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DOI
10.1002/esp.5402
Publication date
2022
Document Version
Final published version
Published in
Earth Surface Processes and Landforms

Received: 9 December 2021 | Revised: 11 March 2022 | Accepted: 22 March 2022
DOI: 10.1002/esp.5402

RESEARCH ARTICLE

ESPL WILEY

Blowout dynamics in lime-rich and lime-poor coastal dunes in the Netherlands

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Funding information
Dutch Ministry of Agriculture, Nature and Food security, through the OBN program, Grant/Award Number: report OBN223-DK

Abstract

Blowouts can mitigate the negative effects of acidification in the topsoil, especially in industrialized countries with high atmospheric nitrogen (N) deposition. However, blowout activity may differ between lime-rich and lime-poor dunes, which creates different regional responses and interactions between processes and patterns.

To further explore this, five Dutch dune sites were selected over the gradient from lime-rich and lime-poor dunes. We mapped blowout activity in 5 years between 1996 and 2017 with aerial photographs, and used transport potential, atmospheric N-deposition and rabbit density as explanatory variables. We also studied soil and plant parameters in the field in different stages of succession.

All sites showed fluctuations, but blowout activity net increased in the lime-rich sites, and decreased in the lime-poor sites. Differences in blowout activity could not be explained by sand transport potential, which differed between years, but not sites. Differences in blowout activity could to some extent be explained by rabbit density and exceedance of the critical N load, although the transition site between lime-rich and lime-poor dunes showed high blowout activity despite low rabbit density.

Differences in blowout activity between lime-rich and lime-poor dunes were also related to differences in topsoil chemistry, especially with respect to lime content, Fe content and different forms of phosphorus (P). High pH was a key factor, which reduced sensitivity to high N deposition through reduced P-availability to the vegetation, higher proportion of arbuscular mycorrhizal plants, which may improve food quality for rabbits, and lower root biomass, which may increase erodibility of the dune soil. High pH and low P availability may even occur in lime-poor dunes with a little lime, as long as blowouts stay active and counteract acidification. However, when pH values drop below 6.5, P availability to the vegetation will increase and start feedback processes leading to blowout stabilization.

KEYWORDS
aeolian activity, atmospheric N deposition, P availability, root biomass, sand transport

1 | INTRODUCTION

The coastal dune landscape is the result of interactions between aeolian and biological processes, and its dynamics produce a wide variation in landforms and vegetation types (Jungerius & Van der Meulen, 1988). In areas with a temperate climate, aeolian processes predominate in the foredunes, but further inland, sand transport may be slowed down by developing vegetation. Plants form a significant obstruction to the flow of air (Wieringa & Rijkoort, 1983; Wolfe & Nicking, 1993), and produce roots and organic matter. This leads to transformation from embryonic and white dunes to coastal dune grasslands, which are called Grey dunes (H2130) in the European habitat directive (European Union, 1992). Nevertheless, in dune grasslands, blowouts and aeolian processes are still a natural part of the landscape, although the scale and activity may vary between dune systems (Arens et al., 2013; Delgado-Fernandez et al., 2019; Hesp, 1991; Jungerius et al., 1981). Blowouts add to the geodiversity of dune environments, which is essential in functional aspects of dune areas such as biodiversity and recreational appreciation. Active blowouts are important to the dune vegetation, as they create deposits of thin sand sheets that can mitigate the negative effects of acidification on the topsoil. This is especially important in industrialized countries, as plant communities in the dunes are threatened by high atmospheric nitrogen (N) deposition and associated acidification (Aggenbach et al., 2017; Kooijman et al., 2017; Remke et al., 2009).

Coastal dunes belong to the most threatened natural ecosystems in the world (Houston, 2008). In Europe, many dune areas are protected by the European Union (EU) Habitat directive (European Union, 1992), but more than 95% of its dune habitats are in an unfavorable conservation status (European Environment Agency, 2015). Increase of dynamics through stimulation of blowout activity is considered as an important restoration measure (Arens et al., 2013; Van Boxel et al., 1997). Blowouts may be stabilized to protect the dunes against erosion (Doody, 2013; Jungerius et al., 1981), but in the Netherlands, this practice was abandoned in the 1980s, and existing blowouts have since then developed in a more natural way. However, activity of blowouts may differ between dune areas. Blowout activity may for example, be higher in lime-rich than in lime-poor dunes, due to differences in topsoil chemistry and sensitivity to high N deposition (Kooijman et al., 2021; Van Dobben & Van Hinsberg, 2008). High N deposition may decrease blowout activity through increased growth of algae, which stabilize the sand (Pluis & Van Boxel, 1993; Sparrius et al., 2012), and higher vegetation biomass, which lowers wind velocities at the soil surface (Remke et al., 2009). Differences in rabbit density may also play a role, as they increase blowout activity through grazing and digging (Drees, 2003, 2007; Van Dam, 2001). In transgressive dunes in Australia, rabbit density was even the main factor linked to vegetation growth and dune stabilization (Moulton et al., 2019). Nitrogen deposition peaked in the 1990s, and rabbit density highly fluctuated during the past decades due to myxomatosis and Rabbit hemorrhagic disease (Drees, 2003, 2007; Provoost et al., 2011), but it is unclear to which extent these changes affected blowout activity. Also, it is not clear how important wind speed and sand transport potential are with respect to blowout activity. Transport potential strongly depends on wind speed and is a function of shear velocity to the third power (Bagnold, 1941; Jungerius et al., 1981; Kawamura, 1951; Sherman & Li, 2012). However, wind speed and transport potential may strongly vary between years. Also, the actual sand transport in blowouts may be unrelated to wind speed (Arens et al., 2004; Hesp & Hyde, 1996; Jungerius et al., 1981). Windflow inside and outside the blowout can differ substantially, and sand transport during heavy storms is often limited by rainfall, as this reduces erodibility of the soil. Jungerius et al. (1981) even found that wind velocities between 8.75 and 10 m s^{-1} are most effective for sand transport in blowouts. This is roughly equivalent to 6 Beaufort, a common wind speed along the North Sea coast in winter (Clemmensen et al., 2014).

The aim of the present study was to further explore relationships between blowout activity, transport potential, N deposition and rabbit density along the gradient from lime-rich to lime-poor dunes, with detailed aerial photographs of 1996–2017 of five Dutch dune sites. In the Netherlands, both lime-rich and lime-poor dunes can be found in the fore dunes due to differences in parent material (Eisma, 1968), which makes the country representative for other parts of northwest Europe. We conducted a field survey in different stages of succession for the analysis of soil and plant characteristics. The research questions were: (i) How did blowout activity change between 1996 and 2017 in the five dune sites? (ii) Could changes in blowout activity be explained by changes in transport potential, atmospheric N deposition and/or rabbit density? (iii) Could differences in aeolian activity between sites be explained by differences in soil chemistry and plant characteristics?

2 | METHODS

2.1 | Analysis of aerial photographs

Five characteristic dune sites were selected for a detailed temporal analysis of blowout activity along the Dutch coast (Figure 1): Hollands Duin (HD) and Amsterdamse Waterleidingduinen (AW), located in the lime-rich Renodunal district, Bergen Zuid (BZ) in the transition zone between lime-rich and lime-poor dunes, and Zwanenwater (ZW) and Texel (TX), typical for the lime-poor Wadden district. In each blowout area, a predefined grid of 75 ha was selected, located landward of and parallel to the foredunes (Figure 2). The sites are all located from the foredunes to approximately 600 m inland. There may be some differences in salt spray and wind velocity over the sea–land gradient, but as distance to the sea is similar in all sites, we assumed this would not affect differences between them. Groundwater tables are well below the surface in all study areas, due to local extraction of groundwater and/or severe coastal erosion in the past hundreds of years, so groundwater does not affect blowout activity. In all sites, the vegetation consists of open dune grassland with some small shrubs. Management is extensive. The sites HD and AW are only naturally grazed by rabbits and fallow deer. In BZ and part of ZW, grazing by cattle is applied in low densities in addition to rabbit grazing. The site TX is only naturally grazed by rabbits. The sites differ to some extent in beach nourishment and morphology. HD and AW were nourished only once on the shoreface. BZ, ZW and TX are heavily nourished on both shoreface and beach. HD has a massive, 150–200 m wide and 20 m high foredune, followed by some dune complexes of medium height (10–15 m). AW has a slightly less wide foredune, equal in height, but with a very homogeneous structure due to intensive management in the past. The dunes at the back are chaotic and small, apart from some larger, partly artificially adapted dunes. Although a considerable part of the dunes consists of deflation valleys, these are all dry due to groundwater lowering. The foredune of BZ is much smaller (70–100 m) and more irregular, but also much higher (25 m), and locally incised by blowouts. The landward dunes consist of large parabolic dunes (locally more than 20 m high) and trailing ridges, alternated by wide deflation valleys. Due to groundwater lowering the slacks are all dry. Foredunes in ZW are much lower, with heights of 12–18 m, backed by parabolic structures of medium height up to

