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Chapter 1

Introduction

Scope of this thesis

In this thesis field surveys and experiments are combined to explain changes in the soil and vegetation of inland dunes over the period 1950-2007. An important part of this work is devoted to the relation between nitrogen deposition and the vegetation. It builds upon previous studies on the vegetation of inland dune landscapes and the effects of nitrogen deposition in dry, acidic habitats.

Compared to the earlier studies on inland dunes, this research project had a wider geographical scope, comprising twenty inland dune areas in a gradient from low to high nitrogen deposition and differing in size and in the extent of active drift sand (bare sand).

The main research questions were:

- At what rate does succession proceed in inland dunes and what is the effect of nitrogen deposition on this succession and its rate?
- What is the impact of nitrogen deposition on species diversity in inland dunes?
- What is the impact of nitrogen deposition on soil processes and nutrient availability in the different succession stages in inland dunes?
- Does nitrogen deposition increase the rate of invasion of the bryophyte *Campylopus introflexus*?

In all chapters, results are translated into management measures, paying particular attention to mitigation of the effects of nitrogen deposition and to the conservation of relict species that occur in primary succession stages. The introductory part mainly describes previously published research. Additionally, it pays attention to topics that do not fit into one of the succeeding chapters, but are relevant for the study as a whole. These include the composition of the parent material, the flora of inland dunes, and the modelling and measuring of nitrogen deposition.

A short history of the Dutch inland dunes

Inland sand dunes occur in a narrow belt running from East England to the Baltic region (Fig. 1.1). In this belt, Weichselian cover sands abound, marked by their uniform grain size and gently sloping landscape (Koster 1995). These sands in particular acted as a source for the eolian drift sands that formed as a result of anthropogenic land degradation during the Late Holocene.

Already in the Bronze Age (3000 BC), extensive logging had resulted in removal of most of the forest on the sand belt (Hacke-Oudemans 1976). Grazing turned the area into heath and, in places, sand started to drift (Koster 2005a; Koster 2009). In the Middle Ages, sod-cutting in heath became popular, sods being used as an addition to manure and to fertilize arable land, resulting in plaggen soils where sod-based manure was applied (Pape 1970; Spek 1992). This practice, in combination with overexploitation (grazing and burning) of the heaths, reached its zenith in the 18th

Fig. 1.1. The European sand belt, the region in which inland dune systems occur (after Koster 2005).

and 19th centuries, inducing a massive degradation of the heaths and concurrent development of drift sands in that period. Radiocarbon dating showed that drift sands were formed between 600 and 1900 (Castel 1991), although recent studies revealed that luminescence dating may yield an improved accuracy (Koster 2005b). There is also some debate on the exact causes for the dramatic expansion of drift sands, with other authors ascribing this expansion to sheep grazing in combination with a relatively cold and windy climate (Heidinga 1984; Koomen *et al.* 2004; Riksen *et al.* 2006; Koster 2010).

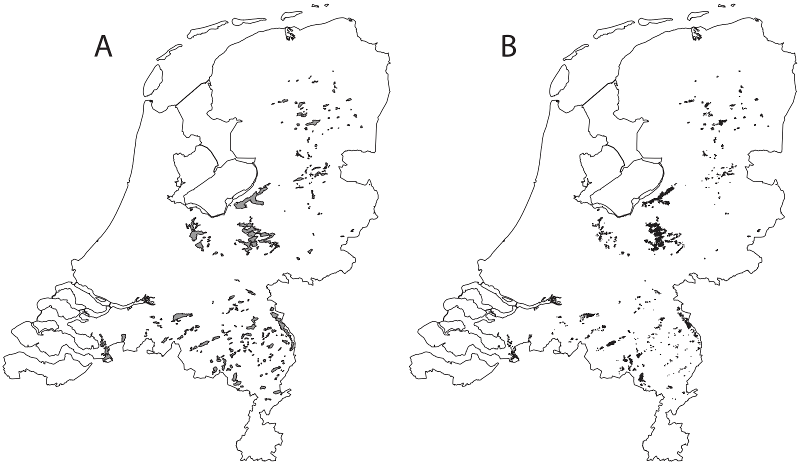

Fig. 1.2. A. The occurrence of drift sands soils in The Netherlands (Jungerius & Riksen 2010); B. Currently non-forested inland dune landscape (source: TOP10Vector 2009).

