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Lime-rich and lime-poor coastal dunes: Natural blowout activity differs with sensitivity to high N deposition through differences in P availability to the vegetation

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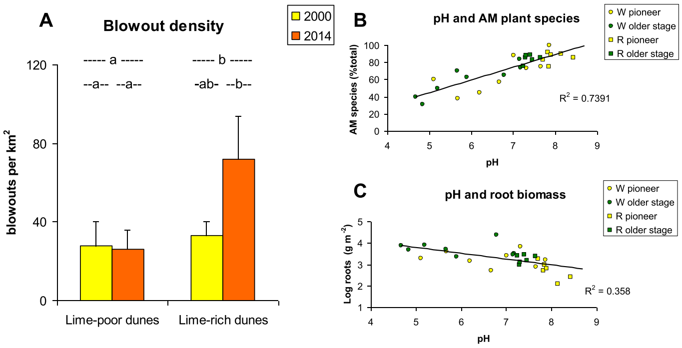
HIGHLIGHTS

- Integrated study on natural blowout activity in coastal dunes with high N deposition
- Blowout activity is higher in lime-rich than in lime-poor dune grasslands.
- Abiotic factors storm activity, landscape position or texture are unimportant.
- Key factors are rabbits and pH effects on P nutrition, plant strategies and roots.
- Blowout activation is a suitable restoration method except in very lime-poor dunes.

GRAPHICAL ABSTRACT

A. Differences in blowout activity between lime-poor and lime-rich dunes in 2000 and 2014. B. Relationship between pH in and around blowouts and the proportion of arbuscular mycorrhizal plant species. C. Relationship between pH in and around blowouts and root biomass. W = lime-poor Wadden district; R = lime-rich Renodunal district.



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ABSTRACT

In industrialized countries, biodiversity is threatened by high atmospheric N deposition. In coastal dunes, blowouts can mitigate this through deposition of fresh sand, but lime-rich and lime-poor dunes may differ in blowout activity. We studied natural blowout activity and explanatory factors in 2000 and 2014 in up to 51 sites along the Dutch coast, representative for other parts of Europe. We further analyzed plant and soil characteristics related to P nutrition in seven sites in 2019 and found that blowout activity was intrinsically linked to interactions between the geosphere, pedosphere and biosphere. Blowout activity was higher in lime-rich than in lime-poor dunes, especially in 2014. This difference could not be explained by wind velocity and only partly by position in the landscape, but was associated with pH, critical N load and rabbit density. At high pH, P availability to the vegetation was low. Arbuscular mycorrhizal (AM) plant species thus predominated, which belong to the most characteristic dune plants and may provide rabbit food of better quality than nonmycorrhizal (NM) or ericoid mycorrhizal (ErM) plants. Root biomass was also low at high pH, which may reduce cohesion of the sand and increase blowout activity, especially in areas with high rabbit density. At low pH, P availability increased, which favored NM and ErM rather than AM plants, and root biomass increased, which increased stability of the blowouts. As a restoration measure, (re)activation of blowouts may improve buffer capacity, characteristic biodiversity and

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Plant mycorrhizal strategies
Root biomass

conservation status of coastal dune grasslands. However, lime-poor dunes are more vulnerable to acidification, increase in P availability and blowout stabilization than lime-rich dunes. In extremely lime-poor dunes, it may even be better to let vegetation develop towards Dune heathlands, which are also EU priority habitats.

1. Introduction

In many ecosystems, biodiversity is threatened by human impact. This is especially true for coastal sand dunes, which are widespread and offer a number of important ecosystem services (Everard et al., 2010), but also belong to the most threatened natural ecosystems in the world (Houston, 2008). A significant part of the coastal dunes has been lost to tourism and residential development, or is fragmented by infrastructure. In the last decades, high atmospheric nitrogen (N) deposition has become a severe problem, especially in industrialized countries (Jones et al., 2004; Remke et al., 2009; Bobbink et al., 2010; Erisman et al., 2015; Kooijman et al., 2017). Resilience of the coastal dunes further decreased due to lower grazing pressure by natural grazers and livestock (Drees, 2003, 2007; Provoost et al., 2011), and decrease of natural dynamics, due to stabilization of the coastline and planting of marram grass or pine forest (Jungerius et al., 1981; Doody, 2013). The combined effects lead to grass-encroachment, scrub development, loss of bare sand patches and acidification of the soil, which all contribute to loss in biodiversity (Provoost et al., 2011; Aggenbach et al., 2017; Kooijman et al., 2017).