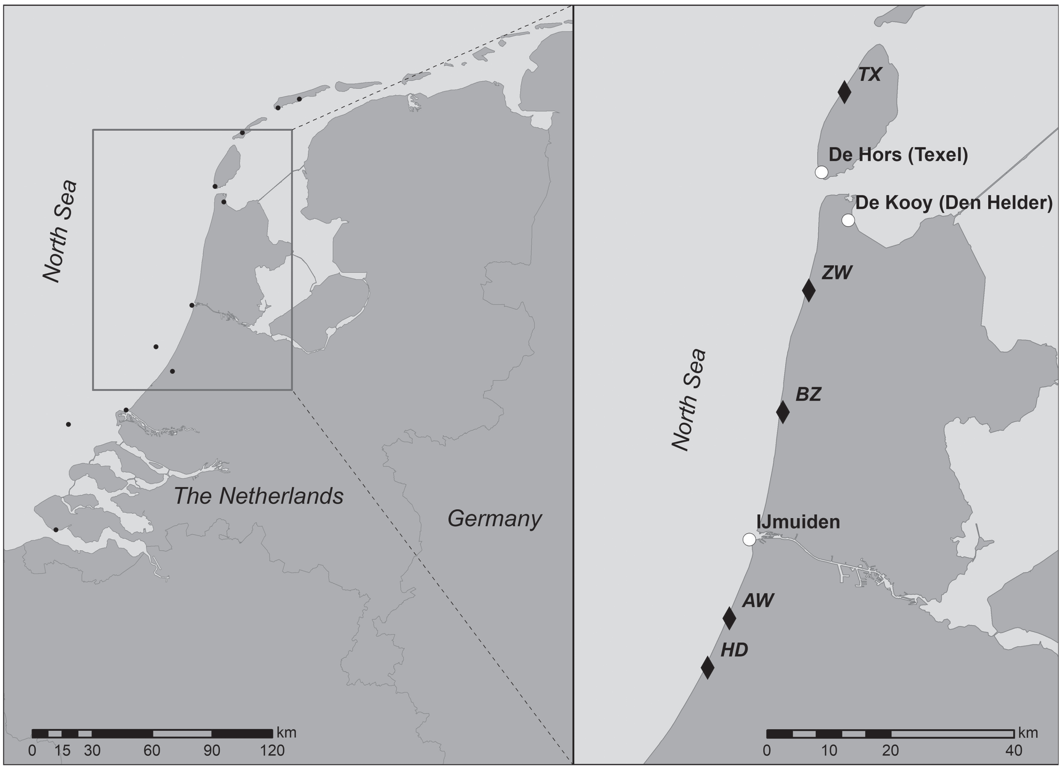

FIGURE 1 Location of weather stations and the five study sites in the Netherlands. The dots on the left represent all weather stations along the Dutch coast, but for the study, only the weather stations de Hors, De Kooy and IJmuiden were used. The dune sites TX (Texel) and ZW (Zwanenwater) are located in the lime-poor dunes of the Wadden district; the site BZ (Bergen Zuid) is located in the transition zone between lime-poor and lime-rich dunes; the sites AW (Amsterdamse Waterleidingduinen) and HD (Hollands Duin) are located in the lime-rich dunes of the Renodunal district

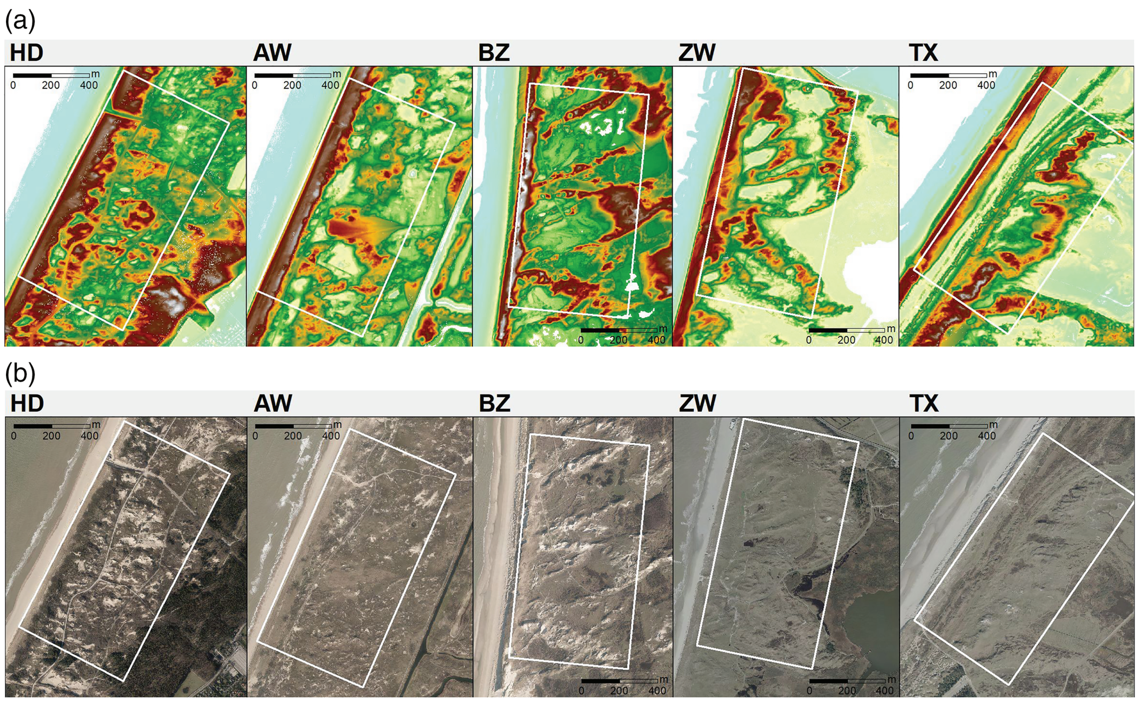

FIGURE 2 Digital elevation maps (a) and aerial photographs of the five dune sites in 2017 (b). The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes. Height of the foredune is 20 m in HD and AW, 25 m in BZ, 12–18 m in ZW and 15 m in TX. All maps are oriented towards the north [Color figure can be viewed at wileyonlinelibrary.com]

15 m. The foredunes of TX are straight structures of 15 m height due to intensive management in the past. Some straight structures behind the foredunes indicate former stuifdykes, induced by man due to the placement of sand fences. Landward are some parabolic structures, ranging in height from 10 to 15 m to over 20 m.

In each blowout area, the predefined grid has been manually mapped through visual interpretation on screen in ArcGIS. Georeferenced RGB (red, green and blue) composite aerial photographs were available for the period 1996–2017, provided by Rijkswaterstaat. After a preselection based on all available years and visual changes in aeolian activity, photographs of October 1996, July 2003, unknown date in 2007, August 2012 and March 2017 were selected for more detailed mapping. Resolution of the photographs gradually increased from 100 cm ×100 cm in 1996 to 50 cm × 50 cm in 2003 and 10 cm × 10 cm in 2017. The scale of mapping was 1:1500, which is suitable for identifying blowouts, deflation and accumulation zones and adjacent vegetation. Polygons were classified in five classes: (1) active deflation zone, (2) bare sand with up to 15% vegetation cover, (3) open pioneer stages with vegetation cover of 15–35%, (4) denser pioneer stages with 35–75% of vegetation cover, and (5) vegetated and inactive with less than 25% bare sand. Classes 1 and 2 were considered as bare sand, classes 1–3 as the area with high aeolian activity, and classes 1–4 as the total active area.