Around 1850, the industrial revolution and associated economic and technological changes, notably the introduction of chemical fertilizer, led to a decrease in sheep grazing. It also led to agricultural reclamation and afforestation of former ‘waste lands’. This is particularly true for drift sands since these were unsuited for agriculture. In The Netherlands, especially between 1910 and 1950, large drift sand areas have been turned into pine forest (Koster 2009). Nowadays, around 2% of the total original drift sand area is still typical drift sand landscape, characterized by open sand and sand dune grasslands. Since 1980, in former drift sand reserves modest attempts started to maintain or even increase open drift sand landscapes through deforestation (Riksen *et al.* 2006). Stimulated by the European Habitat Directive of 1992, these attempts increased and were incorporated in the management plans of most nature conservation organizations. Fig. 1.2 shows the distribution of drift sand soils (total cover: 823 km^2) and the current distribution of non-forested inland dune landscape (total cover: 110 km^2).

Parent material

Inland dune sand largely originates from cover sands, which are Pleistocene eolian deposits (Koster 2005a; Sevink & de Waal 2010). The deflated material includes soils developed in the cover sand, notably podzols that contain fair amounts of organic matter in their various horizons. Drift sand therefore holds a small amount (approximately 0.1%) of organic matter (e.g. Riksen *et al.* 2008).

Texture

Cover sand is the main source of drift sand and the Dutch cover sands have a uniform texture. As a result, differences in soil texture between the main drift sand regions (Fig. 1.3) are small but still significant: The sands in the northern parts of the country (Drenthe), the West (Utrecht) and South (Noord-Brabant) have somewhat higher levels of loam than the other regions, but this is limited to a few mass percentages. The effect of loam is, however, clearly visible in the field, as loam stabilizes dune slopes and erosion rills, which in turn provide a habitat for species confined to vertical soil surfaces such as liverworts and many fauna species (Nijssen *et al.* 2011).

The Veluwe area shows the most uniform soil texture with a grain size of mostly 0.125-0.250 mm (see also Koster 1982). The only significant difference (chi^2: $P < 0.001$) in texture was found in old river dunes of the river Meuse. These sands are essentially cover sands mixed with coarser Holocene river deposits originating from the Ardennes (Tebbens *et al.* 2000), making the average grain size twice as large as in the other drift sands. Within a drift sand reserve, coarser sands may occur in deflation zones, where fine material has been blown away (Riksen & Goossens 2007). Such so-called desert pavements have been sampled by Hasse (2005), who found up to 8% of coarse material (> 2 mm) in some samples.

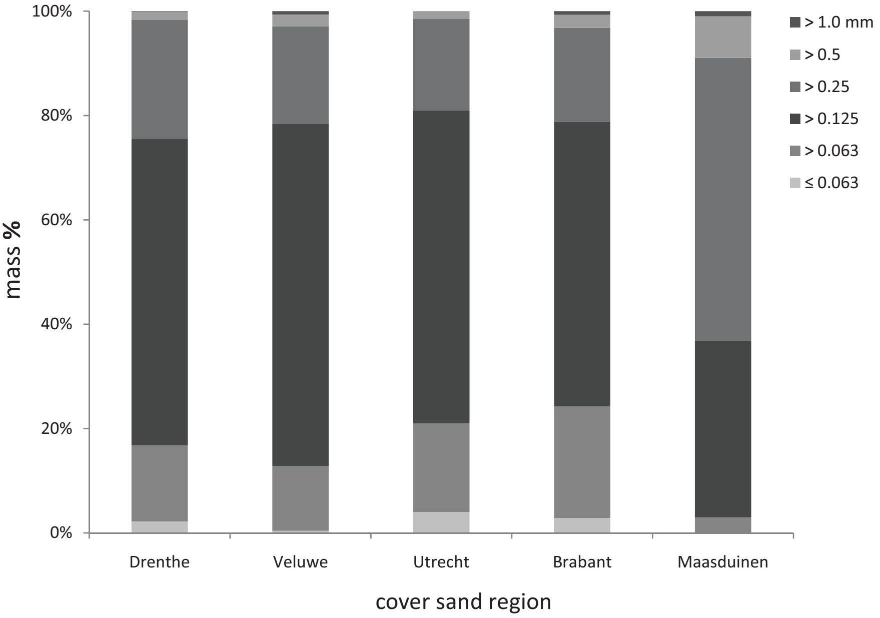

Fig. 1.3. Soil texture from bare sand for five different regions in The Netherlands (n = 31), analyzed using standard sieves varying from 0.063 to 1.0 mm in mesh size, showing minor differences except for the coarser river dune sands (Maasduinen) and absence of a loam fraction in the Veluwe.

Mineralogical composition

The mineralogy of drift sands depends on the origin of the source material and thus is strongly linked to the composition of cover sands, which exhibits regional differences (Crommelin 1964, 1965). Clearly local sources may lead to deviating composition such as the drift sand that is derived from Meuse sediment.