In Europe, many coastal dunes are protected by the EU Habitat directive (European Union, 1992). Nevertheless, 45% of the coastal red list habitats is threatened (Janssen et al., 2016), and more than 95% of the protected dune habitats is in an unfavorable conservation status (European Environment Agency, 2015). Dune grasslands, fixed coastal dunes with herbaceous vegetation which are also called Grey dunes (H2130), are the most threatened part of the dune system and thus belong to the priority habitats (Houston, 2008). Important restoration measures in dune grasslands include (re)activation of blowouts, which could locally counteract acidification of the dune soil, and create open sandy patches for characteristic plant and animal species (Smits and Kooijman, 2012a, 2012b). In the past, dune mobility was seen as a threat to the dune landscape, and blowouts were stabilized as soon as possible (Jungerius et al., 1981; Doody, 2013). However, blowouts are a natural component of dune grasslands, which rejuvenate soil and vegetation, although the scale and activity may vary between dune systems (Jungerius et al., 1981; Hesp, 1991; Arens et al., 2013; Delgado-Fernandez et al., 2019). Since the 1980s, blowouts in the Netherlands are not stabilized any longer (Jungerius et al., 1981), and since the 1990s, various experiments with reactivation of blowouts and rejuvenation of the dunes have been conducted (Van Boxel et al., 1997; Arens et al., 2004, 2013).

Blowout activity is controlled by a number of factors, such as the supply of suitable sediment, but especially its mobility, which depends on wind conditions, soil moisture and stabilization potential of the vegetation (Kok et al., 2012). Wind is important, as wind velocities above a certain threshold are needed to get the sand particles in motion (Bagnold, 1941; Kawamura, 1951; Jungerius et al., 1981; Arens et al., 2004; Sherman and Li, 2012). Transport potential is a function of shear velocity to the third power in many models, but wind velocities between 8.75 and 10 m s^{-1} are most effective for sand transport in blowouts (Jungerius et al., 1981), because they are much more frequent than stronger winds. Windspeeds of 8.75–10 m s^{-1} are roughly equivalent to 6 Beaufort, which is common along the North Sea coast in winter (Clemmensen et al., 2014). Grain size is also important, as threshold wind velocities and transport processes such as creep, saltation and suspension are very sensitive to particle size (Bagnold, 1941; Kok et al., 2012). Blowout activity is also dependent on the vegetation, which reduces erosivity of the wind and erodibility of the sand. Plants form a significant obstruction to the flow of air (Wieringa and Rijkoort, 1983; Wolfe and Nickling, 1993), and produce roots and organic matter. Blowout activity is also influenced by grazing and digging animals, such as rabbits, which increase erosivity of the wind by grazing the vegetation, and erodibility of the sand by their burrowing activities (Van Dam, 2001; Drees, 2003, 2007). Rabbit numbers strongly decreased in NW Europe since the 1950s, due to Myxomatosis disease, followed by the rabbit haemorrhagic disease (RHD), but also showed recovery from time to time (Drees, 2003, 2007; Provoost et al., 2011; Arens et al., 2013).

