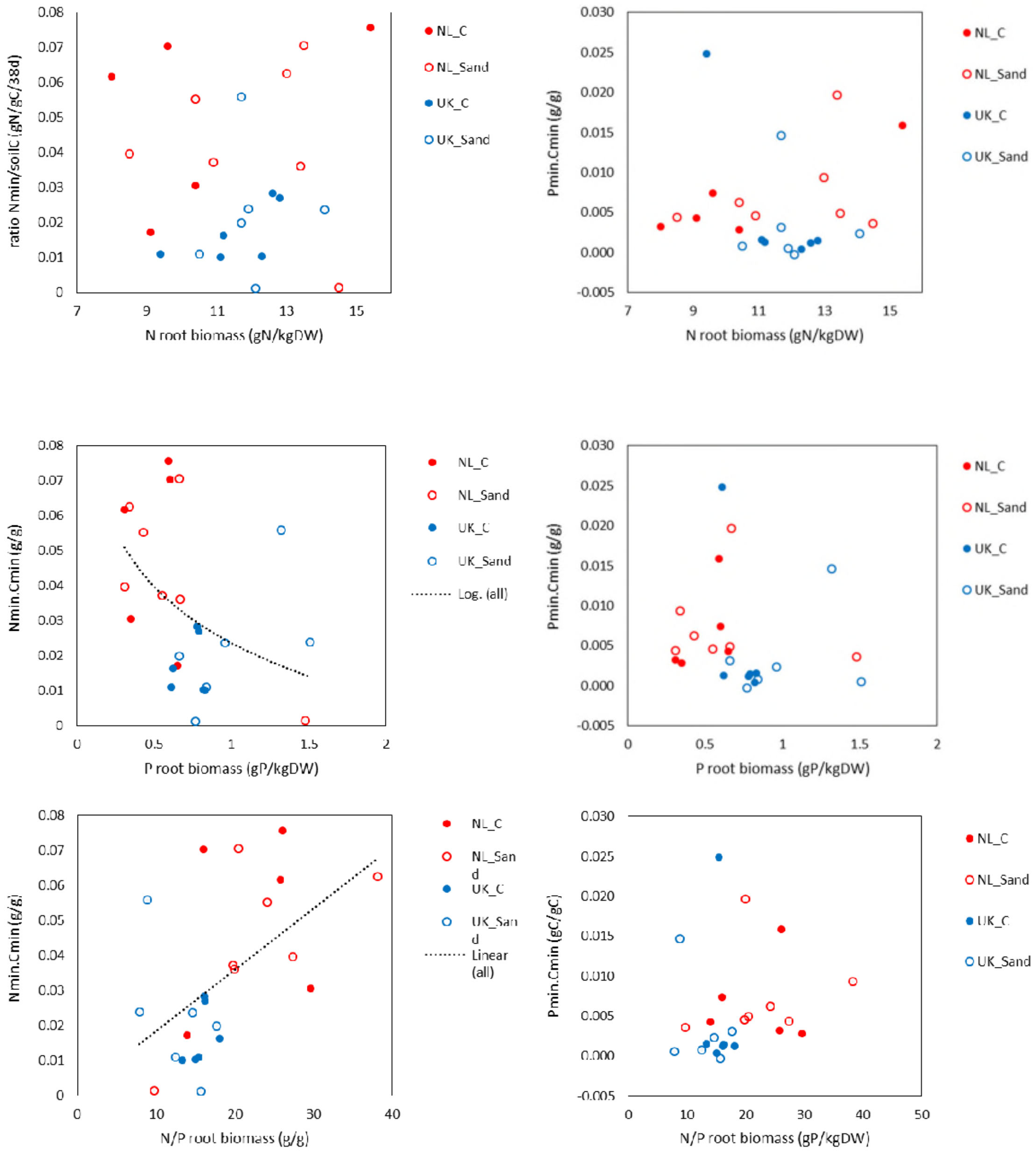


Figure 23: Relation between **N- and P- mineralization with N-content, P-content and N:P ratio in root biomass, and soil pH**. Mineralization is expressed as relative to C mineralization and root biomass in 2018. Significant regressions arshown as dottet lines. . Points depicts each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). The line is the regression for all plots. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

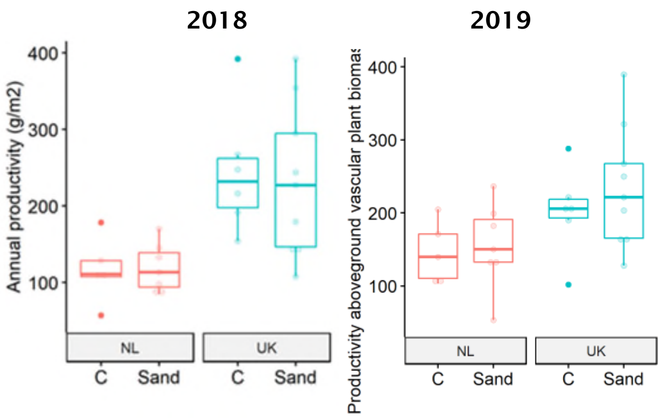
4.4 Effects of sand deposition on plant productivity

There was no significant effect of sand deposition on aboveground plant productivity, peak standing crop, and root biomass in 2018 and 2019 ($p>0.1$; Figure 24). However, all of these parameters were higher in UK than in NL for both years ($p<0.001$ to 0.05). Variability in plant biomass was large among subplots within a plot (Attachment VI), indicating that local habitat conditions play an important role in determining plant productivity. The size of root biomass was not clearly related to the size of aboveground vascular plant biomass (i.e. peak standing crop) (Attachment VI). This might be due to a very small plot surface of root sampling compared to the plot size of aboveground biomass sampling, which fails to capture the representative root sample for the site (see par. 2.7.5).

Compared to the dry year 2018, standing crop of vascular plants was lower and root biomass was higher in 2019 ($p<0.001$). Decline of aboveground standing crop between 2018 and 2019 was stronger in NL. Because this decline was coincidental with an increase of aboveground productivity in the exclosures, it can only be attributed to a high grazing pressure in NL. In both areas the root biomass increased, and might indicate a recovery from severe root die off in 2018. For NL the productivity of aboveground vascular plant biomass was higher in the wetter year of 2019, while this was not the case for UK.

Aboveground plant productivity, and root biomass were not related to soil C content, soil extractible P and soil C:N ratio. Both were weakly and positively related to soil pH-KCl (regression for aboveground plant productivity on pH-KCl: $r_{adj}^2 = 0.26$; $p = 0.008$; regression for root biomass on pH-KCl: $r_{adj}^2 = 0.33$; $p = 0.012$) (Figure 26). In Luchterduinen root biomass was positively related to actual transpiration (calculated by Aggenbach et al. 2020) during the growing season (1 April -31 July). Root biomass was higher in 2019 when precipitation during the growing season, and there water availability was higher indicated by a higher transpiration than in 2018 (Figure 27). Plots with sand deposition, where soil pH is relatively high, had the strongest respond in the wetter conditions in in2019. For aboveground vascular plant productivity there was only a weak positive respond on the higher water availability in 2019.

The root:shoot ratio's which can be calculated for the plots outside the exclosures (Figure 25) was in both years higher in NL than in UK. Only for NL in 2018 management had an effect with higher values for controls. In NL the ratio increased strongly to very high values (ca. 30) due to have heavy grazing of aboveground biomass. In UK the increase was less strong up to values of ca. 15. Within each area in 2019 there was no relation of root/shoot ratio with aboveground vascular plant biomass and pH-KCl.



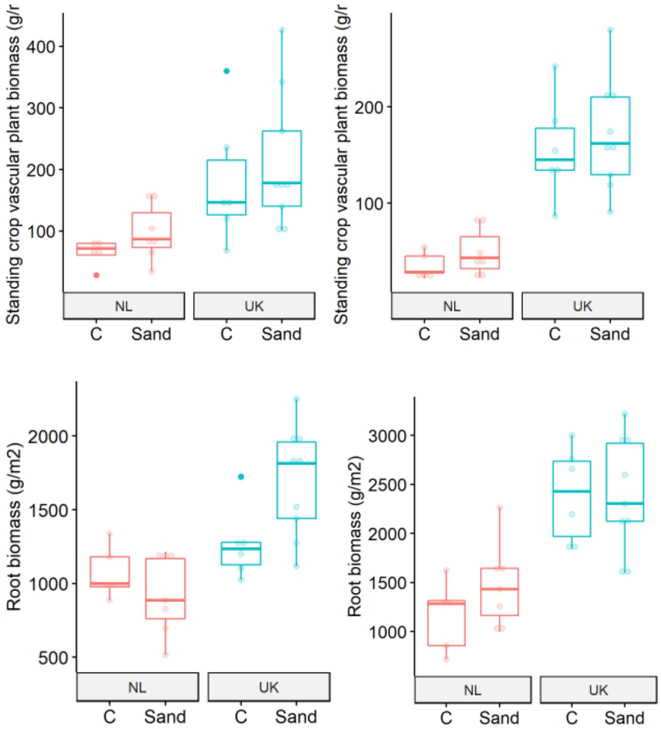


Figure 24. Median and quantiles (25^{th} and 75^{th}) of **plant biomass of flat dune plots** for 2018 (left) and 2019 (right). Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

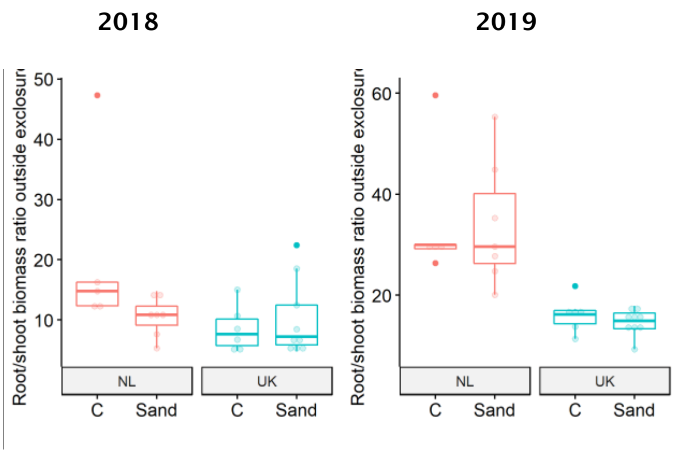


Figure 25: Median and quantiles (25^{th} and 75^{th}) of **root:shoot ratio's of vascular plant biomass of flat dune plots** for 2018 (left) and 2019 (right). Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

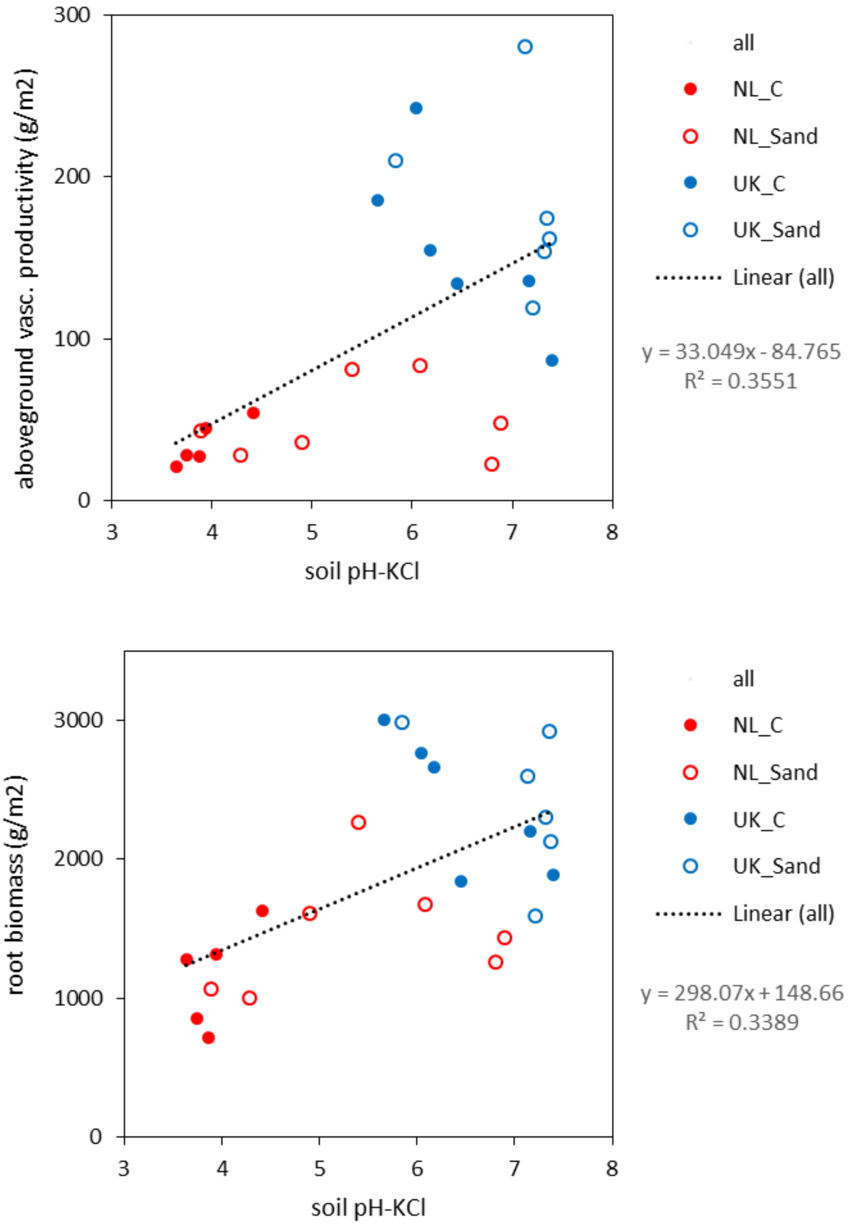


Figure 26: Relation of **aboveground vascular plant productivity and root biomass in 2019 with topsoil pH in flat dune plots** in LD and UK (above), with **topsoil pH** for flat dune plots in NL and UK.

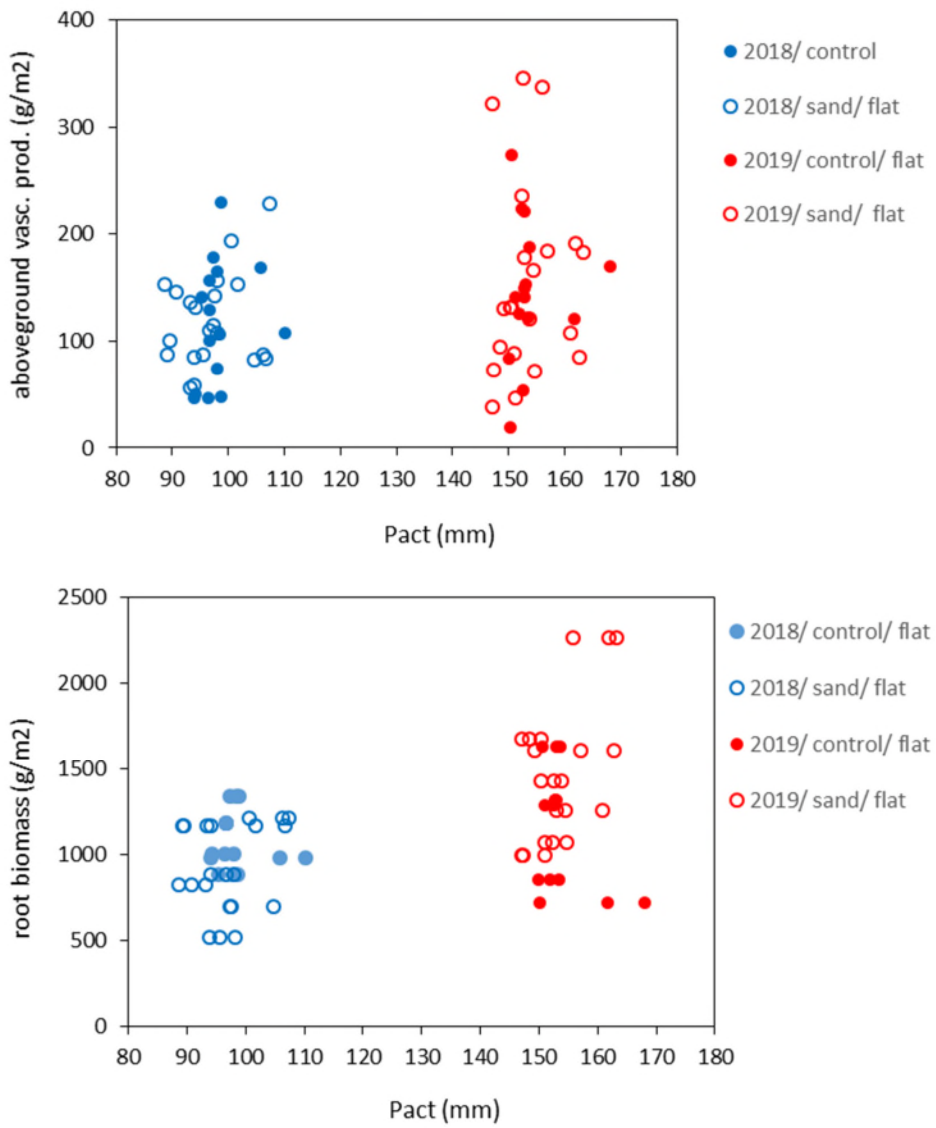


Figure 27: Relation of **aboveground vascular plant productivity and root biomass with actual transpiration** during the growing season (1 April -31 July) **dune plots in NL** in 2018 and 2019. Each point is subplot for which transpiration was calcated from soil properties and meteorological data. For aboveground proiductivity measuremnts on subplot level were used, while for root biomass average values on plot level were used.

4.5 Effects of sand deposition on nutrient concentrations in biomass

Nutrients and nutrient ratios of aboveground vascular biomass and root are presented in Figure 28. For aboveground vascular plant biomass inside the cages (without grazing) there were no effects of area and management on nutrient contents and ratio's. For aboveground vascular plant biomass outside the exclosures N- and P-content do not differ for area, but N:P ratio was higher in NL. In NL the N-content in control plots tended to be higher than in the sand deposition plots (not significant. $p<0.1$).

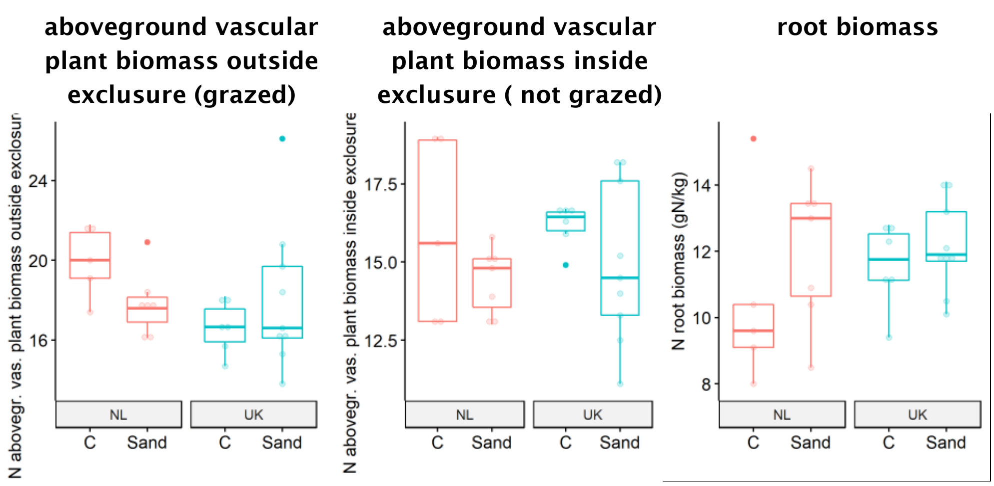
N:P ratio's in aboveground biomass in- and outside the exclosures indicate mostly N-limitation (using criteria of Olde Venterink et al (2003); N:P < 14.5 and N:K < 2.1) . For the biomass outside the exclosures in the control plots P-limitation was indicated

Therefore strong grazing (see par. 4.4) in strongly affected aboveground nutrient stoichiometry due to a very low biomass pool. P:K (not shown) and N:K ratio's indicate no K-limitation (Olde-Venterink 2003).

The patterns of nutrients in root biomass, which were measured outside the exclosures, showed more effects of area and management. In NL P-content is lower and N:P ratio is higher than in UK, while N-content was not different for the areas. Root N-content in the control plots tended to be lower than in the sand deposition plots (not significant, $p>0.1$), which is different from the pattern for aboveground biomass outside the exclosures. Sand deposition had no effect on P-content and N:P ratio

N- and P-content of root biomass is lower than in aboveground biomass, with a strong difference for P-content. Therefore the N:P ratio in roots was higher than in shoots. In NL this difference was most strong. N content of standing crop was not N-content in roots. For P-content there is a weak relation between standing crop and roots (regression: $r_{adj}^2 = 0.17$; $p = 0.029$). Root N-content and P-content are weakly negatively related to soil C:N (regressions resp.: $r_{adj}^2 = 0.14$; $p = 0.046$ and $r_{adj}^2 = 0.0.23$; $p = 0.012$). Root P-content has also a weak positive relation with soil pH-KCl (regression: $r_{adj}^2 = 0.20$; $p = 0.018$) and calcium carbonate content (regression: $r_{adj}^2 = 0.16$; $p = 0.034$), while for root N-content no effect of these two soil variables was present.

Nutrient concentration in mosses were measured at plot level but at sampling sites in the neighbourhood of the plots in order to compare the two dune areas. There were clear differences between the areas (Figure 29) with higher N-concentration in NL, the high N-load area. ($p<0.01$). For P-concentration the pattern was the opposite, with highest values in UK ($p<0.05$). As a consequence N:P ratios were highest in NL ($p<0.001$). N-concentrations in both areas were below the concentration for N-saturation level of 20 gN/kg DW (Harmens et al. 2014).



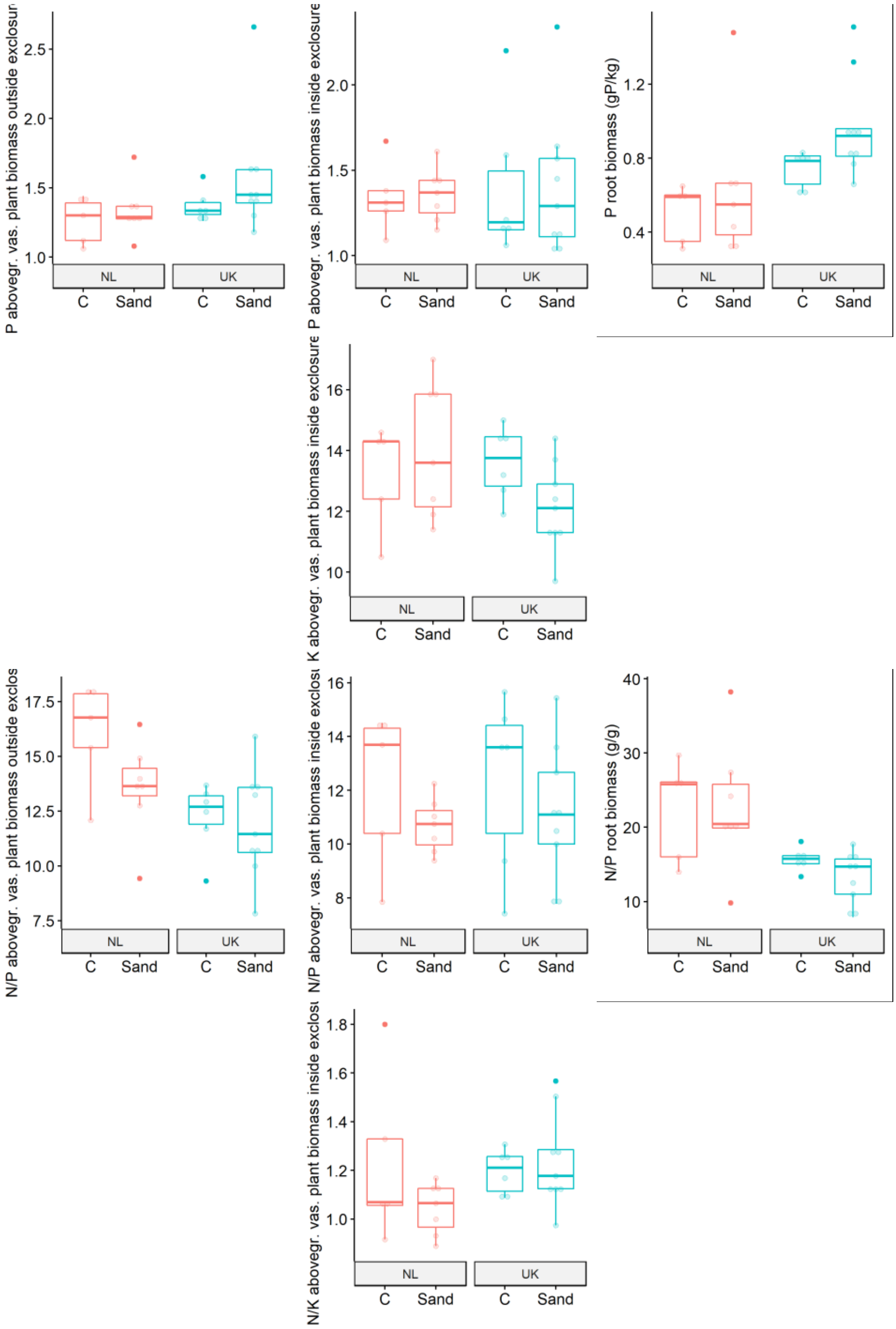


Figure 28: Median and quantiles (25th and 75th) of **nutrient concentrations and ratio's in aboveground vascular plant and root biomass of flat dune plots**, sampled in 2019. Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 6 for UK_Sand (N = 24 in total).

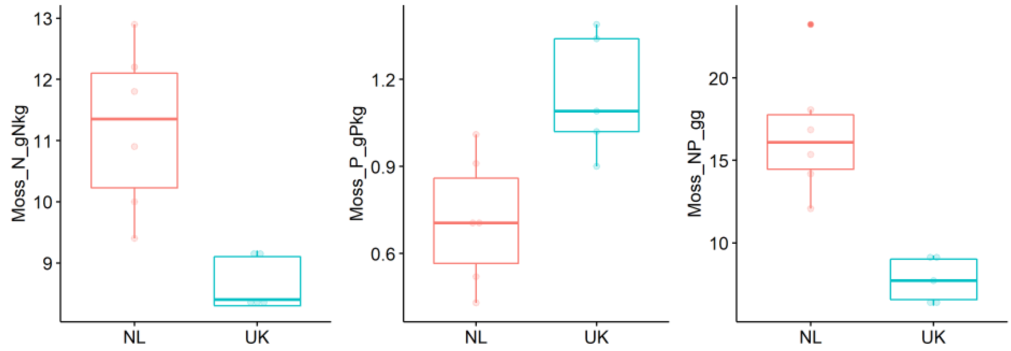


Figure 29: Median and quantiles (25th and 75th) of **nutrient concentrations and ratio's in moss biomass** for area (Luchterduinen ('NL') and Newborough Warren ('UK') sampled in 2019. Points depict the values of each replica. Number of replicas are 6 for NL and 5 for UK.

4.6 Effects of sand deposition on plant community structure

4.6.1 Vegetation structure

There were hardly significant effects of sand deposition on the vegetation structure variables (Figure 30 and Figure 32). Only in 2019 for NL cumulative herb cover was higher in the sand deposition plots than the control plots. However, between NL and UK vegetation structure was different. In UK the sum of vascular plant cover and cumulative herb cover are higher, the total moss cover was lower than in NL in 2018 and 2019 ($p<0.001$) (Figure 31). Grass cover, cover of woody species and the height of the vascular plant stand were only higher in UK in the year 2019 ($p<0.001$ to 0.05). Bare ground cover showed not many differences, and was only for UK in 2019 in plots with sand deposition higher than in control plots. This may indicated an increase of aeolian activity in NB.

Cover of vascular plants and cover of mosses+lichens were negatively correlated (Figure 33), and this indicated that moss growth is supressed by competition for light with vascular plants.

Changes in vegetation structure between 2018 and 2019 were most evident for the vascular plant layer. The trend of total vascular plant cover and grass cover was depended on the area: a decrease in NL (which was in line with the trend of vascular plant standing crop) due to a strong grazing pressure, and an increase in UK. Herb cover increased between 2018 and 2019 ($p<0.001$), and most strongly in UK. For lichens there was a decline between 2018 and 2019 ($p<0.05$). These changes indicated for NL a delayed effect of the strong drought in 2018 on grass biomass in 2019, possibly due to mortality of grasses. In UK such an effect did not occur, and besides herbs, also grasses could recover.

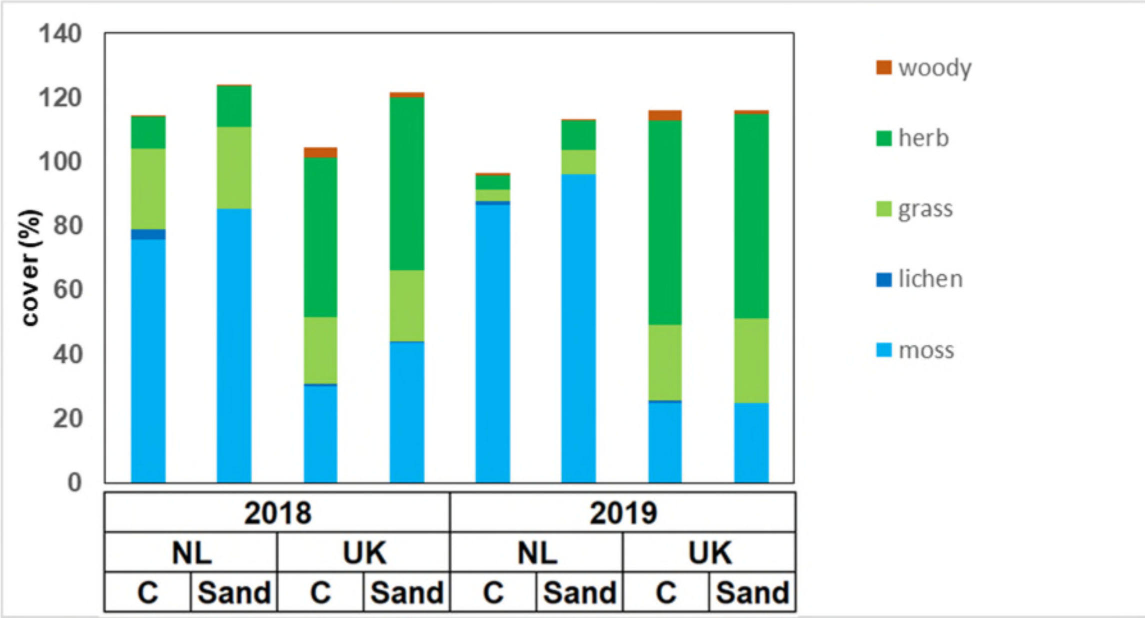


Figure 30. Cumulative **cover of plant functional groups in flat dune plots** (N=27) in 2018 and 2019, split into functional groups, in Luchterduinen ('LD') in NL and Newborough Warren ('NB') in UK. Plots shown with black letters are control plots, whereas those with red letters are sand-deposited plots.

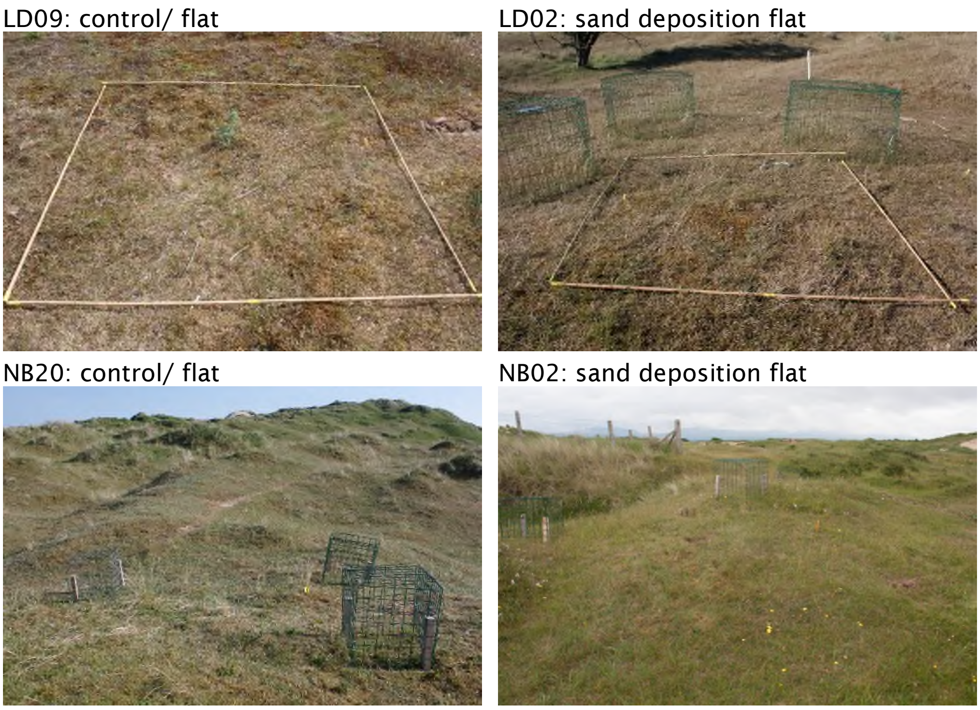
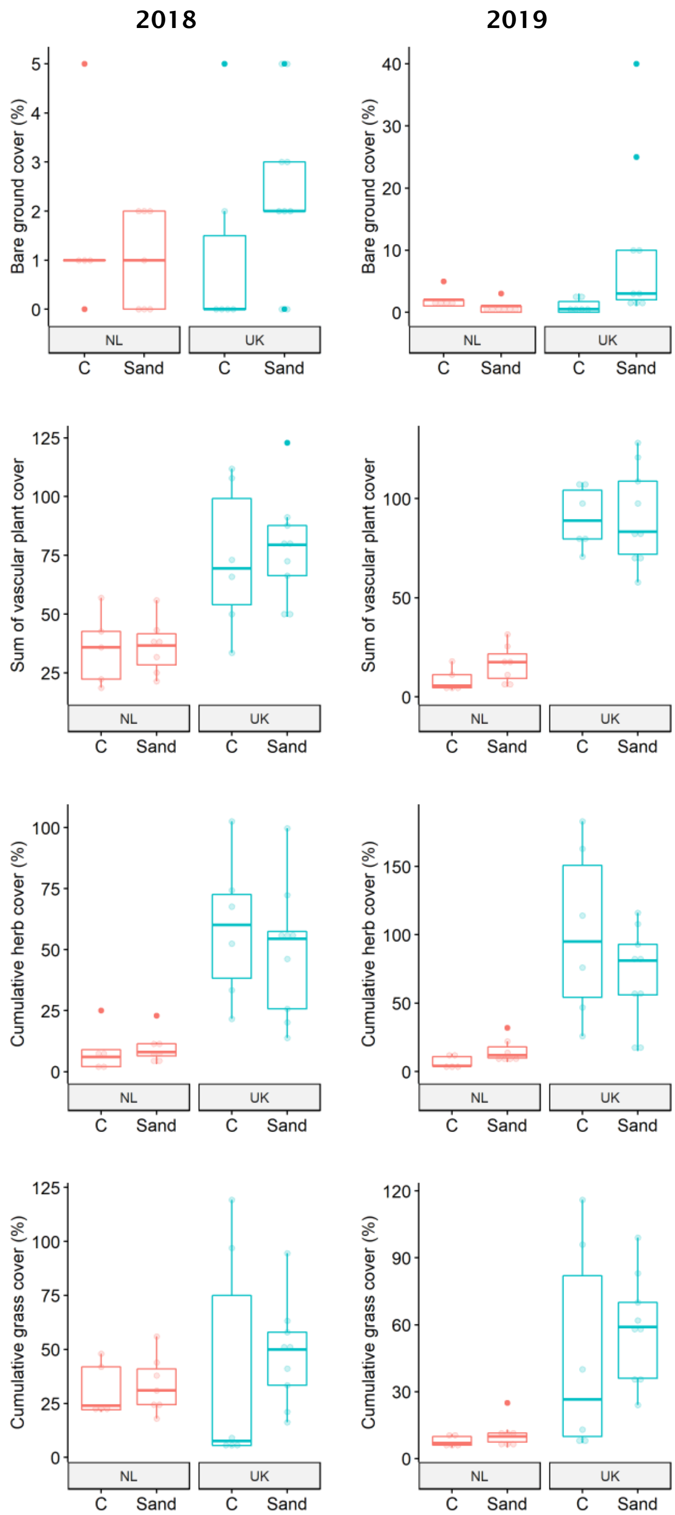


Figure 31: Vegetation of some control and sand deposition plots in in Luchterduinen ('LD') in NL and Newborough Warren ('NB') in UK in June 2018. Note that in the LD plots the vascular plant cover is higher and high moss cover lower than the NB plots. In LD the yellow-brown color of the vegetation indicates stronger drought stress.