2.2 | Explanatory factors

Transport potential is an indicator of the annual amount of sand potentially transported by the wind. Transport potential was calculated according to Kawamura (1951), using the method explained in Arens et al., 2004. The Kawamura equation.

$$q = C_K \frac{\rho}{g}(U_* - U_{*t})(U_* + U_{*t})^2 \quad \text{in kg m}^{-1}\,\text{s}^{-1}$$

with q = calculated transport, C_K = Kawamura's constant (2.78), ρ = air density (1.22 kg m^{-3}), g = gravitational constant (9.81 m s^{-2}), U_* = the friction velocity and U_{*t} = the threshold friction velocity (0.22 m s^{-1}). Friction velocity was derived from the law of the wall:

$$U_z = \frac{U_*}{\kappa} \ln\left(\frac{z}{z_0}\right)$$

where U_z = windspeed at height z and z_0 = roughness length. Wind speeds were derived from the Kooy, IJmuiden and Texel Hors. Measurings height is 10 m and roughness length is 0.0001 m. The calculation of shear stress from wind measurements at a single height is extremely sensitive for the roughness length. Since no accurate data on roughness length are available, and the circumstances for each station can be quite different due to surrounding vegetation or position in the landscape, it was not possible to directly compare transport potential between the stations. Instead, for each weather station, transport potential was expressed as a percentage of the potential in the winter of 1989–1990, which experienced some very heavy storms. For each year of analysis of the aerial photographs, we used transport potential of the preceding winter. For each site, we used the nearest weather station with data for the period 1990–2020. As Valkenburg did not provide data after 2015, this means that weather station IJmuiden was used for the sites HD, AW and BZ, De Kooy for ZW and De Hors for TX. The triple use of one weather station naturally reduced variation between sites, but the weather stations only slightly differed in annual transport potential (Supporting Information Figure S1).

Data on atmospheric N deposition were provided by the Dutch Royal Institute for Public Health and Environment (RIVM) over the period 1981–2015. Deposition of NO_x and NH_y was modeled and mapped with OPS version 4.3.03, and corrected for extra NH_y deposition from the sea (Kooijman et al., 2017; Noordijk et al., 2014). For each blowout area, data on N deposition for different years were extracted from the maps. Exceedance of the critical N load was also calculated, based on the critical N load for lime-poor Grey dunes of 10 kg N ha^{-1} yr^{-1} for the lime-poor dunes, and 15 kg N ha^{-1} yr^{-1} for lime-rich Grey dunes for the lime-rich dunes (Van Dobben & Van Hinsberg, 2008).

Rabbit density was based on data provided by the Dutch Network Ecological Monitoring. Site managers are counting rabbits in many dune areas, in a standardized way in particular transects (Dijkstra et al., 2018). They go out by car in the evening eight times in spring, and eight times in autumn, and count the rabbits appearing in the head lights. For each transect, rabbit numbers in spring and autumn were converted to maximum number of rabbits per year per kilometer of road. In all sites, data were available for more than one transect, which were used to calculate average rabbit density per year for the entire dune area. Rabbit data were available for most sites and years. However, for TX, rabbits were not counted before 1997. Also, HD was not included, and average rabbit density was based on values of adjacent dune areas north and south, which showed more or less similar values and fluctuations over the years. As preceding years are important for the effect of rabbits on blowout activity, average rabbit density was calculated from the value in the year in which the aerial photograph was taken, as well as in the previous 3 years.

2.3 | Field survey

In each of the five sites, three blowouts with five stages of succession in their vicinity were selected according to stratified random sampling procedures. The succession stages were: (1) inside the blowout, (2) young pioneer with vegetation cover < 35%, (3) young pioneer with vegetation cover > 35%, (4) older pioneer stages or blown over stabilized vegetation with a clear Ah horizon in the soil, and (5) stable vegetation with a clear Ah horizon in the soil. These stages more or less coincided with the stages used for the aerial photographs, except that bare sand outside the blowout was not sampled, and an extra stage with older vegetation was included. In each of the five sites, topsoil samples were collected in each of the 15 sampling plots. Soil samples of the upper 5 cm were collected with a metal ring of 100 cm^3, which generally comprised the entire Ah horizon.

In each of the five sites, in the 12 out of 15 sampling plots with vegetation, plant species composition was recorded in a plot of approximately 3 m × 3 m. Cover of bare sand, vascular plants and cryptogam layer was estimated as percentage. Vascular plants were listed as arbuscular mycorrhizal (AM), ericoid mycorrhizal (ErM) or nonmycorrhyzal (NM) species according to Kooijman et al. (2021). Above-ground vascular plant biomass was collected by clipping the vegetation in plots of 25 cm × 25 cm, or 50 cm × 50 cm when vegetation cover was very low. Root samples were collected with a rectangular metal auger with a surface area of 50 cm^2 and a depth of 30 cm (Wardenaar, 1987), in which the majority of roots was present.

2.4 | Laboratory analysis

Vegetation and soil samples were stored at 4°C until further analyses. Above-ground vascular plant biomass and root samples were dried at 70°C. After drying, roots were sieved and thoroughly cleaned by hand, although it was difficult to remove all sand grains from dense root clusters. Dry weight of above-ground and root biomass was determined by weighing. The topsoil samples were dried at 105°C, after which bulk density was determined. After homogenization by hand, pH values were measured in demineralized water, using a 1:2.5 weight/volume ratio. Soil organic matter content was determined with loss on ignition (Westerman, 1990). For each of the five sites, one of the three blowout series was selected, and its five samples milled and used for additional analysis of different fractions of carbon (C), phosphorus (P) and iron (Fe), as well as total N. Total C and N content were determined with a Vario EL cube Elementar CNS analyser. Lime content of the soil was calculated from inorganic C, which was based on measurements of total and organic C with a Shimadzu TOC VCPH analyzer. In one of the older stages in TX, an extreme value for lime content was discarded, as this was incompatible with the relatively low pH and characteristic plant species composition.

Selective extractions of P were applied to dried and ground material of the 25 topsoil samples described earlier. The data should be treated as potential rather than actual amounts, because selective extractions only give a rough indication of different forms, and reactive surfaces are increased due to milling of the samples. Total P was determined after heating the soil at 500°C in order to digest organic matter (Kooijman et al., 1998; Westerman, 1990). Samples were subsequently extracted with sulfuric acid. Total P was measured spectrophotometrically with a Cecil CE1010 spectrometer with a sulfuric acid/ammonium molybdate/ascorbic acid/potassium antimonyl tartrate solution at 880 nm. Inorganic P was extracted in the same way as total P, but with non-heated samples. Organic P was calculated as the difference between total P and inorganic P. Weakly sorbed P was determined according to Mehlich (1984), using ammonium fluoride, glacial acetic acid, ammonium nitrate and nitric acid. In one of the late-successional sites in HD, an extreme value for weakly sorbed P was discarded, which was more than twice as high as in other samples.

Different Fe fractions, important to P sorption, were measured on the same subset of 25 topsoil samples. Total amorphous, poorly crystalline Fe was analyzed according to Schwertman (1964), by extraction in the dark with ammonium oxalate and oxalic acid at pH 3. Amorphous aluminum (Al) was also measured, but this was generally less abundant than amorphous Fe, and showed more or less similar patterns, so this is not further treated. The extracts also included oxalate-extractable P, but they were not further treated, as they were diluted for the measurement of Fe, and often below the detection limit. Organic Fe (and Al), which belongs to complexes of Fe with soil organic matter, were measured according to McKeague et al. (1971) by alkaline sodium-pyrophosphate/sodium hydroxide extraction at pH 9.8. Inorganic amorphous Fe, which belongs to Fe oxides, was calculated as the difference between total amorphous and organic Fe.