For the sand fractions of the drift sands, the mineralogical composition has been studied (e.g. Koster 2005a), showing that the northern sands have a lower mineral content than the southern sands. This is in line with the differences in composition of the cover sand. Drift sands may also be derived from river dunes and thus may consist of a mixture of sand from different sources. The middle to late Quaternary Meuse sediments are e.g. known to contain a relative high amount of Al and lower K and Mg (Tebbens *et al.* 1998), resulting in lower amounts of weatherable minerals (Sevink & de Waal 2010) in drift sands with a significant Meuse component.

As an example, the mineralogy of the soil of two major drift sand regions (Veluwe and Drenthe) was studied. Soil samples of drift sand deposits from the Drenthe region (Aekinge and Drouwen sites; n = 7) and Veluwe region (Kootwijk and Wekerom sites; n = 7) were finely ground, destructed in HF and the total element content measured on an inductively coupled plasma (ICP-OES) analyzer (Jackson 1985). Fig. 1.4 shows the relation between potassium and two combinations of metals occurring in pyroxene

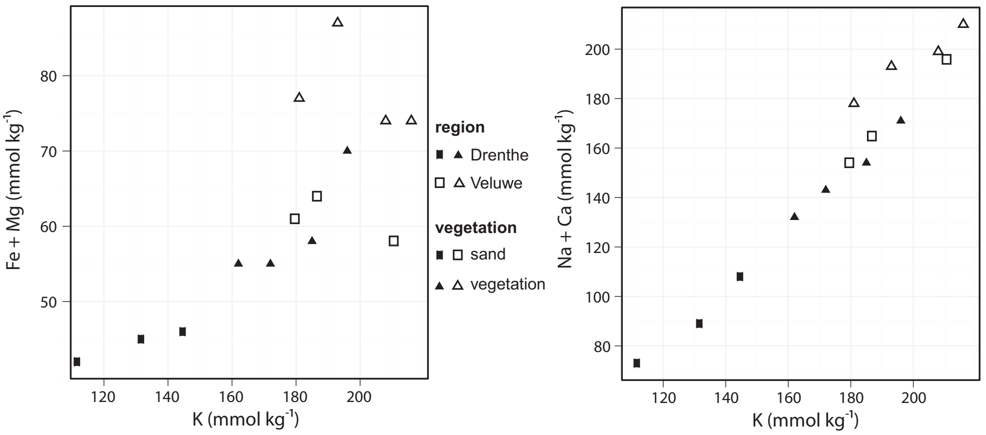

Fig. 1.4. Relations between elements in the upper 5 cm of drift sand soil in two regions for samples from bare sand and below vegetation, which include accumulated elements in the A_h horizon. Upper diagram: elements characteristic for pyroxene and biotite. Lower diagram: elements characteristic for plagioclase.

and biotite (Fe and Mg) and in plagioclase (Na and Ca). Measurements of the element content of bare and vegetated drift sand is included here, to show the effects of soil formation on the total stock of metals in the soil.

Drift sands of the Veluwe area have a significant ($P < 0.05$) higher content of Na, K, Mg, Ca, Al, Fe, Mn and Cr than Drenthe, whereas P content did not differ. The Ca:P ratio was around 10. The K:Al ratio was around 0.4. There was no significant difference in the K:Al, Ca:P and Fe:Mg ratios between the Drenthe and Veluwe regions. This shows that, except for the generally higher mineral content (other than quartz) of the Veluwe drift sands the mineral composition of both regions is more or less equal. The results also show large differences in mineral content within a region and drift sand site. If translated into percentages of non-quartz minerals, including feldspars, micas and pyroxenes, the values most probably range between 5 and 10%, with only some samples reaching values up to 15%. This is in line with the observations by Koster (2005a) and Castel (1991).

Although drift sand is largely derived from cover sand, it can be described as a matured, weathered form of cover sand, with less easily weatherable minerals. This is partly due to the intensive weathering in the Podzols developed in cover sand (see e.g. Sevink *et al.* 1970; Mokma & Buurman 1982). Thus drift sand will contain less easy weatherable minerals than cover sand and once stabilized will release lower amounts of base metals and other weathering products. Consequently, weathering will hardly contribute to the neutralization of acids (e.g. low acid neutralizing capacity of the substrate). Higher levels of base metals in the A_h horizons (Fig. 1.4: sand vs. vegetation) can most probably be attributed to the accumulation of base metals in organic matter (either in structural tissues or adsorbed) and to their supply by atmospheric deposition. The contribution of weathering is likely to be insignificant at the time scale in which these soils have developed and under these conditions.

Drift sands, if not completely derived from eluvial Podzol horizons, contain small amounts of clay minerals and sesquioxides, present as a coating on sand grains (Emmer & Verstraten 1993; Koster 2005a; Sevink & de Waal 2010). These coatings give drift sand its characteristic yellowish colour, though it is rather greyish in comparison with the truly yellow cover sand because of the presence of some organic matter. These clay minerals and sesquioxides are largely responsible for the acid neutralizing capacity of these sands, as was demonstrated by van der Salm (1999) for cover sands.