2018
2019
Bare ground cover (%)
Sum of vascular plant cover
Cumulative herb cover (%)
Cumulative grass cover (%)
NL
UK
C
Sand

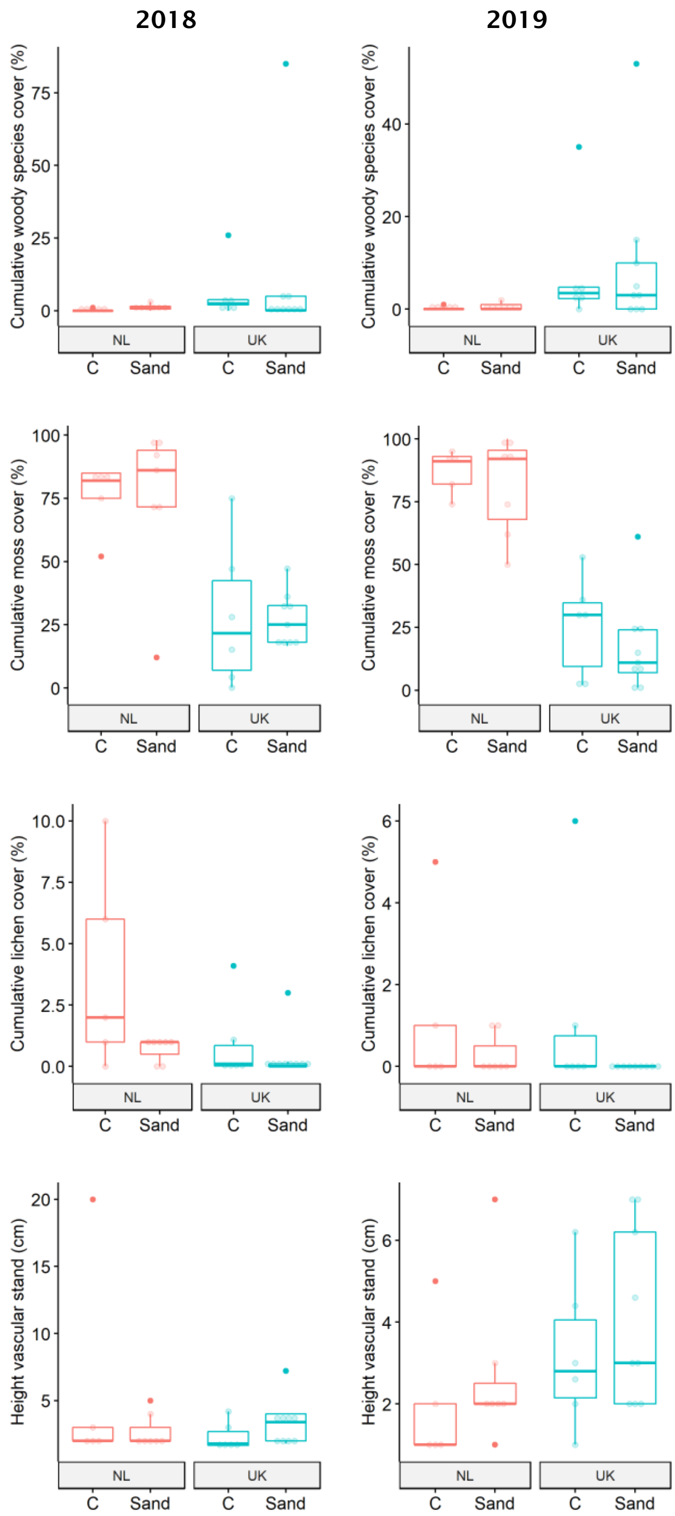


Figure 32: Median and quantiles (25th and 75th) of **vegetation structure variables and plant functional groups of flat dune plots** in 2018 and 2019. Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

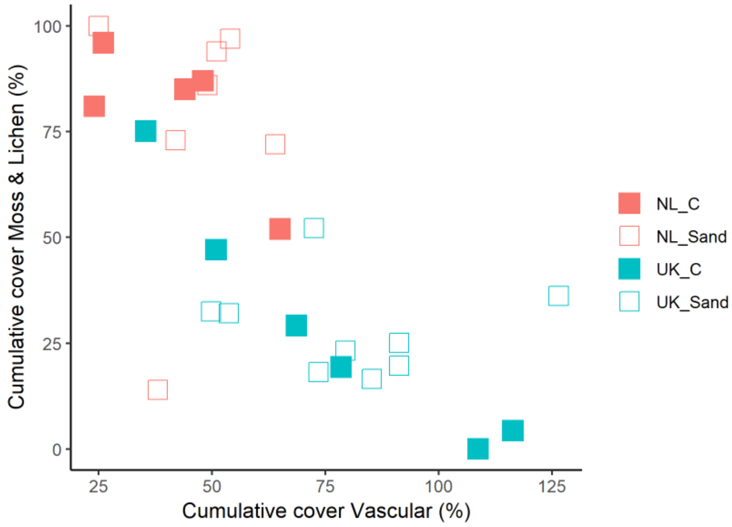
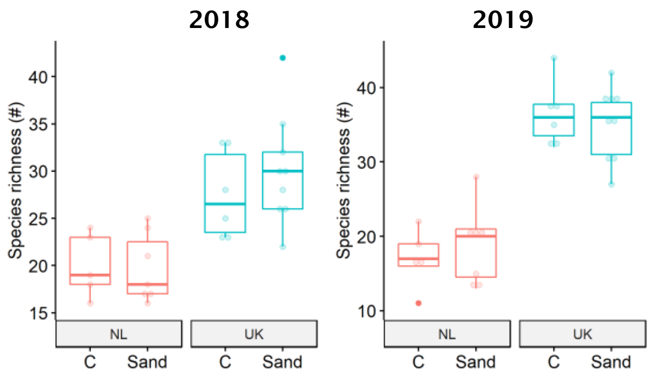


Figure 33. Relationship between cumulative **cover of vascular plants** and cumulative **cover of mosses and lichens** of **flat dune plots** in 2018. N=27.

4.6.2 Number of species

Number of total plant species, of vascular plant species and of moss+lichen species were not significantly different between management types (p>0.1; Figure 34). The total plant species was higher for UK than NL (p<0.001), because UK has a higher number of vascular plant species (p<0.001). The number of moss+lichen species was indifferent between UK and NL (p>0.1) and highest at control plots in NL (in 2018 significant p<0.05). N-fixing species were more abundant in UK than in NL (p<0.001) (Figure 34).

The factor year had an effect on species richness and vascular species richness with higher values in 2019 for UK, while for NL there was no effect of year. The number of mosses+lichens was slightly lower in 2019 for both areas (p<0.01).



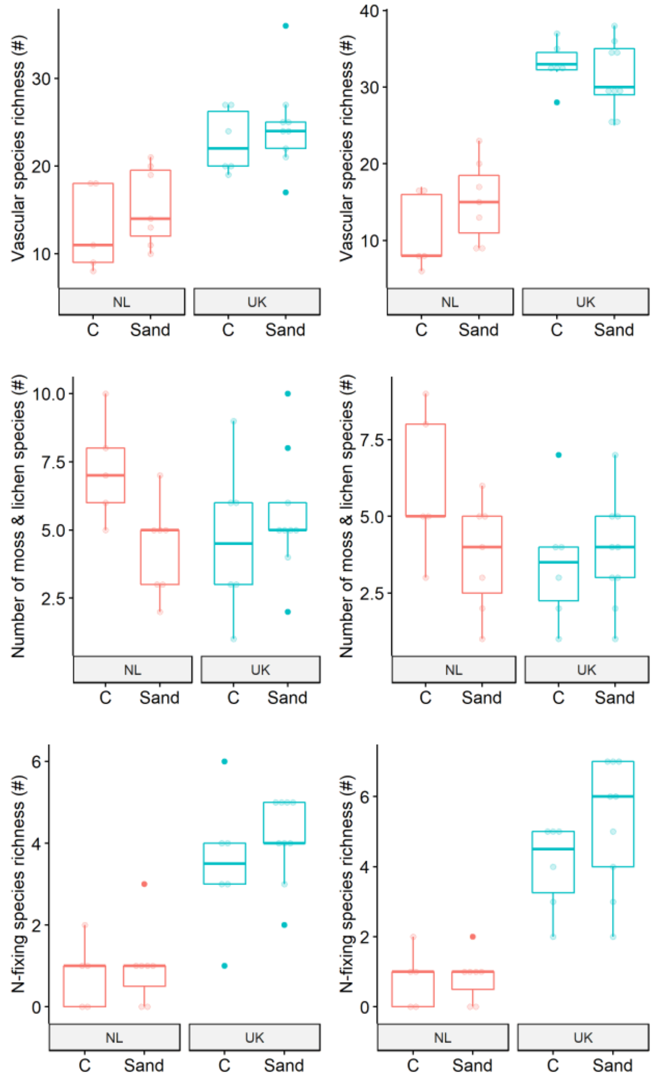
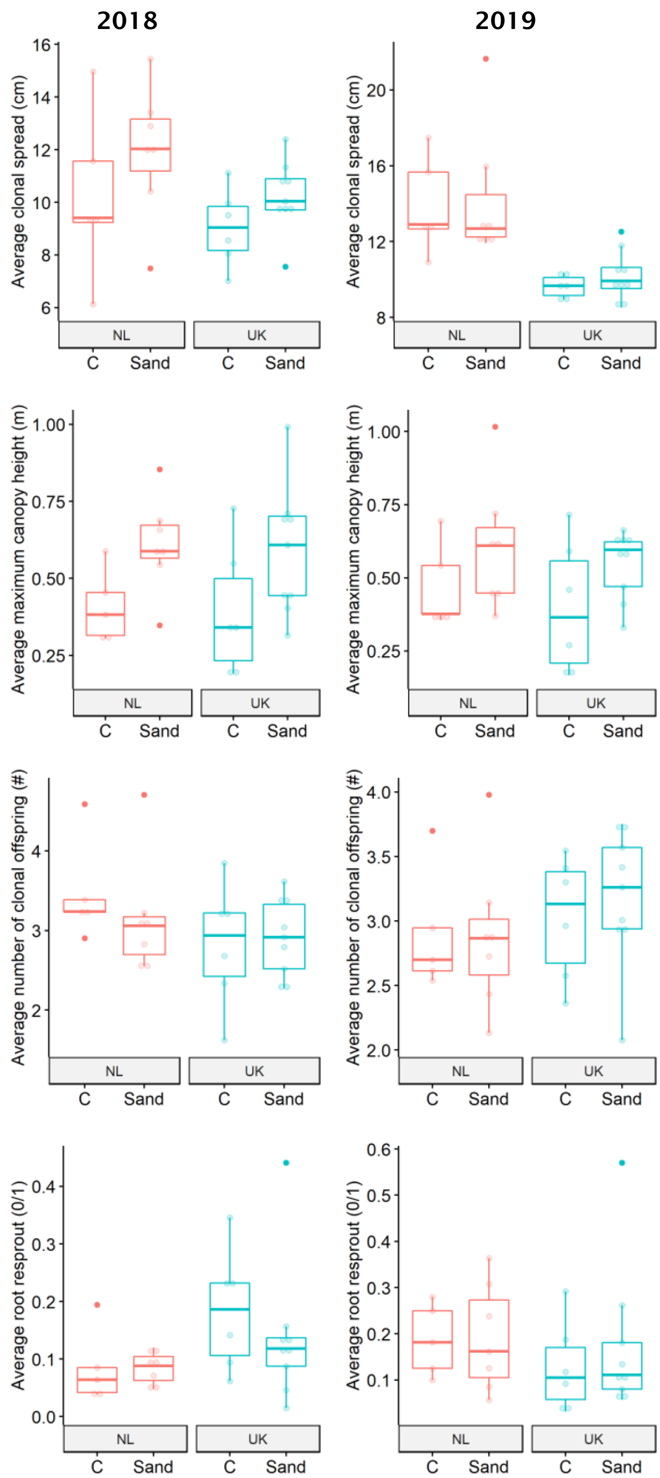


Figure 34. Median and quantiles (25th and 75th) of **indices for species number of flat dune plots** in 2018 and 2019. Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

4.6.3 Species traits

There was limited effect of sand deposition on cover weighted average species traits (Figure 35). Only maximum canopy height is higher in plots with sand deposition (only significant in 2018; $p<0.05$). Effects of area were also limited. Clonal spread was larger in NL (only significant in 2019; $p<0.001$) and might be related to the higher grazing pressure. Shoot life span was lower in NL (only significant in 2019; $p<0.05$) indicating a higher proportion of annuals.

There was also an effect of year with a slightly shorter shoot life span and slightly higher specific leaf area in 2019 for both areas ($p<0.001$ and <0.05). Clonal spread and root resprout increased only in NL. Root resprout declined in the control plots of UK. `



2018
2019
Average clonal spread (cm)
Average maximum canopy height (m)
Average number of clonal offspring (#)
Average root resprout (0/1)
NL
UK
C
Sand

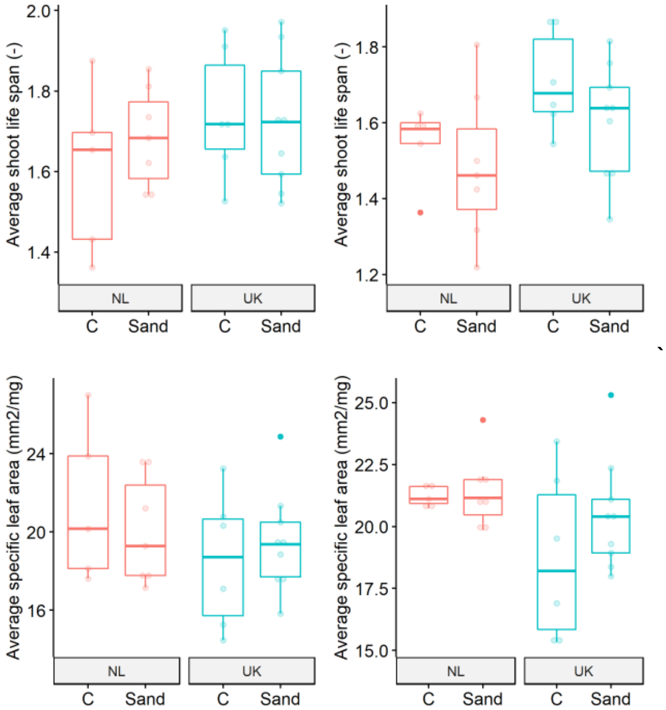


Figure 35: Median and quantiles (25th and 75th) of cover weigthed averaged **plant species traits of flat dune plots** for 2018 and 2019. Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

4.6.4 Species indicator values of environmental conditions

Average Ellenberg values indicated that in 2018 UK plots were slightly (not significantly) more nutrient-rich than NL plots ($p<0.1$), but not so in 2019. Sand-deposited plots were more nutrient-rich than control plots (only significant in 2018; $p<0.01$) (Figure 36). Average Ellenberg acidity values were higher in 2018 and 2019 (which indicate base-rich conditions) for UK than NL ($p<0.001$-0.01) (Figure 36), but there was no significant difference between management types ($p>0.1$). Average Ellenberg moisture values were significantly different between areas (UK is wetter; $p<0.05$), but not for management (Figure 36).

Average Ellenberg nutrient value decreased between 2018 and 2019 in UK, but not in NL. For average Ellenberg moisture and acidity values there was no effect of time.

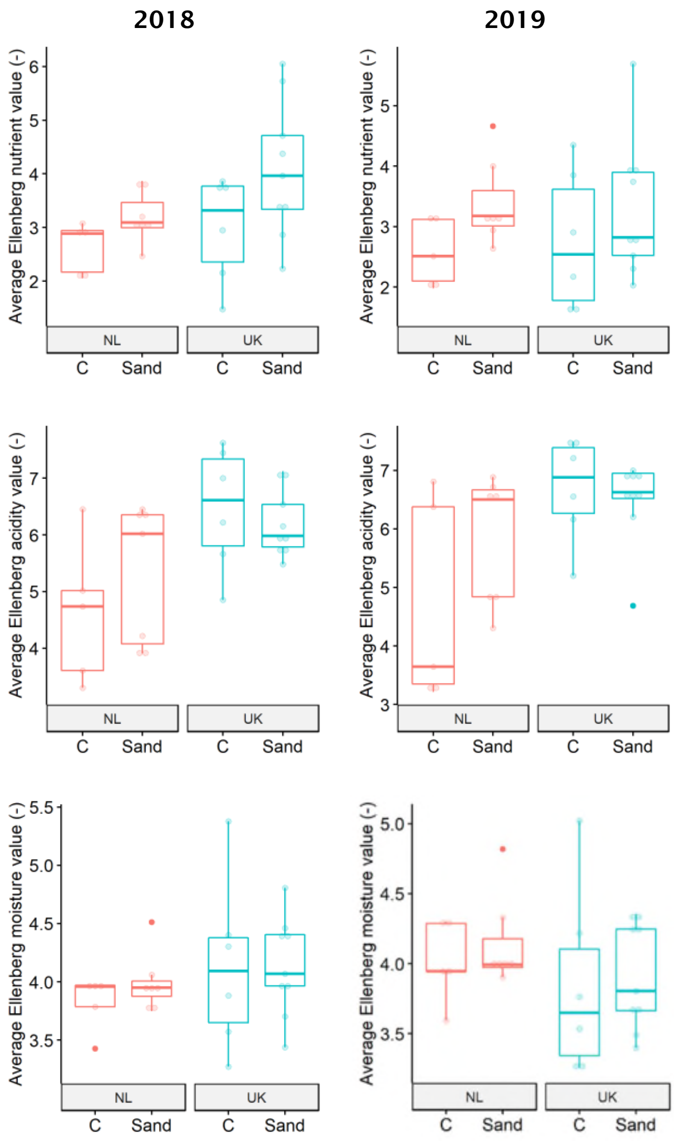


Figure 36. Median and quantiles (25th and 75th) of cover weighted average **plant species indicator values of flat dune plots**. Values are shown separately for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 9 for UK_Sand (N = 27 in total).

4.6.5 Species composition

The dominant moss species had contrasting patterns among plots (Figure 37). *Hypnum jutlandicum*, *Campylopus introflexus* and *Dicranum scoparium*, moss species adapted to acidic conditions, occurred often in control plots in NL. Sand-deposited plots were more often dominated by *Hypnum cupressiforme ssp lacunosum* (which is typical for base-rich conditions) or *Pseudoscleropodium purum*. In sand-deposited sites of UK, *Homalothecium lutescens* was often the most abundant moss species. *Hylocomium splendens*, *Rhytidiadelphus triquetris*, and *R. squarrosus* were recorded in UK but not in NL.

Changes between 2018 and 2019 occurred in NL with an increase of *Hypnum jutlandicum* and *Campylopus introflexus* at the expense of *Dicranum scoparium*, and in UK with a decrease of *Homalothecium lutescens* in plots with sand deposition.

Dominant moss species like *Hypnum cupressiforme ssp lacunosum* and *Pseudoscleropodium purum* showed only minor changes.

Ordination of plots by species composition for 2018 (using DCA) showed that species composition of all plots in NL were very similar, whereas species compositions of UK are more diverse (Figure 38). The clear separation of NL and UK assumedly reflects the strong floristic difference between the regions: of total 111 species recorded in flat dunes, only 23 species occurred in both NL and UK plots (Figure 39). There was no significant difference in indicator values for nutrient, acidity and moisture between species which occurred in NL only, UK only or both ($p>0.05$ with ANOVA) (Figure 40).

Results of CCA for 2018, a constrained ordination method, are shown in Figure 41. Here the dune plots were ordinated by species composition, while constrained by 2 environmental factors (i.e. area and management). The proportion of the total inertia (= a measure of CCA model which represent the variation in the dataset) explained by the constrained axes of CCA was 20.2 %. Permutation test indicated that the effect of area was significant ($p<0.001$) and that of management was nearly significant ($p = 0.075$). The weak contribution of management to the CCA model is most likely due to large overlap between control and sand-deposited plots in terms of soil conditions, as demonstrated earlier with the PCA analysis (see section 4.1). Although the control plots and sand-deposited plots were forcedly separated on the CCA diagram, there are few species which appeared commonly in sand-deposited plots of both area (‘NL_Sand’ and ‘UK_Sand’), or in control plots of both area (‘NL_C’ and ‘UK_C”). An exception is *Pseudoscleropodium purum,* which occurred often (but not exclusively) in sand-deposited area of both NL an UK. In NL, species typical for control plots were identified as: *Campylopus introflexus, Cladina portentosa*. For UK, *Chamerion angustifolium, Homalothecium lutescens* and *Hylocomium splendens* were typical for sand-deposited plots.

Furthermore, the dune plots were ordinated using ‘hard’ variables of soil bulk properties, again using CCA (Figure 42). Here we used only 2 soil variables, pH and soil C, that were indicated to represent the major axes of variation of 10 soil variables, according to the PCA model (see section 4.1). The proportion of the total inertia explained by the constrained axes of CCA was 18.9 %. Permutation test indicated that the effect of pH and soil C was both significant ($p<0.001$ and $p<0.05$, respectively). Here the overlap between control plots and sand-deposited plots are even larger than the CCA model that used management and area as explanatory factors (Figure 41). That confirms again the large overlap in soil factors and species composition between control and sand-deposited plots.

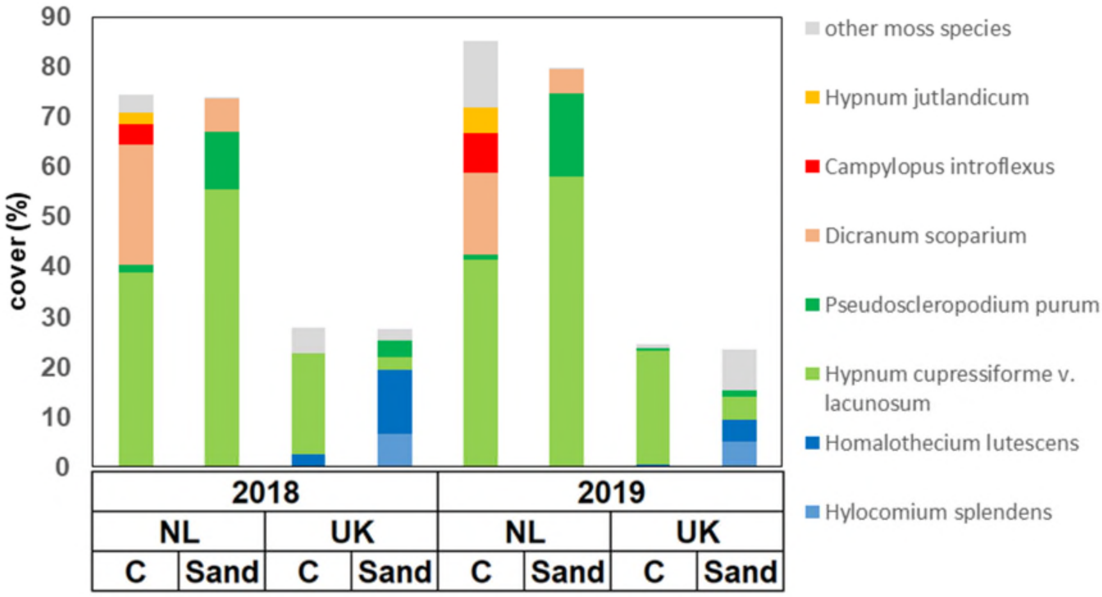


Figure 37. Average of **cover of moss species in flat dune plots** (N=27) in Luchterduinen ('LD') in NL and Newborough Warren ('NB') in UK. Eight common moss species with a (relatively) high cover are indicated .

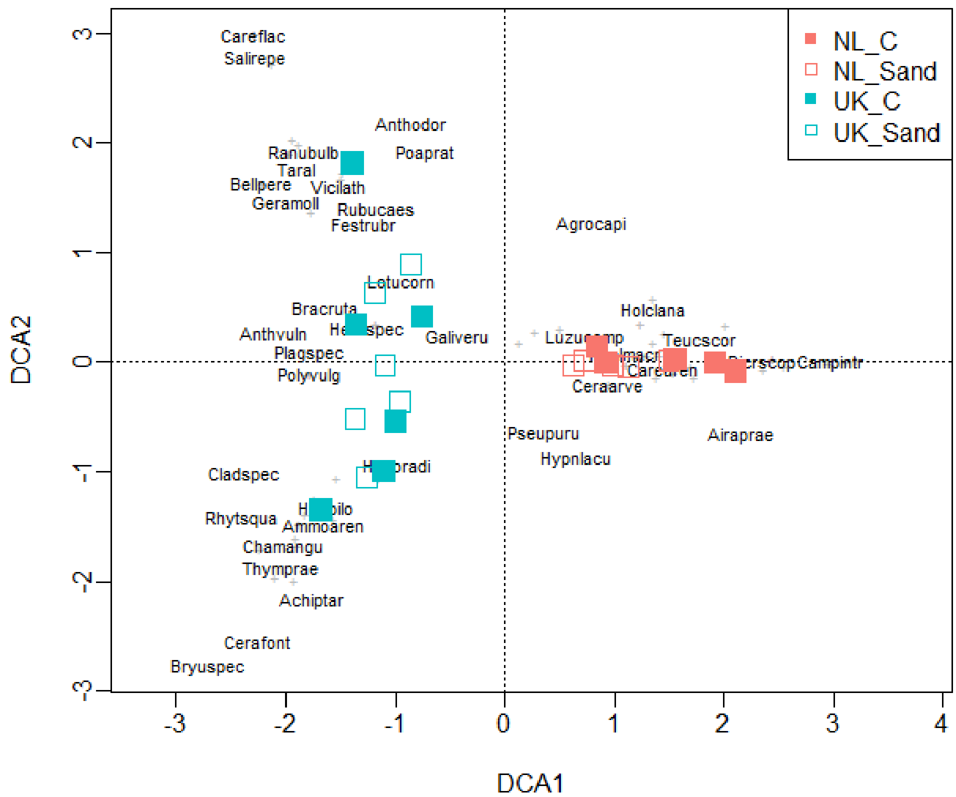


Figure 38. Ordination (DCA) diagram of **vegetation relevees of flat dune grassland plots** (N=27) for 2018. Squares depict the scores of plots on DCA axis 1 and 2. Letters show the loadings of species. When multiple species locate closeby, speices with lower abundance were shown with symbol "+".

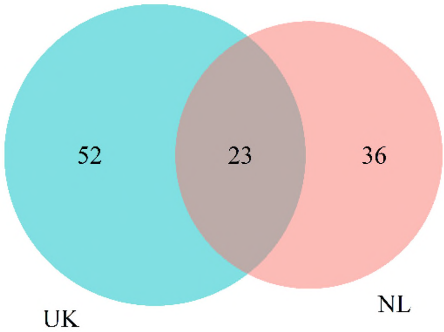


Figure 39. Floristic overlap between UK and NL for 2018. Blue circles depict the number of plant species recorded in at least one of 15 flat dune plots in NB in UK (N = 75). Red circle depicts the number of plant species recorded in at least one of 12 flat dune plots in LD in NL (N = 59). Of total 111 species recorded in LD and/or NB, 23 species appeared in both sites.

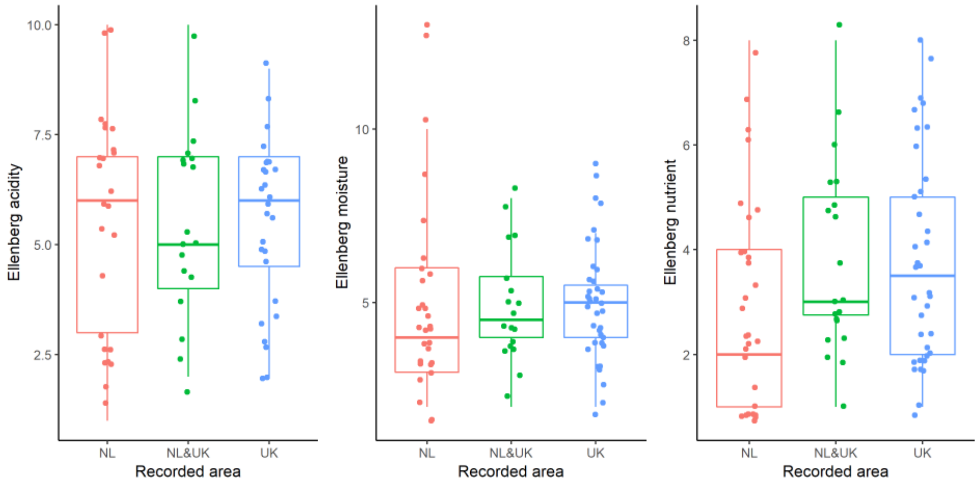


Figure 40. Difference in **Ellenberg indicator values of acidity** (left), **moisture** (middle), and **nutrient** (right) for the species which were recorded in NL only (N=36), NL and UK (N=23), or UK only (N=52) for 2018. Species without a valid indicator value were exluded from the analysis (i.e., 37 species for acidity, 26 species for moisture, 22 species for nutrient).

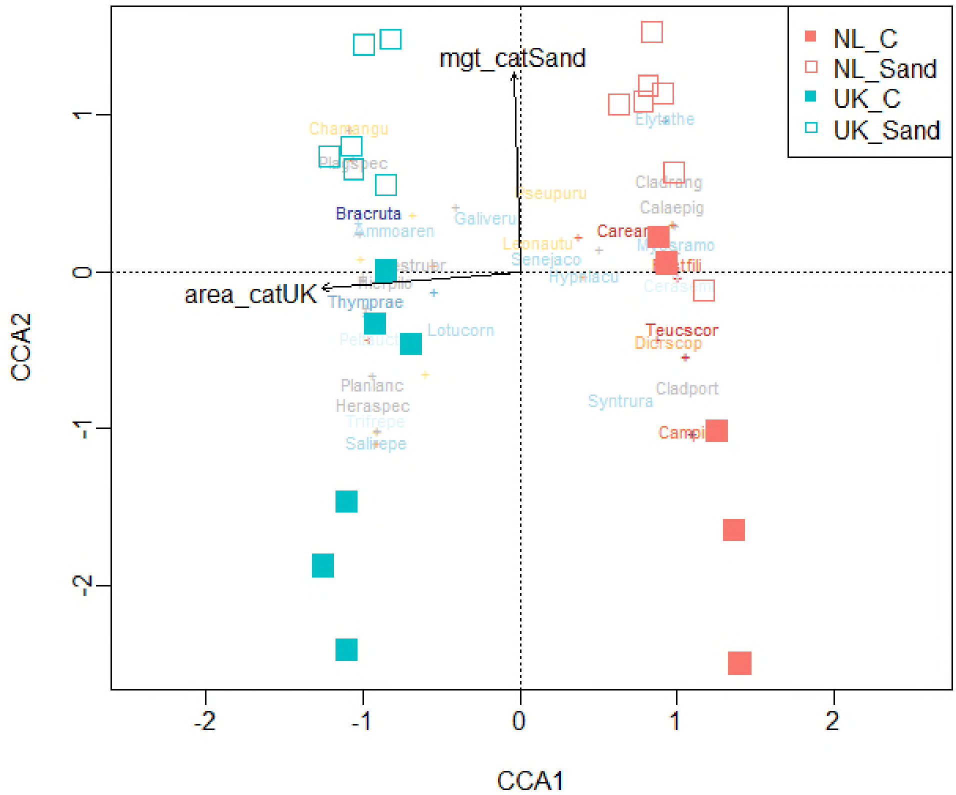


Figure 41. Ordination (CCA) diagram of **flat dune grassland plots** (N=27) for 2018. Circles depict the scores of plots on CCA axis 1 and 2. Arrows depict the loadings of two environmental factors: **area** (NL (0) or UK (1)) and **management** (sand-deposited (1) or Control (0)). Letters show the loadings of species. When multiple species locate close to each other, spieces with lower abundance were shown with symbol “+”.Colors of the species depict their Ellenberg acidity value, ranging from 1 (red; species adapted to acidic conditions) to 10 (blue; species adapted to buffered conditions). Species for which Ellenberg acidity value is unknown are shown with light gray.

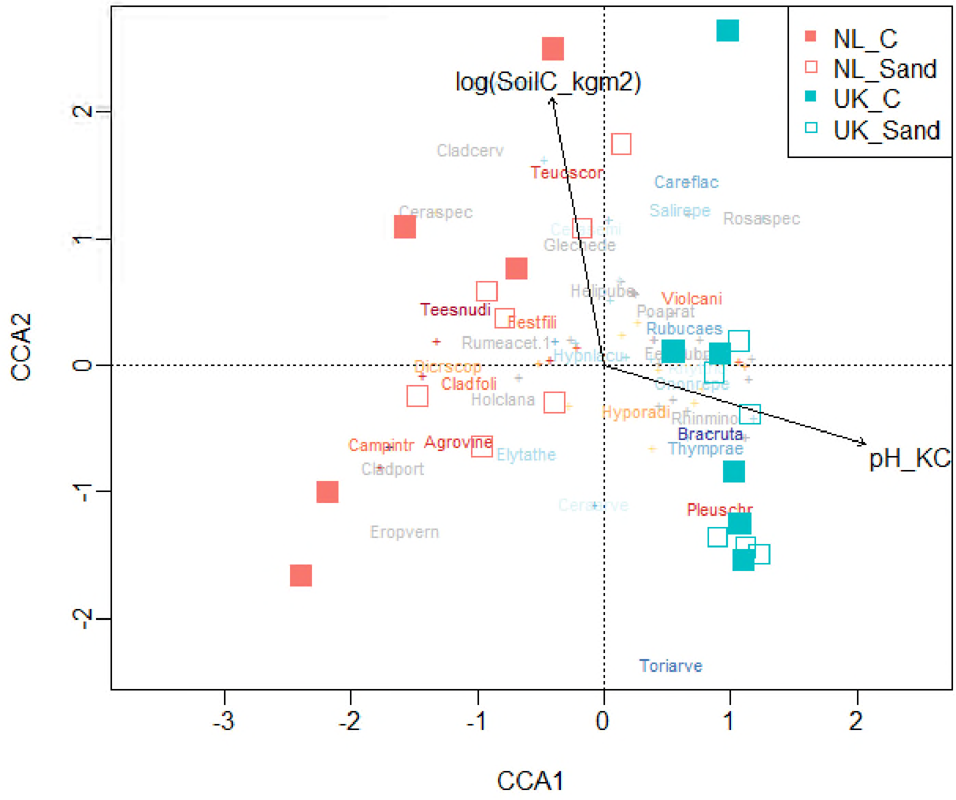


Figure 42. Ordination (CCA) diagram **of flat dune grassland plots** (N=24, for which data of the soil variables are available) for 2018. Squares depict the scores of plots on CCA axis 1 and 2. Arrows depict the loadings of 2 **soil variables**: pH_KCl and log-transformed Soil total organic C (kg C/m^2). Letters show the loadings of plant species. When multiple species are close to each other, spieces with lower abundance were shown with symbol "+". Colors of the species depict their Ellenberg acidity value, ranging from 1(red; species adapted to acidic conditions) to 10 (blue; species adapted to buffered conditions). Species for which Ellenberg acidity value is unknown are shown with light gray.