In the last decades, blowout activity in the dunes of industrialized countries has been affected by high atmospheric N deposition. Atmospheric N deposition mainly consists of nitrogen oxides and ammonia, stemming from fossil fuel combustion and the agricultural sector, and partly of organic N (Cape et al., 2012; Kanakidou et al., 2016; Li et al., 2016). Along the Dutch coast, ammonia is the dominant fraction, due to extra emission from N-rich waters in the coastal zone (Kooijman et al., 2017). High N deposition may lead to increased growth of algae, which stabilize sand particles in early stages of succession (Pluis and Van Boxel, 1993; Sparrius et al., 2012). High N deposition may also increase growth of vascular plants, and locally lead to dominance of a few tall graminoid species (Jones et al., 2004; Remke et al., 2009; Kooijman et al., 2017), which lowers wind velocities at the soil surface, and reduces erodibility of the sand. However, lime-poor Grey dunes are more sensitive to high N deposition than lime-rich dunes (Kooijman and Besse, 2002; Remke et al., 2010). In the Netherlands, the critical load is 10 kg N ha^{-1} $year^{-1}$ for lime-poor Grey dunes, and 15 kg N ha^{-1} $year^{-1}$ for lime-rich Grey dunes (Van Dobben and Van Hinsberg, 2008).

Lime-rich dunes may be less sensitive to high N deposition, because availability of phosphorus (P), which is also an essential nutrient for plant growth, is lower than in lime-poor dunes (Kooijman et al., 1998, 2017, 2020). In lime-rich dunes, the amounts of inorganic P may be high (Walker and Syers, 1976; Hinsinger, 2001), but P availability to the vegetation may be restricted due to low solubility of primary and secondary calcium phosphates at high pH (Lindsay and Moreno, 1966; Hinsinger, 2001). Also, sorbed P may be bound to iron (Fe) oxides rather than to complexes of Fe and organic matter (OM), which constitutes a stronger form of binding (Gerke, 2010; Kooijman et al., 2020). Low P availability in lime-rich dunes may reduce plant productivity and grass-encroachment (Kooijman et al., 2017), especially since many characteristic dune species are arbuscular mycorrhizal (AM) plants (Kooijman et al., 2020). They take up inorganic P with help of their fungal partner (Read and Perez-Moreno, 2003; Smith and Smith, 2011), but in exchange for photosynthesis products, which may limit their growth rates (Koziol and Bever, 2015). In lime-poor dunes, P availability to the vegetation is generally higher than in lime-rich dunes, because calcium phosphates have dissolved at low pH (Lindsay and Moreno, 1966; Hinsinger, 2001). Also, P sorption may have become weaker due to the shift from Fe oxides to Fe-OM complexes (Gerke, 2010; Kooijman et al., 2020). As a result, plant productivity and grass-encroachment are usually higher than in lime-rich dunes (Kooijman et al., 2017), and characteristic AM plant species may disappear (Kooijman et al., 2020).

The goal of this study is to test whether natural blowout activity differs between lime-rich and lime-poor dunes, in order to evaluate suitability of blowout (re)activation as a restoration method in coastal dune grasslands. We studied all 51 natural blowout areas along the Dutch coast, which contains a larger surface of protected dune areas than any other country in the European Union (Houston, 2008). Also, the Dutch dunes are characteristic for countries with lime-rich dunes south of the Netherlands, and lime-poor dunes to the north (Eisma, 1968; Kooijman et al., 1998). Furthermore, artificial stabilization of blowouts stopped already in the 1980s. Natural blowouts have been studied in particular Dutch dune areas before (e.g., Jungerius et al., 1981; Jungerius and Van der Meulen, 1988; Arens et al., 2004, 2013), but differences in blowout activity between lime-rich and lime-poor dunes, and implications for P nutrition and blowout stability have not yet been addressed. We conducted an aerial survey of blowout activity in 2000 and 2014 and explanatory factors in all 51 dune areas, and studied plant and soil characteristics related to P nutrition in a subset of seven.

2. Methods

2.1. Natural blowouts in lime-rich and lime-poor dunes

2.1.1. Analysis of aerial photographs

The analysis of blowout activity along the Dutch coast was based on georeferenced RGB composite aerial photographs of 2000 and 2014, provided by Rijkswaterstaat. The resolution was 50 $*$ 50 cm in 2000, and 25 $*$ 25 cm in 2014. The study focused on natural blowouts, but 1–5% of them may have been influenced by man. In the analysis, 51 dune areas were selected with at least some aeolian activity in one of the years. Of the 51 dune areas, 34 were located in the lime-poor and iron-poor Wadden district in the northern part of the country, and 17 in the lime-rich and iron-rich Renodunal district in the southern part (Eisma, 1968). The area between the districts is a transitional border zone. Based on sand characteristics and chemical analysis of lime, iron and phosphorus contents, sites in the border zone were classified as Wadden sites in this study.