Inland dune soils

In the open inland dune landscape, the vegetation succession is highly correlated with soil development, starting with open sand, poor in nutrients and with a very low amount of organic matter, and ending in A(E)C micropodzols (van Rheenen *et al.* 1995; Koster 2005a). Further development of inland dune soil takes places below later vegetation succession stages, namely forest and heath, where a variety of well-developed soils (mainly podzols) can be formed. Emmer (1995) described the soil development and humus forms in primary *Pinus* forests and first showed the changing nutrient composition in such pine forests over time. However, soil development in the range from open sand to pioneer vegetation has not been thoroughly studied. Among the few studies are those by Paus (1997) and Hasse (2005). Paus investigated the main soil parameters (pH, loss on ignition) for most lichen species occurring in a variety of inland and coastal dunes in Northwest Europe. Hasse (2005) described vegetation classes and included the main soil parameters (pH, loss on ignition, N content, texture) for a limited number of sites where Spergulo-Corynephoretum grasslands occur. These studies showed that during primary succession the amount of organic matter in the mineral soil accumulates and pH(H_2O) decreases from about 5.5 (bare sand) to 3.8 (dry heath).

Primary succession on bare sand and the expansion of naturally established trees have been studied previously, but not on a nation-wide scale (e.g. Ketner-Oostra & Masselink 1999; Hasse 2005; Ujházy *et al.* 2011). The comparison of multiple sites is therefore one of the subjects of this thesis. Different geomorphological units can be recognized, i.e. dunes and blowouts. Due to erosion, vegetation succession may be slower on dunes and faster in blowouts. Quantifying these rates of succession can be used to estimate the efforts needed to conserve a certain area of open sand and pioneer vegetation in inland dunes.

None of the previous studies focussed on the effects of nitrogen deposition on nitrogen availability, soil acidification and succession. These effects were studied by analyzing soil and vegetation properties over gradients in N deposition, adding nutrients to measure the effect of nitrogen addition and through a mineralization experiment. The latter also helped to understand soil processes such as nitrogen mineralization, which is of importance for plant growth and therefore succession rate.

The flora of inland dunes

Inland dunes are known for their plant biodiversity. They are composed of mostly cryptogams, which are adapted to acid, semi-arid environments, the grasses *Corynephorus canescens*, *Festuca ovina* subsp. *hirtula*, *Festuca filiformis* and *Agrostis capillaris*, the bryophytes *Campylopus introflexus* (a neophyte occurring since the 1960s) and *Polytrichum piliferum* and lichens in the genera *Cladonia, Cetraria* and *Stereocaulon* (Masselink 1994; Haveman & van Ravensberg 2003; Hasse & Daniëls 2004) belong to the most common species in this habitat.

Apart from the bryophytes, most species have been the subject of recent taxonomical studies. In the latest edition of Heukels' Flora (van der Meijden 2005), the names of both inland dune *Festuca* taxa were changed following a study by Haveman & van Ravensberg (2003). In older literature, the names *Festuca ovina* and *F. tenuifolia* have been used in a wide sense including both taxa.

Name changes in *Cladonia* species make it especially difficult to compare older and recent vegetation studies in inland dunes. Names of lichens in the genus *Cladonia* have been changing constantly since the 1940s. In the 1970s many chemical varieties in the *Cladonia grayi*-group were recognized by Sipman (1973), including *Cladonia chryptochlorophaea* and *C. novochlorophaea*. Later studies have shown that these varieties reflect only genetic variation within a population of the same species (Culberson *et al.* 1988) and that there was no ecological difference between the varieties (Paus 1997). *Cladonia rei* was included in *Cladonia subulata* for practical reasons, although both species , especially *C. rei,* occur rather infrequent in drift sands. Also *Cladonia bergsohnii, C. bacillaris* and *C. pleurota* are considered chemotypes of *C. floerkeana, C. macilenta* and *C. coccifera,* respectively. The *Cladonia pyxidata*-group appeared to be composed of three distinct taxa: the base-tolerant *Cladonia pocillum*, the montane species *C. pyxidata* and the inland dune species *Cladonia monomorpha* (Aptroot *et al.* 2001). The *Cladonia cervicornis*-group was divided into three distinct species: *Cladonia cervicornis* s.s., *C. pulvinata* and *C. verticillata* (van Herk & Aptroot 2003). Since 1995, another typical inland dunes species is reported in The Netherlands: *Cladonia borealis,* which was formerly included in *Cladonia coccifera*.