2.5 | Statistical analysis

For the temporal analysis of blowout activity in five sites, differences in blowout activity were tested with one-way general linear models, with site (HD, AW, BZ, ZW and TX), district (lime-rich and lime-poor) and year (1996, 2003, 2007, 2012 and 2017) as independent factors (Cody & Smith, 1987). Based on the chemical analysis, the transition site BZ was included in the lime-poor dunes. For blowout parameters, the actual values for the number of blowouts and surface area of different aeolian classes in a particular site and year were used, as well as the changes in blowout number and surface areas compared to 1996. Differences between individual groups were *post hoc* tested with least square means tests. Differences in transport potential, N deposition, N deposition above the critical load and rabbit density were tested in a similar way. Relationships between aeolian parameters and explanatory variables were analyzed with Spearman correlation tests for individual sets of parameters, and Stepwise multiple linear regressions to test which of the explanatory factors was most important (Cody & Smith, 1987). This was done for the actual values of the blowout parameters, but also for changes compared to 1996, as indicator of the cumulative effects.

For the analysis of plant and soil characteristics, if applicable, mean values were calculated for the three replicates of each stage of succession within a particular site, to obtain one value for each stage for the statistical analysis. However, for the number of vascular plants, AM and non-AM plant species, the three replicates were combined in a total list of species for each stage of succession. To further simplify the analysis and increase the number of replicates, pioneer stages 1–3 were combined in one pioneer stage, and older stages 4 and 5 in one older stage of succession. This choice was based on the soil organic matter content, which was usually low for pioneer stages 1–3, and much higher for the older stages 4 and 5. Differences between sites (HD, AW, BZ, ZW and TX) and stages of succession (pioneer and older stage) were tested with two-way general linear models. The same was done for districts (lime-rich and lime-poor) and stages of succession. In almost all cases, interactions between site*stage and district*stage were not significant, and not further shown. Differences between individual groups were *post hoc* tested with least square means tests. Correlations between particular variables were tested with Spearman correlation tests, based on all five (for soil) or four (for vegetation) succession stages in each site.

3 | RESULTS

3.1 | Changes in aeolian activity

On the aerial photographs of 2017, the five dune sites clearly differed in aeolian activity (Figure 2). Areas with bare sand were clearly visible in the lime-rich HD and AW, as well as in the transition site BZ, which chemically belonged to the lime-poor dunes. In BZ, blowout activity was especially high in the crest of its large parabolic dunes. In contrast, aeolian activity was relatively low in the lime-poor ZW and TX.

In the period 1996–2017, blowout numbers and total active area showed significant differences between dune areas (Table 1). The mean number of blowouts and total active area were significantly higher in BZ and HD than in ZW and TX (Figure 3). In AW, the total

TABLE 1 Statistical analysis of the actual values and changes relative to 1996 in blowout numbers and surface areas of different aeolian classes in different dune areas, districts and years ($n = 5–15$)

Parameter	Dune area	District	Year
Actual numbers or surface areas			
Number of blowouts	22.18***	0.09	0.52
Total area with aeolian activity	15.61***	0.90	1.93
Class 1: blowouts	31.29***	1.07	0.43
Class 2: 0–15% vegetation cover	21.16***	10.29**	1.92
Class 3: 15–35% vegetation cover	8.95***	0.02	0.96
Class 4: 35–75% vegetation cover	2.93	0.94	1.84
Bare sand (classes 1 and 2)	21.85***	1.63	0.99
Area with high aeolian activity (classes 1–3)	23.07***	0.54	1.26
Changes relative to 1996			
Number of blowouts	3.50*	1.00	0.32
Total area with aeolian activity	28.18***	32.70***	5.13*
Class 1: blowouts	3.13	0.44	0.52
Class 2: 0–15% vegetation cover	12.99***	29.42***	3.14
Class 3: 15–35% vegetation cover	3.79*	4.80*	1.03
Class 4: 35–75% vegetation cover	29.67***	26.13**	4.54*
Bare sand (classes 1 and 2)	5.69**	14.73**	1.24
Area with high aeolian activity (classes 1–3)	6.90**	15.57***	1.83

Values indicated are *F*-values of the one-way general linear models for a particular parameter. An asterisk indicates that differences between dune areas, districts and/or years for this parameter are significant; $*p < 0.05$; $**p < 0.01$; $***p < 0.01$.

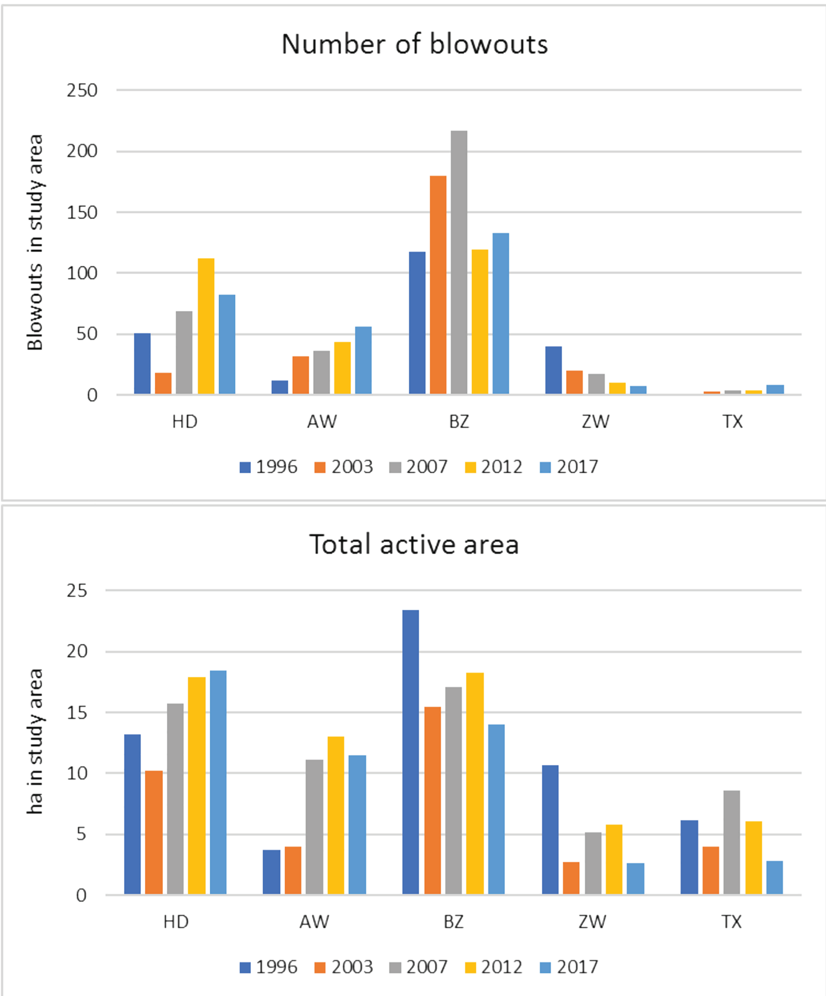

FIGURE 3 The number of blowouts and total active area (in hectares) in different dune areas and years. The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes [Color figure can be viewed at wileyonlinelibrary.com]

active area was also significantly higher than in ZW and TX. Differences between districts were not significant for the actual blowout numbers and surface of the total active area, due to the limited number of sites, and high blowout activity in the transition site BZ, which chemically belonged to the lime-poor dunes. However, lime-rich and lime-poor dunes did differ in changes compared to 1996. The two lime-rich sites showed a significant increase in total active area compared to 1996, and all three lime-poor sites a significant decrease. The number of blowouts and the actual surface of the total active area did not differ between years. However, changes in total active area compared to 1996 were significant, and the total active area showed an overall decrease in 2003, increase in 2007 and 2012 and again a decrease in 2017.

3.2 | Changes in different blowout classes

The actual surface of different aeolian classes mainly differed between dune areas (Figure 4). The surface area of classes 1, 2 and 3, that is, blowouts and open pioneer stages, was significantly higher in the lime-rich HD and the lime-poor BZ than in other sites. The same holds for bare sand (classes 1 and 2) and highly active area (classes 1–3). Differences between districts were only significant for the surface area of class 2, with higher values for lime-rich than lime-poor dunes. However, for almost all aeolian classes, dune districts significantly differed in changes in surface area compared to 1996. Lime-rich dunes showed a general increase in aeolian activity between 1996 and 2017, and lime-poor dunes a decrease. For the actual surface area of aeolian classes, differences between years were not significant. For changes in surface area compared to 1996, differences between years were only significant for class 4. This class showed significantly higher increase in 2012 than in other years, although this was due to both increase (AW) and decrease (TX) in aeolian activity.