We conducted the same analysis for the Dutch flat plots only. DCA analysis (i.e. ordination based on species composition only) did not clearly separate control and sand-deposited plots (Figure 43). When soil variables were included in the ordination (i.e. CCA analysis), sand deposition plots locate on the top-right corner, which corresponds to higher pH (Figure 44). This illustrates that sand deposited sites had higher soil pH, which favored the occurrence of *Rubus caesius* and *Koeleria macrantha* and a high cover of *H. cupressiforme ssp. lacunosum*. Species associated with low-pH control plots (left-bottom) are often those adapted to acidic-conditions, such as *Aira praecox*, *Campylopus introflexus, Dicranum scoparium*.

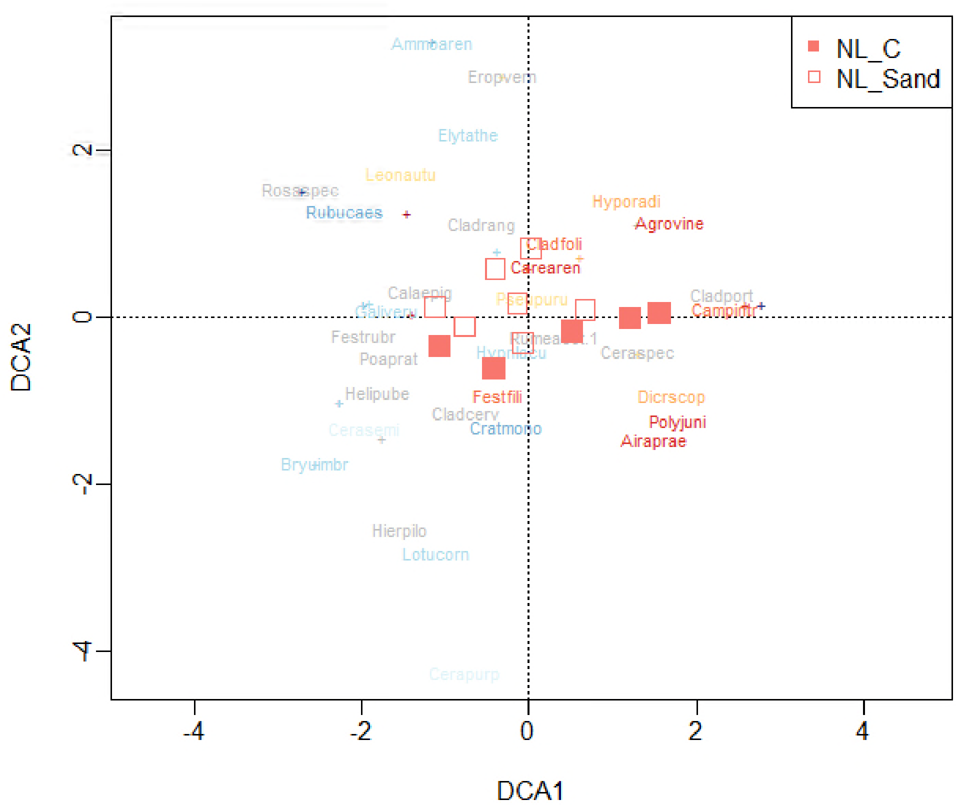


Figure 43. Ordination (DCA) diagram of **Dutch flat dune grassland plots** (N=12) for 2018. Squares depict the scores of plots on DCA axis 1 and 2. Letters show the loadings of species. When multiple species locate closeby, speices with lower abundance were shown with symbol "+".Colors of the species depict their Ellenberg acidity value, ranging from 1(red; species adapted to acidic conditions) to 10 (blue; species adapted to buffered conditions). Species for which Ellenberg acidity value is unknown are shown with light gray.

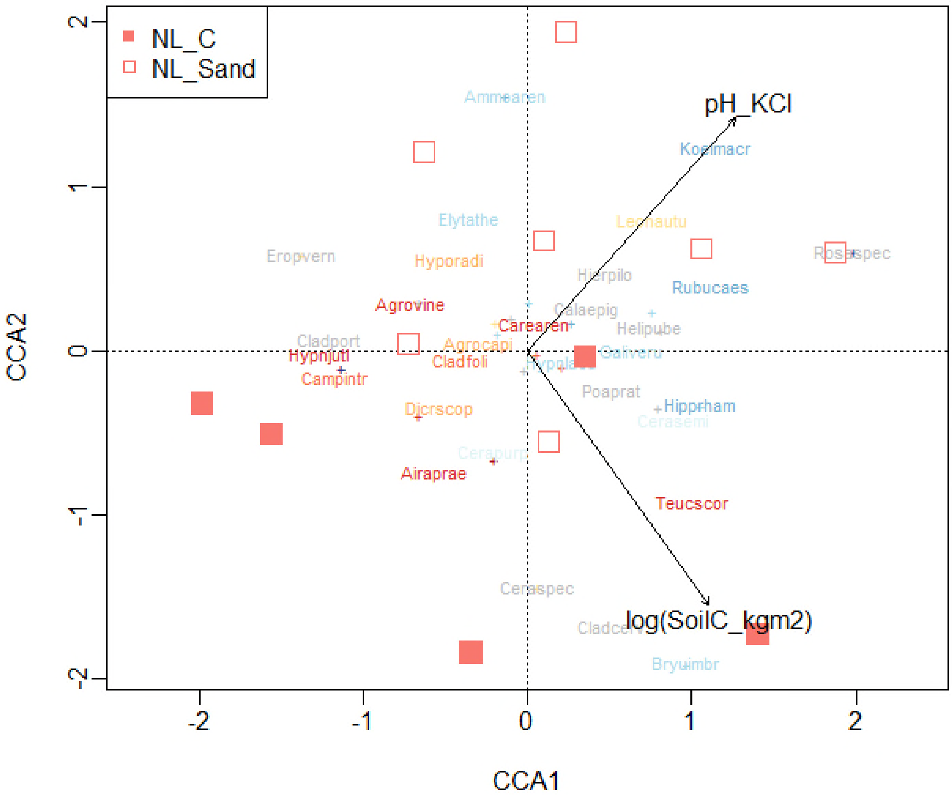


Figure 44. Ordination (CCA) **diagram of Dutch flat dune grassland plots** (N=12). Squares depict the scores of plots on CCA axis 1 and 2. Arrows depict the loadings of 2 soil variables: **pH_KCl** **a**nd log-transformed **Soil total organic C** (kg C/m²). Letters show the loadings of plant species. When multiple speciesare close to each other, spieces with lower abundance were shown with symbol “+”. Colors of the species depict their Ellenberg acidity value, ranging from 1(red; species adapted to acidic conditions) to 10 (blue; species adapted to buffered conditions). Species for which Ellenberg acidity value is unknown are shown with light gray.

4.7 Nitrogen and carbon pools and fluxes

In Figure 45 pools, internal fluxes and external of C and N are presented. The C and N-pools in the soil organic matter were much larger than the pools in the biotic compartments. Major part of the C and N in the biotic compartments was in root biomass. In NL pools in plant biomass were for a major part in living mosses, while in UK aboveground vascular plant biomass was more important. Pools in microbes were (very) small compared to soil organic matter and plant biomass. Note that N-pools in DIN and DON were comparable to N-pools in microbes. Total C and N-pools in plant biomass were lower in NL than UK due to differences in root biomass. Total C and N-pools were lower in plots with sand deposition than plots with sand deposition due to a low soil organic matter pools. In UK the pools in plant biomass had a higher proportion in the total pools.

Internal fluxes showed the following pattern. C- and N-mineralization was higher than storage in vascular plant biomass and microbes. In UK net C-mineralization and storage in aboveground vascular plant biomass were higher than in NL due to a higher decomposition rate and vascular plant productivity. Storage of N microbes was in UK much higher than in NL and was here more or less equal to N-storage in aboveground vascular plant biomass. In NL less N was ended up in microbial biomass and aboveground vascular plant biomass than in UK. Note that in NL mosses can be more important for uptake of N than in UK. However this internal flux is unknown because we did not measure the productivity of mosses.

For external fluxes of N NL has larger input by N deposition and more removal of N in above ground plant biomass by grazing than in UK. There are no clear differences between control plots and plots with sand deposition. Note that N-input by biological N_2-fixation and by large grazers were not measured.

The sum of input by N-deposition and N-mineralization amounted more in NL due to higher N-deposition and net N-mineralization. The larger immobilisation of N in UK contributes largely to this difference, despite of the high C-mineralization rate. Removal of N by grazers was also larger in NL. Due to the lack of measurements in the UK study area itself it was not possible to trace differences in N-leaching between NL and UK. The input of mineral N by grazers is in NL possibly higher due to much higher density of grazers (many fallow deer).

There are no clear differences internal and external fluxes between control plots and plots with sand deposition.

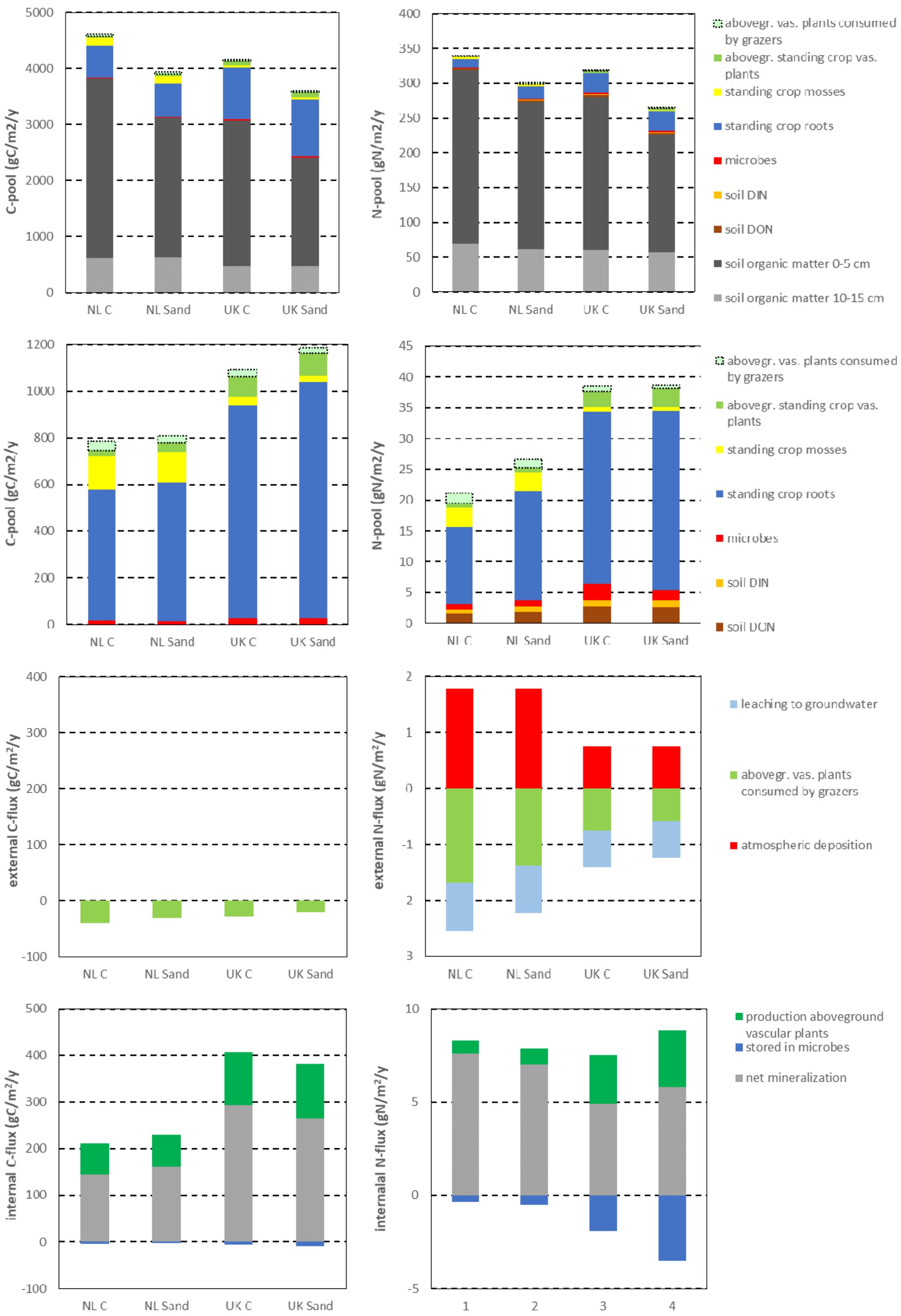


Figure 45: Pools and fluxes of **carbon and nitrogen** for each treatments (control ('C') and sand-deposited ('Sand')) and area (Luchterduinen ('NL') and Newborough Warren ('UK')). The two graphs at the top shows al measured pools, the graphs in the 2th line the small pools, the graphs in the 3th line internal fluxes, and the graphs below internal fluxes. Number of replicas are 5 for NL_C, 7 for NL_Sand, 6 for UK_C, and 6 for UK_Sand (N = 24 in total). For plant biomass pools C-pool was calculated as 50% of the biomass pool.

5 Effects of microclimate (slope) on dune grasslands

Results of all ANOVA analysis related to this section are summarized in Attachment VII.3 and VII.5.

5.1 Effects of slope on bulk density

One could expect that soils on north-facing slopes accumulate organic matter better due to less drought stress, and vice versa for south-facing slope. Such a pattern is indeed indicated in our study: for subsoil (10-15 cm depth), effects of slope was almost significant ($p = 0.058$), with north-facing slopes having lower bulk density (i.e. higher organic matter content). Bulk density of subsoil was lower for UK than NL ($p<0.01$), indicating that organic matter develops better in subsoil in UK. The difference between slopes were more evident in UK than in NL. It probably resulted from difference in grazing. Grazers in UK (cows and ponies) avoid steep slopes, which prevents strong soil compaction, and therefore slope can have a lower bulk density. In contrast, in the NL dune area flat parts and slopes are grazed strongly.

Bulk density of topsoil (0 – 5 cm depth) were not significantly different among slope nor between area ($p>0.05$ for both) (Figure 46a), yet north slope tend to have lower bulk density (i.e. higher organic matter) in both areas.

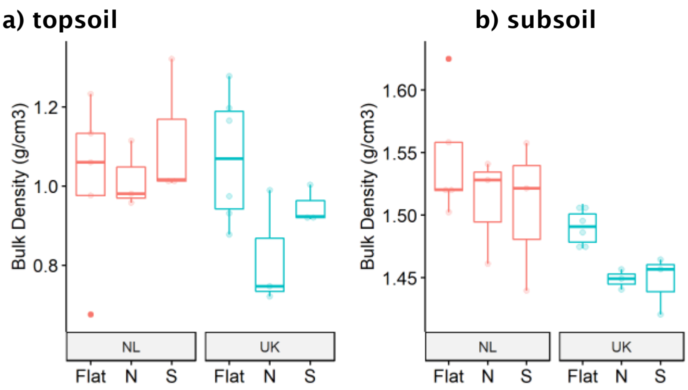


Figure 46. Median and quantiles (25th and 75th) of **soil bulk dentisy of topsoil** (0 – 5 cm depth; left) and subsoil (10-15 cm depth; right) of dune plots. None of the plots are subject to sand deposition. Values are shown separately for slope type (flat ('Flat'), North-facing slope ('N") and south-facint slope ('S')), and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_Flat, 6 for UK_Flat, and 3 for the rest (N = 23 in total).

5.2 Effects of slope on plant productivity

For both years annual productivity of plants (i.e. plant growth inside enclosures) was higher in UK ($p<0.001$), and was not influenced by slope ($p>0.05$) (Figure 47). Peak standing crop (i.e. plant growth outsize enclosures) was also higher in UK than NL ($p<0.001$) (Figure 47). The effect of slope on peak standing crop was not significant ($p>0.05$), but north slopes tend to have slightly higher productivity in both areas in

2018 and 2019. A lower soil bulk density on slopes in UK (see previous section) did not correlate with differences in plant productivity or standing crop.

For productivity and peak standing crop there was an interaction effect of year and area (resp. p<0.01 and <0.001). For productivity changes are not very clear, except for north slopes in UK (higher in 2019). Peak standing decreased in NL and stayed the same in UK

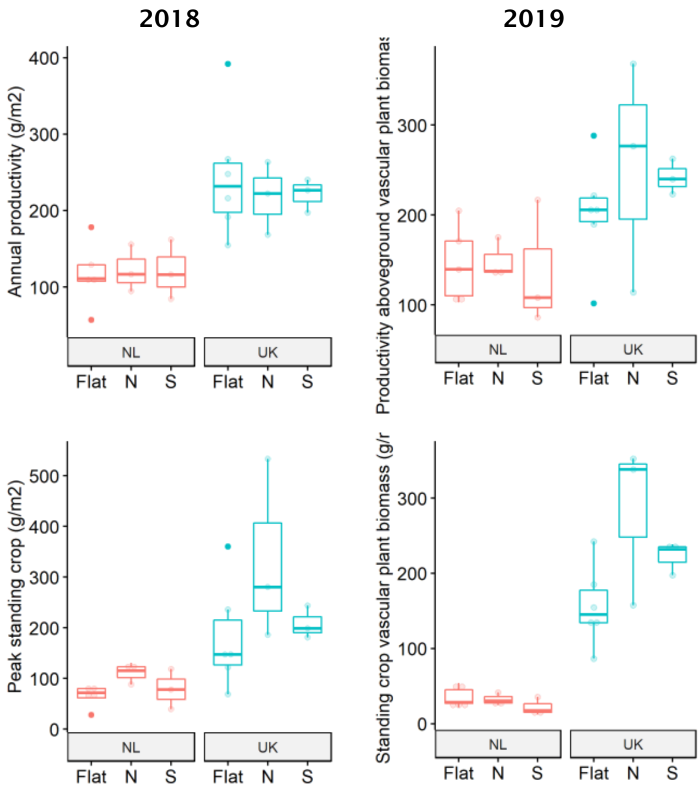


Figure 47. Median and quantiles (25th and 75th) of aboveground **plant annual productivity** and **peak standing crop** of dunes in 2018 an 2019. None of the plots are subject to sand deposition. Values are shown separately for slope type (flat ('Flat'), North-facing slope ('N") and south-facint slope ('S')), and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_Flat, 6 for UK_Flat, and 3 for the rest (N = 23 in total).

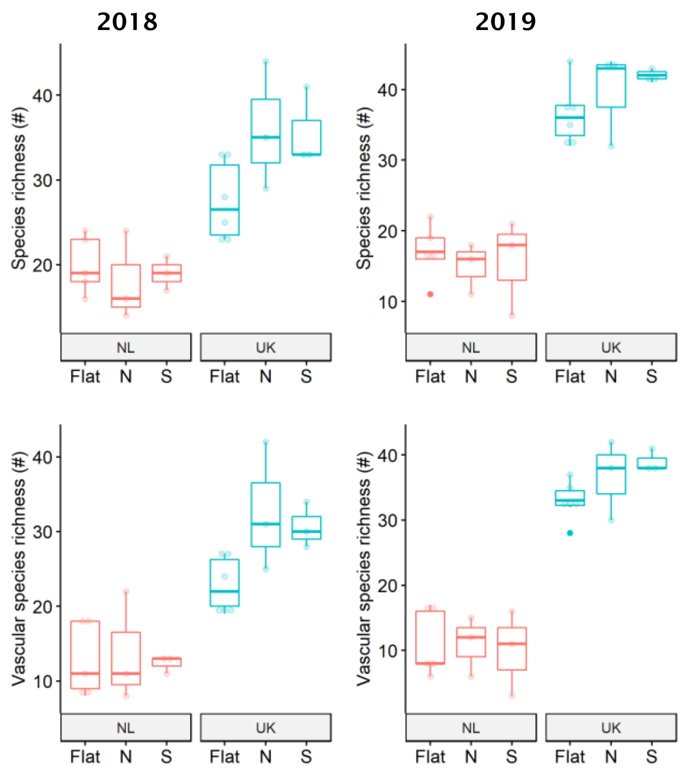
5.3 Effects of slope on plant community structure

The number of vascular plant species was slightly higher on slopes in UK, possibly due to lower grazing pressure (Figure 48b). Species number of mosses and lichens were higher on south-facing and flat slopes than on north-facing slopes in both NL and UK (Figure 48). However these differences were not significant for both years.

Average Ellenberg values for nutrients were significantly ($p < 0.05$) different between slopes, with north-facing slopes associated with more eutrophic species (Figure 48). This is linked to a lower bulk density (see section 5.1). Average Ellenberg values for acidity and moisture were not significantly different between slopes (Figure 48). In UK, north-facing slopes tended to have more species adapted to moist conditions (Figure 48).

In both areas moss cover on north slopes was higher than at south slopes and flat sites by a dominance of *Pseudoscleropodium purum* (Figure 50). This species is adapted to relatively moist and eutrophic conditions. The differences were largest in NL. In UK, more woody species (mainly *Rubus caesius* and *Salix repens*) occur on slopes (Figure 49), due to less intensive grazing pressure by large grazers (ponies and cattle) on slopes in UK. In UK *Poa pratensis* has a preference for north slopes, *Ammophilla arenaria* for south slopes, and *Arrhenatherum elatius* and *Pseudoscleropodium purum* for both north and south slopes. Here herb species like *Thymus praecox* and *Hypochaeris radicata* have the highest cover at flat and south slopes (Figure 50). In NL the clearest effect of slope was a higher moss cover at north slopes (see above). North slopes also had in 2018 less herb cover, and higher grass cover by a high abundance of *Agrostis capillaris+vinialis* (Figure 50). *Dicranum scoparium* tended to occur less on north-facing slopes.

Meteorological conditions (dry in 2018 and relatively wet in 2019) affected the vegetation. The number is vascular plant species increased in UK between 2018 and 2019. The number of moss and lichen species decreased in in both areas. There was no effect year on Ellenberg values for moisture. In NL the strong decrease of grass cover, which occurred in the flat control and sand deposition sites, took also place at north and south slopes. Here all important grass species decreased strongly. In UK herb cover and grass cover increased at flat, north and south sites, by an increase of mainly *Agrostis capillaris* and *Anthoxanthum odoratum*. At flat and south sites also an increase of *Thymus praecox* added to the herb cover increase. In NL moss cover did not change, but in species composition there were some shifts. At flat and south sites *Hypnum jutlandicum* increased and at north sites *Campylopus introflexus*, all at the expense of *Dicranum scoparium*.



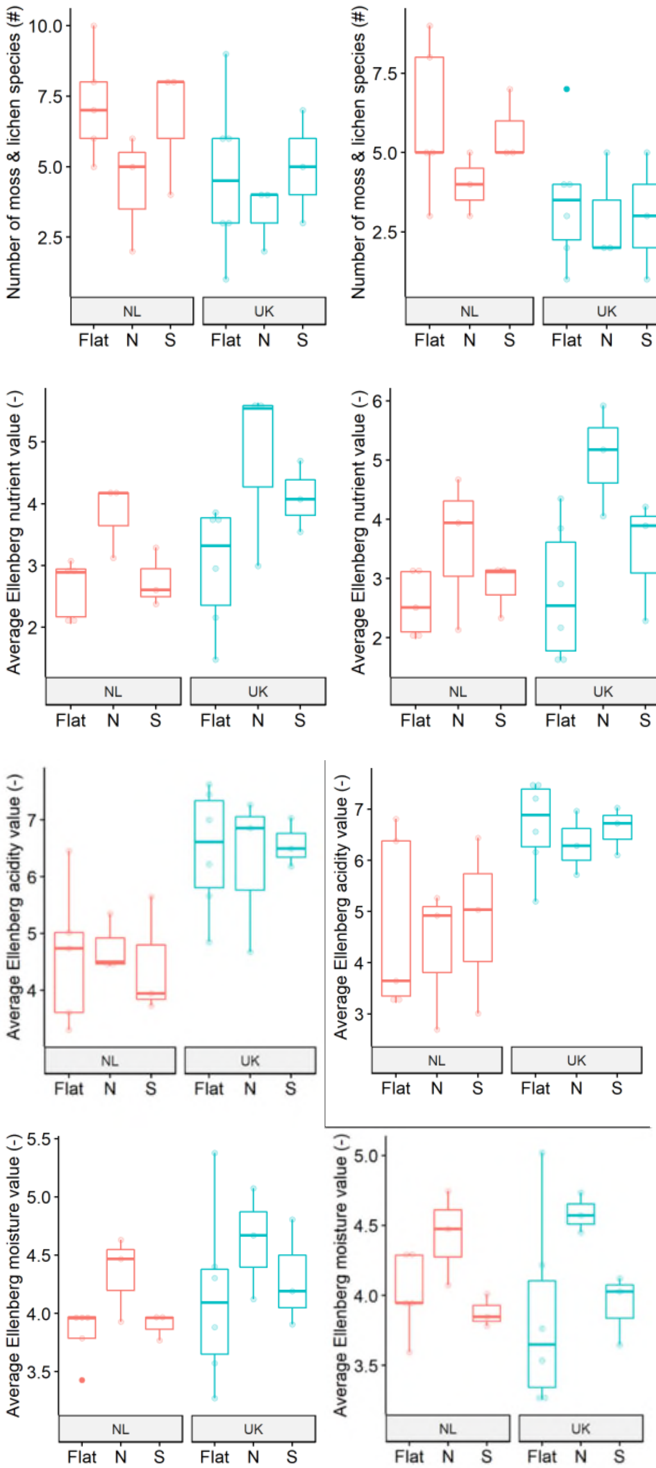


Figure 48. Median and quantiles (25th and 75th) of **species diversity and indicator values of control dune plots** in 2018 and 2019. None of the plots are subject to sand deposition. Values are shown separately for slope type (flat ('Flat'), North-facing slope ('N") and south-facint slope ('S')), and area (Luchterduinen ('NL') and Newborough Warren ('UK')). Points depict the values of each replica. Number of replicas are 5 for NL_Flat, 6 for UK_Flat, and 3 for the rest (N = 23 in total).

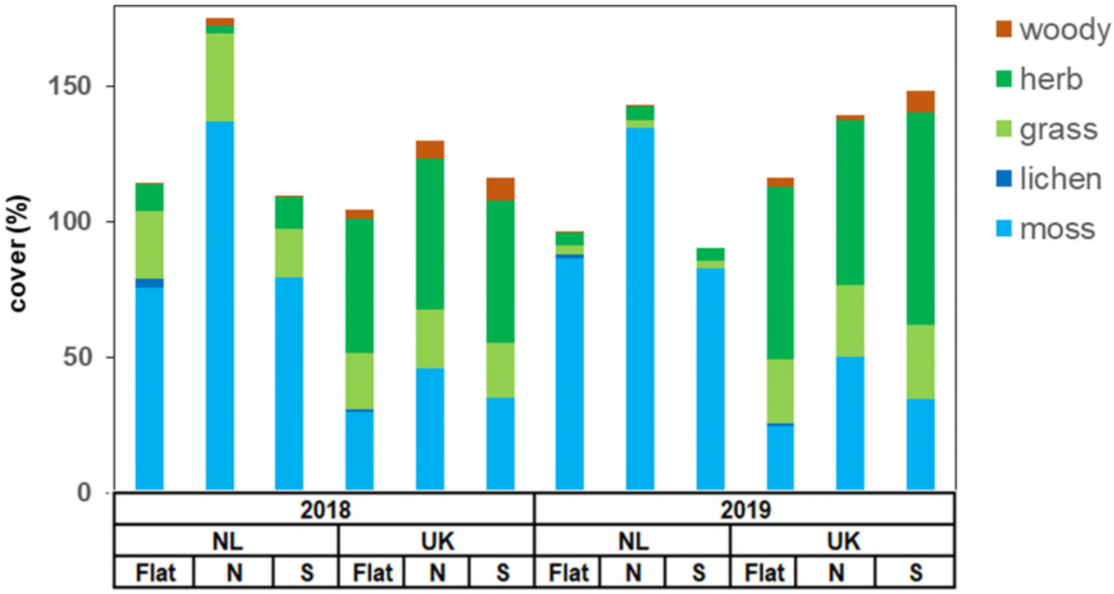


Figure 49. Cumulative cover of **functional plant groups in control dune plots** (N=23), split into functional groups, in Luchterduinen ('LD') in NL and Newborough Warren ('NB') in UK in 2018 and 2019. Plots shown with black letters are flat plots, those with red letters are plots on north-facing slopes, and those with green letters are plots on south-facing slopes.

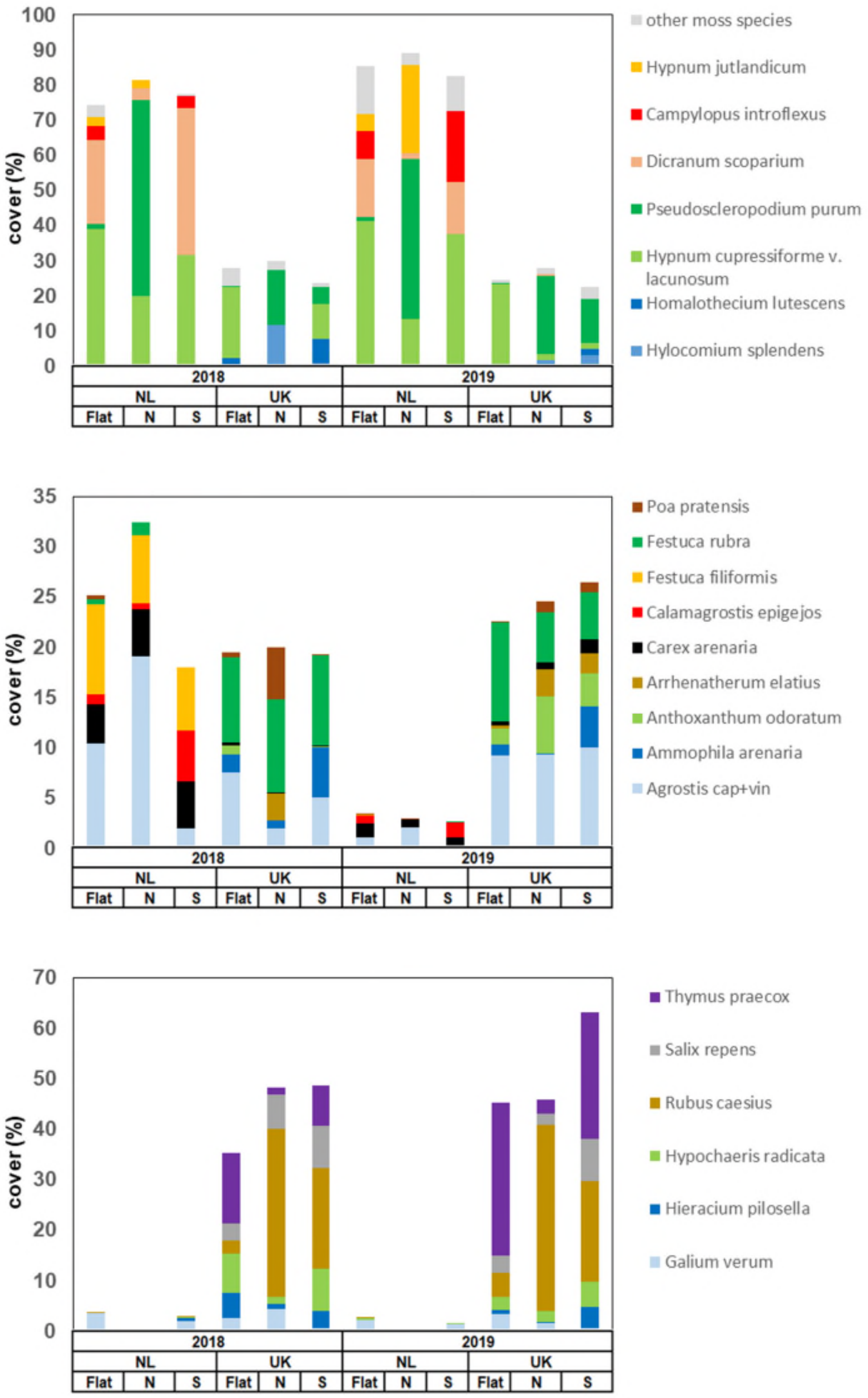


Figure 50. Average cover of **moss** (top), **grass** (middle) and **herb** (bottom) **species in control dune plots** (N=23) in Luchterduinen ('LD') in NL and Newborough Warren ('NB') in UK in 2018 and 2019 diffentiated for flat, north and south exposed sites. Eight common moss species are indicated by color.

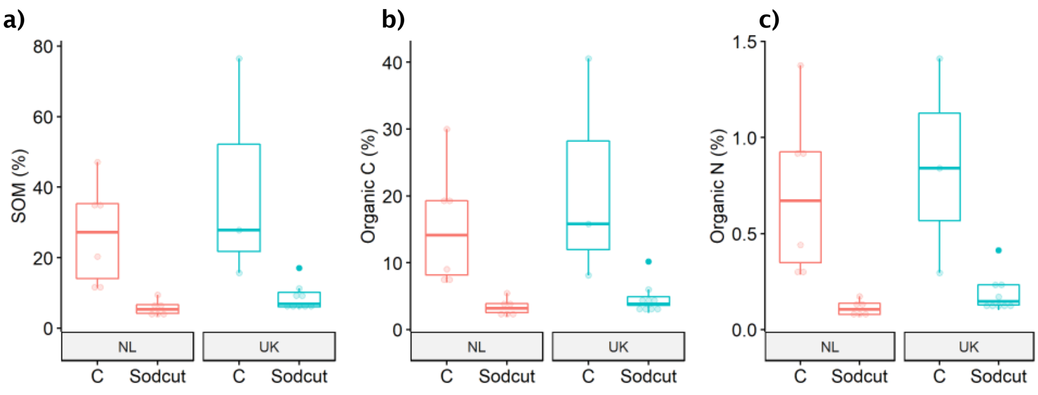
6 Effects of measure (sod-cutting) on heathland

Results of all ANOVA analysis related to this section are summarized in Attachment VII.2.

6.1 Effects of sod-cutting on soil bulk parameters of topsoil and subsoil

Sod cutting obviously reduced soil organic matter, C content, N-content of topsoil ($p<0.001$; Figure 51 a-c). Soil pH was higher for sod cut soils ($p<0.001$ for both pH_KCl and pH_H2O; Figure 51 e & f) due to absence of a strongly acidified thick litter layer. Soil C:N was higher in sod-cut soils ($p<0.01$) especially in NL (interaction effect of management and area $p<0.05$; Figure 51g). Furthermore, dissolved nutrients (N-NH_4, N-NO_3, DON, P-PO_4) were lower in sod-cut soils (Figure 51 h - k).

PCA analysis (Figure 52) indicated that variation of soil parameters of the heathland plots can be summarized with the two major axes: organic matter content of soil (axis 1) and pH gradient (axis 2). The first and second axis explain 70.4% and 10.5% of the total variation, respectively. Control plots and sod-cut plots were clearly separated on the first PCA axis, whereas the overlap between UK and NL sites were large. This means that, irrespective of the difference in N-deposition of the sites, NL and UK had common soil conditions of heathland soils, and the effects of sod-cutting on heathland soils were similar between NL and UK.