In all 51 sites, blowout activity was estimated by manual classification in ArcGIS, at a scale of 1:1500, which is suitable for identifying blowouts and areas with aeolian activity. In each blowout area, all blowouts were counted in 2000 and 2014. In addition, for both years, areas with high and low blowout activity, as well as stable areas were indicated, and surface areas calculated. In stable areas, bare sand was absent, or only present around rabbit holes. In areas with low blowout activity, bare sand accounted for 10–40% of the surface, and in areas with high blowout activity for more than 40%.

2.1.2. Explanatory factors

To explain potential differences in blowout activity, explanatory factors related to weather, site conditions, rabbit density and atmospheric N deposition were also studied. For each of the 51 dune sites, data on average annual wind velocity were collected from the Dutch Royal Meteorological Office over the period 1981–2010 (KNMI, 2011). Transport potential, an indicator of the annual amount of sand potentially transported by the wind, was calculated according to Kawamura (1951) and Arens et al. (2004) for ten weather stations along the Dutch coast. However, it was not possible to compare transport potential values between weather stations directly, due to their different positions in the landscape (Arens et al., 2004). Precipitation data were also provided by KNMI, for 33 weather stations along the Dutch coast. For each of the 51 blowout areas, average precipitation values were calculated for the period 1990–2000 and 2000–2015, based on data from the nearest weather station. The average number of wet days with precipitation of at least 10 mm was also calculated over these periods.

Average distance of the blowout area to the dune foot was measured for all 51 dune sites on the aerial photographs with ArcGIS. Maximum height of the dune area was determined with AHN2, the digital elevation model for the Netherlands, based on eight laser altimetry measurements per m^2, and provided by Rijkswaterstaat. Exposition of the dune areas was determined on the aerial photographs, and classified in 32 sectors of 11.25° each. For each sector, an index was calculated for potential profit of the WSW wind, which is the main wind and net transport direction (Aggenbach et al., 2018). Potential profit of the WSW wind was e.g., 100% for WSW expositions, 75% for W and SW, 50% for WNW, 25% for NW and N and 0% for NNW. Exposure is a proxy for how well a dune area is exposed to wind, based on exposition, distance to the dune foot, height of the dune massive and surrounding vegetation, especially forest. Exposure was classified by the second author based on expert judgement, and expressed in values between 30 and 100%. Exposure would be 100% in high dunes close to the sea with maximum exposition to WSW wind, and 30% in low inland dunes at 1.5 km from the sea surrounded by forest.

The presence of dynamic foredunes and path density was estimated for a subset of 38 of the 51 blowout areas by manual classification of the aerial photographs: 22 in Wadden and 16 in Renodunal. Dynamic foredunes were classified on a scale of 0 to 5, with increasing activity in the fore dune ridge. Path density was classified on a similar scale, from 0 when no paths were present to 5 when path density was very high.

In 40 of the 51 sites (23 in Wadden, and 17 in Renodunal), soil samples were collected in the winter of 2019–2020 for determination of pH and the fine sand fraction < 250 μm (Pit et al., 2020). In 2019–2020, these sites showed more or less similar blowout activity as in 2014 (Schouten, 2019). In each site, samples were collected inside a characteristic blowout, as well as in adjacent open and more vegetated pioneer stages. Soil samples of the upper 5 cm were collected with metal rings of 100 cm^3, dried and manually sieved over a 250 μm sieve. Within a site, differences in the proportion of fine sand between different stages of succession were generally relatively small, and only the blowout samples were used for further analysis. pH values were measured in demineralised water, using a 1:2.5 weight:volume ratio (Westerman, 1990).