All dune areas showed both gains and losses between 1996 and 2017 in almost all aeolian classes, even though the net results differed between sites (data not shown). In the lime-rich sites, the net increase in active blowouts came from the conversion of pioneer classes 2–4, but also from fully vegetated areas. Local losses in the blowouts were mainly due to transitions to pioneer class 2. In the lime-rich sites, net gains in the pioneer classes were mainly due to sand accumulation in fully vegetated areas. In the highly dynamic transition site BZ, most classes showed a net decrease between 1996 and 2017, but mutual transitions were more common than in lime-rich dunes. Blowouts and pioneer class 2 developed from, but mainly converted into the more vegetated pioneer classes 3 and 4, as well as fully vegetated areas. The more vegetated classes 3 and 4 developed into each other, but otherwise from and into fully vegetated areas. The lime-poor sites with low aeolian activity also showed local gains, but mainly a general net decrease between 1996 and 2017. Over this period, blowouts and pioneer classes 2–4 mainly developed into fully vegetated areas.

3.3 | Explanatory factors

In the winters preceding the shooting of the aerial photographs, transport potential was significantly higher for 2007 and 2012 than for other years (Table 2, Figure 5). However, transport potential did not

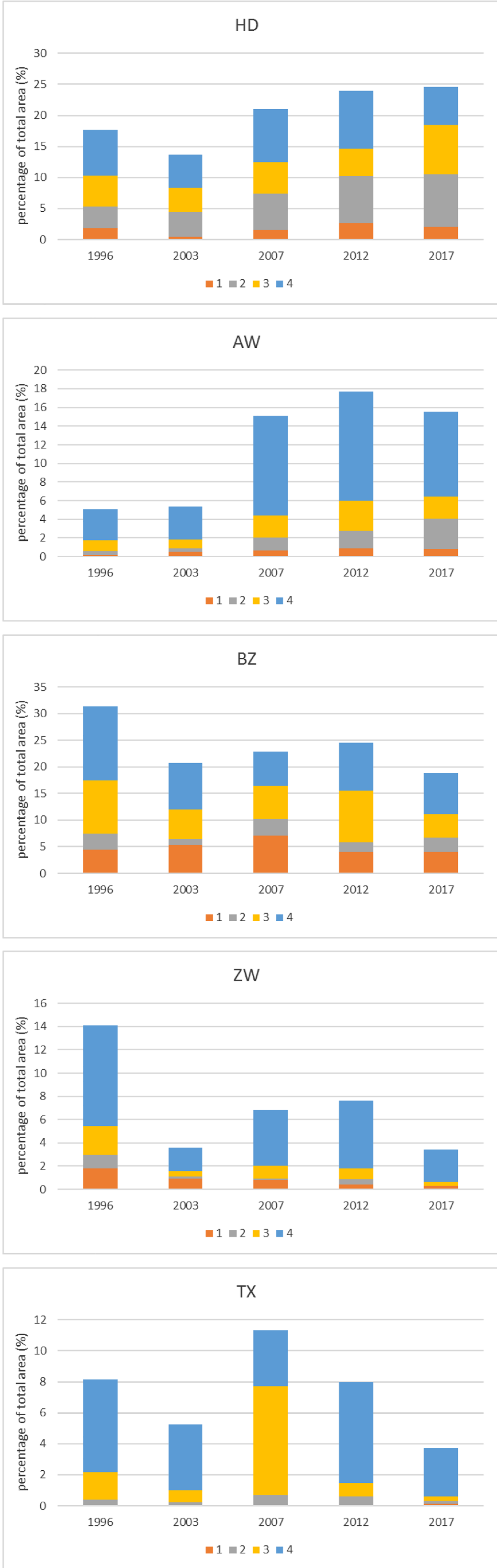

FIGURE 4 The surface area of different blowout classes (in percent of the total area) in different dune areas and years. Class 1 = active deflation zone, class 2 = bare sand with up to 15% vegetation cover, class 3 = open pioneer stages with vegetation cover of 15–35% and class 4 = denser pioneer stages with 35–75% of vegetation cover. The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Statistical analysis of transport potential, total nitrogen (N) deposition, exceedance of the critical N load and rabbit density in different dune areas, districts and years ($n = 5$–15)

Parameter	Dune area	District	Year
Transport potential (percent of winter 1989–1990)	0.78	0.24	53.36***
Total N deposition (kg N ha^{-1} yr^{-1})	39.17***	7.83*	84.33***
Exceedance critical N load (kg N ha^{-1} yr^{-1})	7.77**	0.24	84.33***
Rabbit density (number per kilometer of road)	8.54***	13.52**	4.07*

Values indicated are *F*-values of the one-way general linear models for a particular parameter. An asterisk indicates that differences between dune areas, districts and/or years for this parameter are significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.01$.

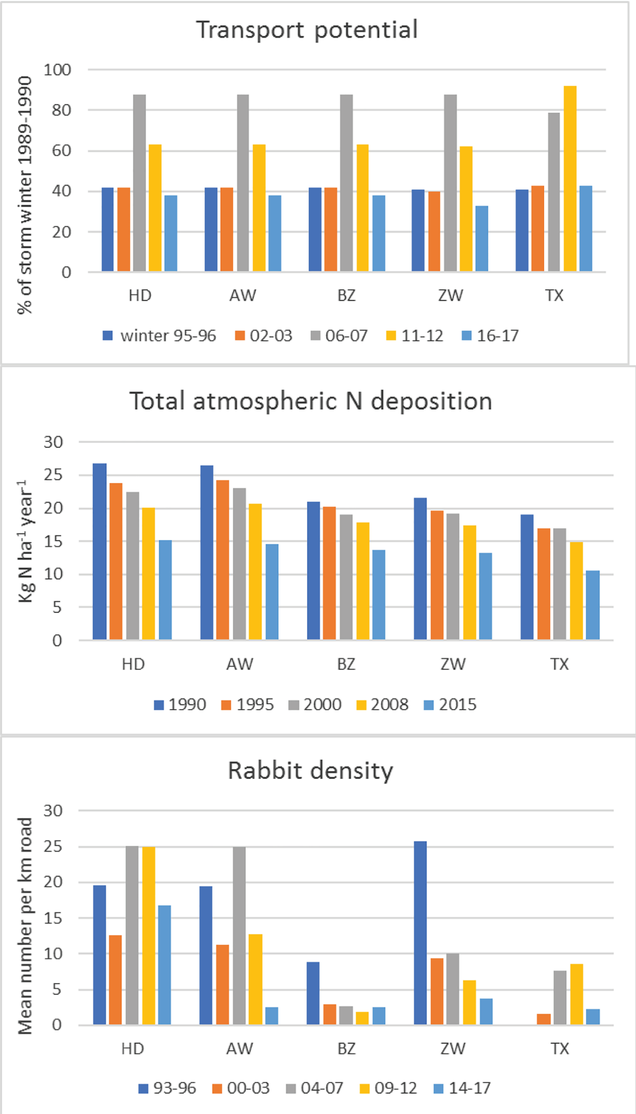

FIGURE 5 Transport potential, total nitrogen (N) deposition, exceedance of the critical N load and rabbit density in different dune areas and years. The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes [Color figure can be viewed at wileyonlinelibrary.com]

differ between dune areas or districts. Also, transport potential did not show any significant correlation with blowout parameters, even though aeolian activity increased between 2003 and 2007 in all five sites (data not shown).