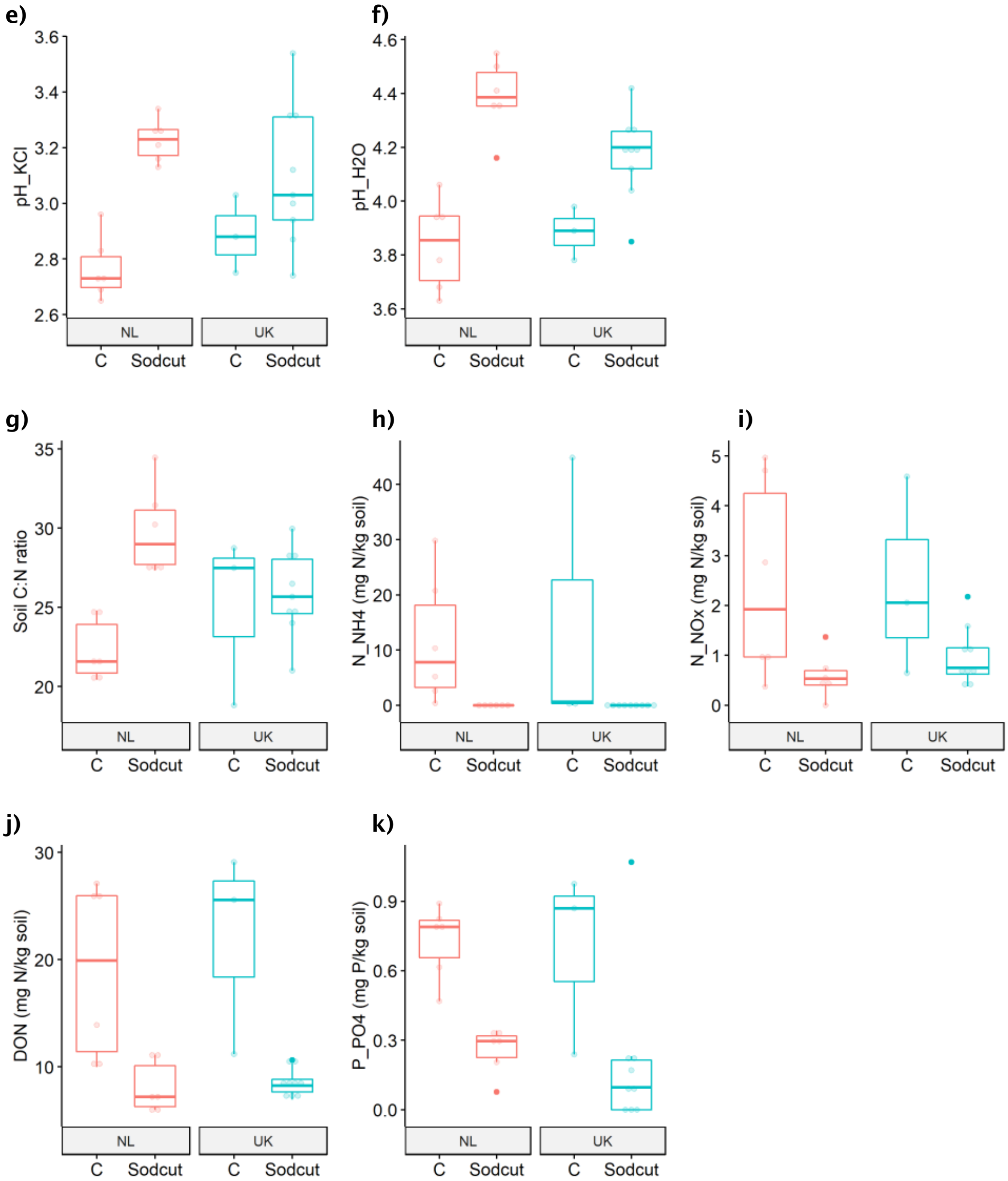


Figure 51. Median and quantiles (25th and 75th) of **soil bulk parameters of topsoil** (0 – 5 cm depth) of **heathland plots**. Values are shown separately for each treatments (control ('C') and sod-cutted ('Sodcut')) and area (Groote Heide ('NL') and Little Budworth Common ('UK')). Points depict the values of each replica. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total).

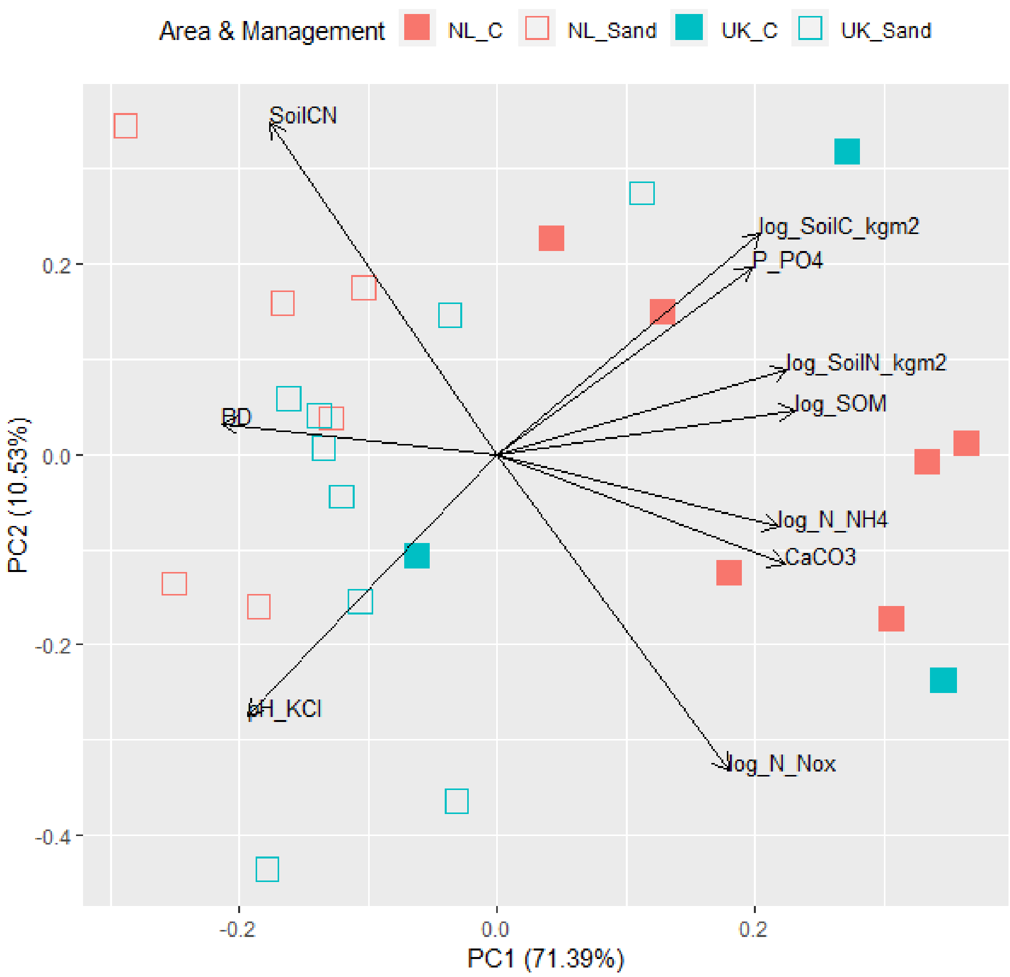


Figure 52. PCA diagram of **heathland plots** (N=24), based on 9 **soil variables of topsoil** (0-5 cm depth): Bulk density (g/cm3), soil organic matter content (%), soil organic C content (kg C/m²), soil organic N-content (kg C/m²), soil C:N ratio, soil pH_KCl, concentrations of N-NH_4, N-NO_x, and P-PO_4 concentration (mg N/kg dry soil and mg P/kg dry soil). Soil organic matter, Soil organic C, soil organic N, N_NH_4 (after adding 0.1), and N-NO_x (after adding 0.1) were log-transformed prior to the analysis.

For subsoil (10 – 15cm depth), we only measured bulk density. Bulk density was higher in sod-cut plots than in control plots in UK only (Figure 53), indicating that soil organic matter content is higher in control sites in UK. On contrast, bulk density was similar between sod-cut plots and control plots in NL.

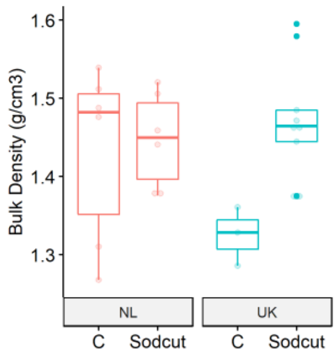


Figure 53. Median and quantiles (25th and 75th) of **soil bulk density of subsoil** (10 – 15 cm depth) of **heathland plots**. Values are shown separately for each treatments (control ('C') and sod-cutted ('Sodcut')) and area (Groote Heide ('NL') and Little Budworth Common ('UK')). Points depict the values of each replica. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total).

6.2 Effects of sod-cutting on N- and P-mineralization of topsoil

N-mineralization rate was lower in sod-cut plots compared to control plots ($p<0.001$) (Figure 54a). Most of the sod-cut plots have very little N-mineralization or net N-immobilization. P mineralization rate was higher for UK than NL ($p<0.05$) and lower for sod-cut plots than control plots ($p<0.05$) (Figure 54b).

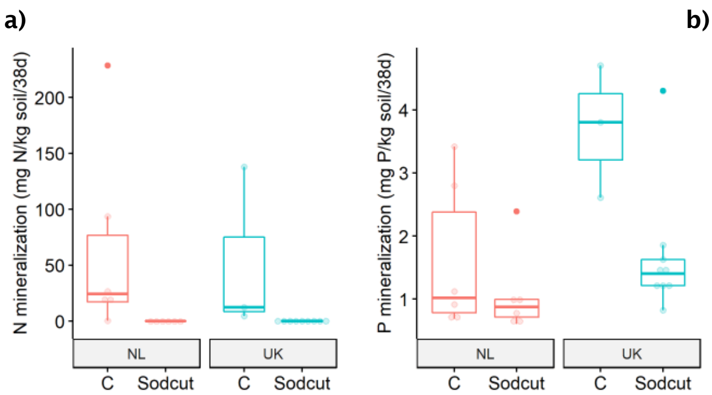


Figure 54. Median and quantiles (25th and 75th) of **mineralization rates of of topsoil** (0 - 5 cm depth) of **heathland plots**. Values are shown separately for each treatments (control ('C') and sod-cutted ('Sodcut')) and area (Groote Heide ('NL') and Little Budworth Common ('UK')). Points depict the values of each replica. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total).

6.3 Effects of sod-cutting on plant productivity

Peak standing crop of heathlands was higher for UK than NL ($P<0.001$; Figure 55). The effect of sod-cutting was contrasting between UK and NL (interaction effect $p<0.001$): peak standing crop was similar between control and sod-cut plots in NL, whereas in UK it was much higher in control plots than in sod-cut plots. The small difference in peak standing crop in NL, irrespective of much higher soil organic matter content in control plots, may be because drought stress, besides nutrient availability, is limiting the productivity of the vegetation (see section 6.4 for species indicator values for moisture). In addition. the extreme dry summer of 2018 caused in NL much more dying off of *Calluna vulgaris* leaves than in UK. Then also some in NL *Molinia caerulia* suffered strongly from drought stress in 2018 (nearly no growth).

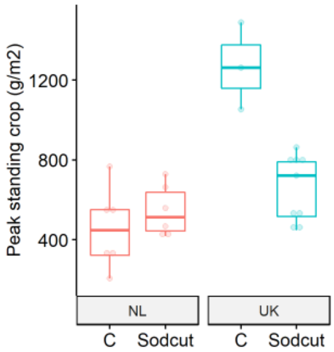


Figure 55. Median and quantiles (25th and 75th) of aboveground **peak standing crop** of **heathland plots**. Values are shown separately for each treatments (control ('C') and sod-cutted ('Sodcut')) and area (Groote Heide ('NL') and Little Budworth Common ('UK')). Points depict the values of each replica. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total).

GH08: control

GH03: sod cut

LB06: control

LB03: sod cut

Figure 56: Vegetation of some control and sod cut plots in Groote Heide ('GH') in the Netherlands and Little Budworth Common ('LB') in UK.

6.4 Effects of sod-cutting on plant community structure

The number of species was not different between areas nor between management (p>0.05), in terms of total plant species, vascular plant species, and moss+lichen species (Figure 57 a - c). Average Ellenberg indicator values for acidity and nutrient were not different among management nor area (p<0.05 for both; Figure 57 d & e).

Cover of functional groups in each plot is illustrated in Figure 58. Most plots had a high cover of *Calluna vulgaris* (Figure 56). Two control plots in NL were dominated by grass (i.e. *Molinia caerulea)*, and these plots had a lower moss cover than the *Calluna* dominated plots. Moss cover was higher in UK than NL

Dominant moss species were contrasting between control and sod-cut plots (Figure 59). In NL, *Hypnum jutlandicum* dominates in control plots, whereas *Campylopus introflexus* dominates in sod-cut plots. Presumably, *C. introflexus* benefits from the open conditions created by sod-cutting. In UK, on contrast, *H. jutlandicum* is often (and partly *Pleurozium schreberi*) the dominant moss-species in control and sod-cut plots.

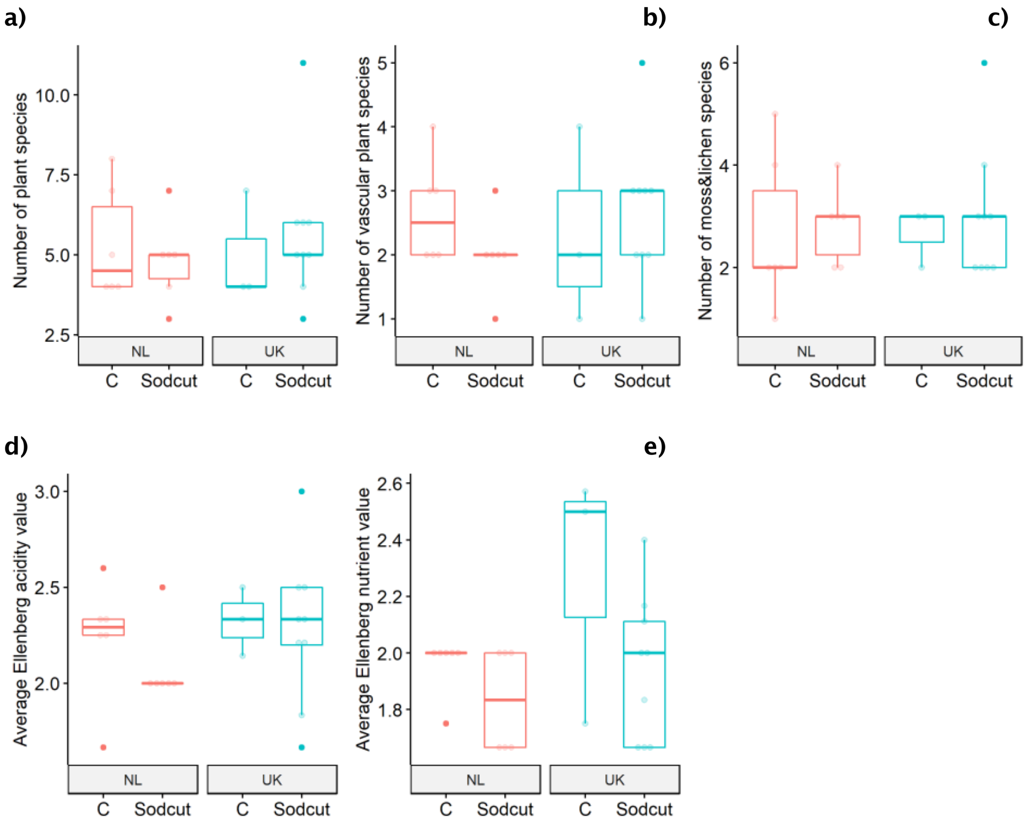


Figure 57. Median and quantiles (25th and 75th) of s**pecies number and average Ellenberg indicator values of heathland plots**. Values are shown separately for each treatments (control ('C') and sod-cutted ('Sodcut')) and area (Groote Heide ('NL') and Little Budworth Common ('UK')). Points depict the values of each replica. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total).

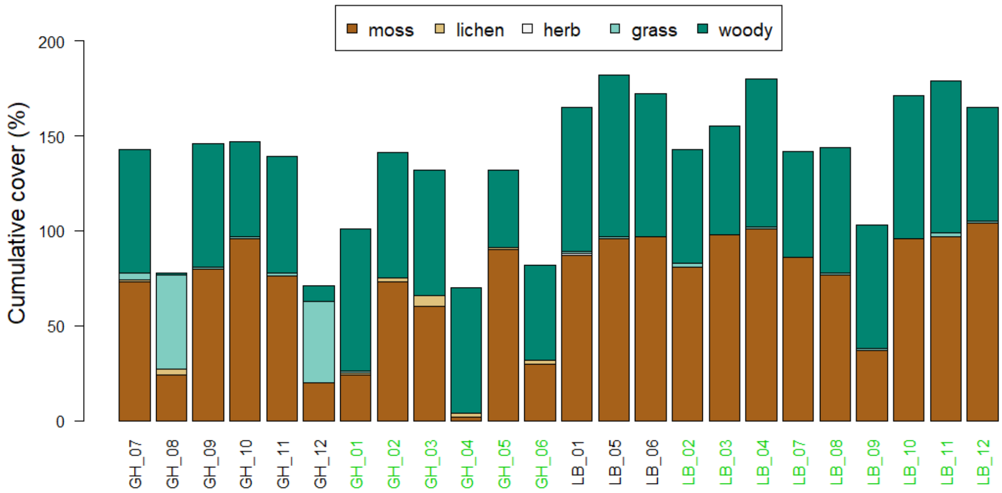


Figure 58. Cumulative cover of **plant functional groups in heathland plots** (N=24), split into functional groups, in Groote Heide ('GH') in NL and Little Budworth Common ('LB') in UK. Plots shown with black letters are control plots, and those with green letters are sod-cut plots.

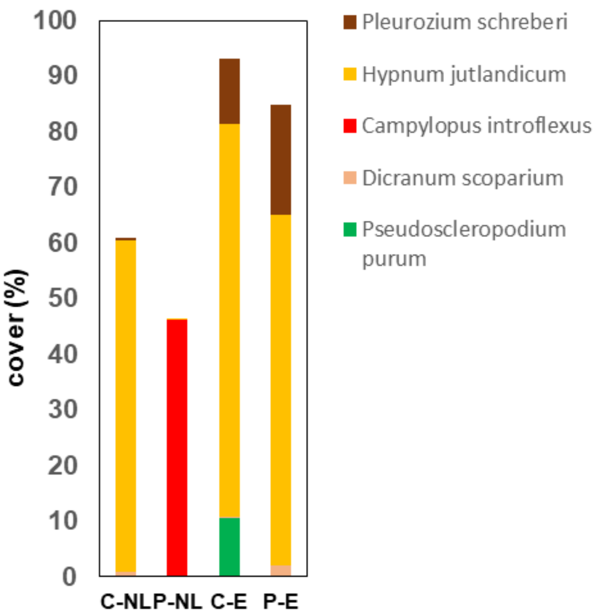


Figure 59. Cumulative cover of **moss species in heathland plots** (N=24) in Groote Heide ('GH') in NL and Little Budworth Common ('LB') in UK. Five common moss species are indicated by color. Plots shown with black letters are control plots, and those with green letters are sod-cut plots.

6.5 Pools and fluxes of nitrogen and carbon

In Figure 61 pools and fluxes of C and N are presented. The C pool of the topsoil was much higher than that of the standing crop of vascular biomass. Net N-mineralization in control plots is the most important for availability of mineral N and was much higher than N-deposition. In sod cut plots N-mineralization is neglectable. Leaching of N (only measured in NL) is small compare to the N-deposition for the control plots and negligible in the sod-cut plots.

For the sod cut plots we compared the N-pool in the topsoil in 2018 with the cumulative N-deposition after sod cutting (Figure 60). The deposition is based on modelled N-profile (par. 3.2). There is a considerable part of the topsoil N-pool which cannot be explained by the cumulative N-deposition. For NL this fraction is ca. 50% and in UK ca. 40% of the topsoil N-pool. Explanations for this can be 1) the actual N-deposition was higher than modelled values, 2) after sod cutting there was still a significant amount of soil organic matter left in the new topsoil, and 3) biological N-fixation adds strongly to N-accumulation.

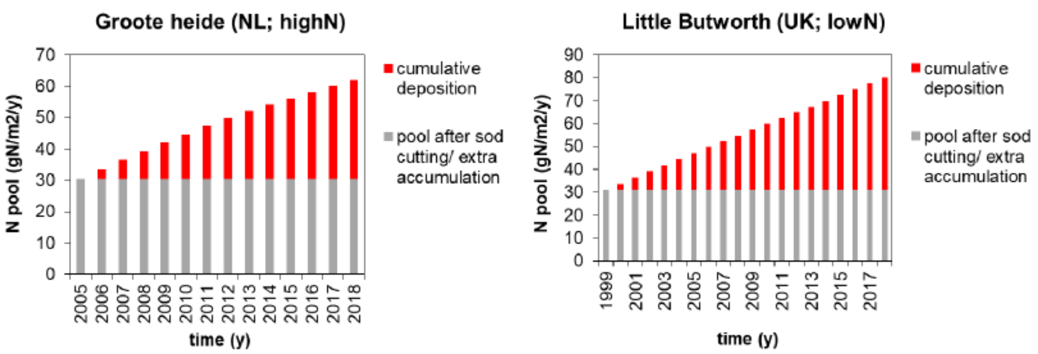


Figure 60: Backward reconstruction of the the developement of **soil N-pool in the topsoil** at sod cut plots 0-5 cm topsoil. Calculation are based on the measured N-pool in 2018 and cumulative N-deposition (red) after sod cutting based on modelled N-deposition. The pool indicated by grey bars is not explained by accumulation of the modelled N-deposition.

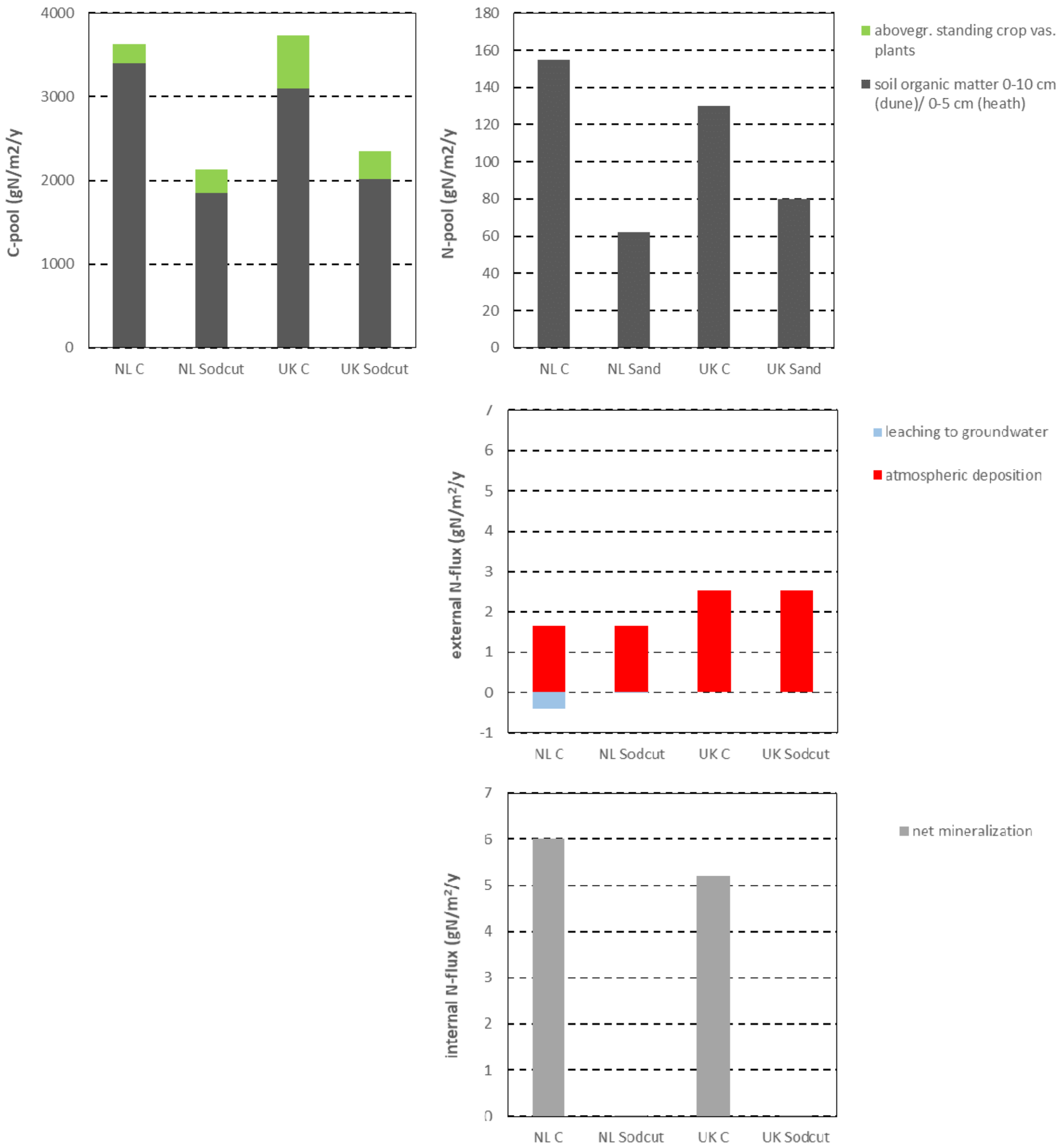


Figure 61: Pools and fluxes of **carbon and nitrogen** for each treatments (control ('C') and sod cutting ('Sodcut')) and area (Groote Heide ('NL') and Little Butworth Common ('UK')). The graphs above shows pools, the graph in the middle the external fluxes, and the graph bolow the internal fluxes. Number of replicas are 6 for NL_C, 6 for NL_Sodcut, 3 for UK_C, and 9 for UK_Sodcut (N = 24 in total). Leaching to groundwater was not measured in UK.

7 Effects of sand deposition and sod-cutting on N-leaching

In dune grasslands in NL, NO_x concentration in groundwater in two control plots was higher than in four sand-deposited plots (Figure 62). A high N-concentration in groundwater could be caused by a low uptake by plants or a high net N-mineralization in the topsoil. However, our dataset showed that the two control plots did not have lower plant annual productivity nor lower net N-mineralization rates. Looking at the entire dataset of Stuyfzand et al. (2019), there was no indication that dune grasslands under influence of sand deposition are associated with lower N-concentrations (Figure 63). Thus, from this small dataset of one-time measurement in summer, we cannot conclude that sand-deposited plots have lower N-leaching rates.

In heathlands in NL, NO_x concentrations were higher in two control plots than in two sod-cut plots (Figure 64). This is in line with much higher net N-mineralization in control plots. This confirms that the sod-cut plots are a N-sink, leaking almost no N to groundwater.

Using the empirical relationship and annual precipitation of 582 mm in 2018, annual recharge was calculated as approximately 214 mm for dune grasslands and 108 mm for heathlands. With these values, N-leaching rates of the six dune plots in LD were estimated to range between 0.14 and 1.57 g N/m^2/year (= 1.4-15.7 kg N/ha/y). Identically, average N-leaching rates of the control and sod-cut heathlands in GH were estimated as ca. 0.39 and 0.008 g N/m^2/year, respectively (=3.9 and 0.1 kg N/ha/y). The estimated N-leaching rates were notably lower than the level of atmospheric N-deposition in the last years (e.g. 2-3 g N/m^2/year). This indicates that both dune grasslands and heathlands function to retain N in their system by assimilating it, which limits leakage of the deposited N from atmosphere into groundwater. The capacity to retain N seems to be higher for heathlands, especially the sod-cut heathlands. Note that N-leaching in the sod-cut heathlands was for ca. half by organic bound nitrogen (DON).

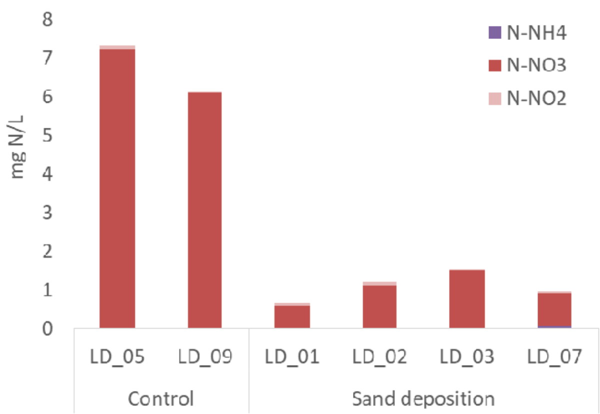


Figure 62. Concentations of **N-NH_4, N-NO_3, N-NO_2 in shallow groundwater** in adjacent to six dune plots of Luchterduinen.

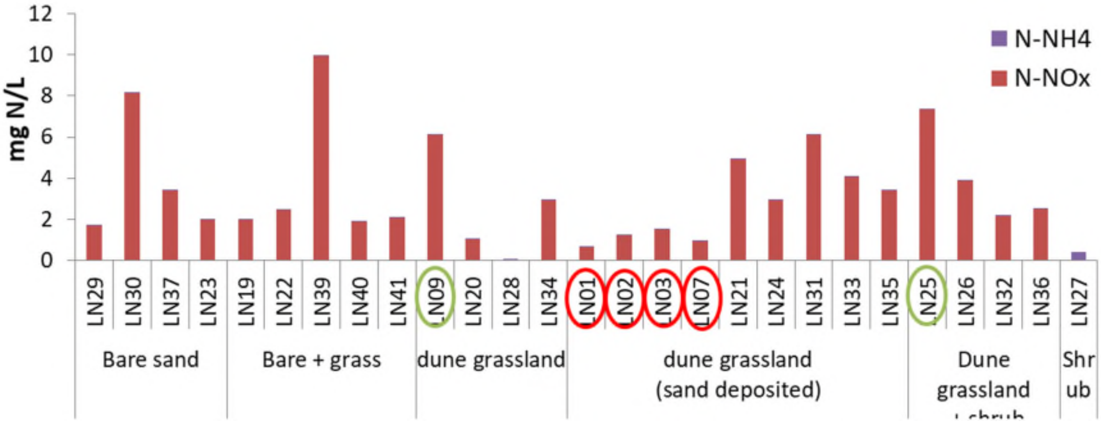


Figure 63. Concentrations of dissolved **N (N-NO$_x$ and N-NH$_4$) in shallow groundwater in Luchterduinen** (Stuyfzand et al. 2019). The samples circled are those sampled in adjacent to the plots of this study (green circle : control, red cicle: sand-deposted). The correcpondence between sample code and plot ID is as follows: LN09: LD_09, LN01: LD_01, LN02: LD_02, LN03: LD_03, LN07: LD_07, LN25: LD_05.

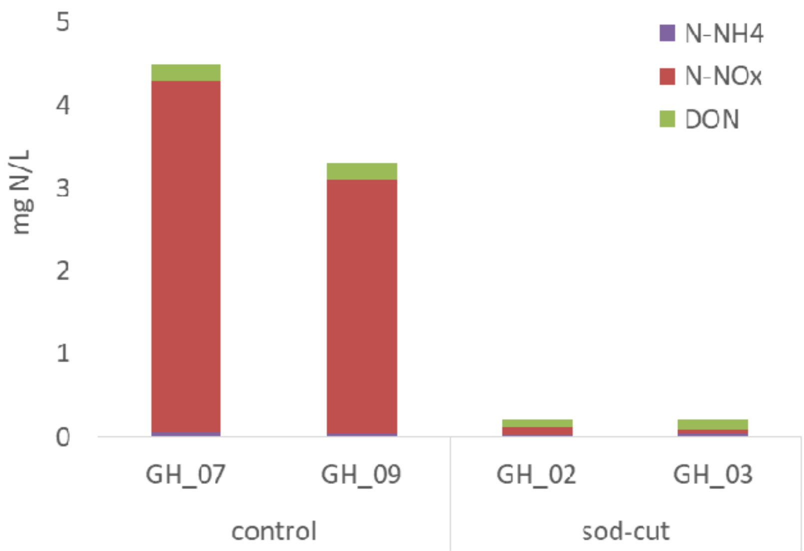


Figure 64. Concentations of **N-NH$_4$, N-NO$_x$** (i.e. N-NO$_3$ + N-NO$_2$), **dissolved organic N** (DON in **shallow groundwater** in adjacent to 4 heathland plots of Groote Heide.

8 Synthesis: effects of N-deposition, sand deposition and microclimate on dune grasslands

In this paragraph we discuss the effects of N-deposition, sand deposition and microclimate on the N-cycling and vegetation of dune grasslands. A summary of these effects is given in Table 3 and Figure 65. We primarily assumed that the two areas (NL and UK) had similar conditions except N deposition levels. However, in reality, the high N-deposition area had a high grazing pressure, relatively dry climate (more drought stress) and deeper decalcified soil (lower topsoil pH), while the low N-deposition area had a low grazing intensity, relatively wet climate (less drought stress) and less decalcified soil (higher topsoil pH). Therefore, when comparing the two areas, we also take effects of grazing pressure, climate and soil pH into account, in addition to the effects of N-deposition.

8.1 Effects of atmospheric N-deposition level on N-cycles and vegetation

N-cycle

Irrespective of the contrasting N-deposition levels, we observed similar patterns of N cycles in dry grasslands of LD in the Netherlands and NB in the UK. Both areas have comparable size of N pool in soil. This is in line with an earlier chronosequence study of dune grasslands of the same areas: speed of N accumulation was similar (or even slightly faster in UK) as succession proceeds (Aggenbach et al. 2017). Our study showed that turnover rate of C in soil was faster in UK than NL, due to the high soil pH. However, relative turnover of N compared to C (i.e. ratio of N-mineralization to C mineralization) was slower for UK than NL, resulting that N-mineralization rate per square meter was comparable between NL and UK. Another possible consequence of slow N-turnover relative to C turnover in NB might be a lower soil C:N ratio of UK.

Although accumulation of soil N and N mineralization rates are similar between NL and UK, we observed several crucial differences in the underlying processes. First, soil C turnover rate was faster in UK than NL, which can be caused by higher pH and greater proportion of microbes in UK. Because plant productivity is higher in UK (due to their relatively wetter climate) and therefore plant litter input is higher, the accumulation rate of soil C is similar between NL and UK. N turnover rate compared to C turnover rate was relatively slower in UK than NL, resulting in similar N mineralization rate between UK and NL.

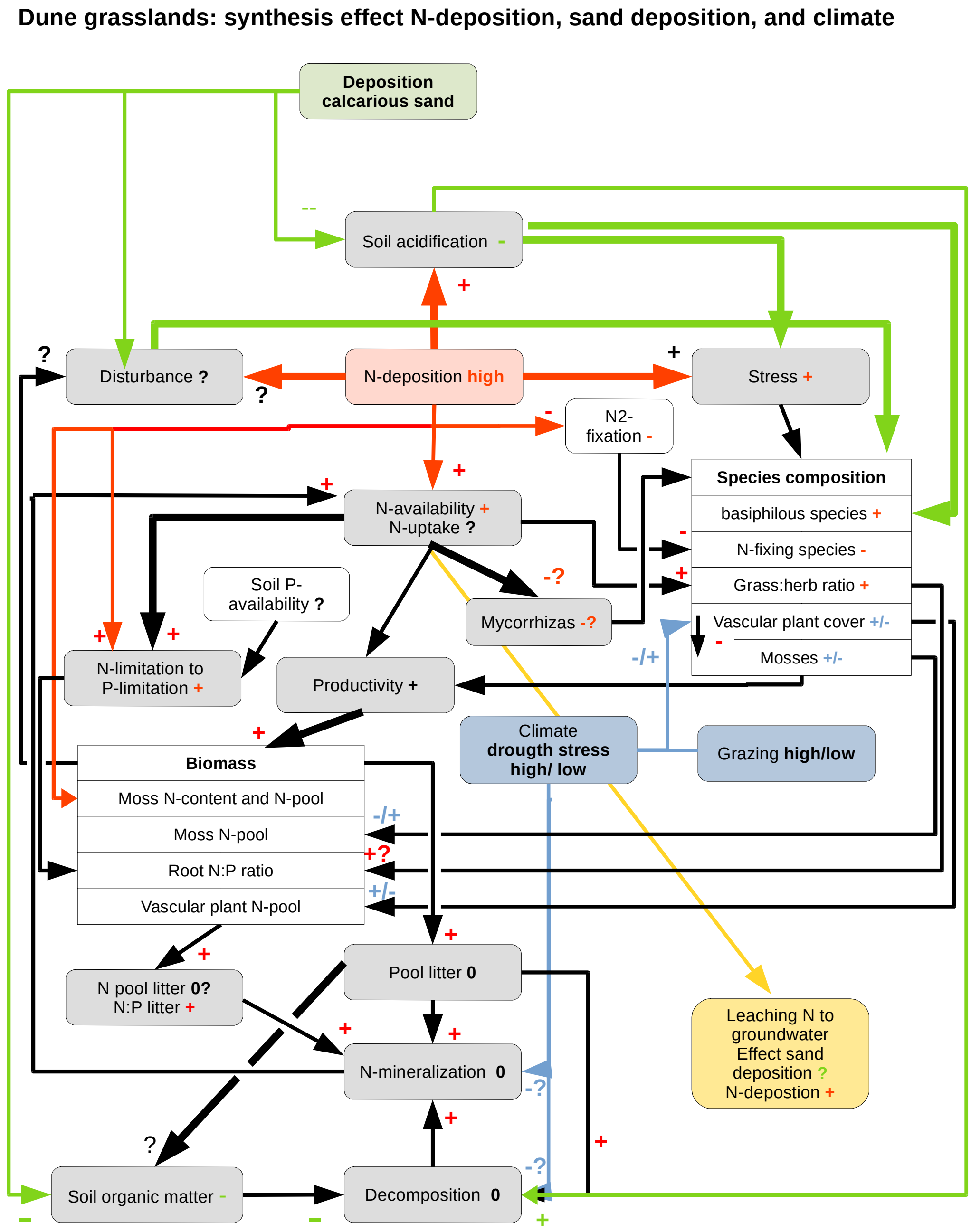


Figure 65: Scheme of impacts of sand deposition of calcarious sand, N-deposition, climate (drought stress) and grazing on **dry dune grassland**. Thick lines indicate long-term and thinn lines for short-term effects. Colors: green = effects of sand deposition on soil and vegetation; red = effects of N-deposition; blue = effects of climate and grazing; black = indirect effects. Effects: + = increase; - = decrease; -- = strong decrease; ? unknown

Table 3:Summary of the effects of N-deposition (high and low N), Management (control/ sand deposition) and microclimate (flat, north slope, south slope) on **dune grassland** in Luchterduinen (LD) and Newborough (NB). Note that high N deposition area (NL) is associated with relatively dry climate and high grazing pressure, and low N deposition area (UK) is associated with relatively wet climate and low grazing pressure. Thus, these comfounding factors also influenced the response of the dune grassland. When possible, the responsed caused by these confounding factors are specified with the following codes: Hd/Ld/Hg/Lg/Dc/Wc (see legend below); NA = not measured. Green indicates positive, and red negative effects of low N-deposition and management.