In 37 of the sites visited for soil sampling (21 in Wadden and 16 in Renodunal) plant species composition in open and more vegetated pioneer stages was recorded in plots of approximately 3 × 3 m, with nomenclature according to Van der Meijden (2005) for vascular plants, and Van Tooren and Sparrius (2007) for bryophytes. Species composition was partly recorded in winter, but in the temperate coastal dune grasslands of the Netherlands many species are perennials or winter annuals. Data of the open and more vegetated pioneer plots were combined to obtain a list of all plant species present in each site. Vascular plants were listed as arbuscular mycorrhizal (AM), ericoid mycorrhizal (ErM) or nonmycorrhyzal (NM) species according to various sources (Read et al., 1976; Ernst et al., 1984; Cairney and Meharg, 2003; Wang and Qiu, 2006; Brundett, 2009). *Sedum acre* was classified as AM according to Ernst et al. (1984), although this species was NM in Olsson and Tyler (2004). Also, some plant species may be negatively affected by AM fungi rather than positively (Johnson et al., 1997; Koziol and Bever, 2015). As *Koeleria macrantha* was negatively affected by AM fungi in Dixon (2000), this was classified as non-AM species.

Rabbit density was based on data provided by the Dutch Network Ecological Monitoring (NEM). In many dune areas, site managers are counting rabbits in a standardized way in particular transects (Dijkstra et al., 2018). Eight times in spring, and eight times in autumn, site managers go out by car in the evening, and count the rabbits appearing in the head lights. Rabbit data were available for 21 of the 51 blowout sites in 2000 (14 in Wadden and 7 in Renodunal), and 33 sites in 2014 (25 in Wadden and 8 in Renodunal). For each transect, rabbit numbers in spring and autumn were converted to maximum number of rabbits per year per km road. In many sites, data were available for more than one transect, which were used to calculate average rabbit density per year for the entire dune area. As preceding years are also important for the effect of rabbits on blowout activity, average rabbit density was also calculated for the period 1996–2000 and 2010–2014.

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 modelled and mapped with OPS version 4.3.03, and corrected for extra NH_y deposition from the sea (Noordijk et al., 2014; Kooijman et al., 2017). Deposition of organic N was not taken into consideration, but based on data for Rotterdam in Cape et al. (2012), this fraction probably accounted for only 2–3% of the total N deposition in both Wadden and Renodunal district. For each blowout area, data on N deposition for different years were extracted from the maps. Transgression 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} $year^{-1}$ for the lime-poor Wadden district, and 15 kg N ha^{-1} $year^{-1}$ for lime-rich Grey dunes for the lime-rich Renodunal district (Van Dobben and Van Hinsberg, 2008). For the site Solleveld, located in the Renodunal district, but on much older lime-poor sand than the generally lime-rich younger dunes, critical load was assumed to be 10 kg N ha^{-1} $year^{-1}$. We also used a critical N load based on pH values in the blowout, with values of 15 kg N ha^{-1} $year^{-1}$ for soils with $pH > 8$, and 10 kg N ha^{-1} $year^{-1}$ for soils with $pH < 8$, but this did not really change the response patterns.

2.2. Plant and soil characteristics related to P nutrition

2.2.1. Field survey

For the analysis of plant and soil characteristics, seven characteristic dune sites were selected, four in Wadden (Texel Slufter Zuid, Zwanenwater, Schoorlse duinen, Bergen Zuid), and three in Renodunal (Amsterdamse Waterleidingduinen I and II, and Hollands Duin). In each site, a predefined grid of two by one kilometers was located parallel to the foredunes (Fig. 1). In each site, three blowouts with five succession stages in their vicinity were selected according to stratified random sampling procedures: (1) inside the blowout, (2) open pioneer with vegetation cover up to 35%, (3) denser pioneer with vegetation cover of 35–75%, (4) older pioneer stages with a clear Ah horizon in the soil or blown over stabilized vegetation, and (5) stable vegetation with a clear Ah horizon in the soil. In each of the 15 sampling localities in each site, soil profiles were collected with a rectangular metal auger with a surface area of 50 cm^2 and a depth of 36 cm, and soil descriptions were made according to FAO guidelines (FAO, 2006). Thickness of the fresh sand layer on top of older soil horizons was measured, or set at 36 cm when Ah horizons were absent. Topsoil samples (0–10 cm) were collected for analysis of basic soil characteristics and fractionation of Fe and P. For bulk density, additional samples were collected with a metal ring of 100 cm^3.