Large collections of distribution data on cryptogams became available over the past ten years and can now be used in spatial analyses. Data from the Dutch Bryological and Lichenological Society and the Dutch Mycological Society were combined with the map in Fig. 1.2a. All species with a distribution pattern overlapping for 20% or more with drift sand soils are listed in Table 1.1. Surprisingly, most common, vegetation-forming species are absent in this list, e.g. all common drift sand bryophytes and most vascular plants. Apparently most of the common species of drift sands occur just in the margin of their ecological niche. Most species in the list are generally rare and are present on the Red List of endangered species in The Netherlands. Most of the listed bryophytes and the lichens *Cladonia squamosa, Cladonia sulphurina* and *Pycnothelia papillaria* are on the verge of extinction. Mycorrhizal fungi occur mostly in forest margins, where they live on young soils with a thin solum and litter layer.

Table 1.1 Species of plants, bryophytes, lichens, and macrofungi with a distribution pattern which falls for 20% or more within drift sand areas. Data is based on occurrence data in a km square grid for the period 1800-2008 (source: Dutch Bryological and Lichenological Society and Dutch Mycological Society, January 2010). * The exact number of km^2 squares is not available for *Festuca ovina* ssp. *hirtula*, and an expert guess is used instead.

Species group	% in drift sands	km^2 squares in drift sands	km^2 squares total
Vascular plants			
Festuca ovina ssp. hirtula	c. 50%	c. 200 *	c. 400 *
Bryophytes			
Barbilophozia floerkei	50%	3	6
Barbilophozia kunzeana	27%	49	182
Oligotrichum hercynicum	27%	59	220
Scapania compacta	20%	46	235
Tetraplodon mnioides	33%	2	6
Lichens			
Cetraria islandica	38%	17	45
Cladonia borealis	57%	43	76
Cladonia crispata	51%	163	320
Cladonia gracilis	29%	91	318
Cladonia monomorpha	58%	42	72
Cladonia phyllophora	50%	4	8
Cladonia pulvinata	47%	98	209
Cladonia squamosa	48%	11	23
Cladonia strepsilis	61%	113	185
Cladonia sulphurina	50%	4	8
Cladonia uncialis	33%	78	235
Cladonia verticillata	56%	39	70
Cladonia zopfii	52%	174	333
Micarea leprosula	50%	31	62
Micarea viridileprosa	33%	17	52
Placynthiella oligotropha	45%	36	80
Pycnothelia papillaria	33%	1	3
Stereocaulon condensatum	79%	79	100
Stereocaulon saxatile	27%	4	15
Mycorrhizal fungi			
Coltricia perennis	20%	92	455
Cortinarius fusisporus	37%	59	159

Species group	% in drift sands	km^2 squares in drift sands	km^2 squares total
Gomphidius roseus	20%	65	331
Hebeloma cylindrosporum	56%	9	16
Hygrophorus hypothejus	22%	62	276
Pseudoomphalina pachyphylla	33%	19	57
Psilocybe polytrichi	33%	16	49
Rhizopogon luteolus	33%	111	336
Rhodocybe parilis	39%	7	18
Tricholoma albobrunneum	36%	54	151
Tricholoma equestre	34%	60	176
Tricholoma portentosum	36%	38	106

Vegetation succession in inland dunes

The succession from open sand to heath and forest has been described by many authors (Fanta 1986, Prach *et al.* 1993, Hasse 2005, Ketner-Oostra & Sýkora 2008). Hasse (2005) and Ketner-Oostra & Sýkora (2008) defined several vegetation classes to which the various primary succession stages can be attributed. Fig. 1.5 shows the simplified chronosequence of the vegetation classes used in this study. The main classes were used for interpretation of aerial photographs, whereas more detailed subclasses were used for vegetation mapping.

Sand dune vegetations belong to the association of the Spergulo-Corynephoretum, which is usually subdivided into three categories, i.e. typicum, inops (species poor variant) and cladonietosum (dominated by lichens) (Weeda *et al.* 1996). More detailed descriptions of associations within the Spergulo-Corynephoretum include bryophytes, lichens and algae, and are called microsynusiae (Biermann & Daniëls 1997). These microsynusiae have been used in further studies by these authors and co-workers (Biermann & Daniëls 2001; Hasse *et al.* 2002; Hasse & Daniëls 2004; Daniëls *et al.* 2008). In this thesis, syntaxonomy is not often used. Instead, vegetation classes, combining soil, vegetation structure and geomorphological units are defined. Table 1.2 shows how vegetation classes and subclasses are related to the syntaxonomy of inland dunes vegetation types.