Effect	N-deposition/ climate effect/ grazing intensity		Management effects (effect of sand deposition are listed)		Slope effects	
N-deposition	High N	Low N	High N	Low N	High N	Low N
Area	NL (LD)	UK (NB)	NL (LD)	UK (NB)	NL (LD)	UK (NB)
pH	- Hd,Dca	+ Sca	++	+	NA	NA
Soil organic matter	=	=	-?	-?	=	- N
Soil C:N	=	=	-	-	NA	NA
Soil compaction	=	=	=	-	=	+? flat Hg N,S
Nutrients content above ground vas. plant biomass	(N: + Hg?) P: = K: = N/P: + Hg?	N = P = K = N/P: - Ld?	=	=	NA	NA
Nutient content root biomass	N: - Hg? P: - Hd? N/P: + Hd?	N = P: + Ld? N/P: - Ld?	=	=	NA	NA
N content moss biomass	N: + Hd N/P: + Hd	N: - Ld N/P:-Ld	=	=	NA	NA
Decompostion	-	+	+	=	NA	NA
N mineralization	=	=	=	=	NA	NA
Vascular plant cover/ productivity	- Hg,Dc	+ Lg,Wc	=	=	=	+ N
Vascular stand heigth	- Hg,Dc	+ Lg,Wc	=	=	NA	NA
Moss cover/ productivity	+ Hd?,Hg,Dc	- Ld?,Lg,Wc	=	=	++ N	+ N
Nutrient pools aboveground vascular plant biomass	NPK: - Hg,Dc	NPK + Lg,Wc	=	=	NA	NA
Nutrient pools moss biomass	+ Hd,Hg,Dc	- Ld,Lg,Wc	NA	NA	NA	NA
Nutrient pools root biomass	- Hg?,Dc	+ Lg?,Wc	NA	NA	NA	NA
Vascular plant species number, number of N-fixing species	- dD,Hg,Dc	+Hd,Lg,Wc	=	=	=	+ N,S
Number of moss+lichen species	=	=	=	=	+ S	+ S
Species composition						
- nutrients rich species	=	=	-	+	+ N	+ N
- moist species	- Dc	+ Wc	=	=	+ N	+ N
- basiphilous species	- Hd,Sca	+ Ld,Dca	+	=	=	=
- herb cover	- Hd,Hg,Dc	+ Ld,Lg,Wc	+	=	=	=
- proportion annuals	+ Dc	- Wc	=	=	=	=
- woody plant cover	=	=	=	=	=	+ N,S
- clonal spread	+ Hg	- Lg	=	=	=	=

effects	
++	strongly increase
+	increase
-	decrease
=	neutral
?	unsure

factor area	
Hd	high N-deposition
Ld	low N-deposition
Hg	high grazing intensity
Lg	low grazing intensity
Dc	relativily dry climate
Wc	relativily wet climate
Sca	shallow decalcification/ high topsoil pH
Dca	rel. deep decalcification/ low topsoil pH

factor slope	
flat	flat
N	north facing slope
S	south facing slope

Soil C mineralization and N mineralization are strongly coupled processes, and theoretically their ratio can deviate due to three factors: soil C:N ratio, microbial C:N ratio, or microbial yield efficiency (i.e. fraction of decomposed C which is assimilated, instead of respired; also known as carbon use efficiency). Using the generic kinetics of decomposition processes (Manzoni & Porporato 2009), the influence of these factors on ratio of N mineralization and C mineralization can be written as:

$$Nmin/Cmin = (NCs - e\ NCm) / (1-e)$$

Where NCs is the N:C ratio of soil substrate, NCm is the N:C ratio of microbes, and e is microbial yield efficiency. Nmin/Cmin increases with increasing soil N:C ratio, decreasing microbial N:C ratio, and increasing microbial yield efficiency (under the condition that NCs is lower than NCm, which is usually the case).

In our dataset, neither soil C:N ratio nor microbial C:N ratio did explain the pattern. However, the fact that microbes of UK immobilized much more N during incubation period (without competition with plants) indicates that microbial demand for N is higher in UK than NL, promoting higher N retention in soil. We did not identify composition of soil microbes, but higher microbial N:P ratio in NL indicates that NL soil is more dominated by fungi than bacteria, as N:P ratio of fungi tend to be higher than that of bacteria (Cleveland & Liptzin 2007). Higher dominance of fungi in NL soil may be a consequence of their low pH and high mineral N input, as shown in the experimental study of Silva-Sanchez et al (2019). Since microbial yield efficiency is generally higher for bacteria than fungi (Silva-Sanchez et al 2019), bacterial dominance in UK soil can be the mechanism to explain the relatively low N mineralization rate compared to C mineralization rate. Further research is therefore needed to clarify if and how microbial community differs between the two areas, and if they have structural difference in functioning such as yield efficiency and stoichiometry, and what their impacts are on C and N cycles of dry grasslands.

The nutrient content and stoichiometry of fresh litter input from the vegetation can affect the pattern of mineralisation. Root biomass was the largest pool of living biomass. We have no measurement to estimate how much of the roots annually flow into the soil organic matter pool as litter. A study of four grass species of hay meadows estimated that life span of roots is not much longer than 1 year (Van der Krift & Berendse 2002). This may imply that in the dune grasslands probably litter input from roots is far larger than that from aboveground vascular plant biomass in dry grasslands.

N concentrations in living roots and aboveground vascular plant biomass were not different between UK and NL. Thus, stoichiometry of plant materials are probably not the cause of lower soil C:N ratio in UK. There was however a consistent pattern in plant P concentrations: in NL, P concentrations was lower and N:P ratio was higher in roots and aboveground biomass outside exclosure. Together with higher N:P ratio in microbes of NL, these trends in CNP stoichiometry indicate that the dune ecosystem of NL is relatively more limited by P than that of UK (although the degree of P limitation is not very severe, judged from the aboveground plant N:P ratio in NL). Also the N:P ratio in moss biomass is different with higher values in NL. In NL input of litter to the soil by mosses is stronger than in UK because of a higher standing crop of moss biomass in NL. Therefore, the lower soil decomposition rate in NL might be, at least partly, due to P limitation in the soil and/or in the root and moss litter. Moreover, other root biomass properties important for decomposition rates (e.g. lignin, biogenic silicates) might be correlated with P-content and N:P ratio.

Root quality might be affected by the pattern of vascular plant species composition. In NL the cumulative cover of herbs and of woody species was much less than in UK, while the cumulative cover of grasses was for 2018 the same. Therefore the ratio of cumulative grass cover too cumulative herb+woody species cover is much higher in NL. Plant functional groups can strongly differ in nutrient stoichiometry, with legumes having lower C:N ratio's than forbs and grasses, and grasses having higher C:P ratio's then legumes and forbs (Di Palo & Fornara, 2015). These differences in vascular plant species composition might affect the biochemical properties of the root biomass, and therefore also the soil microbial community and its functioning in decomposition, mineralization, and immobilization.

The N-balance we constructed lacks the input of N by biological N_2-fixation. In temperate grasslands symbiotic N_2 fixation ranges 0.01–1.0 gN/m^2/y, and non-symbiotic N_2 fixation 0.01–2.1 g N/m^2/y (Reed et al., 2011). In UK the cover of N_2-fixing plant species was about twice as high as in NL. This means the differences of mineral N-input between UK and NL (about 1.5 to 2 g N/m^2/y) by N-deposition and N-mineralization could be smaller or even out levelled. A high mineral N-input can switch off much of the symbiotic N_2-fixation (Tang et al. 1999; Kato et al., 2007; Macduff et al., 1996; Keuter et al., 2014). Therefore at low N-deposition N_2-fixing species may have more advantage than at high N-deposition. This effect may explain why cover of N_2-fixing species is higher in UK. In NL non-N_2-fixing species can profit more from the mineral N-input. Mosses can also serve as a microhabitat for algae. In boreal regions N_2-fixation by (cyano)bacteria in the moss layer contributes significantly to input of mineral N, but here N_2-fixation is turned off at a N-deposition level of 3-4 g/m^2/y (Salamaa et al. 2019). To what extend this process is relevant for moss-rich vegetation in dune grasslands is not well known. Generally N_2-fixation is higher at higher moisture level of the mosses (Salamaa et al. 2019). However in NB, the relatively wet dune area in our study, measurements on N_2-fixation in mosses appeared to be low (data CEH/ Tom DeLuca). This may indicate that N_2-fixation in mosses is not important in temperate, dry dune grasslands.

The N-balance calculation also lacked denitrification. In general grasslands can have denitrification, and this process is enhanced by wet conditions, high NO_3 and/or NH_4 concentrations, a high soil pH and a high temperature (Cameron et al. 2013). As far we could check, there is no specific literature on denitrification rates in dry dune grasslands soils. In dune grasslands denitrification may occur during wet periods and at (temporary) anaerobic, organic-rich micro-spots in the soil. In dry ecosystems considerable losses of N form the ecosystem may occur by denitrification in the moss layer. Bähring et al. (2017) could not trace back 50 % of ^{15}N input to the moss layer in other ecosystem compartments of dry heathland. They attribute this to denitrification in the moss layer during water saturation after rain events.

N-leaching was measured only in the NL study site and ranged from 0.14 and 1.57 g N/m^2/year (= 1.4-15.7 kg N/ha/y). Because this range was below the atmospheric N-deposition of the last years (1,7-2.7 g/m^2/y) the dune grasslands accumulate a small to major part of the N-deposition. One measurement of 0.65 gN/m^2/y in a dune area in Wales with low N-deposition (Merthyr Mawr) indicates a relatively low leaching rate (Jones et al (2014). The higher range of leaching rates in NL was still high, and indicates that the system is mostly N-saturated. An older study in LD (Stuyfzand et al. 1991) during the N-deposition peak revealed high N-leaching in dune grasslands mainly consisting of mosses (3.4-4.3 g $N/m^2/y$) and lower, but variable N-leaching in dune grasslands dominated by grasses (0.03-1.7 g $N/m^2/y$). This indicates that at high N-deposition moss rich vegetation can accumulate less N than grass-dominated vegetation, and only a limited part of N-deposition. The limited N-accumulation by moss vegetation is in line with a maximum N-content of moss biomass because of saturation with N. For moss species common in dune grasslands the saturation point for N-content is at 20 gN/kg DW at a bulk N-deposition higher than 2.0 g $N/m^2/y$ (Harmsen et al. 2014). In 2019 the average N-content in moss in LD was 11.2 g N/kg DW, indicating the moss biomass is not saturated anymore, as it will have been in the '80. Although the moss tissue in LD not saturated, this does not mean it will capture the whole N-deposition flux. The high N-content is still a sign that the ecosystem is oversaturated. In UK moss N-content (scaled to the content of *Hypnum cupressiforme*) was much lower than in NL, on average 6.2 g N/kg DW, which fits to the much lower N-deposition in UK.

It should be noted that several confounding factors, which contrast between NL and UK, could play an important role in regulating processes of N in soil and plant. These factors consist of decalcification/ acidification, climate, and grazing intensity.

In NL decalcification depth and topsoil acidity were greater than in UK, which was also indicated by the lower average indicator values for acidity in NL. Because decomposition was positively related to soil pH, decomposition in the incubation experiment was higher in UK. The higher soil pH in UK is also in favour of N_2-fixing plant species, which consist mainly of basiphilous species, and therefore also in favour of more (potential) N_2-fixing. Root biomass and P-content is weakly and positively affected by soil pH. This indicates soil base status may affect the input and nutrient stoichiometry of belowground litter input.

A climate with more drought stress in NL was indicated by a stronger desiccation of the dune grassland vegetation in the dry 2018 summer. More drought stress suppresses above and below ground vascular plant productivity. The severe summer drought of 2018 led to stronger drop of the vascular plant productivity in NL than in UK. Because of a low vascular plant cover in NL light limitation for mosses was low, which favours a high moss cover and biomass. In UK drought stress was less and only evident in extreme dry years like 2018. The wetter conditions were in favour of vascular plant productivity, often resulting in a low and dense canopy. This causes stronger light limitation for mosses, and as a consequence in UK moss cover and standing crop of moss biomass were relatively low compare to NL. Better soil moisture conditions might also result in stronger decomposition.

Grazing intensity was in NL much higher due to overpopulation with fallow dear. Here the strong grazing pressure was indicated by poor recovery of vascular plant standing crop, grass cover and root biomass in 2019 after the extreme dry 2018 summer. The stronger grazing pressure strongly limited the cover and standing crop of vascular plants and thus favours moss productivity and biomass.

The drier climate and higher grazing pressure in NL worked both in favour of high cover and standing crop of mosses and a low aboveground standing crop of vascular plant and relatively low root biomass. In combination with a relatively high N-content of moss biomass due the high N-deposition, most N in aboveground biomass was stored in mosses, and the moss N-pool had a relative high proportion in total N-pool in plant biomass. In contrast, in UK moss cover and biomass are lower and above and below ground vascular plant biomass were higher. Therefore, and because the moss N-content was low due to a low N-deposition, N-pool in mosses was lower than the aboveground vascular plant N-pool, and was a small fraction of the total biomass N-pool. Therefore in NL mosses should be more important for the ecosystem N-fluxes by uptake of N-deposition and N-mineralization than in UK. Yet the contribution of the decomposing moss biomass to N-mineralization is unknown, because the thin dead moss litter horizon was not included in the soil samples for the incubation experiment. In the case during wet periods strong denitrification occurs in the N-rich moss layer (see above) the large moss biomass in NL might be important for N-losses to the atmosphere.

We conclude that there are striking differences in the N-balance and N-fluxes between the high N and low N dune areas. Differences in soil acidity affect the pattern of decomposition (i.e faster decomposition rate in the base rich, low N-area). Nevertheless, due to relatively faster N-mineralization rate compared to C mineralization rate in the high N-area, N-turnover per m^2 is similar for both areas. Differences in microbial community and stoichiometry of nutrients (in particular N:P in soil microbes, roots and mosses), and other unknown parameters which influence quality of decomposed substrates may play a role in regulating N-mineralization and immobilisation. Furthermore, a high N-deposition, together with a stronger soil acidity and a higher grazing pressure leads to many directional changes in plant community composition, such as increased ratio of grasses compared to herbs. Such changes in species composition might influence the structure of the microbial community and quality of plant litter. Besides the vascular plant biomass, the moss layer is in the drier and strongly grazed high N-area more important in the N-cycling than in the low N-area, while in the wetter, extensively grazed low N-area vascular plant biomass is dominant in the N-cycling.

Vegetation

In the high N-area, LD, the vegetation does not indicate a higher nutrient level than in the low N-area. Higher N-deposition is thus not reflected in the cover weighted average of the nutrient indicator values. In aboveground vascular biomass N, P, K content, and ratios of these nutrients were hardly different for both areas, and indicating N-limitation. A higher N-content and N:P ratio was only present in control plots of NL outside the exclosures. Because this pattern was absent for the biomass in the exclosures, we attribute the elevated values to an effect of extreme grazing in NL during 2019. In contrast, effects of high N-deposition caused an elevated N-content and N:P-ratio in the moss biomass. For root biomass P-content was lower and N:P-ratio higher in NL. Because N-content was not different it is unsure if the N-deposition level had no direct effect on root nutrient stoichiometry. Unknown is whether P-availability in the soil in involved (higher in UK), which is possibly related to the soil base status (higher pH and more calcium carbonate in UK) or there is an effect of vascular plant species composition (see below).

In NL the dune grassland was more acidic due to the deeper decalcification and stronger acidification of the topsoil. This was reflected in a higher cover of acidiphilous moss species and plant species like *Teucrium scorodonia* and *Aira praecox*. In NL cumulative cover of herbs was lower than NB and cumulative grass cover was not different between the areas in 2018. As a consequence the ratio of grasses cover too herb cover was higher in NL, and might be a (combined) effect of higher N-deposition, stronger acidification, and higher grazing pressure in NL. A high N-load enhances grass encroachment in dune grasslands (Kooijman et al. 2017). In old dune grasslands in LD herb cover is higher in calcareous grasslands than in acidic grasslands (Aggenbach et al. 2013). Comparison of the vegetation outside and inside the exclosures of LD for 2019 reveals a higher herb cover in the non-grazed exclosures. (Aggenbach et al. 2020). In LD the high grazing pressure of fallow deer has caused a strong suppression of herbs, because fallow deer strongly graze on non-grassy and non-woody plants (herbs) (Mourik 2015). Probably the drier climate in LD is not in favour of more grass cover. For LD grass cover showed a delayed effect of the summer drought in 2018 (Aggenbach et al. 2020). Outside the exclosures grass cover was very low, which was probably a combined effect of dying off in 2018 and strong grazing preventing recovery. Inside the exclosures grass cover was in 2019 lower than in 2018 which also indicated a delayed effect of drought stress on grass cover. In conclusion in UK the wetter climate, higher soil pH, lower grazing intensity, and low N-deposition work in favour of herbs. In NL the drier climate, lower soil pH and higher grazing pressure suppresses herbs and high N-deposition is in favour of grasses.

NL and UK have a strong floristic difference between the regions: of total 111 species recorded in the flat plots, only 23 species occurred in both NL and UK plots. The question is then if this large difference affects ecosystem functioning. Major part of the plant and moss species which have a high cover, occur in both areas and are mostly common species in these areas. This implies nutrient and carbon cycling is only to a low extend influences by differences in regional species pools. In NL *Agrostis capillaris+vinealis, Carex arenaria, Calamagrostis epigejos* and *Festuca filiformis* contribute most to plant cover, while in UK most important species are *Festuca rubra, Galium verum, Hieracium pilosella, Hypochaeris radicata, Rubus caesius, Salix repens* and *Thymus praecox*. These differences in vascular plant species composition might affect the biochemical properties of the root biomass, and therefore also the soil microbial community and its functioning in decomposition, mineralization, and immobilization. The only species with high cover which is only present in one area is *Thymus praecox* in UK. Notwithstanding, the poor overlap in species pools and also the outcomes of multivariate analyses reflect strong floristic differences in dune grassland vegetation between the two areas. On plot scale topsoil pH is an important factor for species composition with lower topsoil pH in NL due to stronger decalcification. Species like *Galium verum, Hieracium pilosella Rubus caesius* and *Thymus praecox* which were abundant in the UK plots also grow in calcareous Dutch dune grasslands. This indicates differences in decalcification depth and topsoil pH are important for the species composition if the vegetation.

Also species richness of vascular plants and N_2-fixing species was lower in LD. The lower presence of N_2-fixing species can be partly attributed to a lower soil pH, because most N-fixing plant species prefer base rich conditions. Also the higher input of mineral N by deposition will decrease the beneficial effect of symbiotic N_2-fixation for plants (see above).

Tall, grasslike species favoured by a high N-deposition (*Carex arenaria, Calamagrostis epigejos* (Van den Berg et al. 2005; Kooijman et al. 2017) had a higher cover and/or frequency in LD. The same was true for *Campylopus introflexus,* which is promoted by high N-deposition (Sparrius & Kooijman 2011). *Ammophila arenaria*, which is enhanced by high N-deposition in acidic dune grasslands (Kooijman et al. 2017), is more abundant in NB than in LD, but cover is still low (1-5 %) compare to acidic dune grasslands with strong *Ammophilla* encroachment in the '90. In LD the moss layer had a high cover. *Pseudoscleropodium purum* had a higher cover in LD, while in NB *Rhytidiadelphus triquetrus* was only occurring in NB and *Hylocomium splendens* had a higher cover and frequency in NB. It is not clear if this pattern is related to differences in N-deposition, or a wetter climate or soil pH. In the Middel- and Oostduinen (in NL) an increase of *Pseudoscleropodium purum* in dune grassland was correlated with an increase of the local N-deposition (data KWR/ Evides; Hensen et al. 2018). In Luchterduinen this species increased since the '90 (pers. com, M. van Til) while N-deposition decreased. These trends may indicate the species reacts on an increase of precipitation. *Rhytidiadelphus triquetrus* and *Hylocomium splendens* occur in Luchterduinen where they have a preference for north slopes (Van Til & Mourik 1999).

In summery N-deposition might affect the species composition, with higher cover of several tall grass species, a lower cover of herb species and lower cover of N_2-fixing plant species in the high N-area. A stronger acidification of the topsoil and a higher grazing pressure in LD by fallow deer enhances grasses and suppress herbs. The effect of a high N-load on the species composition of the moss layer is unsure, but may have a strong effect because a large part of the N-deposition is transferred by the moss layer to the soil-root compartment. A slightly drier climate and stronger grazing pressure in the high N-area strongly favours moss production above vascular plant production and standing crop. A lower soil acidity, wetter climate and lower grazing pressure are in favour of higher vascular plant species numbers in the low N-area.

8.2 Effects of sand deposition on N-cycles and vegetation

Effect on N-cycling

Although sand deposition did not have a clear effect on the content of soil organic matter, organic C, and organic N (yet with a tendency of sand-deposited plots having less organic matter content in the 0-5 cm topsoil), it had a significant (but small) effect on soil organic matter turnover. Namely, sand-deposited sites had a slightly faster C turnover rate (i.e. higher respiration rate per soil total C). As the C turnover rate was strongly correlated with topsoil pH, it was indicated that sand deposition influence C turnover via modulating the soil acidity. The higher C turnover rate of sand-deposited plots in the topsoil, however, did not lead to higher N mineralization rate, because ratio of N mineralization over C mineralization was slightly (though not significantly) lower in sand-deposited plots. In this study we did not measure soil properties and mineralisation rates in the soil layer at 5 to 10 cm depth. This has implications for interpreting e.g. total soil C or total soil N. If sand is deposited on top, it effectively moves the existing soil layers lower in the profile, but they are mostly still there and can add to decomposition and N-mineralisation. When sand deposition is low and the sand mix with the humus rich topsoil the sand burial effect can be of less importance.

There was little effect of sand deposition on N, P, K concentrations and ratio's in above-belowground vascular plant biomass. However input of calcareous sand may (weakly) affect the P availability, which is indicated by a higher P-content in root biomass with higher soil pH. Sand deposition can counteract the negative acidification effect of atmospheric N-deposition: it increases soil pH, especially in the Dutch dune area LD which was stronger acidified and had been exposed for decades to a high acidifying deposition level.

Effect on vegetation

In LD, plots with sand deposition had a high cover of species adapted to base-rich conditions (such as *Hypnum cupressiforme var. lacunosum*), while the control plots had a moss layer with a high proportion of acidiphilous moss species (e.g. *Dicranum scoparium* and *Hypnum jutlandicum*). The effect on soil pH was not reflected in the cover weighted average indicator values for acidity, but this can be regarded as an artefact, because for this trait no distinction is made for *H. jutlandicum* and *H. cupressiforme var. lacunosum*. The later 'species' has no Ellenberg indicator value for acidity. In LD sand deposition had no clear effect on species number of vascular plants and mosses, but it had a noticeable effect on species composition. In NB the effect of sand deposition on soil pH is limited or absent because the topsoil is buffered by calcite. Therefore the effect on species composition is limited and has no effect on average indicator values for acidity. In the moss layer *Homalothecium lutescens* is promoted by sand deposition. Although there are effects of sand deposition on vegetation, there is large overlap in species composition between plots with and without sand deposition. A reason for this is that the intensity of sand deposition was relatively low and started in an existing old fixed dune grassland. Therefore a large overlap in soil conditions between control and sand-deposited plots exists. In both areas sand deposition has no effect on cover and species number of functional plant groups, and limited effect on cover weighted averaged species traits. In plots with sand deposition the relative abundance of species with a higher canopy height is larger.

Conclusion

With this study is proven that sand deposition works out positively under the current N deposition level in NL. The beneficial effect of deposition of calcareous sand does have a clear positive effect on restoring a higher base status of the topsoil and promotes basiphilous dune grasslands species. Therefore promoting sand deposition with small scale aeolian activity (blowouts) is an effective measure for restoring calcareous dune grasslands and also its fauna (Aggenbach et al. 2018). However this mitigating measure for the adverse effects of high N-deposition does not work for lowering the N-cycling in the ecosystem, but on the other hand there was no prove for increase N availability by accelerating N turnover rate neither. In a longer term, N_2-fixing species may increase and plant and microbial composition may change, but as seen in little difference between NL and UK in net N-mineralization (in gN/m^2), we do not expect much changes in N-accumulation and N-mineralization. If N-deposition increases again, then sand deposition cannot mitigate the increased N-availability and therefore nitrate leaching to the groundwater will probably increase. If then grass encroachment occurs depends on the grazing pressure: with low grazing tall grasses will increase and with strong grazing these grasses will be suppressed. If N deposition decreases, soil pH does not improve immediately, so the need of sand deposition for improving soil base status remains. Moreover this measure is also necessary to preserve calcareous grasslands which suffer from strong acidification of the topsoil during the high sulphur deposition peak in the 20th century.

8.3 Effects of microclimate on soil and vegetation

In the NL and UK dune area we look at the effect of north and south slopes in order to gain insight in the effect of microclimate on soil and vegetation. South slopes have more solar radiation and also (at least for the SW exposed part) more rain because the most intense rain showers occur with southwest winds. North facing slopes have less solar radiation and rain. Plots located on slopes are expected to have contrasting water availability due to their difference in soil development: soils on north slopes develop more organic matter and therefore better soil moisture retention properties. In contrast, south slopes may have a less developed soil and therefore retain less rain water in the topsoil, have less vascular plant biomass, having less evapotranspiration than north slopes. Because north slopes soils retains rain water better in the topsoil, evapotranspiration is here larger and groundwater recharge less (Voortman et al. 2016). With these assumptions, our intention was to project the effects of slopes to the effects of changing climate, with south slope representing hotter and drier conditions (and therefore resembling future climatic conditions).

Slopes and exposition had an effect on soil conditions and vegetation. Soil organic matter content and peak standing crop (i.e. plant biomass outside exclosure) was higher on north slopes, especially in UK. In both areas, vegetation tended to indicate wetter and more nutrient rich conditions at north slopes than at south slopes and flat areas. North slopes had in both areas more moss cover with dominance of *Pseudoscleropodium purum*, which might indicate wetter microclimatic conditions. In NL north slopes also had in 2018 (before the effects summer drought on vegetation worked out completely) a higher grass cover by a high cover of *Agrostis capillaris+vinialis* and a lower herb cover.

Our results showed, however, that the difference between slopes in the dry grasslands reflect not only microclimate but also grazing effects. These patterns can be explained by the differences in grazing pressure and types of grazers. In UK grazing pressure is lower than in NL, and here the cows and ponies avoid steep dune slopes, while flat parts are grazed more intensely, also by rabbits. The soil of slopes is less trampled and plant biomass is less grazed, and therefore have more woody cover and more vascular plant species. Probably the combination of a low grazing pressure and the steep dune slopes in UK (steeper than in LD) are important factors in avoidance of the slopes by grazers. The NL dune area is strongly grazed by a large the fallow deer population. Here flat areas as well slopes were strongly grazed. An indication for a strong grazing pressure in LD was the very low vascular plant standing crop in 2019 when drought stress was limited, while in this year the productivity measured in the exclosure was higher than in 2019.

8.4 Effect of severe drought

The summer of 2018 was extremely dry because of low precipitation and high temperatures. Calculation of actual transpiration indicated for NL an extreme long period with drought stress of more than two months. Therefore drought stress affected strongly the vegetation. The effects in vegetation structure and species composition were partly different for the two areas. The drought supressed the aboveground vascular plant productivity only in NL, indicating that drought stress was here stronger than in UK. In both areas root biomass and root:shoot ratio's were in 2018 much lower than in 2019. This might be caused by root mortality already occurred quickly in the dry summer. It also points to a high dynamics in belowground biomass. In NL the drought also had a delayed effect on grass cover which became low in 2019, probably due to strong die off. Such an effect was absent in UK and here grass cover increased after the drought. Both areas had a recovery of herb cover. During the 2018 drought moss cover stayed high and in NL it increased afterwards. In NL aboveground vascular plant biomass dropped to very low values in 2019, despite a recovery of productivity in the exclosures. This was probably an effect of an increase of the grazing pressure of fallow dears to a very high level. After the severe drought in the 2018 summer there was not much biomass left in the autumn and winter. As a consequence the grazing pressure became extreme and prevented the recovery vascular plant cover and standing crop (Aggenbach et al. 2020). The strong difference between 2018 and 2019 for the number of vascular plant species in NB indicates that the 2018 drought temporarily excludes the presence of species. Such an effect was absent in LD, where in normal meteorological years substantial drought stress regularly occurs, and therefore the flora consists of plant species which adapt to the climatic conditions. Here the stronger drought stress promotes a higher proportion of species with a short (annual) shoot life span. These species survive strong drought stress in the seedbank (lower presence in 2018) and can complete their life cycle in wetter years (higher presence in 2019).

We conclude the strong fluctuations in meteorological conditions affects to far extend the water availability for the vegetation and caused fast changes in below and aboveground vascular biomass pools, cover of plant functional groups and presence of annuals. Partly these effects differ due to differences in climate. In NL interaction of the severe 2018 drought and a high grazing pressure prevented the recovery of aboveground vascular plant biomass in the year after.

9 Synthesis: effects of N-deposition level and sod-cutting on heathlands

In this paragraph we discuss the effects of N-deposition and sod cutting on the N-cycling and vegetation of dry heathlands. In Table 4 and Figure 66 a summary of these effects is given. The high N-deposition area had a relatively dry climate (more drought stress), while the low N-deposition area had a relatively wet climate (less drought stress). Therefore for differences between the two areas we also evaluated effects of climate in addition to the effects of N-load.

Table 4: Summary of the **effects of sod cutting of heahtlands** with high N-deposition (Groote Heide (GH) in NL) and low N-deposition (Little Budworth Common (LB) in UK.

Effect	**N-deposition/ climate effect**		**Management effects (effect of sod cutting are listed)**	
N-deposition	**rel. High N**	**rel. Low N**	**rel. High N**	**rel. Low N**
Area	**NL (GH)**	**UK (LB)**	**NL (GH)**	**UK (LB)**
pH	- Hd	- Hd	+	+
Soil organic matter, C, N pool	++ Hd	++ Hd	--	--
N accumulation	+ Hd	+ Hd	**++ Hd**	**++Hd**
Soil C:N	?	?	++	+
N mineralization	+ Hd	+ Hd	--	--
P mineralization	- Lm?	+ Hm?	-	--
Vascular plant standing crop	? Hd	++ HdWc	=	-
Moss cover	-? Dc	+ Wc	=	=
Vascular plant species number	=	=	=	=
Number of moss+lichen species	=	=	=	=
Species composition				
- nutrients rich species	=	=	=	=
- moist species	- Dc	+ Wc	=	=
- basiphilous species	=	=	=	=
- dominant moss species	**Hypjut**	**Hypjut + Plesch**	**Campint**	**Hypjut**

effects	
++	strongly increase
+	increase
-	decrease
=	neutral
?	unsure

factor area	
Hd	high N-deposition
Ld	low N-deposition
Dc	relativily dry climate
Wc	relativily wet climate
Hm	rich in easily weatherable minerals
Lm	poor in easily weatherable minerals

moss species	
Hypjut	Hypnum jutlandicum
Plesch	Pleurozium schreberi
Camint	Campylopus introflexus

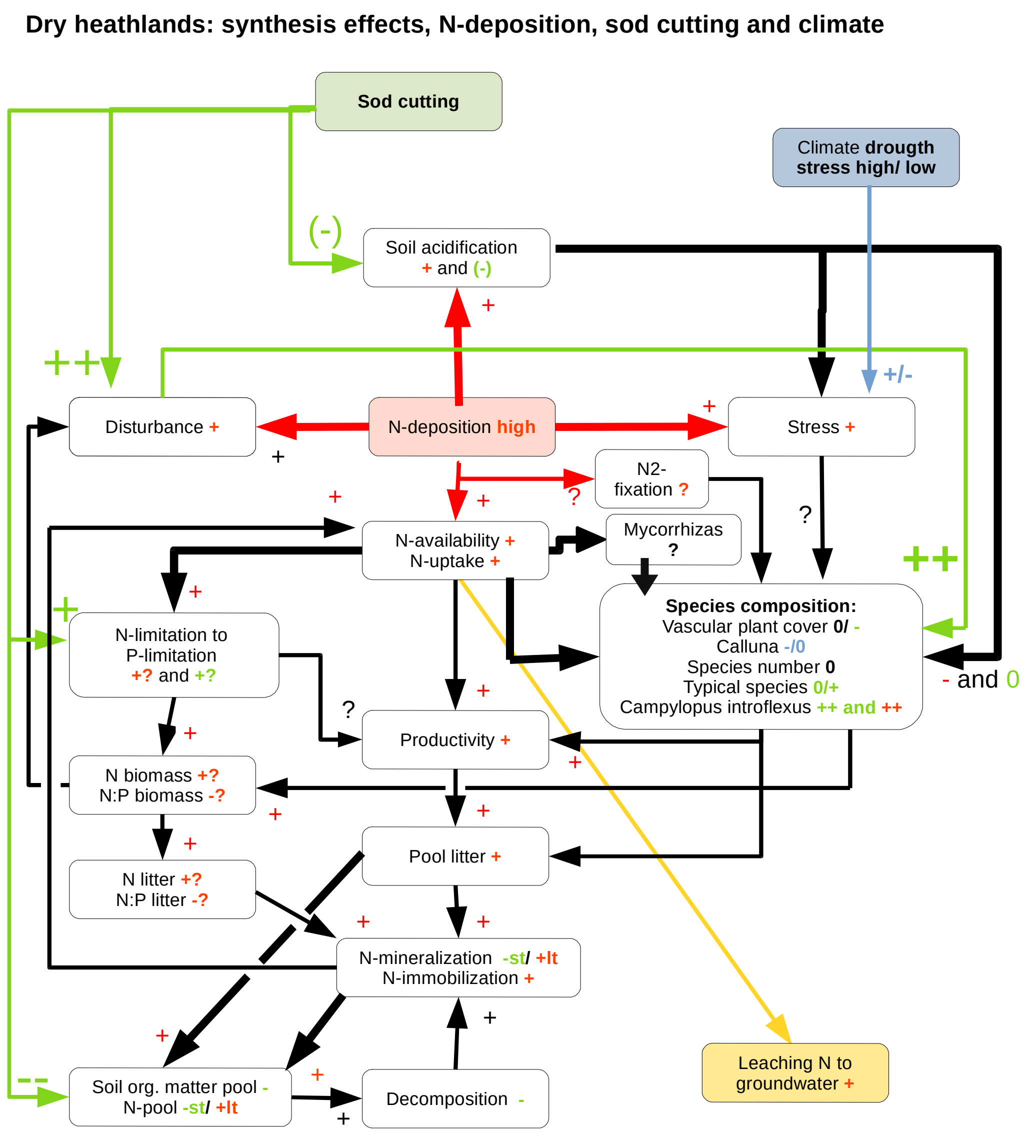


Figure 66: Scheme of impacts of s**od cutting N-deposition and climate** (drought stress) on d**ry heathlands**. Thick lines indicate long-term and thinn lines for short-term effects. Colors: green = effects of sand deposition on soil and vegetation; red = effects of N-deposition; blue = effects of climate and grazing; black = indirect effects. Effects: + = increase; ++ = strong increase; - = decrease; -- = strong decrease; ? unknown; st = short-term, lt = long-term.