In each of the seven sites, plant species composition was recorded in a plot of approximately 3 ∗ 3 m in the 12 sampling localities with vegetation as described in the foregoing section. Cover of bare sand, vascular plants and cryptogam layer were estimated in percentage. Aboveground vascular plant biomass was collected by clipping the vegetation in plots of 25 ∗ 25 cm, or 50 ∗ 50 cm when vegetation cover was very low. Root samples were collected with the rectangular auger of 36 cm depth described above, in which the majority of roots was present.

2.2.2. Laboratory analysis

Vegetation and soil samples were stored at 4 °C until further analyses. Aboveground vascular plant biomass and root samples were dried for 48 h 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 aboveground and root biomass was determined by weighing. The topsoil samples were dried for 48 h at 105 °C, after which bulk density was determined. After homogenization by hand, pH values were measured in demineralised water, using a 1:2.5 weight:volume ratio. Soil organic matter content was determined with weight loss on ignition (Westerman, 1990).

For analysis of different fractions of C, P and Fe, as well as total N, we used only one of the three replicate series in each site, and analyzed five samples in each of the seven sites. The samples were ground before analysis.. Total C and N content were determined with a Vario EL cube Elementar CNS analyzer. Lime content of the soil was measured with a Shimadzu TOC VCPH analyzer, and further used to calculate total organic C.

Selective extractions of P were applied to dried and ground material of the 35 topsoil samples described above. 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 grinding of the samples. Total P was determined after heating 1 g of soil at 500 °C in order to digest organic matter (Westerman, 1990; Kooijman et al., 1998, 2009). Samples were subsequently extracted with 50 ml 0.5 M H_2SO_4. Total P was measured spectrophotometrically with a Cecil CE1010 spectrometer with a sulphuric 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 0.015 M ammonium fluoride, 0.20 M glacial acetic acid, 0.25 M ammonium nitrate and 0.013 M nitric acid.

Different Fe fractions, important to sorption of P, were measured on the same subset of 35 topsoil samples. Total amorphous Fe was determined according to Schwertmann (1964), by extraction in the dark

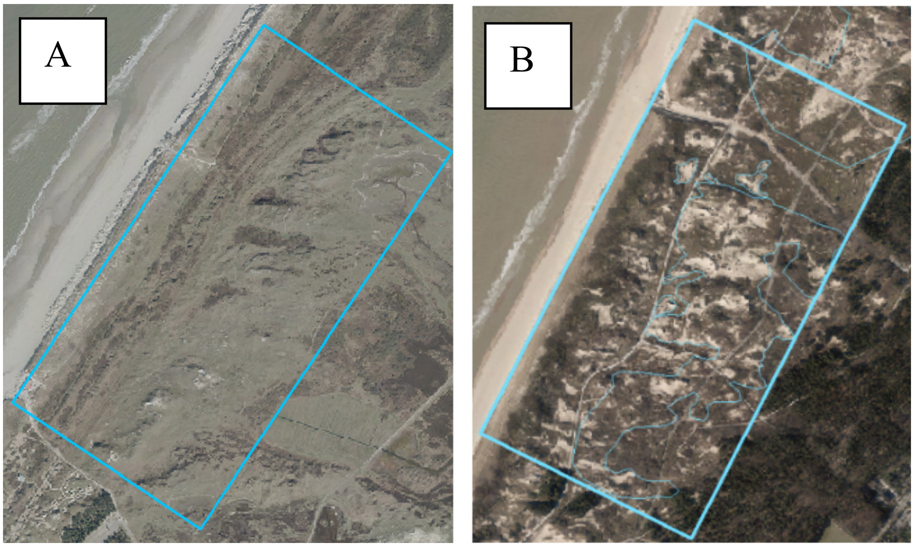

Fig. 1. Aerial photographs of 2017 of two characteristic dune areas. A = Zwanenwater, characteristic for the lime-poor Wadden district; B = Hollands Duin, characteristic for the lime-rich Renodunal district. Data are derived from Schouten (2019).