Total atmospheric N deposition significantly differed between dune areas, districts and years. In all sites, N deposition gradually decreased between 1996 and 2017. In the lime-rich sites HD and AW, N deposition amounted to more than 26 kg N ha^{-1} yr^{-1} in 1990, but decreased to approximately 15 kg N ha^{-1} yr^{-1} in 2015, which is the current critical N load for lime-rich Grey dunes (Van Dobben & Van Hinsberg, 2008). In the lime-poor sites ZW, TX and BZ, N deposition ranged around 20 kg N ha^{-1} yr^{-1} in 1990, and decreased to 11–14 kg N ha^{-1} yr^{-1} in 2015, which is higher than the critical N load for lime-poor Grey dunes of 10 kg N ha^{-1} yr^{-1}. Nevertheless, exceedance of the critical N load did not differ between districts, but only between dune areas and years, with significantly higher values for BZ than for HD, AW and TX. Also, correlations of total N deposition or the amount exceeding the critical N load with blowout parameters were mostly insignificant. However, exceedance of the critical N load showed a negative correlation with the increase in surface area compared to 1996 for class 2 and the total area with bare sand.

Rabbit density differed between dune areas, districts as well as years. Significantly higher rabbit densities were found in the lime-rich sites HD and AW, and for the years 1996 and 2007. Correlations between rabbit density and blowout parameters were significant for the actual surface of class 2, and the changes compared to 1996 for class 2, class 4, total active area and the areas with bare sand and high activity. All these correlations were positive.

In a stepwise multiple linear regression with transport potential, exceedance of the critical N load and rabbit density as independent factors, significant effects were usually low when based on the actual blowout numbers and surface area of blowout classes (Table 3). However, with changes relative to 1996 rather than actual values, explanatory factors became more prominent, especially for combined classes, such as total active area, bare sand and area with high aeolian activity. Transport potential remained unimportant, but exceedance of the critical N load and rabbit density together explained 41–74% of the variance. Exceedance of the critical N load always showed a negative effect on blowout parameters, and rabbit density a positive effect.

3.4 | Differences in soil and plant parameters

Soil chemical parameters mainly differed between dune areas and districts, although succession stage was important to some of them (Table 4, Figure 6). Lime content and total or inorganic Fe content were significantly higher in the lime-rich HD and AW than in the lime-poor BZ, ZW and TX. These results were not unexpected, but

TABLE 3 Stepwise multiple linear regression of the actual values and changes relative to 1996 in blowout numbers and surface areas of different aeolian classes ($n = 24$)

Parameter	Transport potential	Exceedance critical N load	Rabbit density	Total model R^2
Actual values				
Number of blowouts	–	–	–	ns
Total aeolian active area	–	–	–	ns
Class 1: blowouts	–	–	–	ns
Class 2: 0–15% vegetation cover	–	0.19	0.19	0.38*
Class 3: 15–35% vegetation cover	–	–	–	ns
Class 4: 35–75% vegetation cover	–	–	–	ns
Bare sand (classes 1 and 2)	–	–	–	ns
Area with high aeolian activity (classes 1–3)	–	–	–	ns
Changes relative to 1996				
Number of blowouts	–	–	–	ns
Total aeolian active area	0.02	0.16	0.35	0.53**
Class 1: blowouts	–	–	–	ns
Class 2: 0–15% vegetation cover	–	0.35	0.39	0.74***
Class 3: 15–35% vegetation cover	–	–	–	ns
Class 4: 35–75% vegetation cover	–	0.10	0.31	0.41*
Bare sand (classes 1 and 2)	–	0.23	0.25	0.48*
Area with high aeolian activity (classes 1–3)	0.02	0.19	0.28	0.49*

Independent factors were transport potential, exceedance of the critical nitrogen (N) load and rabbit density. Values given are partial R^2 values of the model for each factor, as well as total R^2 values for the entire model. Only significant correlations ($p < 0.05$) are indicated; ns = not significant.

TABLE 4 Statistical analysis of chemical topsoil characteristics in different dune areas, districts and succession stages ($n = 5$–15)

Parameter	Dune area	District	Stage of succession
Lime content (%)	6.35*	32.25***	5.13*
Soil organic matter content (kg m^{-2})	1.39	5.81*	12.14**
Nitrogen (N) content (g m^{-2})	0.84	2.33	16.12**
Total iron (Fe) content (g m^{-2})	277.47***	235.30***	0.67
Inorganic Fe content (g m^{-2})	197.19***	333.18***	14.44**
Organic Fe content (g m^{-2})	3.38*	8.81**	6.33*
Total phosphorus (P) content (g m^{-2})	18.98***	53.48***	0.62
Inorganic P content (g m^{-2})	284.25***	97.18***	1.27
Organic P content (g m^{-2})	0.76	2.50	1.19
Log weakly sorbed P (g m^{-2})	6.12*	19.51***	13.91**
Weakly sorbed P (percent of total P)	6.45**	9.13*	1.05

Values indicated are *F*-values of the one-way general linear models for a particular parameter. An asterisk indicates that differences between dune areas, districts and/or years for this parameter are significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.01$.

highlighted that the transition site BZ with high aeolian activity chemically belonged to the lime-poor (and Fe-poor) dunes. Soil organic matter and N content did not differ between dunes areas and only partly between districts, but were significantly higher in older than in pioneer stages of succession (Supporting Information, Table S1). Organic Fe also increased from pioneer to older succession stages, but mainly differed between districts, with higher values for lime-rich than lime-poor dunes. With respect to P, total and inorganic P were significantly higher in lime-rich than in lime-poor sites, while organic P did not differ between dune areas, districts or succession stages. However, weakly sorbed P significantly differed between dune areas, districts and succession stages, and the amount and proportion of this fraction were higher in lime-poor than in lime-rich dunes. In the lime-poor ZW, the proportion of weakly sorbed P increased to 30% of total P. Also, in lime-poor dunes, weakly sorbed P was already high in pioneer stages, while lime-rich pioneer stages showed very low amounts. In addition, correlations between weakly sorbed P and pH were significantly negative for both amount and proportion of total P ($R = -0.66$ and -0.72 respectively).

Like lime content, pH values of the topsoil significantly differed between dune areas, districts and succession stages (Table 5, Figure 7). However, in the lime-poor BZ, pH values were as high as in the lime-rich HD and AW, in spite of the lower lime content. In all three cases, pH values ranged around 8 in pioneer stages, and around

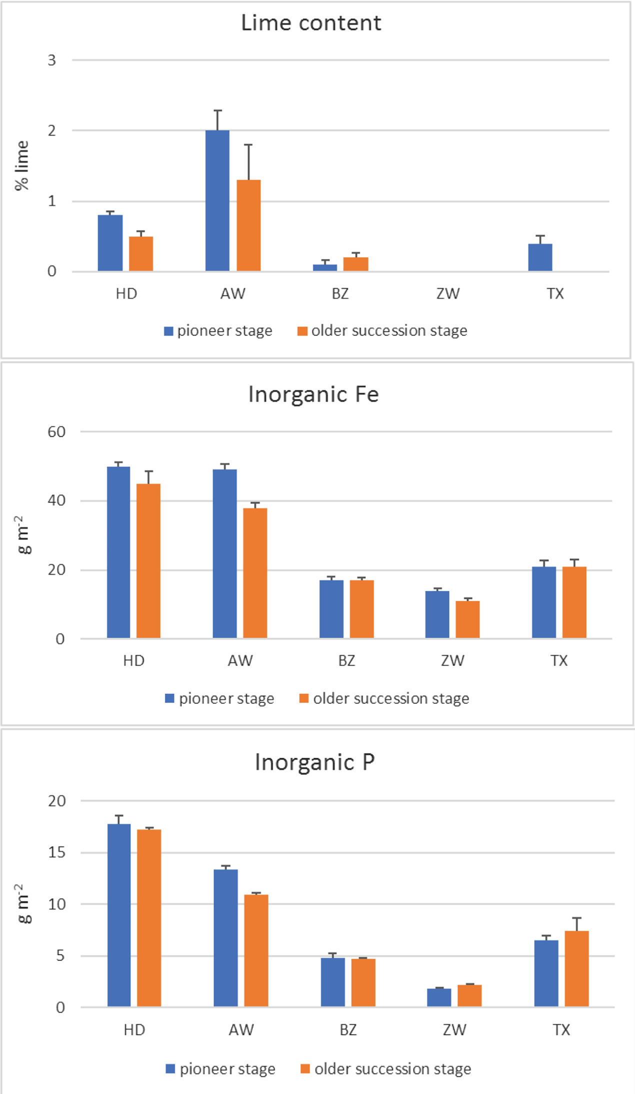

FIGURE 6 Lime content, inorganic iron (Fe) and inorganic phosphorus (P) in the topsoil (0–5 cm) in different dune areas and succession stages ($n = 2–3$). The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes [Color figure can be viewed at wileyonlinelibrary.com]