9.1 Effects of atmospheric N-deposition level on N-cycles and vegetation

Effect of N-deposition on nutrient cycling

Recent bulk N-deposition levels were similar for both the NL and UK heathland areas, while during the 1970s to '90s N-deposition was higher in NL, implying a much higher cumulative N-load during the last 40 years. Another relevant difference is a strong increase of the ratio of NH_y/NO_x in the deposition in UK. While this ratio was in the '70s similar for both areas, it increased in the UK strongly between 1990 and 2010 due to a strong increase of NH_y and decrease of NO_x deposition. In NL the ratio of NH_y/NO_x remained stable. Although the area Little Budworth Common in UK was selected as a lowN site, this turned out to be not the case in respect to the recent total N-deposition and for heathlands disadvantageous high NH_y/NO_x ratio. However, this area can be considered a relatively lowN-area with respect to the cumulative N-deposition during the last 40 years.

The variation of soil parameters of the heathland plots is mainly depicted by a cluster of variables correlated with organic matter content of the topsoil, and to a minor extend to soil pH gradient. Soil N, soil C, NH_4 and bulk density are strongly correlated with soil organic matter. Soil pH is less correlated with this cluster. Control plots and sod-cut plots are clearly separated on the soil organic matter content, whereas the overlap between UK and NL sites is large. This means that, irrespective of the different cumulative N-deposition, NL and UK have common soil conditions, and the effects of sod-cutting on heathland soils are similar between NL and UK. A lower standing crop in control and sod cut plots in NL compared to UK was partly caused by a low productivity in the dry summer of 2018. This led even to dying of *Calluna vulgaris* shrubs and a very low productivity of *Molinia caerulea*. Another factor for a higher standing crop in UK might be a generally better soil water availability in UK because of a slightly wetter climate. The control plots in UK, which have the highest standing crop, may also have extra soil water availability due to a high soil organic matter content of the subsoil (higher than control plots in NL).

N-mineralization did not differ between NL and UK. Control plots had net N-mineralization. Leaching to the groundwater in the NL control plots was 0.39 g $N/m^2/y$ which is a small part of the total N-deposition (ca. 2.4 g $N/m^2/y$). This implies major part is of the N-input is retained or leaves the heathland system as N_2 because of denitrification. We conclude that dry heathland ecosystems can accumulate major part of the N-deposition at high atmospheric N-input. These findings fit with other studies in heathlands (Berendse 1990; Bobbink et al. 2010). In other studies on N-leaching dry heathlands in the Netherlands Fujita et al. (2018) measured a leaching rate of 0.1 $gN/m^2/y$ at N-deposition of 1.3-2.4 $gN/m^2/y$, and Beier et al. (2009) a higher leaching rate of 2.45 $gN/m^2/y$ at N-deposition of 4.1 $gN/m^2/y$. When comparing with our measurements in the Groote Heide we can conclude that N-leaching in old heathlands is low when N-deposition is not extremely high, but is much higher at levels which occurred during the N-deposition peak. Bobbink & Hettelingh (2000) concluded from a review that there is a threshold for N-accumulation above which net N-mineralisation occurs.

The N-leaching in the Dutch study site consisted for about 50% of DON. This is also in line with measurements of Fujita et al. (2018) were the N in the leachate and soil pore water under the soil was dominated by DON (89 - 99%). Obviously the podzol soils release organic particles to the pore water. In the meantime leaching of nitrate is very limited because of the very low soil pH nitrification of ammonium is strongly inhibited. Leaching of ammonium is low because of strong immobilisation and this ion is adsorbed easily at the cation adsorption complex.

Although dry heathlands have a very strong retention of the N-input, even at relatively high N-deposition levels, this not necessarily means they always have a low N-retention and N-leaching. In a recent field study soil porewater measurements indicated that during and shortly after the drought of 2018 much NH4 is released from the soil. This effect was also reproduced in a mesocosms experiment with a drought period of 5 months (Bobbink et al. 2019). For our Dutch study site, Groote Heide, at the beginning of the drought period extractible NH4 and NO3 concentrations in the topsoil were much higher (average values resp. 11.5 and 2.5 mgN/ kg DW) than similar measurements carried out in an old heathland at the Veluwe in the less dry year2017 by Fujita et al. (2018) (resp. 1.7 and 0.2 mgN/ kg DW). This may indicate that at the beginning of the drought period already considerable mobilization started. It is unclear by which processes a severe drought event causes release of mineral N. A possible explanation is mobilization of N stored in microbial and root biomass which dies off. Because of drought stress also uptake of mineral N by microbes and roots will stop. This drought effect on N-cycling indicates that dry heathlands, which immobilize for a long period the high atmospheric N-input, can act as a 'N-bomb' when the ecosystem has a strong disturbance. Also disturbance by heather beetles can enhance N-leaching to the subsoil (Nielsen et al. 2000).

Effect on vegetation

The dry heathlands were species poor. Species number of vascular plants and mosses+lichens did not differ between UK, neither did average indicator values for nutrient level and acidity. Generally sod cut plots had after 12 to 20 year a high cover of *Calluna vulgaris*, forming high plants with in between open patches with moss lawns. In NL *Molinia cearulea* had high cover in some of the control plots. In the moss layer there were major differences for dominant species. In the NL *Hypnum jutlandicum* was the dominant species in the control plots, and *Campylopus introflexus* in the sod cut sites. In UK *H. jutlandicum* and *Pleurozium schreberi* were codominant in the control and sod cut plots. *M. caerulea* and *C. introflexus* can get a high cover in dry heathlands at high N-deposition levels and high NH_y/NO_x ratios (Bobbink et al. 2010; Sparrius & Kooijman 2014). Because the N-deposition was not very different between sites and the NH_y/NO_x ratio was higher in UK, this a remarkable result. In the UK area both species occurred only with a low frequency and always with a very low cover (<1%) despite the current high N-deposition. An explanation for low presence of *Molinia* in the old control stands in UK could be that the species only has comparative advantage on *Calluna* in early successional stages of heathlands (Heil and Bruggink 1987, Aerts et al. 1990). An increase of *Molinia* in an existing *Calluna* stand can only occur after a disturbance (like heather beetle invasion, frost injury or severe drought stress) which opens the shrub canopy (Bobbink et al. 2010). This explanation holds not true for the sod cut sites which were exposed to a high N-load when succession started. Possibly there is an interaction effect of climate and N-deposition because plants exposed to a high N-load have a higher shoot:root ratio and therefore more susceptible for drought stress (Wang et al. 2018). Possibly such an interaction effect depends on the plant species. *Calluna* is more sensitive for drought stress when exposed to high N-deposition (Meyer-Grunefeldt et al. 2016; Southon et al. 2012). During the extreme dry summer of 2018 drought stress was stronger in NL and here the *Calluna* stand died off for a major part. In UK only very little dying off was noticed.

9.2 Effects of sod cutting

Effects on nutrient cycling

We investigated soil and vegetation in sod cuts plots of 12 to 20 years old. Sod-cutting of heathland soils had similar effects on soil conditions for NL and UK. It had clear effects in reducing soil organic matter soil, N-pool, NH_4, NO_3, DON and PO_4. Soil pH increased slightly, which was opposite to the expectation.

N-mineralization rate did not differ between NL and UK and was much lower in sod cut plots than in control plots. After sod cutting hardly any net N-mineralization occurs, implying that most of the mineralized N is immobilized. N-leaching from the sod cut plots in NL was also very low (0.008 g N/m^2/y), and indicates that nearly all N-deposition (ca. 2.4 g N/m^2/y) was accumulated in the soil and plant biomass. When we compared the N-pool in the topsoil layer (0-5 cm; for NL and UK resp. 62 and 80 gN/m^2) with the cumulative deposition after sod cutting, on average 31 gN/m^2 (=310 kgN/ha) of the N-pool did not originate from the N-deposition in both areas. This pool was either already there just after sod cutting, is caused by a too low estimate of the N-deposition (by modeling), or consist of the contribution of non-symbiotic N_2-fixation. We conclude that sod-cut dry heathland ecosystems can accumulate major part of the N-deposition at high atmospheric N-input, and that sod cutting increases the retention capacity. The strong retention is caused by a low nitrification of ammonia because of a low soil pH and a strong ammonium immobilization in the soil (Dorland et al. 2003). This prevents leaching of nitrate (Bobbink et al. 2010). However the increased N-availability stimulates biomass and most of the N-input will accumulate in the litter horizon. This will cause over time an increase of the N-mineralization (Berendse 1990). The control plots in the old heathland had a thick litter layer and net N-mineralization. Sod cutting also effects the P cycling by lowering the net P mineralization.

We conclude sod cutting decreases the net N-mineralization temporarily, but it does not prevent strong N-accumulation due to high N-deposition.

Effects on vegetation
Sod cutting led a lower standing crop of vascular plants in NL, but not in UK. The higher standing crop in UK in sod cut plots is attributed to a wetter climate. In both areas the vascular stands were dominated by *C. vulgaris*. Sod cutting did not increase species number of vascular plants and mosses+lichens. In UK *Juncus squarrosus* and the moss *Ptilidium ciliare* were present with low cover and frequency in the sod cut plots. These typical heathland species did not occur in control plots. The moss layer responded very different to sod cutting for both areas: in NL *Campylopus introflexus* became the dominant species while in UK *Hypnum jutlandicum* and *Pleurozium schreberi* became (co)dominant. *C. introflexus* is enhanced in cover by a high N-deposition, while the other two mosses species can be dominant at low N-deposition. *C. introflexus* start to dominate at high ammonia concentrations of the air corresponding with a N-deposition of 3.0 gN/m^2/y (Sparrius & Kooijman 2011) which is close to the average N-deposition of last 20 years (2.8 gN/m^2/y in NL). Because both areas had similar N-deposition levels (2.8 and 2.6 gN/m^2/y for respectively NL and UK)) during the last 20 years and sod cutting was done 12 to 20 years ago, the difference in dominant moss species is striking. Unclear is if this is caused by differences in climate (UK wetter) or in nutrient stoichiometry. *Pleurozium schreberi* and *Hypnum jutlandicum* have preference for dry conditions, and *Campylopus introflexus* can grow on even more dry soils (Siebel 1995). So differences in moisture conditions could explain the pattern. However *H.*

jutlandicum was also dominant in the control plots of NL. Moss vegetation dominated by *C. introflexus* are P limited (Sparrius 2011), so the species can cope very well in a N-rich and P-poor environment, which is present at sod cut plots in NL. Establishment of the species is enhanced by soil disturbance and a relatively high organic matter content (soil C > 0.75 % DW) of the topsoil (Sparrius & Kooijman 2011). Because after sod cutting some organic rich substrate is left, initial organic matter content of the new topsoil could have been easily above mentioned C-content value. In the NL area sod cutting of a P-poor podzol soil and a high N-deposition provided all conditions for successful invasion by *C. introflexus*. Possibly a better availability of P in UK prevented dominance of *C. introflexus*. However, unknown is if species *Pleurozium schreberi* and *Hypnum jutlandicum* can compete better because of relatively high P availability or better moisture conditions.

The slight increase of soil pH by sod cutting was in line with our hypothesis, but was not reflected by a higher in average indicator values for acidity than control plots. The topsoil pH of the sod cut plots was still low (average pH_H2O 4.1 and 4.2 for NL and UK). A relatively high soil pH and base status is an important factor for the occurrence of several typical heathland species (Bobbink et al. 2010). Except for *Juncus squarrosus,* no other heathland species with a preference for a better soil base status were recorded.

We conclude that the effects of sod cutting in areas with high N-deposition, as in the NL area, do not contribute to a better quality of the dry heathland habitat. In contrast, sod cutting had a negative effect by causing dominance of the invasive exotic moss species *C. introflexus.* In the UK area small positive effects of sod cutting on vegetation were observed as some typical heathland species were enhanced. Strong acidification of the heathland soils, which was enhanced by acidifying N- and S deposition in the past, limits the recovery of typical dry heathland plant species.

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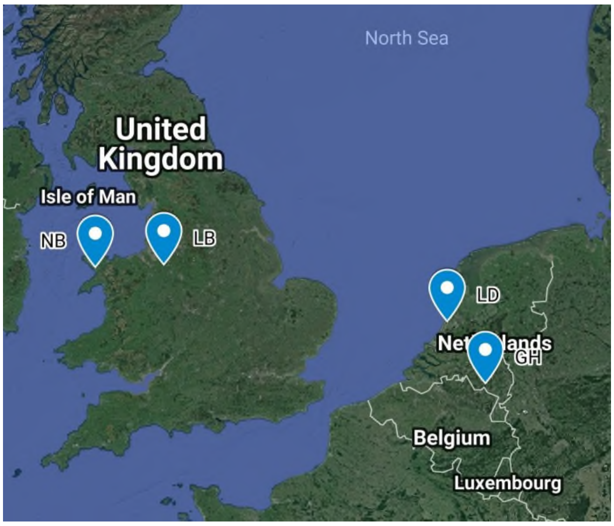
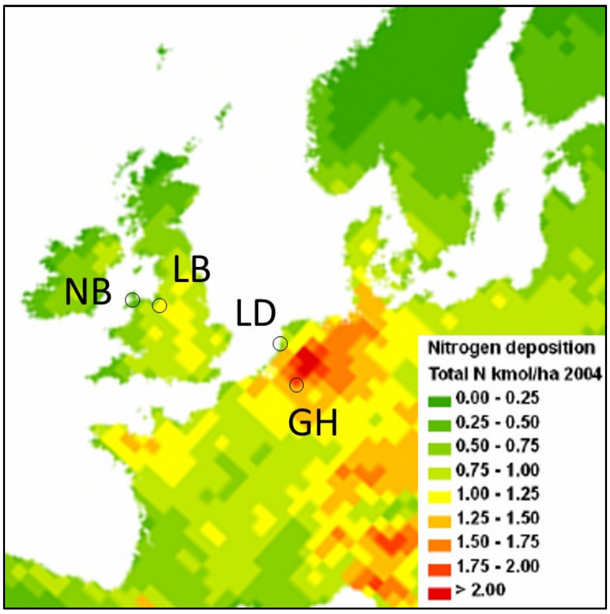
Attachment I Locations of research sites

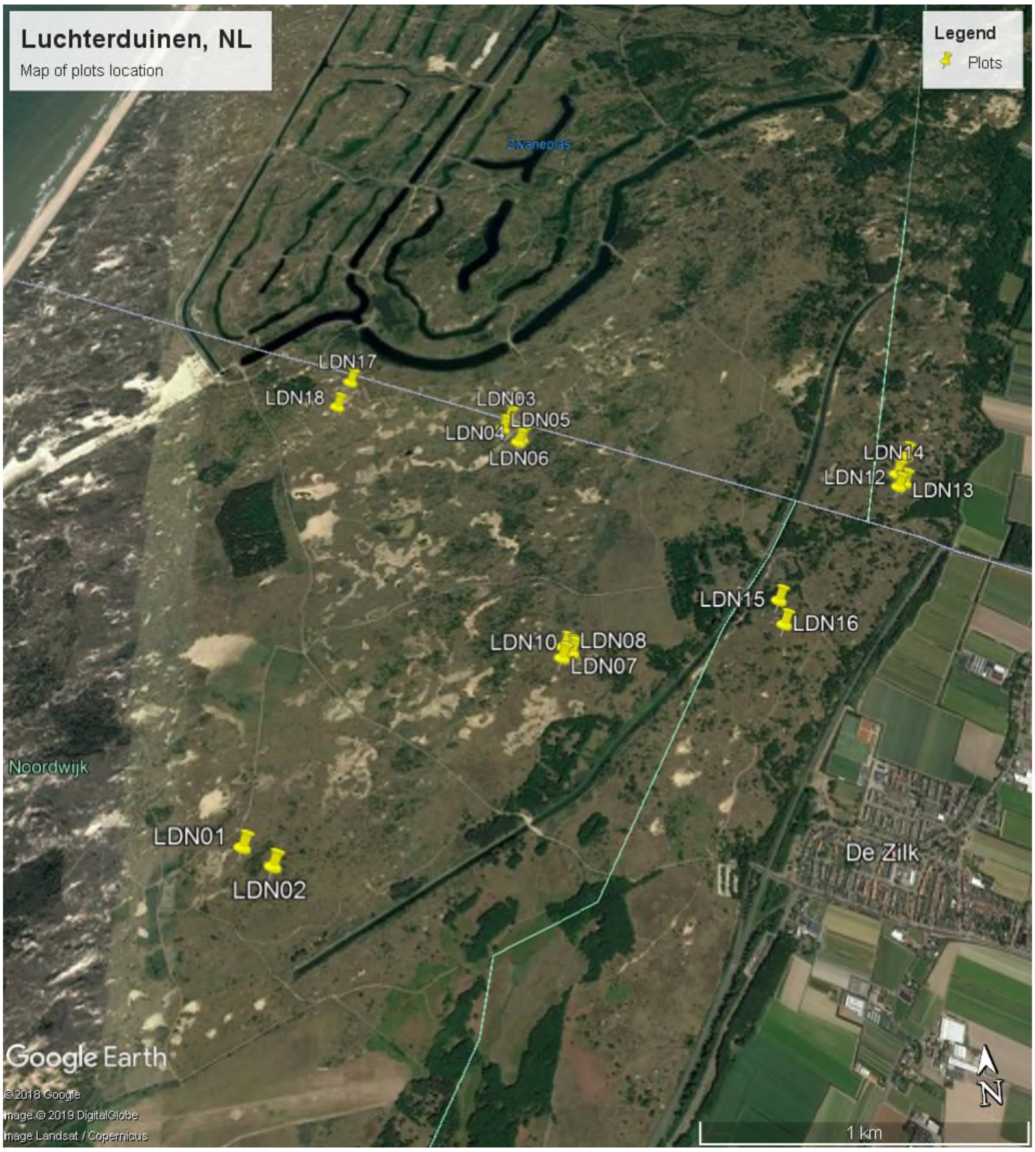


Study areas: dune area LD Luchterduinen (‘LD’) in NL, dune area Newborough Warren (‘NB’) in Wales (UK), heathland area Groote Heide ('GH') in NL, heathland areas Little Budworth ('LB') in England (UK).



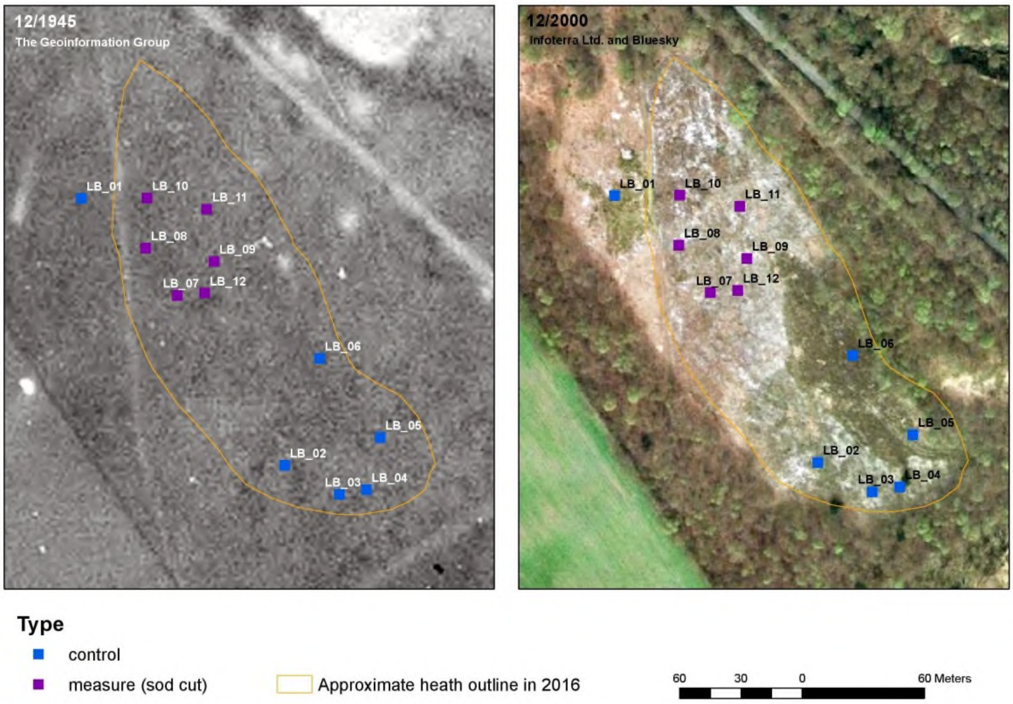
Study areas (black circles) projected on a map with modelled total N-depositioni in the EMEP grid square in 2004.

I.1 Luchterduinen (LD)



I.2 Newborough Warren (NB)

I.3 Little Budworth Common (LB)

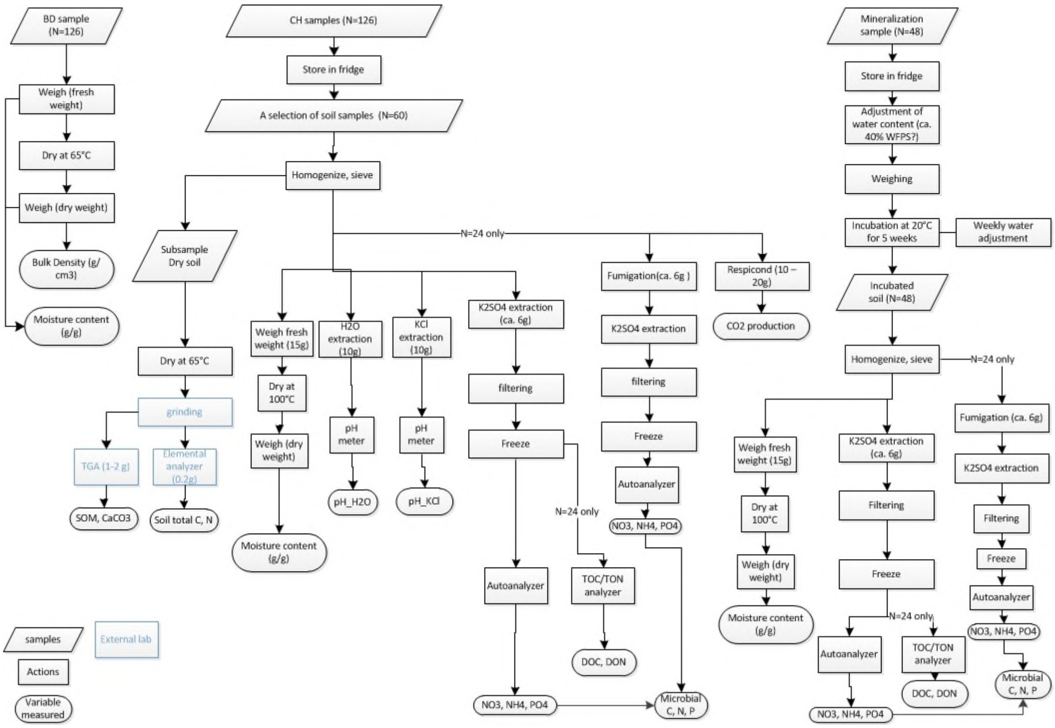


Note that three plots (LB02, LB03, LB04), which were supposed to be 'control' at the planning phase, turned out to be sod-cut in the past. Therefore , in the end, we have 3 control and 9 sod-cut plots.

I.4 Groote Heide (GH)

GH_x are plots, GH_X_GWBUIS are groundwater wells.

Attachment II Lab analysis schema



Attachment III Soil moisture content of N-mineralization experiment

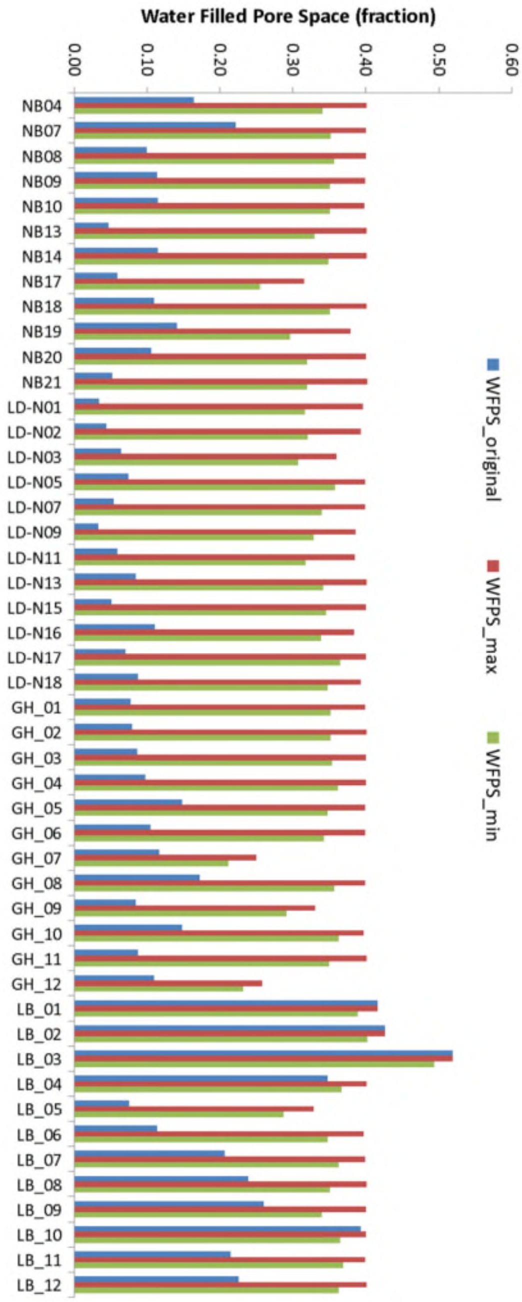
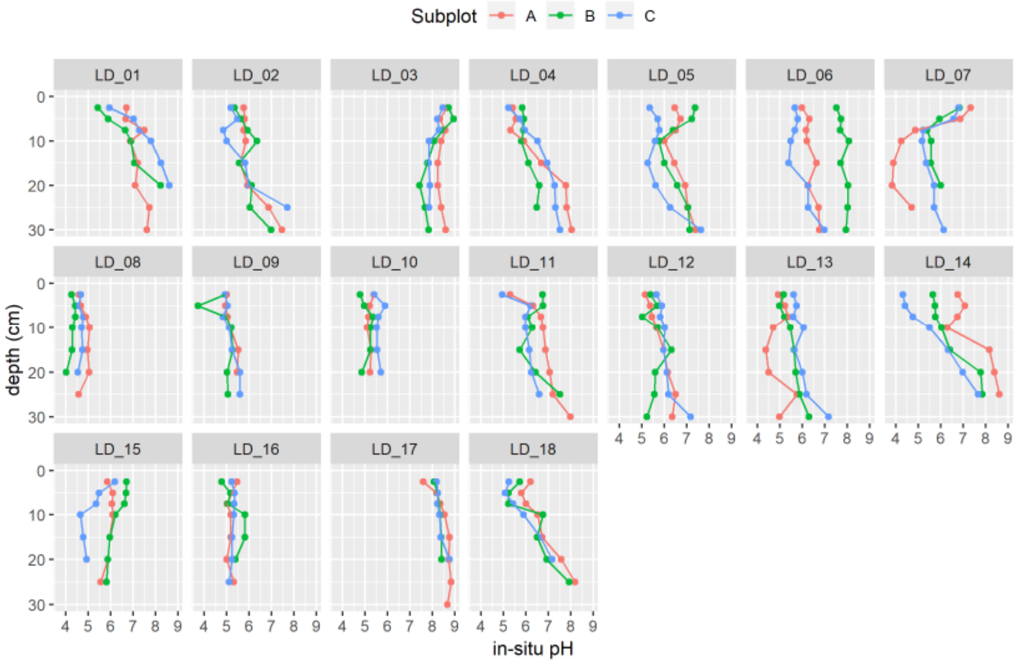


Figure 67. Water filled pore space (WFPS) of soil samples. WFPS_original is WFPS in field condition, estimaed from bulk density samples. For N-minerization experimen, we attempted to adjust WFPS to approximately 0.4. WFPS_max is the highest WFPS achieved during the experiment, whereas PS_min is the lowest WFPS achieved during the experiment.

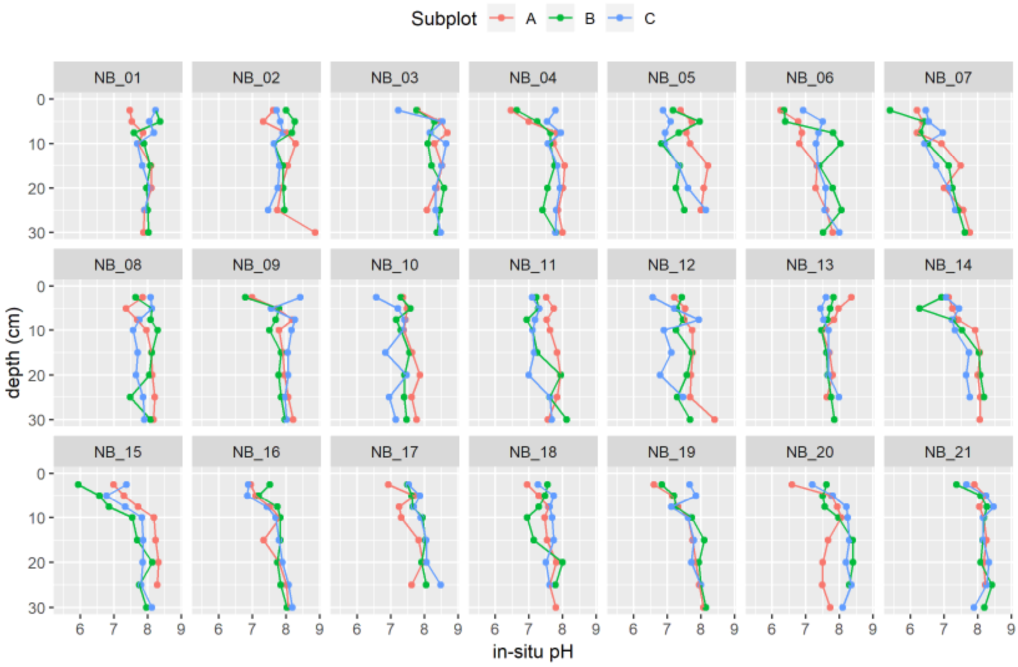
Attachment IV Soil humus profile

IV.1 In-situ pH

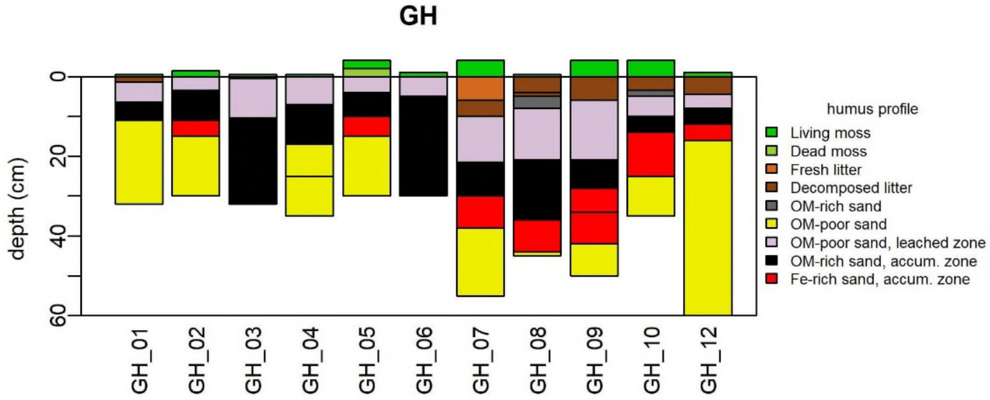
Luchterduinen (LD)

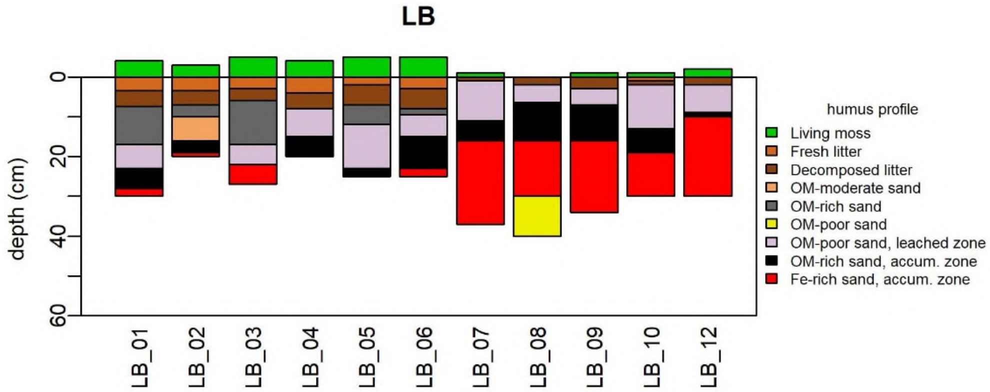


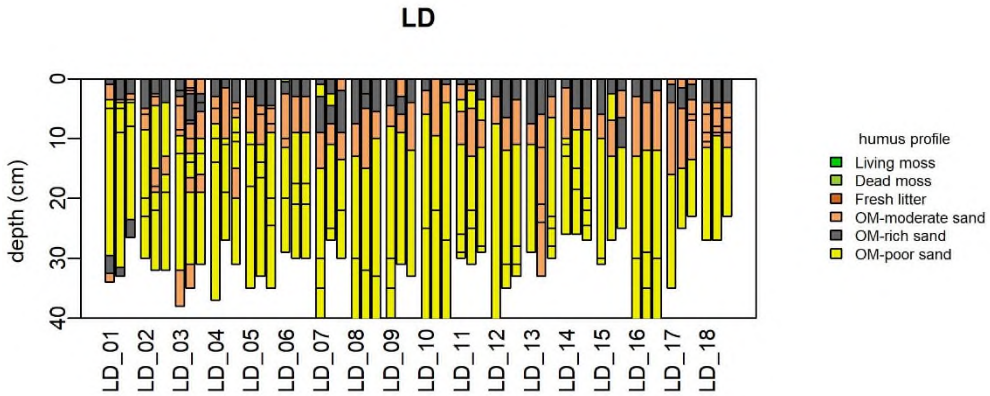
Newborough Warren (NB)