with 0.073 M ammonium oxalate and 0.05 M oxalic acid at pH 3. Amorphous Al was also measured, but because this was generally less abundant than amorphous Fe, and showed more or less similar patterns, this is not further treated. The extracts also included oxalate-extractable P, but as they were diluted for the measurement of Fe, many P values were below the detection limit, and not further treated. Organic Fe (and Al), which belongs to complexes of Fe with soil organic matter, were measured according to McKeague et al. (1971) by alkaline Na-pyrophosphate/NaOH extraction at pH 9.8. Inorganic amorphous Fe, present as Fe oxides, was calculated as the difference between total amorphous and organic Fe. As already mentioned, selective extractions should be used with some care. Part of the organic Fe may consist of small inorganic particles, especially in podzol soils with mobilization and precipitation of Fe (Jeanroy and Guillet, 1981). However, in the lime-poor dunes of this study, podzolisation did not yet occur.

2.3. Statistical analyses

Differences in blowout activity between dune districts and years were tested with two-way general linear models with district (Wadden and Renodunal) and year (2000 and 2014) as independent factors (Cody and Smith, 1987). Differences were significant when $P < 0.05$. Differences between individual groups were post-hoc tested with Least square means tests (Cody and Smith, 1987). Differences in explanatory variables were tested with two-way GLM as described above when data for both 2000 and 2014 were available, and otherwise with one-way GLM, with dune district as independent factor. To test whether the frequency of particular plant species in pioneer vegetation differed between Wadden and Renodunal districts, chi-square tests were applied, with average frequency for the two districts as expected frequency (Mason et al., 1994). To test relationships between blowout density in 2014, pH and plant characteristics, Spearman correlation tests were applied (Cody and Smith, 1987). A correlation-based network analysis was conducted to test relationships between blowout activity in 2014 and explanatory variables, based on Spearman correlation tests for individual sets of parameters. Stepwise multiple linear regressions were applied to test which of the explanatory factors was most important (Cody and Smith, 1987).

For the analysis of plant and soil characteristics in the P nutrition study, the seven sites were grouped into four Wadden and three Renodunal sites. For variables analyzed in the three replicate succession series within a particular site, values were combined in one mean value for each stage of succession. However, for plant species, the three replicates were combined in a total list of species, from which total number and number of AM and non-AM plants could be derived. We also combined succession stages in two groups rather than four (vegetation) or five (soil) stages, as stages 1 (if present), 2 and 3 closely resembled each other, as well as stages 4 and 5. Differences between dune districts and stages of succession were tested with two-way general linear models, with district (Wadden and Renodunal) and stage (pioneer and older stage) as independent factors. Differences between individual groups were post-hoc tested with least square means tests. For particular plant species, differences in frequency between Wadden and Renodunal were tested with chi-square tests, with average frequency for the two districts as expected frequency. To further explore relationships between pH and plant or soil characteristics, Spearman correlation tests were applied, based on the values for each of the five (for soil) or four (for vegetation) succession stages in each site. A correlation-based network analysis was conducted to test relationships between variables related to site conditions, nutrients and plant characteristics, based on Spearman correlation tests for individual sets of parameters.

3. Results

3.1. Natural blowouts in lime-rich and lime-poor dunes

3.1.1. Blowout activity

In the 51 sites of the dune survey, blowout activity statistically differed between dune districts rather than years (Supporting materials Table S1). Blowout density per km^2 was significantly higher in the lime-rich Renodunal than in the lime-poor Wadden, and showed a clear increase between 2000 and 2014 (Fig. 2). The total active area was higher in Renodunal than in Wadden in both years. The areas with high and low activity were also generally higher in Renodunal than in Wadden, but the area with high activity increased from 2000 to 2014, while the area with low activity decreased. In Wadden, the areas with high and low aeolian activity remained low in both years.