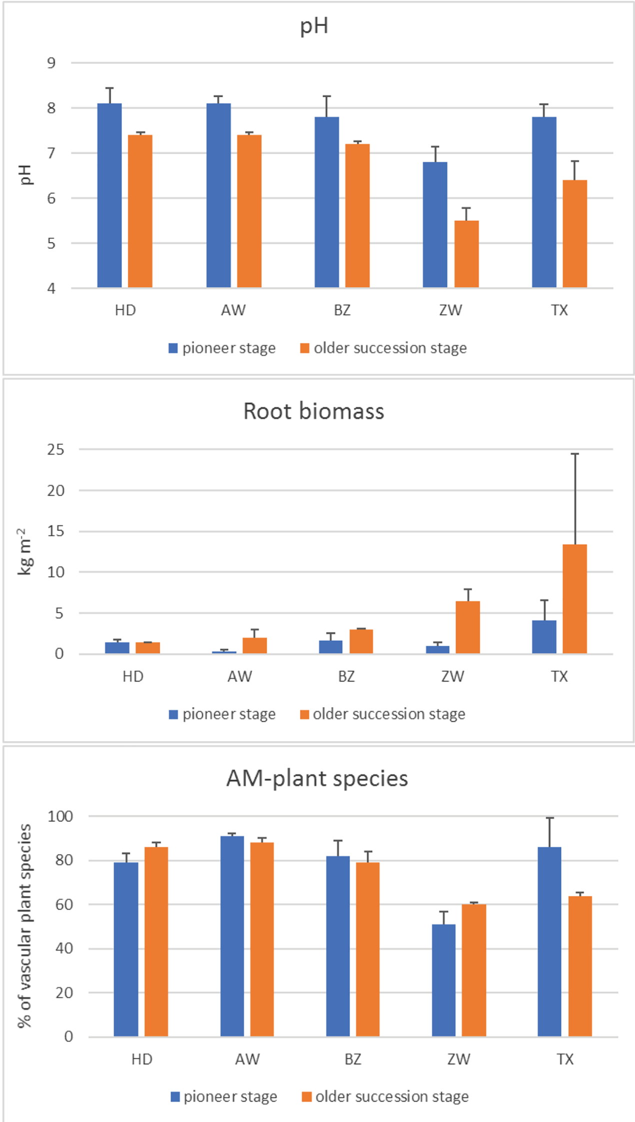

FIGURE 7 Topsoil pH, root biomass and proportion of arbuscular mycorrhizal (AM) plant species in different dune areas and succession stages ($n = 2–3$). The dune sites HD (Hollands Duin) and AW (Amsterdamse Waterleidingduinen) are located in the lime-rich dunes, the site BZ (Bergen Zuid) in the transition zone between lime-poor and lime-rich dunes, and ZW (Zwanenwater) and TX (Texel) in the lime-poor dunes [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 5 Statistical analysis of topsoil pH and plant characteristics in different dune areas, districts and succession stages ($n = 5–15$)

Parameter	Dune area	District	Stage of succession
pH	8.14**	8.88**	21.75***
Above-ground biomass (g m^{-2})	2.31	2.90	27.23***
Log root biomass (kg m^{-2})	3.21	7.71*	8.88*
AM-plant species (nr)	2.30	0.00	2.38
Non-AM plant species (nr)	3.04	11.69**	3.76
AM-plant cover (%)	1.09	1.17	1.97
Non-AM plant cover (%)	1.78	0.08	1.01
AM-plant species (percent vascular plant species)	7.75**	6.53*	0.43

AM-plant species = arbuscular mycorrhizal plant species; non-AM plant species = plant species without arbuscular mycorrhizal. Values indicated are *F*-values of the one-way general linear models for a particular parameter. An asterisk indicates that differences between dune areas, districts and/or years for this parameter are significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.01$.

7.3 in older stages of succession. In fact, pH values only decreased when lime content was close to zero, such as in ZW and older succession stages of TX.

Above-ground biomass was significantly lower in pioneer stages than in older stages of succession, but did not differ between dune areas or districts. Root biomass did not differ between dune areas, but was significantly higher in lime-poor than in lime-rich dune districts, especially in older stages of succession. Also, the correlation between root biomass and pH was significantly negative when expressed on a log base ($R = -0.53$).

The number and cover of AM- and non-AM plant species did not differ between dune areas, districts or succession stages, although the number of non-AM plants was higher in lime-poor than in lime-rich dunes. However, the proportion of AM-plant species significantly differed between dune areas and districts, and showed high values especially in sites with high pH. The correlation between pH and the proportion of AM-plant species was also significant ($R = 0.77$).

4 | DISCUSSION

The aim of this study was to further explore changes in blowout activity over the last decades over the gradient from lime-rich to lime-poor dunes, in relation to explanatory factors such as transport capacity, N deposition, rabbit density and plant and soil characteristics. Although we could only analyze five sites in more detail, they were representative for the Dutch coastal dunes, as well as lime-rich and lime-poor dunes in other northwest European countries. We traced changes from 1996 onwards, because dunes were not stabilized any longer after the 1980s (Jungerius et al., 1981). Blowout activity differed between dune sites rather than between lime-rich and lime-poor districts, due to the limited number of sites and selection of the lime-poor transition site BZ with high aeolian activity. However, blowout activity showed an overall increase between 1996 and 2017 in lime-rich dunes, and decrease in lime-poor dunes, in accordance with Kooijman et al. (2021).

4.1 | Transport potential

Wind speed and transport potential probably contributed to changes in aeolian activity to a limited extent. The general increase in blowout activity between 2003 and 2007 may be explained by the significantly higher transport potential in the winter of 2006–2007, after a few years with low storm activity. However, transport potential differed between years rather than between dune areas and districts, and could not explain differences in blowout activity between the latter. Also, wind speeds are generally higher in the northern part of the Netherlands with lime-poor dunes (KNMI, 2011). We used relative values for transport potential in each weather station rather than absolute ones, but this means that actual values for transport potential may have been higher in lime-poor dunes than in the lime-rich south, even though blowout activity was lower. This further supports that differences in blowout activity between dune sites cannot be explained by differences in transport potential.

4.2 | Rabbits and atmospheric N deposition

Changes in blowout activity relative to 1996 could to some extent be explained by rabbit density and atmospheric N deposition, which showed opposite effects. Rabbits may increase aeolian activity through grazing and digging (Drees, 2003, 2007; Moulton et al., 2019; Van Dam, 2001), while high N deposition would stabilize the sand (Pluis & Van Boxel, 1993; Remke et al., 2009). Relationships with the actual surface area of different blowout classes were however obscured by the transition site BZ, which showed high aeolian activity despite low rabbit density and high exceedance of the critical N load. However, in BZ, rabbit numbers were much higher before 1996, and amounted to 26 per kilometer of road in 1989–1992. Also, the critical N load for BZ was set at 10 kg ha^{-1} yr^{-1} because of its lime-poor sand, but the dunes may be less sensitive to high N deposition due to the relatively high pH in the topsoil, which is associated with relatively low P availability (Kooijman et al., 2020, 2021). The use of a higher critical load for BZ only slightly changed the results, but rabbit density and exceedance of the critical N load now explained 25% of the variance in total active area, instead of 3%. We explored different scenarios for rabbit density and N deposition with the regression equation for the total active area (in hectares) $= 11.8 + 0.3 \times$ rabbit density – $0.8 \times$ exceedance of the critical N load, and high and low values for these parameters of 25 and 0 rabbits per kilometer of road, as well as 10 and 0 kg N ha^{-1} yr^{-1} above the critical N load. In the best scenario with high rabbit density and low N deposition, total active area amounted to 19.3 ha, or 26% of the area. In intermediate scenarios with low rabbit density or high N deposition, total active area would decrease to 15%. With low rabbit density and high N deposition, the active area would further decrease to 5%. When the transition site BZ was excluded, the equation slightly changed and the variance explained increased to 68%, but patterns in total active area stayed more or less the same. The actual values in these scenarios should thus be treated with care, but the analysis shows that both rabbits and N deposition are important, and that their effects reinforce each other.