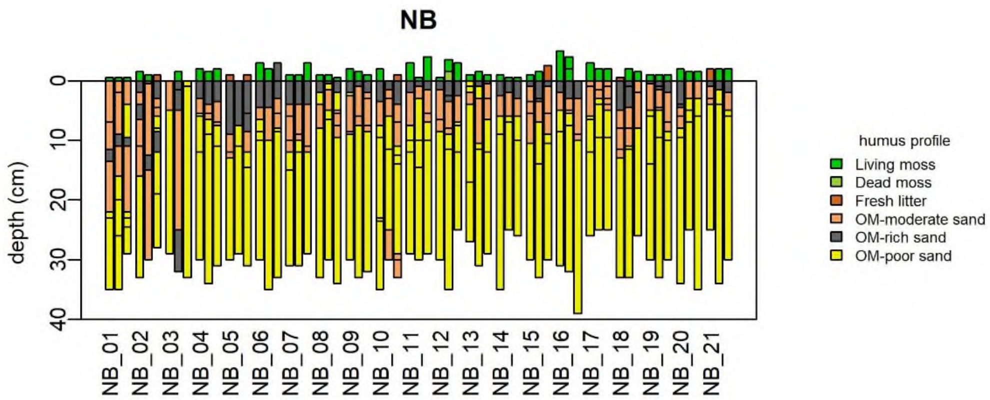


IV.2 Humus profiles

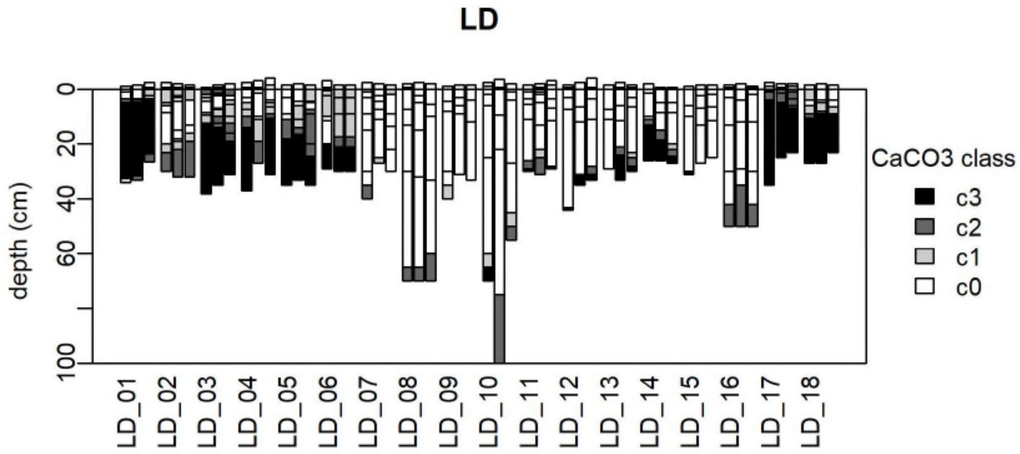


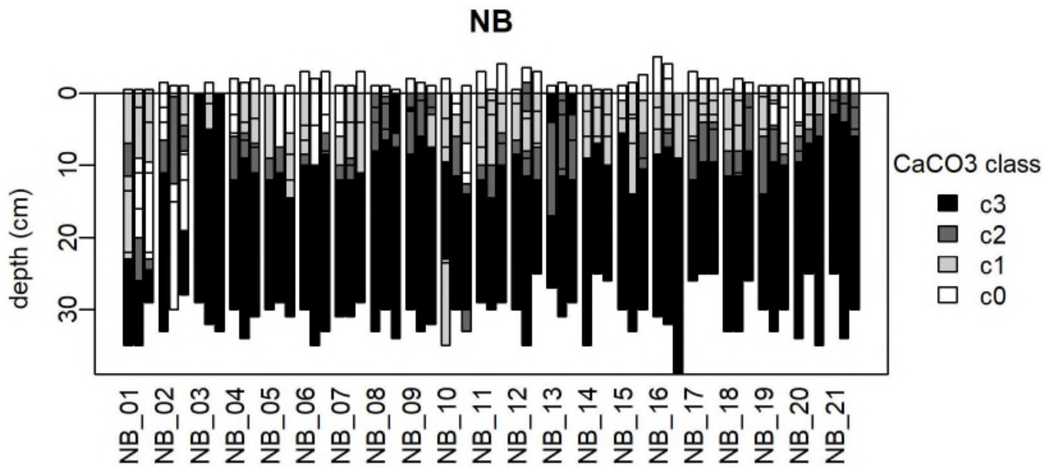




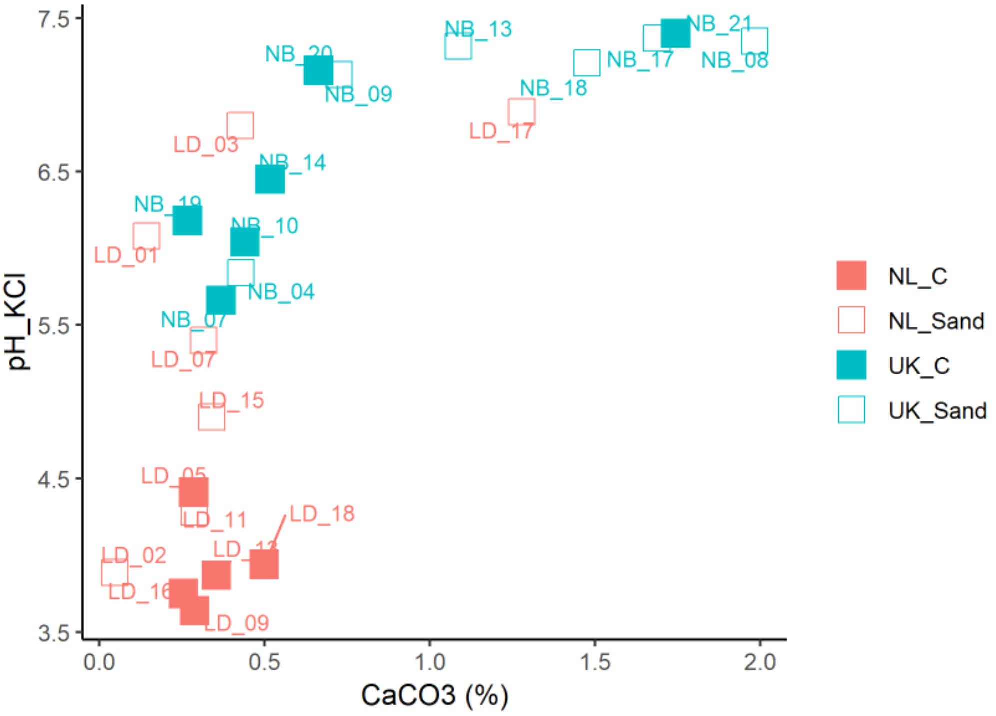


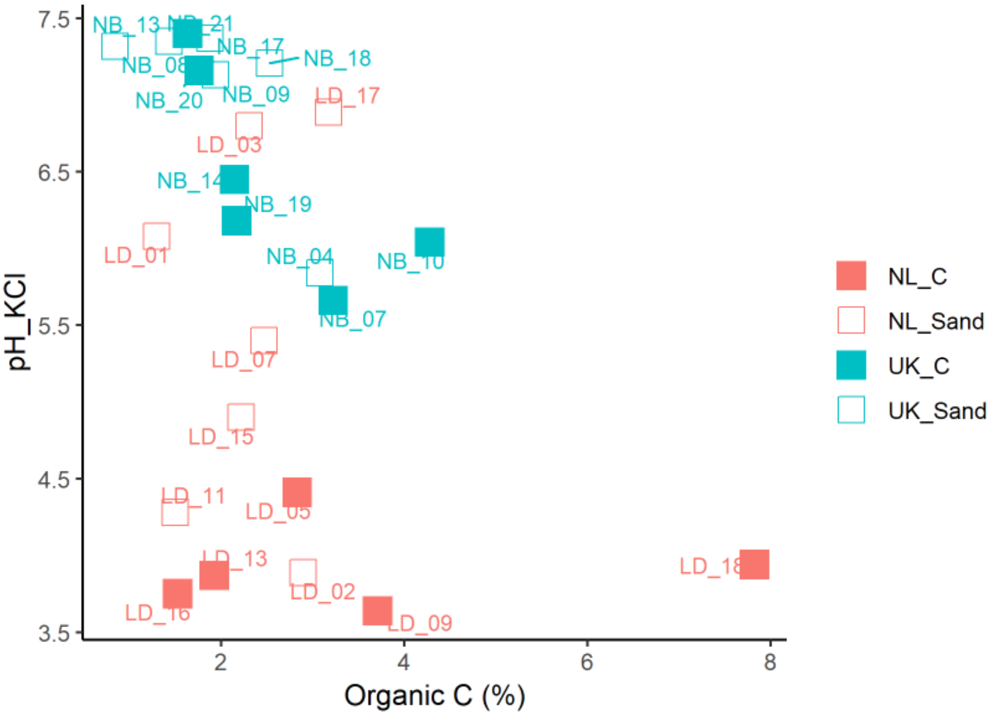
IV.3 $CaCO_3$ profiles



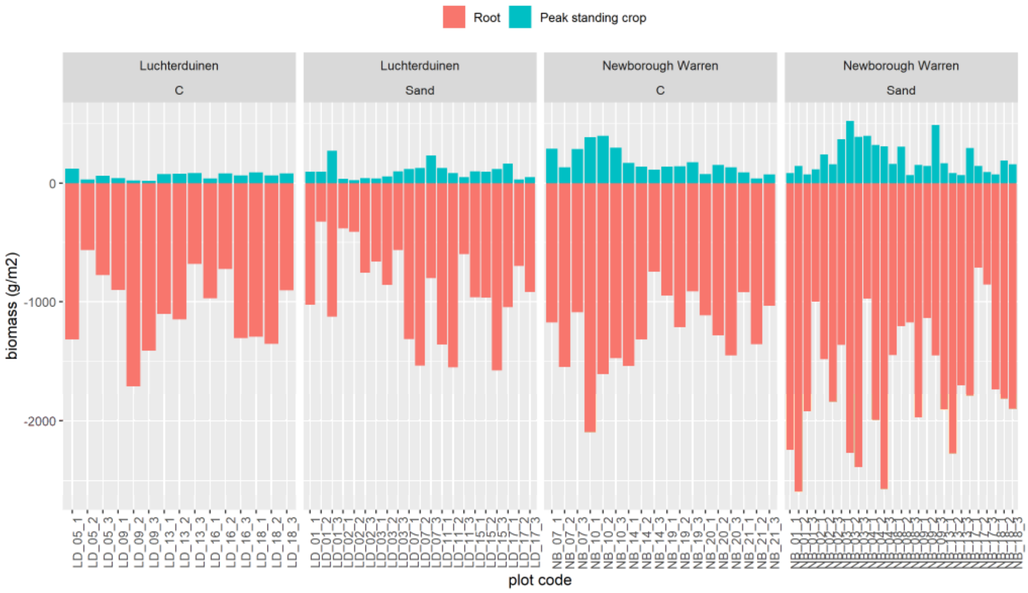


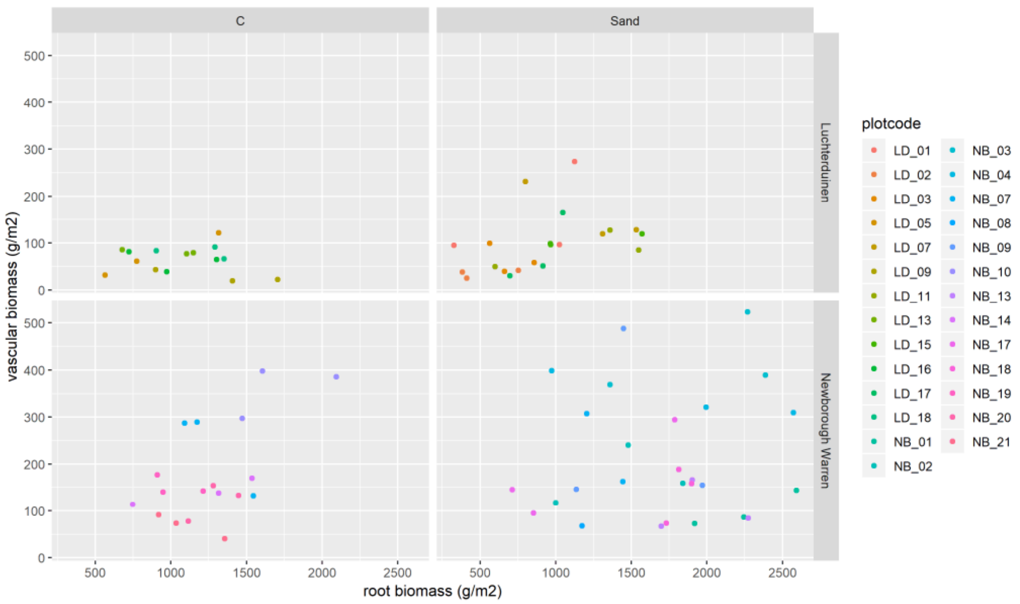
Attachment V Variation in soil pH





Attachment VI Variation in plant biomass





Attachment VII Results of ANOVA

VII.1 ANOVA for the effects of sand deposition and area on flat dune grasslands

Results of 2-way ANOVA of flat dune plots for the effect of management (control / sand deposition), area (Luchterduinen (LD) / Newborough Warren (NB)), and their interactions. The number of plots (N), which are different among the parameters, are shown separately for each parameter group. F values and their significance level (p-values) of ANOVA are shown. P-values are shown with simbols; ***p<0.001, **: p<0.01, *: p<0.05, (*): p<0.1, ns: p>=0.1. For each area, the treatment means and standard deviations are shown. Log-transformed variables are indicated with 'Ln'. For these variables, the means and SEs are also shown as natural logarithm.

Variabele	Tranformed	Year	2-way ANOVA for each year seperately (N=27)					LD Control	LD Sand	NB Control	NB Sand
			Effect			ShapiroWilcoxon P	LevenesTest P				
			Area	Manage-ment	Inter-action						
Top soil (0 – 5 cm)								N=5	N=7	N=6	N=9
Bulk Density (g/cm3)	not	2018	0.0 ns	0.7 ns	0.7 ns			1.02 (0.09)	1.12 (0.04)	1.07 (0.07)	1.08 (0.04)
								N=5	**N=7**	**N=6**	**N=6**
Bulk Density (g/cm3)	not	2018	0.1 ns	0.3 ns	1.2 ns			1.02 (0.09)	1.12 (0.04)	1.07 (0.07)	1.04 (0.05)
SOM (%)	ln(x+1)	2018	0.1 ns	1.9 ns	0.0 ns			1.61 (0.28)	1.35 (0.11)	1.51 (0.15)	1.28 (0.18)
pH_KCl	not	2018	**35.3 *****	**10 ****	2.3 ns			3.92 (0.13)	5.46 (0.45)	6.48 (0.27)	7.04 (0.24)
pH_H2O	not	2018	**30.6 *****	**8.2 ****	2.6 ns			5.23 (0.10)	6.29 (0.31)	6.99 (0.21)	7.28 (0.19)
CaCO3 (%)	ln(x+1)	2018	**10.8 ****	0.8 ns	2.2 ns			-1.12 (0.12)	-1.30 (0.38)	-0.61 (0.26)	0.09 (0.24)
Organic C (%)	ln(x+1)	2018	1.0 ns	2.7 ns	0.0 ns			1.10 (0.28)	0.77 (0.12)	0.87 (0.15)	0.59 (0.19)
Organic N (%)	ln(x+1)	2018	0.6 ns	1.8 ns	0.0 ns			-1.45 (0.28)	-1.69 (0.12)	-1.60 (0.15)	-1.85 (0.19)
Organic C (kg C/m2)	not	2018	2.2 ns	3.8 (*)	0.0 ns			3.21 (0.63)	2.49 (0.24)	2.60 (0.28)	1.94 (0.25)
Organic N (kg N/m2)	not	2018	1.4 ns	2.5 ns	0.0 ns			0.25 (0.05)	0.21 (0.02)	0.22 (0.02)	0.17 (0.02)
Soil C:N ratio	not	2018	3.3 (*)	**6.8 ***	1.2 ns			12.77 (0.18)	11.77 (0.29)	11.90 (0.32)	11.50 (0.21)
N_NH4 (mg N/kg soil)	not	2018	1.2 ns	0.7 ns	1.3 ns			4.69 (1.67)	4.16 (0.84)	4.60 (1.54)	7.67 (2.22)
N_NOx (mg N/kg soil) + 0.1	ln(x+1)	2018	0.4 ns	0.1 ns	0.5 ns			0.55 (0.32)	0.19 (0.50)	0.08 (0.09)	0.19 (0.19)
DIN (dissolved inorganic N) (mg N/kg soil)	not	2018	0.2 ns	0.6 ns	1.1 ns			6.70 (1.77)	6.17 (1.35)	5.61 (1.52)	8.88 (2.37)
DON (dissolved organic N) (mg N/kg soil)	not	2018	**18.9 *****	1.6 ns	0.4 ns			6.28 (1.44)	6.90 (0.86)	9.86 (0.73)	11.62 (0.78)
P_PO4 (mg P/kg soil)	not	2018	0 ns	3.4 (*)	1.4 ns			0.94 (0.29)	1.14 (0.17)	0.67 (0.26)	1.57 (0.44)
N mineralization rate (mg N/kg soil/38d)	not	2018	1.1 ns	0 ns	0.7 ns			34.87 (10.62)	27.22 (5.83)	20.27 (4.27)	25.16 (9.16)
N mineralization rate (g N/m2/38d)	not	2018	1.4 ns	0 ns	0.2 ns			3.20 (0.78)	2.95 (0.63)	2.08 (0.39)	2.46 (0.81)
N turnover rate Nmin/C (mgN/gC/38d)	not	2018	0 ns	1.7 ns	0.4 ns			0.98 (0.18)	1.13 (0.22)	0.80 (0.13)	1.27 (0.36)
Respiration rate(mg CO2/g soil/38d)	ln(x+1)	2018	**27.8 *****	0.1 ns	0 ns			0.80 (0.15)	0.78 (0.08)	1.44 (0.14)	1.37 (0.10)
C turnover rate Cmin/C (mgC_CO2/gC/38d)	not	2018	**54.7 *****	**6.1 ***	0.7 ns			21.20 (2.80)	27.90 (1.99)	48.45 (2.86)	61.85 (6.86)
Nmin/Cmin (ratio)	not	2018	**10.9 ****	0 ns	0.7 ns			0.05 (0.01)	0.04 (0.01)	0.02 (0.00)	0.02 (0.01)
P mineralization rate (mg P/kg soil/38d) + 1	ln(x+1)	2018	1.7 ns	0.0 ns	0.2 ns			1.51 (0.34)	1.60 (0.23)	1.20 (0.37)	1.01 (0.45)
Nitrification rate (mg N/kg soil/38d)	not	2018	2.0 ns	0.7 ns	1.4 ns			32.23 (10.31)	19.68 (4.33)	15.40 (4.70)	17.25 (5.50)
% nitrification (% of net N mineralization)	not	2018	1.4 ns	0.6 ns	0.8 ns			89.09 (4.21)	73.63 (7.85)	69.05 (9.85)	70.04 (11.35)
NOx:NH4 (ratio) + 0.1	ln(x+1)	2018	1.7 ns	1.3 ns	0.1 ns			-0.52 (0.37)	-0.90 (0.33)	-0.98 (0.18)	-1.24 (0.16)
Microbial fraction (g microbe C/kg total C)	ln(x+1)	2018	**16.2 *****	0.1 ns	0.7 ns			1.46 (0.29)	1.10 (0.41)	2.33 (0.05)	2.47 (0.18)
microbial C (mgC/kg dry soil)	ln(x+1)	2018	**8.4 ****	1.5 ns	0.6 ns			4.86 (0.33)	4.18 (0.44)	5.50 (0.17)	5.36 (0.28)
microbial N (mgN/kg dry soil)	not	2018	**11.9 ****	1.6 ns	3.3 (*)			7.48 (1.51)	9.53 (1.09)	25.47 (4.99)	15.13 (4.15)
microbial P (mgP/kg dry soil)	not	2018	**13.2 ****	0.3 ns	0.4 ns			1.12 (0.65)	1.39 (0.35)	12.90 (3.79)	9.80 (3.98)
microbial C:N ratio	ln(x+1)	2018	0.4 ns	0.3 ns	3.5 (*)			2.94 (0.44)	1.97 (0.52)	2.37 (0.07)	2.86 (0.30)
(microbial C:P ratio)^-1	not	2018	**7.0 ***	0.1 ns	3.2 (*)			0.01 (0.00)	0.02 (0.01)	0.04 (0.01)	0.03 (0.01)
microbial N:P ratio	ln(x+1)	2018	**12.7 ****	0.1 ns	0.1 ns			2.38 (0.73)	2.15 [a)] (0.35)	0.86 (0.18)	0.86 (0.35)
microbial C incubated soil (mgC/kg dry soil)	not	2018	**16.0 *****	0.2 ns	0.8 ns			210.10 (36.37)	154.33 (24.08)	328.62 (47.93)	344.41 (48.40)
microbial N incubated soil(mgN/kg dry soil)	not	2018	**27.7 *****	0.6 ns	0.1 ns			11.40 (3.38)	14.55 (6.05)	43.33 (4.85)	49.83 (8.84)
microbial P incubated soil(mgP/kg dry soil)	not	2018	**8.2 ****	0.0 ns	0.4 ns			6.98 (3.79)	4.68 (2.53)	15.53 (5.09)	18.54 (4.30)
(Microbial C:N incubated soil)^-1	not	2018	**14.4 ****	0.8 ns	0.7 ns			0.05 (0.01)	0.08 (0.03)	0.14 (0.02)	0.14 (0.01)
(Microbial C:P incubated soil)^-1	not	2018	3.9 (*)	0.2 ns	0.3 ns			0.03 (0.01)	0.02 (0.01)	0.04 (0.01)	0.05 (0.01)
Microbial N:P incubated soil	ln(x+1)	2018	0.1 ns	0.4 ns	0.5 ns			1.27 (0.50)	0.66 [b)] (0.73)	1.13 [a)] (0.33)	1.13 (0.23)
Microbial C increase (mgC/kg dry soil/38d)	not	2018	0.5 ns	0.0 ns	0.1 ns			48.47 (40.65)	27.64 (70.08)	65.46 (30.15)	81.03 (50.20)
Microbial N increase (mgN/kg dry soil/38d)	not	2018	**14.3 ****	2.5 ns	1.9 ns			3.92 (2.58)	5.02 (5.99)	17.86 (5.69)	34.70 (6.69)
Microbial P increase (mgP/kg dry soil/38d)	not	2018	0.2 ns	0.3 ns	1.9 ns			5.85 (3.17)	3.28 (2.54)	2.63 (3.52)	8.74 (3.30)

Sub soil (10 – 15 cm)								N=5	N=7	N=6	N=9
Bulk Density (g/cm3)	not	2018	**7.8 ***	0.9 ns	0.0 ns			1.55 (0.02)	1.53 (0.02)	1.49 (0.01)	1.47 (0.03)
								N=3	N=3	N=3	N=3
Bulk Density (g/cm3)	not	2018	2.0 ns	0.7 ns	0.7 ns			1.57 (0.03)	1.51 (0.03)	1.49 (0.01)	1.49 (0.05)
SOM (%)	not	2018	0.1 ns	0.4 ns	0.0 ns			0.87 (0.16)	0.98 (0.17)	0.84 (0.09)	0.90 (0.14)
pH_KCl	not	2018	**23.8 ****	0.9 ns	1.5 ns			4.12 (0.11)	5.47 (1.20)	7.89 (0.20)	7.74 (0.23)
pH_H2O	not	2018	**29.8 *****	1.8 ns	1.3 ns			5.46 (0.16)	6.41 (0.71)	7.98 (0.17)	8.06 (0.14)
CaCO3 (%)	not	2018	**30.5 *****	2.4 ns	0.9 ns			0.23 (0.01)	0.42 (0.23)	1.59 (0.43)	2.34 (0.34)
Organic C (%)	not	2018	0.8 ns	0.0 ns	0.0 ns			0.39 (0.14)	0.42 (0.10)	0.32 (0.04)	0.32 (0.07)
Organic N (%)	not	2018	0.1 ns	0.1 ns	0.0 ns			0.04 (0.01)	0.04 (0.01)	0.04 (0.00)	0.04 (0.01)
Organic C (kg C/m2)	not	2018	1.1 ns	0.0 ns	0.0 ns			0.61 (0.22)	0.63 (0.13)	0.48 (0.06)	0.47 (0.08)
Organic N (kg N/m2)	not	2018	0.3 ns	0.2 ns	0.0 ns			0.07 (0.02)	0.06 (0.01)	0.06 (0.00)	0.06 (0.01)
Soil C:N ratio	not	2018	2.4 ns	1.5 ns	0.4 ns			8.54 (0.65)	10.08 (1.28)	7.72 (0.68)	8.25 (0.60)
N_NH4 (mg N/kg soil)	not	2018	**14.9 ****	0.4 ns	0.8 ns			0.00 (0.00)	0.12 (0.12)	1.75 (0.48)	1.20 (0.54)
N_NOx (mg N/kg soil)	not	2018	0.9 ns	0.6 ns	0.8 ns			0.99 (0.09)	1.01 (0.34)	1.42 (0.05)	1.03 (0.29)
DIN (Dissolved inorganic N) (mg N/kg soil)	not	2018	**9.6 ***	0.6 ns	1.0 ns			0.99 (0.09)	1.13 (0.41)	3.17 (0.52)	2.23 (0.82)
DON (Dissolved organic N) (mg N/kg soil)	not	2018	**8.9 ***	0.0 ns	0.8 ns			5.88 (0.49)	6.93 (1.46)	11.07 (1.33)	9.70 (1.71)
P_PO4 (mg P/kg soil)	not	2018	**10.9 ***	0.5 ns	0.5 ns			0.04 (0.04)	0.22 (0.22)	0.57 (0.10)	0.56 (0.11)
Plant biomass								N=5	N=7	N=6	N=9
Standing crop vascular plant biomass (g/m2)	ln(x+1)	2018	**18.2 *****	2.1 ns	0.2 ns	**0.577**	**0.916**	4.10 (0.20)	4.48 (0.20)	5.06 (0.23)	5.24 (0.16)
Standing crop vascular plant biomass (g/m2)	not	2019	**50.4 *****	0.9 ns	0.0 ns	**0.242**	**0.152**	35.29 (6.14)	49.03 (9.22)	156.39 (21.62)	170.48 (19.15)
Productivity aboveground vascular plant biomass (g/m2)	not	2018	**17.2 *****	0.0 ns	0.1 ns	**0.268**	**0.078**	116.57 (19.51)	119.04 (11.90)	244.77 (33.66)	231.76 (33.05)
Productivity aboveground vascular plant biomass (g/m2)	not	2019	**7.3 ***	0.8 ns	0.2 ns	**0.711**	**0.527**	145.78 (19.05)	155.32 (22.28)	202.17 (24.54)	234.39 (27.74)
Root biomass (g/m2)	not	2018	**21.0 *****	2.4 ns	**6.2 ***	**0.934**	**0.301**	1076.20 (81.15)	924.78 (101.64)	1261.38 (107.22	1694.19 (125.80)
Root biomass (g/m2)	not	2019	**30.1 *****	0.7 ns	0.7 ns	**0.561**	**0.514**	1159.14 (165.48	1473.05 (163.89	2392.77 (197.65	2389.41 (194.48)
Nutrients plant biomass								N=5	N=7	N=6	N=9
N abovegr. vas. plant biomass inside exclosure (gN/kg)	not	2019	0.3 ns	2.8 ns	0.0 ns	**0.321**	0.020	15.94 (1.31)	14.41 (0.40)	16.17 (0.28)	14.96 (0.86)
P abovegr. vas. plant biomass inside exclosure (gP/kg)	ln(x+1)	2019	0.0 ns	0.0 ns	0.0 ns	0.035	**0.419**	0.28 (0.07)	0.30 (0.04)	0.30 (0.11)	0.30 (0.09)
K abovegr. vas. plant biomass inside exclosure (gK/kg)	not	2019	2.1 ns	0.5 ns	2.9 ns	**0.523**	**0.416**	13.22 (0.78)	14.00 (0.84)	13.60 (0.49)	12.12 (0.48)
N/P abovegr. vas. plant biomass inside exclosure (g/g)	not	2019	0.1 ns	1.9 ns	0.0 ns	**0.635**	**0.436**	12.15 (1.31)	10.69 (0.38)	12.38 (1.32)	11.14 (0.83)
N/K abovegr. vas. plant biomass inside exclosure (g/g)	not	2019	1.7 ns	0.6 ns	2.3 ns	**0.061**	**0.336**	1.23 (0.16)	1.04 (0.04)	1.19 (0.04)	1.24 (0.06)
N abovegr. vas. plant biomass outside exclosure (gN/kg)	ln(x+1)	2019	2.0 ns	0.1 ns	**3.2 (*)**	**0.212**	**0.255**	2.99 (0.04)	2.88 (0.03)	2.81 (0.03)	2.88 (0.06)
P abovegr. vas. plant biomass outside exclosure (gP/kg)	ln(x+1)	2019	**3.3 (*)**	1.8 ns	0.2 ns	0.004	**0.677**	0.23 (0.06)	0.28 (0.05)	0.31 (0.03)	0.42 (0.08)
N/P abovegr. vas. plant biomass outside exclosure (g/g)	not	2019	**8.8 ****	2.4 ns	1.5 ns	**0.240**	**0.734**	16.02 (1.09)	13.54 (0.82)	12.23 (0.65)	11.89 (0.81)
N root biomass (gN/kg)	not	2019	0.5 ns	1.8 ns	0.4 ns	**0.725**	**0.678**	10.50 (1.29)	12.03 (0.81)	11.57 (0.52)	12.13 (0.46)
P root biomass (gP/kg)	ln(x+1)	2019	**13.1 ****	2.4 ns	0.1 ns	**0.349**	**0.207**	-0.74 (0.15)	-0.59 (0.20)	-0.31 (0.06)	-0.06 (0.09)
N/P root biomass (g/g)	not	2019	**14.3 *****	0.3 ns	0.4 ns	**0.329**	**0.220**	22.32 (3.08)	22.84 (3.28)	15.70 (0.63)	13.27 (1.14)
N abovegr. vas. plant biomass inside exclosure (gN/m2)	not	2019	**7.5 ***	0.0 ns	0.1 ns	**0.633**	**0.971**	2.40 (0.49)	2.26 (0.35)	3.28 (0.42)	3.40 (0.30)
P abovegr. vas. plant biomass inside exclosure (gP/m2)	not	2019	**8.7 ****	1.6 ns	0.3 ns	**0.501**	**0.579**	0.20 (0.03)	0.21 (0.03)	0.26 (0.02)	0.32 (0.03)
K abovegr. vas. plant biomass inside exclosure (gK/m2)	not	2019	**4.0 (*)**	0.3 ns	0.1 ns	**0.253**	**0.627**	1.91 (0.26)	2.22 (0.38)	2.74 (0.35)	2.84 (0.33)
N abovegr. vas. plant biomass outside exclosure (gN/m2)	not	2019	**60.0 *****	1.2 ns	0.1 ns	**0.165**	**0.306**	0.71 (0.14)	0.88 (0.17)	2.63 (0.40)	2.95 (0.23)
P abovegr. vas. plant biomass outside exclosure (gP/m2)	ln(x+1)	2019	**93.0 *****	**3.3 (*)**	0.2 ns	**0.686**	**0.555**	-3.18 (0.18)	-2.84 (0.21)	-1.59 (0.12)	-1.40 (0.11)
N root biomass (gN/m2)	not	2019	**24.4 *****	1.2 ns	0.7 ns	**0.604**	**0.428**	12.60 (2.72)	17.75 (2.15)	28.04 (3.33)	28.71 (2.23)
P root biomass (gP/m2)	not	2019	**30.3 *****	**3.9 (*)**	0.0 ns	**0.173**	**0.396**	0.58 (0.10)	0.97 (0.28)	1.79 (0.21)	2.26 (0.21)
Vegetation structure								N=5	N=7	N=6	N=9
Sum of vascular plant cover	not	2018	**23.3 *****	0.2 ns	0.0 ns	**0.826**	**0.212**	35.28 (6.95)	36.29 (4.40)	73.72 (12.72)	77.87 (7.49)
Sum of vascular plant cover	ln(x+1)	2019	**133.3 *****	**3.2 (*)**	**3.5 (*)**	**0.983**	**0.101**	1.96 (0.30)	2.65 (0.25)	4.49 (0.07)	4.48 (0.09)
Total moss-lichen cover (%)	not	2018	**29.6 *****	0.1 ns	0.0 ns	**0.202**	**0.330**	77.50 (7.39)	76.01 (12.02)	28.62 (11.62)	27.53 (3.85)
Total moss-lichen cover (%)	not	2019	**72.7 *****	1.0 ns	0.0 ns	**0.551**	**0.736**	86.82 (4.42)	79.80 (7.21)	24.73 (8.04)	19.29 (6.84)
Total moss cover (%)	not	2018	**28.9 *****	0.0 ns	0.0 ns	**0.226**	**0.294**	74.38 (6.31)	75.89 (12.02)	27.87 (11.75)	27.26 (3.90)
Total moss cover (%)	not	2019	**72.4 *****	0.7 ns	0.0 ns	**0.633**	**0.756**	85.38 (4.44)	79.74 (7.21)	23.87 (7.96)	19.28 (6.84)
Total lichen cover (%) + 0.1	ln(x+1)	2018	1.2 ns	**3.2 (*)**	1.1 ns	0.005	**0.360**	-0.15 (0.90)	-1.58 (0.20)	-1.27 (0.57)	-1.68 (0.34)
Total lichen cover (%) + 0.1	ln(x+1)	2019	0.9 ns	**3.8 (*)**	0.2 ns	0.001	**0.210**	-0.89 (0.87)	-1.95 (0.17)	-1.53 (0.65)	-2.23 (0.08)
Height vascular stand (cm)	ln(x+1)	2018	0.1 ns	0.0 ns	2.1 ns	0.001	**0.753**	1.23 (0.45)	0.92 (0.15)	0.77 (0.16)	1.11 (0.15)
Height vascular stand (cm)	ln(x+1)	2019	**4.3 ***	1.9 ns	0.0 ns	**0.444**	**0.950**	0.46 (0.32)	0.83 (0.22)	1.01 (0.26)	1.28 (0.18)
Bare ground cover (%) + 0.1	ln(x+1)	2018	0.1 ns	0.8 ns	2.7 ns	**0.138**	**0.909**	-0.08 (0.63)	-0.66 (0.59)	-1.14 (0.74)	0.35 (0.51)
Bare ground cover (%) + 0.1	ln(x+1)	2019	2.5 ns	1.9 ns	**13.5 ****	0.008	**0.255**	0.66 (0.28)	-0.78 (0.55)	-0.82 (0.68)	1.64 (0.44)