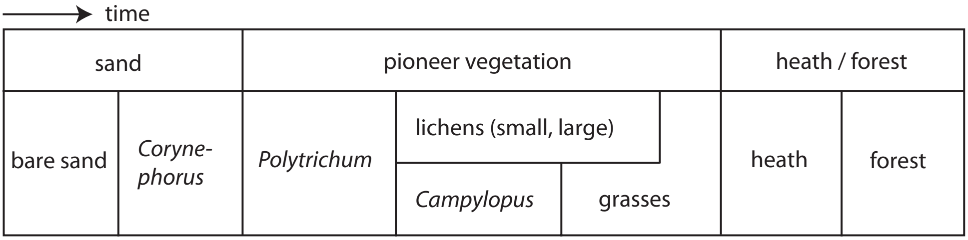

Fig. 1.5. Vegetation succession in inland dunes using a classification in main (above) and subclasses (below) based on Hasse (2005).

Table 1.2. Description of the vegetation subclasses and translation to syntaxa in Weeda *et al.* (1996) and Hasse (2005).

Vegetation subclasses	**Main syntaxon (Weeda et al. 1996)**
Open sand (no vegetation)	-
Corynephorus canescens and algal crusts on open sand	Spergulo-Corynephoretum inops
Polytrichum piliferum mats, few grasses present	Spergulo-Corynephoretum inops
Campylopus introflexus mats, few grasses present	Spergulo-Corynephoretum (*Campylopus introflexus* derivate association)
Small cup-lichens and grass tussocks (with abundant *Cladonia pulivinata, C. cervicornis, C. glauca, C. strepsilis, C. borealis, Festuca* spp.)	Spergulo-Corynephoretum cladonietosum
Large reindeer lichens and dense grasses (with abundant *Cladonia portentosa, C. unicialis, C. zopfii, Agrostis vinealis*)	Spergulo-Corynephoretum cladonietosum
Grasses dominant, with sparse mosses and lichens, including logging sites with stumps, *Deschampsia flexuosa* & *Carex arenaria* and forest floor bryophytes	*Carex arenaria* derivate of the Koelerio-Corynephoretea
Calluna vulgaris heath, usually with abundant lichens between the shrubs	Genisto anglicae-Callunetum (including the Juncus squarrosus-Oligotrichum hercynicum derivate of the Corynephorion canescenstis)
Pinus sylvestris and *Quercus robur* forest	Dicrano-Pinion, Betula-Quercetum

Vegetation subclasses	**Microcommunity (Hasse 2005)**
Open sand (no vegetation)	Grünalgen-Typ p.p. without vascular plants
Corynephorus canescens and algal crusts on open sand	Grünalgen-Typ p.p. with vascular plants
Polytrichum piliferum mats, few grasses present	*Polytrichum*-Typ
Campylopus introflexus mats, few grasses present	*Campylopus*-Typ
Small cup-lichens and grass tussocks (with abundant *Cladonia pulivinata, C. cervicornis, C. glauca, C. strepsilis, C. borealis, Festuca* spp.)	*Cladonia zopfii*-Typ + *Cladonia strepsilis*-Typ
Large reindeer lichens and dense grasses (with abundant *Cladonia portentosa, C. unicialis, C. zopfii, Agrostis vinealis*)	*Cladonia mitis*-Typ p.p. with low grass-cover
Grasses dominant, with sparse mosses and lichens, including logging sites with stumps, *Deschampsia flexuosa* & *Carex arenaria* and forest floor bryophytes	*Cladonia mitis*-Typ p.p. with high grass cover
Calluna vulgaris heath, usually with abundant lichens between the shrubs	*Cladonia mitis*-Typ p.p. as patches between heath
Pinus sylvestris and *Quercus robur* forest	-

Nitrogen deposition and its effect on soil and vegetation in dry, acid habitats

Without human activities, nitrogen deposition would be much lower in inland dunes in The Netherlands. In inland dunes, nitrogen deposition is 10 to 20 times higher than the natural background value of 1-2 kg N ha^{-1} yr^{-1}. Nitrogen is deposited in two ways: dry and wet. Dry deposition includes dust particles, such as $(NH_4)_2SO_4$ and absorbed gases (mainly NH_3) on humid surfaces. Wet deposition comprises the nitrogen dissolved in precipitation and includes NH_4^+ and NO_3^- ions. Industry and traffic are the most important sources of oxidized nitrogen, whereas livestock farms form the main source of ammonia. Livestock farms form the main source of nitrogen deposited in nature reserves and circa 60% of the wet deposition (de Haan *et al.* 2008).