In the present study, N deposition showed a clear decrease since the 1990s. The actual values were higher in lime-rich than in lime-poor dunes, because they are located closer to seaports and industrial complexes. However, the decrease in N deposition was also larger than in lime-poor dunes, and current values are close to the critical N load for lime-rich Grey dunes of 15 kg ha^{-1} yr^{-1} (Van Dobben & Van Hinsberg, 2008). In the lime-poor dunes of this study, N deposition was still higher than the critical N load, mainly because the latter is lower than for lime-rich Grey dunes, with values of 10 kg ha^{-1} yr^{-1}. However, N deposition is still higher than the critical load in most of the Dutch lime-poor dunes (Kooijman et al., 2021), which means that further measures to reduce N deposition are still needed, especially in areas close to agricultural lands.

Rabbit populations decreased since the 1960s due to illnesses such as myxomatosis, and since the 1990s due to viral hemorrhagic disease (VHD), which killed many animals (Provoost et al., 2011). In the lime-poor TX, rabbits were not counted before 1997, but the clear decrease in rabbit density in BZ and ZW was probably due to VHS. In lime-rich dunes, rabbits largely recovered after 2003, which may explain the increase in aeolian activity since then, together with the decrease in N deposition. In AW, new blowouts may even have started from collapsed rabbit holes and pipes. The current blowouts did not exist in 1928 or 1938, and were formed in dune grasslands which stabilized between these years (Schouten, 2019). However, at present, many rabbit populations in the lime-rich dunes are threatened by a new variant of VHS, and rabbit numbers dropped dramatically since 2020 (Mark van Til, personal communication). If rabbits are indeed so important, blowout activity may decrease again.

4.3 | Topsoil and plant characteristics

Lime-rich and lime-poor dune areas clearly differed in chemical composition of the topsoil, in accordance with existing literature (Eisma, 1968; Kooijman et al., 1998). Lime content, inorganic Fe and inorganic P were significantly higher in lime-rich than in lime-poor dunes. Surprisingly, the transition site BZ, located in the transition zone between lime-rich and lime-poor dunes, chemically belonged to the lime-poor dunes. Due to its location, as well as its high aeolian activity, we had expected intermediate values for lime content and inorganic Fe and P, but this was not the case. However, in BZ, pH values of the topsoil were as high as in the lime-rich dunes, even in older stages of succession. In a survey along the entire Dutch coast, pH of the parent material inside the blowouts appeared to be the best explanatory factor for aeolian activity, even in lime-poor dunes (Kooijman et al., 2021).

In the present study, pH values were above 7 in both lime-rich sites and the lime-poor BZ, even in older stages of succession. This is above the dissolution threshold for calcium phosphate of pH 6.5 (Hinsinger, 2001; Lindsay & Moreno, 1966), and means that P availability to the vegetation is still relatively low. This was supported by the predominance of AM plants, which profit from uptake of inorganic P by their fungal partner especially when P is a limiting factor (Hoeksema et al., 2010; Kooijman et al., 2021). Also, pH showed negative correlations with the amount and proportion of weakly sorbed P, an indicator for high P availability to the vegetation. The relatively low P availability in HD, AW and BZ may in turn explain why root biomass was relatively low, which may increase erodibility of the sand. High pH and low P availability to the vegetation may also have affected aeolian activity through higher food quality for rabbits, due to predominance of AM plants (Kooijman et al., 2020). It is unclear yet whether high food quality can help recover rabbits from viral diseases, but higher food quality may at least explain why rabbits are generally more abundant in lime-rich than in lime-poor dunes.

The results of this study support that high pH is a key factor to blowout activity, and reduces sensitivity to high N deposition by decreasing the availability of P. Lime-rich dunes are protected against acidification and increase of P availability as long as lime is present in the topsoil (Blume et al., 2016). In contrast, lime-poor dunes such as BZ and TX may show high pH initially due to some lime in the parent material, but they are sensitive to acidification as soon as blowout activity is reduced. In the lime-poor TX, where aeolian activity was low, the lime content of the parent material was high enough for high pH in pioneer stages, but too low to maintain this in older stages of succession. Acidification of the topsoil may be further stimulated in areas with high atmospheric deposition (Aggenbach et al., 2017). In the lime-poor BZ, however, high blowout activity is probably the reason why pH remained high even in older stages of succession, which reduced P availability and root biomass, and increased food quality for rabbits. High blowout activity in BZ could only partially be explained by rabbits and N deposition, and may be due to the form, location and history of the dunes. In BZ they consist of large parabolic dunes, with many blowouts in their crests, which for a large part were already present in 1938 (Schouten, 2019). They may be more active than many other lime-poor dunes due to their exposition, which is more favourable to the predominant west-southwest winds (Kooijman et al., 2021). Also, the coastline in this area is strongly erosive, and large scarps in the fore dunes were still present in 1957 (Schouten, 2019). Past human activity may have played a role as well, as the BZ dunes are located close to the former fishing village of Egmond. Between AD 1500 and AD 1900, dunes around fishing villages were intensively used for grazing and collection of biomass for fuel, which increased their vulnerability to erosion (Slings, 1994).

4.4 | Concluding remarks

This study shows that changes in aeolian activity in lime-rich and lime-poor dunes over the last decades in the Netherlands cannot be explained by transport potential, although the stormy winter of 2006–2007 may have temporarily increased blowout activity in all sites. In contrast, blowout activity is probably regulated by interactions and feedback mechanisms between rabbits, N deposition, soil chemistry and vegetation. Blowout activity was probably positively affected by rabbit density and negatively by N deposition, especially when this exceeded the critical N load. Blowout activity was generally high in dunes with high pH, probably due to low P availability to the vegetation and low root biomass, which increase erodibility of the soil. Also, high pH and low P availability may increase the proportion of AM plant species and food quality for rabbits, which stimulate blowout activity themselves. Because pH is a key factor, differences in sensitivity to acidification between lime-rich and lime-poor dunes are important. In lime-rich dunes, pH remains high and P availability low as long as lime is present in the topsoil, and blowouts may remain active, especially when N deposition does not exceed the critical load, and rabbits are present. In lime-poor dunes, pH values in the topsoil may initially be high due to some lime in the parent material, and may remain high as long as blowouts are active, especially in well exposed areas with strong coastal erosion. However, lime-poor dunes are sensitive to acidification, and probably develop low pH values in the topsoil as soon as aeolian activity decreases, especially in areas with high atmospheric deposition. This may lead to increased P availability and root biomass, and further reductions in aeolian activity.

ACKNOWLEDGMENTS

The authors would like to thank Bas van Dalen, Marijn Nijssen, Erik Noordijk and Mark van Til for valuable support and contributions; Jitske Esselaar (Natuurmonumenten), Luc Geelen (Waternet), Hubert Kievit (PWN), Erik van der Spek (Staatsbosbeheer) and Casper Zuyderduyn (Staatsbosbeheer) for information and access to the field; Rutger van Hall and Eva de Rijke for instructions and support in the laboratory and Thijs de Boer for help with the geographic information system (GIS). Part of the study was financially supported by the Dutch Ministry of Agriculture, Nature and Food Security, through the OBN program of the VBNE (report OBN223-DK).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR'S CONTRIBUTIONS

AK, BA and EC conceived the ideas and designed the methodology; AK, BA, MS and AP collected and analyzed the data; AK, BA and EC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data will be published in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Kooijman, A., Schouten, M., Postema, A., Cammeraat, E. & Arens, B. (2022) Blowout dynamics in lime-rich and lime-poor coastal dunes in the Netherlands. *Earth Surface Processes and Landforms*, 47(11), 2695–2708. Available from: https://doi.org/10.1002/esp.5402