Variabele	**Tranformed**	**Year**	**2-way ANOVA for each year seperately (N=27)**					**LD Control**	**LD Sand**	**NB Control**	**NB Sand**
			Effect			**ShapiroWilcoxon P**	**LevenesTest P**				
			Area	**Manage-ment**	**Inter-action**						
Number of species								N=5	N=7	N=6	N=9
Species richness (#)	not	2018	**25.7 *****	0.6 ns	0.6 ns	**0.168**	**0.751**	20.00 (1.52)	19.71 (1.38)	27.50 (1.89)	30.11 (1.95)
Species richness (#)	not	2019	**92.0 *****	0.0 ns	0.8 ns	**0.680**	**0.881**	17.00 (1.82)	18.86 (1.99)	36.50 (1.77)	35.11 (1.62)
Vascular species richness (#)	not	2018	**27.8 *****	1.6 ns	0.1 ns	**0.267**	**0.973**	12.80 (2.18)	15.43 (1.70)	22.83 (1.49)	24.56 (1.72)
Vascular species richness (#)	not	2019	**108.6 *****	0.5 ns	2.6 ns	**0.193**	**0.584**	11.00 (2.28)	15.14 (2.01)	33.00 (1.24)	31.33 (1.53)
Moss species richness (#)	not	2018	0.1 ns	0.9 ns	**4.6 ***	**0.469**	**0.580**	7.20 (0.86)	4.29 (0.64)	4.67 (1.17)	5.56 (0.77)
Moss species richness (#)	not	2019	1.6 ns	1.3 ns	2.7 ns	**0.489**	**0.927**	6.00 (1.10)	3.71 (0.68)	3.50 (0.85)	3.78 (0.60)
N-fixing species richness (#)	not	2018	**42.6 *****	1.1 ns	0.2 ns	**0.659**	**0.529**	0.80 (0.37)	1.00 (0.38)	3.50 (0.67)	4.11 (0.35)
N-fixing species richness (#)	not	2019	**56.2 *****	2.1 ns	1.2 ns	**0.166**	**0.184**	0.80 (0.37)	0.86 (0.26)	4.00 (0.52)	5.22 (0.62)
Species indicator values environmental conditions											
Average Ellenberg nutrient value (-)	not	2018	3.6 (*)	**5.5 ***	0.5 ns	**0.954**	**0.079**	2.62 (0.21)	3.19 (0.18)	2.99 (0.40)	4.08 (0.42)
Average Ellenberg nutrient value (-)	not	2019	0.0 ns	3.1 (*)	0.1 ns	**0.126**	**0.380**	2.57 (0.25)	3.38 (0.26)	2.76 (0.47)	3.30 (0.38)
Average Ellenberg acidity value (-)	not	2018	**10.3 ****	0.1 ns	1.5 ns	**0.314**	**0.330**	4.62 (0.56)	5.32 (0.46)	6.47 (0.44)	6.18 (0.19)
Average Ellenberg acidity value (-)	not	2019	**8.3 ****	0.9 ns	2.4 ns	**0.264**	**0.315**	4.66 (0.80)	5.81 (0.42)	6.68 (0.37)	6.48 (0.24)
Average Ellenberg moisture value (-)	not	2018	1.4 ns	0.2 ns	0.2 ns	**0.403**	**0.054**	3.82 (0.10)	4.00 (0.09)	4.13 (0.30)	4.13 (0.14)
Average Ellenberg moisture value (-)	not	2019	1.5 ns	0.3 ns	0.0 ns	**0.080**	**0.310**	4.01 (0.13)	4.15 (0.12)	3.84 (0.28)	3.91 (0.13)
Species cover with Ellenberg moisture value (%)	not	2018	**6.6 ***	0.0 ns	0.1 ns	**0.329**	**0.996**	71.65 (2.76)	73.03 (2.50)	66.07 (2.17)	65.93 (2.41)
Species cover with Ellenberg moisture value (%)	not	2019	**5.8 ***	0.5 ns	0.0 ns	**0.087**	**0.640**	78.38 (4.83)	76.27 (3.54)	71.02 (2.95)	68.90 (1.55)
Functional groups and traits								N=5	N=7	N=6	N=9
Cumulative moss cover (%)	not	2018	**31.6 *****	0.0 ns	0.0 ns	**0.140**	**0.340**	75.80 (6.22)	75.29 (11.31)	28.30 (11.66)	27.16 (3.51)
Cumulative moss cover (%)	not	2019	**83.2 *****	1.4 ns	0.0 ns	**0.789**	**0.726**	87.00 (3.94)	81.29 (7.36)	25.67 (8.10)	17.22 (6.18)
Cumulative lichen cover (%) + 0.1	ln(x+1)	2018	**5.7 ***	2.6 ns	0.2 ns	**0.719**	**0.754**	0.53 (0.81)	-0.59 (0.44)	-1.03 (0.62)	-1.64 (0.37)
Cumulative lichen cover (%) + 0.1	ln(x+1)	2019	1.0 ns	**3.0 (*)**	0.3 ns	0.001	**0.263**	-1.04 (0.81)	-1.62 (0.44)	-1.22 (0.72)	-2.30 (0.00)
Cumulative herb cover (%)	ln(x+1)	2018	**44.6 *****	0.1 ns	1.2 ns	**0.335**	**0.508**	1.72 (0.48)	2.13 (0.24)	3.95 (0.23)	3.74 (0.21)
Cumulative herb cover (%)	ln(x+1)	2019	**54.7 *****	0.6 ns	**4.8 ***	**0.133**	**0.890**	1.77 (0.30)	2.60 (0.20)	4.41 (0.31)	4.06 (0.24)
Cumulative grass cover (%)	ln(x+1)	2018	0.1 ns	**3.1 (*)**	2.0 ns	**0.067**	**0.136**	3.38 (0.17)	3.45 (0.15)	2.78 (0.61)	3.74 (0.18)
Cumulative grass cover (%)	ln(x+1)	2019	**31.9 *****	**3.9 (*)**	0.6 ns	**0.917**	0.001	2.01 (0.15)	2.29 (0.19)	3.29 (0.50)	3.98 (0.15)
Cumulative woody species cover (%) + 0.1	ln(x+1)	2018	2.9 ns	0.0 ns	**3.0 (*)**	**0.515**	**0.509**	-1.82 (0.48)	-0.35 (0.53)	0.83 (0.73)	-0.18 (0.77)
Cumulative woody species cover (%) + 0.1	ln(x+1)	2019	**9.7 ****	0.0 ns	0.5 ns	**0.385**	**0.391**	-1.82 (0.48)	-1.18 (0.53)	1.03 (0.78)	0.66 (0.80)
Shannon index (-)	not	2018	**12.7 ****	0.0 ns	**3.8 (*)**	**0.519**	**0.434**	2.02 (0.11)	1.72 (0.14)	2.18 (0.18)	2.43 (0.11)
Shannon index (-)	not	2019	**91.0 *****	0.1 ns	**3.1 (*)**	**0.288**	**0.215**	1.60 (0.16)	1.36 (0.11)	2.57 (0.19)	2.80 (0.08)
Average maximum canopy height (m)	not	2018	0.1 ns	**7.7 ***	0.0 ns	**0.657**	**0.549**	0.41 (0.05)	0.61 (0.06)	0.39 (0.09)	0.59 (0.07)
Average maximum canopy height (m)	not	2019	0.8 ns	**4.1 (*)**	0.0 ns	**0.222**	**0.319**	0.47 (0.07)	0.60 (0.08)	0.40 (0.09)	0.55 (0.04)
Average minimum canopy height (m)	not	2018	1.1 ns	**11.1 ****	0.0 ns	**0.090**	**0.427**	0.11 (0.01)	0.17 (0.01)	0.10 (0.01)	0.15 (0.02)
Average minimum canopy height (m)	not	2019	**3.9 (*)**	**4.4 ***	0.0 ns	**0.258**	**0.717**	0.13 (0.02)	0.17 (0.02)	0.09 (0.02)	0.13 (0.01)
Average specific leaf area (mm2/mg)	not	2018	1.5 ns	0.0 ns	0.9 ns	**0.143**	**0.557**	21.35 (1.79)	20.05 (1.04)	18.52 (1.41)	19.50 (0.87)
Average specific leaf area (mm2/mg)	ln(x+1)	2019	**3.9 (*)**	1.6 ns	1.0 ns	**0.350**	0.003	3.05 (0.01)	3.06 (0.03)	2.92 (0.07)	3.01 (0.04)
Average shoot life span (-)	not	2018	1.6 ns	0.2 ns	0.6 ns	**0.296**	**0.767**	1.60 (0.09)	1.68 (0.05)	1.74 (0.07)	1.72 (0.06)
Average shoot life span (-)	not	2019	**5.3 ***	1.8 ns	0.2 ns	**0.926**	**0.597**	1.54 (0.05)	1.48 (0.08)	1.71 (0.05)	1.60 (0.05)
Average number of clonal offspring (#)	not	2018	2.6 ns	0.1 ns	0.6 ns	**0.272**	**0.793**	3.47 (0.29)	3.15 (0.28)	2.82 (0.32)	2.91 (0.16)
Average number of clonal offspring (#)	not	2019	1.3 ns	0.2 ns	0.2 ns	**0.999**	**0.966**	2.90 (0.21)	2.88 (0.22)	3.03 (0.20)	3.18 (0.17)
Average clonal spread (cm)	not	2018	**3.3 (*)**	2.8 ns	0.1 ns	**0.675**	**0.414**	10.26 (1.46)	11.95 (0.95)	9.03 (0.60)	10.24 (0.45)
Average clonal spread (cm)	ln(x+1)	2019	**29.9 *****	0.2 ns	0.1 ns	**0.072**	**0.578**	2.62 (0.08)	2.63 (0.08)	2.26 (0.03)	2.32 (0.04)
Average root resprout (0/1)	ln(x+1)	2018	2.8 ns	0.5 ns	1.1 ns	**0.238**	**0.674**	-2.66 (0.29)	-2.53 (0.13)	-1.85 (0.26)	-2.31 (0.31)
Average root resprout (0/1)	ln(x+1)	2019	1.6 ns	0.2 ns	0.5 ns	**0.941**	**0.695**	-1.75 (0.20)	-1.83 (0.26)	-2.33 (0.34)	-2.01 (0.24)

[a)] 1 sample was excluded from ANOVA because microbial P-content was 0 and therefore N:P could not be computed.

[b)] 3 samples were excluded from ANOVA because microbial P-content was 0 and therefore N:P could not be computed.

VII.2 ANOVA for the effects of sod-cutting and area on heath

Results of 2-way ANOVA of heath plots for the effect of management (control / sod-cutting), area (Groote Heide (GH) / Little Budworth Common (LB)), and their interactions. The number of plots for each category was 6 (GH control), 6 (GH sod-cut), 3(LB control), and 9 (LB sod-cut. F values and their significance level (p-values) of ANOVA are shown. P-values are shown with simbols; ***p<0.001, **: p<0.01, *: p<0.05, (*): p<0.1, ns: p>=0.1. For each area, the treatment means and standard deviations are shown. Log-transformed variables are indicated with 'Ln'. For these variables, the means and SEs are also shown as natural logarithm.

	ANOVA			Means (SE)			
Variable	Area	Management	Interaction	GH Control	GH Sod-cut	LB Control	LB Sod-cut
Topsoil (0 – 5 cm)							
Bulk Density (g/cm3)	0.9 ns	67.3 ***	0.0 ns	0.52 (0.08)	1.14 (0.05)	0.32 (0.06)	0.91 (0.06)
Ln SOM (%)	0.0 ns	43.4 ***	0.0 ns	3.15 (0.25)	1.68 (0.16)	3.47 (0.46)	2.08 (0.13)
pH_KCl	0.4 ns	20.5 ***	2.5 ns	2.77 (0.05)	3.23 (0.03)	2.89 (0.08)	3.10 (0.08)
pH_H2O	0.1 ns	43.7 ***	3.8 (*)	3.84 (0.07)	4.39 (0.06)	3.88 (0.06)	4.17 (0.05)
CaCO3 (%)	0.4 ns	45.6 ***	0.1 ns	0.39 (0.06)	0.07 (0.01)	0.42 (0.09)	0.13 (0.03)
Ln Organic C (%)	0.1 ns	41.1 ***	0.0 ns	2.59 (0.24)	1.15 (0.15)	2.85 (0.47)	1.47 (0.14)
Ln Organic N (%)	0.0 ns	48.2 ***	0.4 ns	-0.51 (0.26)	-2.24 (0.15)	-0.35 (0.46)	-1.78 (0.15)
Organic C (kg C/m2)	0.9 ns	12.3 **	0.4 ns	6.80 (0.84)	3.71 (0.44)	6.19 (2.03)	4.03 (0.38)
Organic N (kg N/m2)	1.1 ns	18.8 ***	1.4 ns	0.31 (0.04)	0.12 (0.01)	0.26 (0.09)	0.16 (0.02)
Soil C:N ratio	0.1 ns	13.2 **	6.5 *	22.27 (0.79)	29.82 (1.15)	25.01 (3.12)	25.90 (0.90)
Ln N_NH4 (mg N/kg soil) + 0.1	7.2 *	40.9 ***	1.6 ns	1.78 (0.62)	-2.30 (0.00)	0.38 (1.80)	-2.30 (0.00)
N_NOx (mg N/kg soil)	0.1 ns	9.4 **	0.2 ns	2.47 (0.82)	0.59 (0.19)	2.43 (1.15)	0.98 (0.20)
Ln DIN (mg N/kg soil) + 0.1	0.6 ns	20.6 ***	1.2 ns	2.05 (0.56)	-0.63 (0.37)	1.54 (1.24)	-0.04 (0.17)
DON (mg N/kg soil)	0.6 ns	26.6 ***	0.3 ns	18.90 (3.37)	8.10 (0.97)	21.94 (5.48)	8.51 (0.42)
Ln P_PO4 (mg P/kg soil) + 0.1	6.1 *	15.7 ***	0.3 ns	-0.20 (0.08)	-1.08 (0.14)	-0.35 (0.37)	-1.52 (0.26)
Ln N-mineralization rate (mg N/kg soil/38d) + 2	3.6 (*)	37.3 ***	0.0 ns	3.37 (0.64)	0.70 (0.11)	3.16 (0.92)	0.66 (0.12)

Ln N-mineralization rate (g N/m2/38d) + 1	2.1 ns	16.2 ***	0.2 ns	0.99 (0.32)	0.01 (0.03)	0.79 (0.59)	0.00 (0.02)
Ln N-turnover rate Nmin/C (mgN/gC/38d) + 0.1	2.0 ns	21.1 ***	0.1 ns	-1.08 (0.36)	-2.29 (0.09)	-1.20 (0.63)	-2.29 (0.06)
Ln P mineralization (mg P/kg soil/38d)	5.9 *	5.9 *	1.5 ns	0.27 (0.28)	-0.04 (0.20)	1.28 (0.17)	0.41 (0.15)
Subsoil (10 – 15 cm)							
Bulk Density (g/cm3)	0.0 ns	4.1 (*)	3.4 (*)	1.43 (0.05)	1.45 (0.02)	1.32 (0.02)	1.47 (0.03)
Plant productivity							
Peak standing crop (g/m2)	19.8 ***	7.7 *	20.9 ***	455.90 (83.08)	545.51 (52.12)	1268.38 (125.71)	662.57 (54.32)
Plant community structure							
Number of plant species	0.3 ns	0.0 ns	0.5 ns	5.33 (0.71)	4.83 (0.54)	5.00 (1.00)	5.67 (0.75)
Number of vascular plant species	0.4 ns	0.3 ns	1.3 ns	2.67 (0.33)	2.00 (0.26)	2.33 (0.88)	2.67 (0.37)
Number of moss&lichen species	0.1 ns	0.2 ns	0.0 ns	2.67 (0.61)	2.83 (0.31)	2.67 (0.33)	3.00 (0.44)
Average Ellenberg nutrient value	1.8 ns	4.0 (*)	0.9 ns	1.96 (0.04)	1.83 (0.07)	2.27 (0.26)	1.95 (0.09)
Average indicator value for nutrient	0.6 ns	4.3 (*)	0.1 ns	1.81 (0.22)	2.54 (0.33)	1.53 (0.37)	2.09 (0.26)
Average Ellenberg acidity value	1.1 ns	0.6 ns	0.2 ns	2.24 (0.13)	2.08 (0.08)	2.33 (0.10)	2.29 (0.13)
Average indicator value for acidity	0.2 ns	2.2 ns	2.3 ns	2.70 (0.15)	2.75 (0.36)	1.83 (0.60)	2.83 (0.22)
Average Ellenberg moisture value	4.4 *	0.3 ns	0.7 ns	5.97 (0.23)	6.00 (0.00)	6.78 (0.40)	6.39 (0.25)
Weighted average Ellenberg nutrient value	1.4 ns	0.1 ns	1.0 ns	1.71 (0.08)	1.78 (0.19)	1.74 (0.18)	1.57 (0.03)
Weighted average indicator value for nutrient	0.0 ns	1.4 ns	2.2 ns	1.07 (0.02)	1.07 (0.02)	1.03 (0.02)	1.08 (0.02)

VII.3 ANOVA for the effects of slope and area on dune grasslands

Results of 2-way ANOVA of dunes for the effect of slope (flat / north-facing slope / south-fading slope), area (Luchterduinen (LD) / Newborough Warren (NB)), and their interactions. None of the plots are subject to management (i.e. sand deposition). The number of plots for each category was 5 (LD flat), 3 (LD north-facing slope), 3 (LD south-facing slope), 6 (NB flat), 3 (NB north-facing slope), and 3 (NB south-facing slope). F values and their significance level (p-values) of ANOVA are shown. P-values are shown with simbols; ***p<0.001, **: p<0.01, *: p<0.05, (*): p<0.1, ns: p>=0.1. For each slope of each area, the means and standard deviations are shown. Log-transformed variables are indicated with 'Ln'. For these variables, the means and SEs are also shown as natural logarithm.

Variable	ANOVA			Means (SE)					
	Area	Slope	Interaction	LD Flat	LD North	LD South	NB Flat	NB North	NB South
Topsoil (0 – 5 cm)									
Bulk Density (g/cm3)	1.0 ns	1.3 ns	1.6 ns	1.02 (0.09)	1.02 (0.05)	1.12 (0.10)	1.07 (0.07)	0.82 (0.09)	0.95 (0.03)
Subsoil (10 – 15 cm)									
Bulk Density (g/cm3)	13.2 **	3.4 (*)	0.0 ns	1.55 (0.02)	1.51 (0.02)	1.51 (0.03)	1.49 (0.01)	1.45 (0.00)	1.45 (0.01)

Variabele	**Tranformed**	**Year**	**2-way ANOVA for each year seperately (N=27)**				
			Effect			**ShapiroWilcoxon P**	**LevenesTest P**
			Country	**slope**	**interaction**		
Productivity aboveground vascular plant biomass (g/m2)	not	2018	**23.8 *** **	0.1 ns	0.2 ns	**0.174**	**0.569**
Productivity aboveground vascular plant biomass (g/m2)	not	2019	**9.0 ** **	0.4 ns	0.4 ns	**0.516**	**0.405**
Standing crop vascular plant biomass (g/m2)	nl(x)	2018	**25.4 *** **	3.5 (*)	0.0 ns	**0.849**	**0.728**
Standing crop vascular plant biomass (g/m2)	nl(x)	2019	**150.9 *** **	1.4 ns	3.4 (*)	**0.527**	**0.807**
Species richness (#)	not	2018	**40.6 *** **	1.7 ns	3.2 (*)	**0.161**	**0.756**
Species richness (#)	not	2019	**134.8 *** **	0.4 ns	1.2 ns	**0.704**	**0.813**
Vascular species richness (#)	not	2018	**45.6 *** **	2.6 ns	2.1 ns	**0.401**	**0.499**
Vascular species richness (#)	not	2019	**165.8 *** **	0.7 ns	1.2 ns	**0.289**	**0.747**
Average Ellenberg acidity value (-)	not	2018	**17.1 *** **	0.0 ns	0.1 ns	**0.840**	**0.691**
Average Ellenberg acidity value (-)	not	2019	**13.8 ** **	0.2 ns	0.0 ns	**0.507**	**0.654**
Average Ellenberg moisture value (-)	not	2018	2.3 ns	2.0 ns	0.0 ns	**0.245**	**0.255**
Average Ellenberg moisture value (-)	not	2019	0.1 ns	**4.3 * **	0.3 ns	0.045	**0.316**
Average Ellenberg nutrient value (-)	not	2018	4.1 (*)	**6.0 * **	0.7 ns	**0.075**	**0.743**
Average Ellenberg nutrient value (-)	not	2019	2.1 ns	**5.9 * **	0.9 ns	**0.534**	**0.603**
Number of moss & lichen species (#)	not	2018	3.9 (*)	1.8 ns	0.2 ns	**0.606**	**0.672**
Number of moss & lichen species (#)	not	2019	**6.8 * **	0.8 ns	0.4 ns	**0.521**	**0.822**

Variabele	NL Flat	NL North	NL South	UK Flat	UK North	UK South
Productivity aboveground vascular plant biomass (g/m2)	116.57 (19.51)	122.37 (18.01)	120.91 (22.67)	244.77 (33.66)	217.81 (27.59)	221.25 (12.82)
Productivity aboveground vascular plant biomass (g/m2)	145.78 (19.05)	149.33 (13.03)	136.93 (40.40)	202.17 (24.54)	253.05 (74.27)	242.06 (11.45)
Standing crop vascular plant biomass (g/m2)	64.30 (9.65)	111.43 (12.54)	78.62 (22.91)	179.99 (42.29)	333.09 (103.69)	207.83 (18.59)
Standing crop vascular plant biomass (g/m2)	35.29 (6.14)	32.18 (4.95)	21.74 (7.03)	156.39 (21.62)	282.78 (62.75)	222.72 (12.69)
Species richness (#)	20.00 (1.52)	18.00 (3.06)	19.00 (1.15)	27.50 (1.89)	36.00 (4.36)	35.67 (2.67)
Species richness (#)	17.00 (1.82)	15.00 (2.08)	15.67 (3.93)	36.50 (1.77)	39.67 (3.84)	42.00 (0.58)
Vascular species richness (#)	12.80 (2.18)	13.67 (4.26)	12.33 (0.67)	22.83 (1.49)	32.67 (4.98)	30.67 (1.76)
Vascular species richness (#)	11.00 (2.28)	11.00 (2.65)	10.00 (3.79)	33.00 (1.24)	36.67 (3.53)	39.00 (1.00)
Average Ellenberg acidity value (-)	4.62 (0.56)	4.76 (0.30)	4.44 (0.61)	6.47 (0.44)	6.26 (0.80)	6.57 (0.25)
Average Ellenberg acidity value (-)	4.66 (0.80)	4.29 (0.81)	4.79 (0.98)	6.68 (0.37)	6.32 (0.36)	6.62 (0.27)
Average Ellenberg moisture value (-)	3.82 (0.10)	4.34 (0.21)	3.90 (0.07)	4.13 (0.30)	4.62 (0.28)	4.30 (0.27)
Average Ellenberg moisture value (-)	4.01 (0.13)	4.43 (0.19)	3.88 (0.07)	3.84 (0.28)	4.59 (0.08)	3.93 (0.15)
Average Ellenberg nutrient value (-)	2.62 (0.21)	3.82 (0.36)	2.75 (0.27)	2.99 (0.40)	4.72 (0.87)	4.10 (0.33)
Average Ellenberg nutrient value (-)	2.57 (0.25)	3.58 (0.75)	2.86 (0.26)	2.76 (0.47)	5.05 (0.54)	3.46 (0.59)
Number of moss & lichen species (#)	7.20 (0.86)	4.33 (1.20)	6.67 (1.33)	4.67 (1.17)	3.33 (0.67)	5.00 (1.15)
Number of moss & lichen species (#)	6.00 (1.10)	4.00 (0.58)	5.67 (0.67)	3.50 (0.85)	3.00 (1.00)	3.00 (1.15)

VII.4 LMM or year, area and management on dune grasslands

Results of 3-way lineair mix model with plot as random factor of dunes for the effect of year (2018/ 2019), management (control/ sand depostion), area (Luchterduinen (LD) / Newborough Warren (NB)), and their interactions. P-values are shown with simbols; ***p<0.001, **: p<0.01, *: p<0.05, (*): p<0.1, ns: p>=0.1. The number of plots for each category was 5 (LD flat), 3 (LD north-facing slope), 3 (LD south-facing slope), 6 (NB flat), 3 (NB north-facing slope), and 3 (NB south-facing slope). F values and their significance level (p-values) of LMM are shown.

Variable	Trans-formation	area	man	year	area * man	area * year	man * year	man * year * area	Shapiro p	Levene p	Random Effect p
Average clonal spread (cm)	nl(x+1	**14.83 *** **	2.34 ns	**8.91 ** **	0.00 ns	**6.52 ***	1.71 ns	0.25 ns	**0.902**	**0.511**	0.092
Average Ellenberg acidity value (-)	not	**13.27 ** **	1.10 ns	0.02 ns	0.95 ns	4.01 (*)	0.04 ns	4.75 *	**0.862**	**0.067**	**0.000**
Average Ellenberg nutrient value (-)	nl(x+1	0.58 ns	**5.20 ***	**5.00 ***	0.01 ns	**6.22 ***	0.24 ns	1.73 ns	**0.905**	**0.497**	**0.000**
Average maximum canopy height (m)	nl(x+1	0.43 ns	**7.38 ***	0.00 ns	0.03 ns	0.51 ns	0.98 ns	0.09 ns	**0.065**	**0.355**	**0.000**
Average minimum canopy height (m)	nl(x+1	2.98 (*)	**9.23 ** **	0.08 ns	0.00 ns	1.60 ns	0.71 ns	0.04 ns	0.028	**0.430**	**0.002**
Average number of clonal offspring (#)	not	0.21 ns	0.00 ns	0.09 ns	0.58 ns	**6.34 ***	0.43 ns	0.21 ns	**0.842**	**0.987**	0.053
Average root resprout (0/1)	not	0.24 ns	0.00 ns	**7.57 ***	0.00 ns	**9.79 ** **	2.41 ns	1.64 ns	**0.380**	**0.576**	**0.000**
Average shoot life span (-)	nl(x+1	3.97 (*)	0.30 ns	**16.38 *** **	0.41 ns	1.21 ns	**4.29 ***	0.32 ns	**0.539**	**0.763**	**0.001**
Average specific leaf area (mm2/mg)	nl(x+1	2.64 ns	0.40 ns	**4.47 ***	1.04 ns	0.06 ns	1.72 ns	0.14 ns	**0.385**	0.041	**0.000**
Bare ground cover (%)	nl(x+1	3.25 (*)	2.68 ns	3.40 (*)	**9.39 ** **	1.51 ns	0.53 ns	2.61 ns	**0.425**	**0.319**	0.274
Cumulative grass cover (%)	nl(x+1	**7.83 ***	3.84 (*)	**8.14 ** **	1.43 ns	**38.82 *** **	0.03 ns	0.74 ns	**0.940**	**0.320**	**0.001**
Cumulative herb cover (%)	nl(x+1	**56.01 *** **	0.13 ns	**15.57 *** **	2.70 ns	0.63 ns	0.42 ns	2.84 ns	**0.114**	**0.221**	**0.000**
Cumulative lichen cover (%)	nl(x+1	2.74 ns	**4.28 ***	**10.34 ** **	0.20 ns	**4.52 ***	0.21 ns	3.37 (*)	0.004	**0.488**	**0.000**
Cumulative moss cover (%)	not	**66.74 *** **	0.35 ns	0.01 ns	0.01 ns	4.13 (*)	0.71 ns	0.02 ns	0.023	**0.781**	**0.005**
Cumulative woody species cover (%)	not	2.38 ns	0.13 ns	0.00 ns	0.05 ns	0.05 ns	0.36 ns	0.14 ns	0.000	**0.215**	**0.000**
Height vascular stand (cm)	nl(x+1	0.79 ns	0.51 ns	0.11 ns	0.61 ns	**6.14 ***	1.37 ns	2.59 ns	0.022	**0.716**	**0.006**
Moss species richness (#)	nl(x+1	0.80 ns	0.62 ns	**11.97 ** **	3.95 (*)	0.75 ns	0.16 ns	0.44 ns	**0.849**	**0.666**	**0.000**
N-fixing species richness (#)	not	**73.75 *** **	1.95 ns	2.60 ns	0.94 ns	2.93 ns	0.24 ns	0.45 ns	**0.663**	**0.457**	0.085
Productivity aboveground vascular plant biomass (g/m2)	not	**13.98 ** **	0.10 ns	0.38 ns	0.00 ns	**5.77 ***	1.88 ns	0.85 ns	**0.200**	**0.056**	**0.000**
Root biomass (g/m2)	not	**44.59 *** **	1.67 ns	**38.39 *** **	0.31 ns	**6.13 ***	0.02 ns	4.54 *	**0.822**	**0.120**	0.535
Shannon index (-)	not	**50.43 *** **	0.02 ns	0.57 ns	4.14 (*)	**50.41 *** **	0.04 ns	0.09 ns	**0.126**	**0.547**	**0.000**
Species richness (#)	not	**65.98 *** **	0.17 ns	**13.97 ** **	0.00 ns	**28.83 *** **	0.63 ns	3.77 (*)	**0.986**	**0.840**	**0.001**
Standing crop vascular plant biomass (g/m2)	nl(x+1	**46.69 *** **	1.82 ns	**27.68 *** **	0.35 ns	**15.41 *** **	0.55 ns	0.00 ns	**0.644**	**0.753**	**0.000**
Sum of vascular plant cover	nl(x+1	**112.29 *** **	1.75 ns	**19.15 *** **	1.24 ns	**57.50 *** **	1.17 ns	3.75 (*)	**0.587**	**0.146**	**0.040**
Total lichen cover (%)	nl(x+1	0.79 ns	**4.39 ***	**5.15 ***	1.09 ns	0.39 ns	0.11 ns	2.82 ns	0.000	**0.574**	**0.000**
Total moss cover (%)	not	**59.75 *** **	0.11 ns	0.02 ns	0.00 ns	2.80 ns	0.46 ns	0.04 ns	0.036	**0.731**	**0.007**
Total moss-lichen cover (%)	not	**60.33 *** **	0.27 ns	0.05 ns	0.00 ns	2.53 ns	0.37 ns	0.01 ns	0.043	**0.768**	**0.007**
Vascular species richness (#)	nl(x+1	**55.61 *** **	1.49 ns	**15.91 *** **	1.74 ns	**37.04 *** **	0.01 ns	3.84 (*)	**0.872**	**0.952**	**0.000**

VII.5 LMM or year, area and slope on dune grasslands

Results of 3-way lineair mix model with plot as random factor of dunes for the effect of year, slope (flat / north-facing slope / south-facing slope), area (Luchterduinen (LD) / Newborough Warren (NB)), and their interactions. P-values are shown with simbols; ***p<0.001, **: p<0.01, *: p<0.05, (*): p<0.1, ns: p>=0. None of the plots are subject to management (i.e. sand deposition). F values and their significance level (p-values) of LMM are shown.

Variable	Trans-formation	area	slope	year	area * slope	area * year	slope * year	slope * area * year	Shapiro p	Levene p	Random Effect p
Standing crop vascular plant biomass (g/m2)	ln	**73.53 *** **	2.56 ns	**87.83 *** **	0.87 ns	**79.47 *** **	**4.60 ***	**6.08 ***	**0.827**	**0.502**	**0.000**
Productivity aboveground vascular plant biomass (g/m2)	ln	**17.45 *** **	0.06 ns	1.82 ns	0.08 ns	**7.57 ***	0.54 ns	2.26 ns	**0.260**	**0.890**	**0.000**
Species richness (#)	non	**103.57 *** **	1.18 ns	**5.63 ***	2.63 ns	**30.29 *** **	0.81 ns	0.72 ns	**0.538**	**0.977**	**0.012**
Vascular species richness (#)	non	**105.99 *** **	1.73 ns	**20.69 *** **	1.72 ns	**53.41 *** **	2.18 ns	1.20 ns	**0.522**	**0.841**	**0.000**
Moss species richness (#)	ln	**6.73 ***	1.05 ns	**5.19 ***	0.25 ns	0.56 ns	0.51 ns	0.38 ns	**0.673**	**0.848**	**0.013**
N-fixing species richness (#)	non	**63.73 *** **	0.80 ns	0.40 ns	0.09 ns	1.04 ns	0.19 ns	**4.23 ***	**0.752**	**0.958**	**0.014**
Shannon index (-)	ln	**46.86 *** **	0.63 ns	0.05 ns	2.73 (*)	**22.47 *** **	0.19 ns	0.85 ns	**0.995**	**0.585**	**0.019**
Average Ellenberg nutrient value (-)	ln	2.13 ns	**5.52 ***	1.49 ns	0.50 ns	0.29 ns	0.26 ns	1.89 ns	**0.375**	**0.972**	**0.000**
Average Ellenberg acidity value (-)	non	**19.91 *** **	0.16 ns	0.04 ns	0.05 ns	0.01 ns	0.12 ns	0.61 ns	**0.885**	**0.751**	**0.003**
Species cover with Ellenberg moisture value (%)	ln	**10.86 ** **	0.06 ns	**7.02 ***	0.78 ns	2.48 ns	1.69 ns	**5.38 ***	**0.888**	**0.946**	**0.008**
Cumulative moss cover (%)	non	**39.88 *** **	0.11 ns	1.42 ns	0.02 ns	**6.63 ***	0.42 ns	0.36 ns	**0.938**	**0.746**	**0.000**
Cumulative lichen cover (%)	non	1.49 ns	2.11 ns	2.97 ns	0.24 ns	**4.56 ***	0.49 ns	1.00 ns	0.000	**0.282**	**0.013**
Cumulative herb cover (%)	ln	**71.01 *** **	0.94 ns	**4.86 ***	1.22 ns	**5.69 ***	0.10 ns	1.63 ns	**0.131**	**0.611**	**0.006**
Cumulative grass cover (%)	non	3.51 (*)	0.03 ns	**10.83 ** **	0.02 ns	**20.10 *** **	0.69 ns	0.10 ns	**0.512**	**0.993**	**0.000**
Cumulative woody species cover (%)	ln	**24.66 *** **	2.15 ns	0.00 ns	2.03 ns	0.76 ns	0.79 ns	0.12 ns	**0.164**	**0.238**	**0.000**
Average maximum canopy height (m)	ln	0.10 ns	1.61 ns	0.72 ns	0.93 ns	**15.74 *** **	0.53 ns	2.69 (*)	**0.629**	**0.541**	**0.000**
Average minimum canopy height (m)	ln	0.12 ns	**4.57 ***	0.41 ns	2.48 ns	**4.96 ***	0.22 ns	0.70 ns	**0.210**	**0.139**	**0.003**
Average specific leaf area (mm2/mg)	ln	**4.63 ***	2.50 ns	0.72 ns	0.17 ns	0.41 ns	0.23 ns	0.31 ns	**0.405**	**0.741**	**0.013**
Average shoot life span (-)	non	**4.66 ***	0.73 ns	**6.61 ***	0.89 ns	0.24 ns	1.18 ns	1.70 ns	**0.401**	**0.584**	**0.017**
Average number of clonal offspring (#)	non	**6.18 ***	0.51 ns	0.14 ns	0.95 ns	1.27 ns	0.26 ns	1.06 ns	**0.742**	**0.948**	0.510
Average clonal spread (cm)	ln	**7.33 ***	0.70 ns	**18.93 *** **	0.25 ns	**18.40 *** **	0.78 ns	0.69 ns	**0.268**	**0.859**	**0.001**
Average root resprout (0/1)	non	2.11 ns	**3.94 ***	**4.54 ***	1.25 ns	**22.22 *** **	1.72 ns	0.35 ns	**0.113**	**0.914**	**0.001**

Attachment VIII Estimate of moss biomass from cover and height

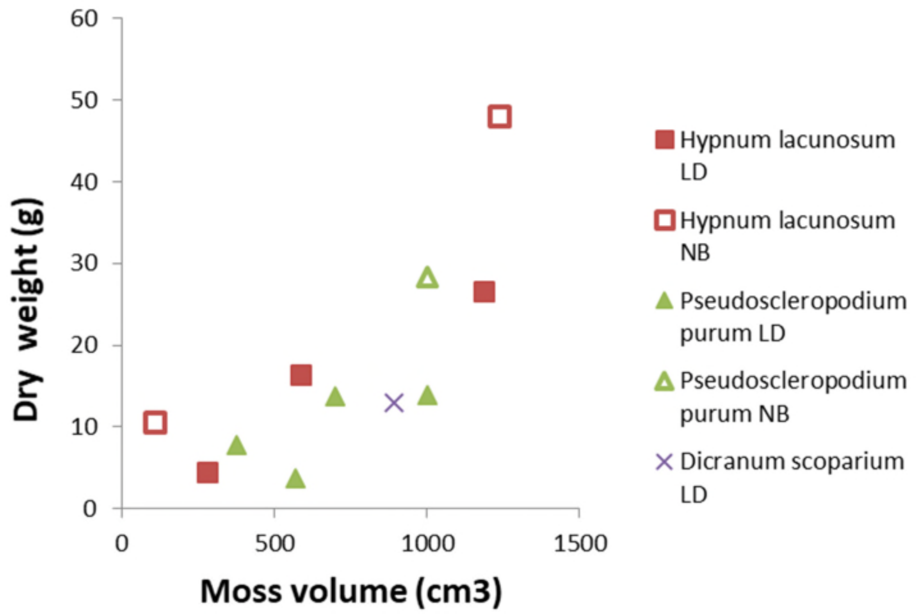


Figure 68. Relation between dry weight and volume of moss. Volume was estimated by multiplying average height and coverage of moss within 25 x 25 cm plot. Results are shown separately for plots which were dominated by different moss species. Mosses were sampled in 7 plots in Luchterduinen ('LD') and 3 plots in Newborough Warren ('NB').