Little information is available on the effect of nitrogen on soil and plants in inland dunes, but the main effects are likely to be comparable to those in *Calluna*-dominated heath on podzols and Scots pine forest on acid sandy soils, as for example described by Bobbink *et al.* (2010). The main form of nitrogen deposited in nature reserves in The Netherlands, reduced nitrogen (NH_x), can be toxic or inhibit seed germination (de Graaf *et al.* 1997, 1998; van den Berg *et al.* 2005). Nitrification of ammonium causes soil acidification (Tietema & Verstraten 1992) and leaching of metals in acid soils, such as aluminium (Al^{3+}) that can reach toxic levels for plants (Aerts & Bobbink 1999; Smit & Kooijman 2001). Addition of nitrogen changes the vegetation. In dry heaths, soil ammonium and also the Al:Ca ratio is negatively correlated with species diversity (de Graaf *et al.* 2009; Duprè *et al.* 2010; Maskell *et al.* 2010; Stevens *et al.* 2010). Lichens are widely used as highly sensitive bioindicators for ammonia, mostly by evaluating epiphytic lichen communities (e.g. van Herk 1999). Lichens are also used as a biomonitor, by analysing the nitrogen content in the lichen thallus (Hyvärinen & Crittenden 1998; Cape *et al.* 2009a; Remke *et al.* 2009; Olsen *et al.* 2010).

Local dominance of the bryophyte *Campylopus introflexus* was also related to nitrogen deposition (Ketner-Oostra & Sýkora 2008) and disturbance (Daniëls & Krüger 1996). However, strong evidence for the relation with nitrogen was lacking. As the species is a neophyte introduced during the 1960s, its expansion in Europe is still ongoing (Hassel & Söderström 2005). As the species was still expanding in the Netherlands, an increase of the species in long-term plot studies (e.g. Ketner-Oostra & Sýkora 2008) cannot be automatically attributed to atmospheric deposition. Therefore, in this thesis, sites with high and low N deposition are compared with respect to the abundance of *C. introflexus*.

Field and experimental studies

In the following chapters, field and experimental studies are described based on the research questions and hypotheses described in this introductory chapter.

In **chapter 2**, the large-scale vegetation development in the study areas is described for the period 1950-2007 in eight inland dune reserves. The effect of factors such as recreation and nitrogen deposition is studied. A prediction of the future development of the main vegetation classes (bare sand, pioneer vegetation and forest) is made.

In **chapter 3**, the soil and vegetation characteristics of the succession stages in inland dunes are presented. The influence of nitrogen deposition on soil acidification and concurrent alteration of the vegetation is discussed.

Chapter 4 zooms into the level of cryptogam mats and studies the potential mineralization of nitrogen in the soil in different succession stages in inland dunes under high and rather low N deposition. In this chapter, the authors also focus on the role of the ectorganic layer of bryophytes and lichens in N cycling.

Chapter 5 describes the results of a two-year field experiment with nitrogen and phosphorus addition that has been carried out in two inland dune sites, which particularly differ in nitrogen deposition.

Chapter 6 provides evidence for the relation between *Campylopus introflexus* dominance, soil organic matter content and nitrogen deposition.

In the synthesis, **chapter 7**, the conclusions of the chapters are briefly discussed in order to find an answer to the main research questions.

Fig. 1.6. Location of the eight main study sites.

Description of the study areas

Field studies were carried out in twenty inland dune sites, of which eight have been studied in more detail. Fig. 1.6 shows the location of the eight main study sites. Table 1.3 gives a summary of the main characteristics of the sites, including the total size of the reserve and the selected part for vegetation mapping. The sites are chosen to reflect a range in nitrogen deposition, size and geological history (northern, central and southern cover sands; former river dunes).

Table 1.3. General data on the eight main study sites.

Site name	Province	Total size (ha)	Studied area (ha)	Annual visitors x 1000	Rainfall mm a^{-1}	Geology
Aekingerzand	Friesland	100	39.6	50	750	Northern cover sands
Drouwenerzand	Drenthe	150	40.5	10	775	-
Lemelerberg	Overijssel	30	20.2	20	750	-
Loonse en Drunense duinen	Noord-Brabant	225	47.1	500	700	Southern cover sands
Kootwijkerzand	Gelderland	400	45.8	250	800	Central cover sands
Otterlosche zand	Gelderland	300	26.0	45	800	-
Wekeromse zand	Gelderland	100	86.0	50	800	-
Bergerheide	Limburg	20	15.1	0.5	700	River dunes

Nitrogen deposition: measuring, modelling and critical loads

Measuring nitrogen deposition

In this study, nitrogen deposition was measured in eight sites, using precipitation collectors and ammonia diffusion tubes. However, converting results from these measurements into actual deposition data is not as simple as it seems. There are different approaches to calculate the total nitrogen deposition, all based on the wet deposition and a contribution of dry deposition based on either terrain roughness or particle deposition velocity. High vegetation adsorbs or traps more dry deposition than low vegetation. Cape *et al.* (2009b) presented a formula to calculate the deposition of ammonia from the ammonia air concentration in combination with the particle deposition velocity, which actually reflects the adsorption of ammonia by the vegetation. High vegetation, like forest, traps more ammonia than low vegetations, such as grassland or bogs. This is supported by similar findings in inland dunes (forest versus grassland) in The Netherlands (Daniëls & Pott 2008).

Modelled nitrogen deposition

The so-called OPS (Operationeel model Prioritaire Stoffen) model in The Netherlands is based on emission data and terrain roughness and has been developed to predict the nitrogen deposition for any location (van Jaarsveld 2004) in a 1 x 1 km grid cell. Many inland dunes are situated within forested areas and the predicted deposition can be too high when a grid cell contains both forest and pioneer vegetation. The air concentrations of nitrogen compounds are calculated at 5 km resolution and downscaled to 1 km resolution, based on average terrain roughness. This data set is the most complete data source for nitrogen deposition, although little difference can be made between low vegetation and adjacent forest sites. Also errors in modelled deposition values can reach 20-30% (van Jaarsveld 2004).

Deposition data used in this study

In this study, nitrogen deposition has been measured during 2008-2009 by sampling wet deposition with monthly replaced precipitation traps, and dry deposition with monthly replaced ammonia diffusion tubes (Nijssen *et al.* 2011). The results are presented in Table 1.4, showing total wet deposition and the average ammonia concentration. The wet deposition consisted for 60-80% of NH_4^+. The total nitrogen deposition could then be calculated in two ways. First, assuming that terrain roughness is so low that almost no dry deposition occurs; the measured wet deposition can then be regarded as the lowest estimate for N deposition. Second, the total deposition can be calculated from the ammonia air concentration with a formula by Cape *et al.* (2009b) assuming a low particle deposition velocity of 15 mm s^{-1}. The latter is regarded here as an average estimate. OPS data, which are modelled from nitrogen emissions, are regarded as a high estimate.

Table 1.4. Different approaches to estimate the nitrogen deposition in pioneer vegetation in inland dunes. The measured data (2008-2009) can be regarded as a low estimate. An average estimate is based only on the atmospheric ammonia concentration (Cape *et al.* 2009b) for a particle deposition velocity of 15 mm s^{-1}. Modelled data (here for 2006) can be regarded as a high estimate. * source: Velders *et al.* (2002).

Site name	**Measurements**		**Calculated deposition**	**Modelled data**
	N_{wet}	NH_3	N_{tot} (Cape *et al.*)	Ntot (OPS)*
	kg (mol) ha^{-1} yr^{-1}	µg m^{-3}	kg (mol) ha^{-1} yr^{-1}	kg ha^{-1} yr^{-1}
Aekingerzand	11.0	5.8	24	28.9
Drouwenerzand	11.1	6.6	26	25.3
Lemelerberg	12.7	7.6	30	36.7
Loonse en Drunense duinen	-	7.5*	29	42.7
Kootwijkerzand	12.3	7.9	30	34.3
Otterlosche zand	-	7.0*	28	35.2
Wekeromse zand	13.9	9.7	41	50.3
Bergerheide	12.8	10.0	42	39.2

Modelled OPS data are used for ranking, describing or grouping sites, i.e. in chapter 2, 3 and 5. In chapters 4 and 6, the air concentration itself or deposition values calculated from ammonia air concentrations are used, by using the formula presented by Cape *et al.* (2009b). In order to estimate the ammonia air concentration for other sites, measurements dating from 2000-2001 are used (Velders *et al.* 2002). These are currently the best available data. The ammonia air concentration has dropped by 10-20% since 2001. However, the error in the measurements is of a similar order and differences in atmospheric ammonia concentration between sites are relatively large.

Critical load and critical level

A critical load for atmospheric deposition is the highest deposition that will not cause chemical changes leading to long term harmful effects on ecosystem structure and function (Nilsson & Grennfelt 1988). The critical load of nitrogen deposition for inland dune vegetation has been modelled by van Dobben *et al.* (2006), based on historical relevees and nitrogen deposition data. Their calculations resulted in a critical load of 10.4 kg N ha^{-1} yr^{-1}, a value which is below even the lowest estimate of N deposition (wet deposition only) in the studied sites (Table 1.4).

The critical level for ammonia was defined as “the concentration in the atmosphere above which direct adverse effects on receptors, such as plants, ecosystems or materials, may occur according to present knowledge” and has been estimated at 8 µg NH_3 m^{-3} (Posthumus 1988). This value is around the median value of the studied sites (Table 1.4).

Other studies have shown that for cryptogams, based on the exact definition of the critical load, this load is already met at very low N deposition and atmospheric ammonia concentrations. For example, chemical changes in bryophytes were already detected at values as low as 1 µg NH_3 m^{-3} in a study on the response of tissue N content to elevated N levels in bryophytes (Cape *et al.* 2009a). This shows that the critical load values must be interpreted with care and that they are usually within a range of gradual changes to the ecosystem.

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