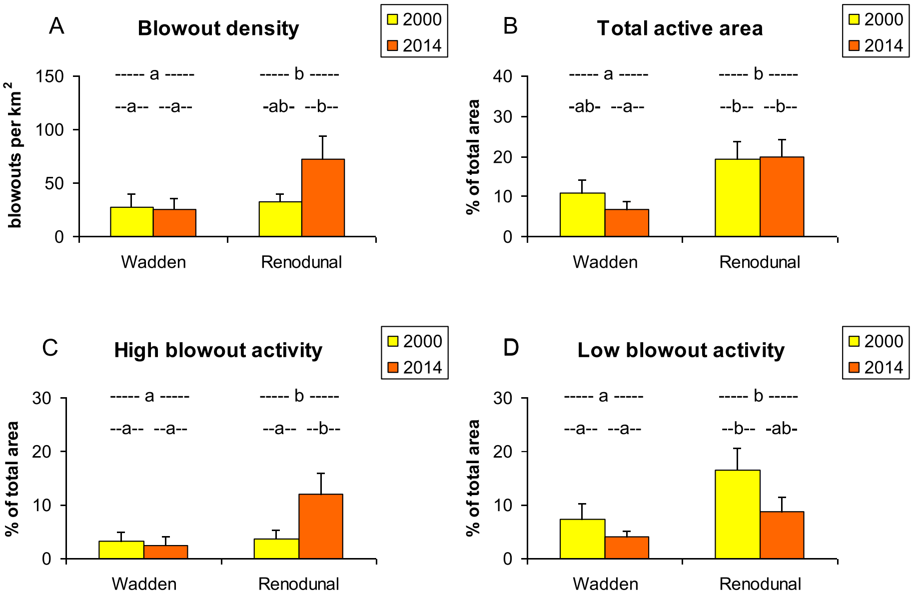

Fig. 2. Blowout activity in 2000 and 2014 in the lime-poor Wadden ($n = 34$) and lime-rich Renodunal ($n = 17$). A = Blowout density (numbers km^{-2}), B = total active area (% of total dune area); C = area with high blowout activity (% of total dune area) and D = area with low blowout activity (% of total dune area). Values are mean values and standard errors. Different letters indicate significant differences between individual mean values ($P < 0.05$).

Table 1
Mean and standard errors for explanatory factors in the lime-poor Wadden district ($n = 23–34$) and the lime-rich Renodunal district ($n = 15–17$).

	Wadden district	Renodunal district
Average wind velocity (m s^{-1})	5.8 (0.1)	5.2 (0.2)*
Presence of dynamic foredunes (class value)	2.7 (0.3)	1.4 (0.3)*
Exposition to WSW wind (% of maximum)	37 (5)	48 (6)
Distance to dune foot (m)	713 (82)	606 (96)
Height dune massif (m)	19.8 (1.0)	22.8 (7.6)
Exposure of dune area (% of maximum)	80 (3)	78 (3)
Path density (class value)	0.8 (0.1)	1.1 (0.2)
Fine sand fraction (%)	39 (4)	46 (5)
Annual rainfall (mm)	850 (8)	876 (14)*
Number of wet days	23 (0)	26 (1)*

* Significant differences between Wadden en Renodunal ($P < 0.05$).

3.1.2. Explanatory factors

Higher blowout activity in Renodunal than in Wadden could not be explained by factors related to erosivity of the wind (Table 1). Average wind velocity was significantly higher in Wadden than in Renodunal, but blowout activity lower rather than higher. Dynamic fore dunes, which may facilitate sand transport between beach and hinter lying dunes, were also more common in Wadden than in Renodunal. Exposition to WSW winds, distance to the dune foot, height of the dune massif and exposure of the dune area did not differ between districts. Factors related to erodibility of the sand could also only partly explain differences in blowout activity. Path density and the fraction of fine sand < 250 μm did not differ between districts. Annual rainfall and number of wet days did show differences between districts, but values were slightly higher in Renodunal than in Wadden, instead of lower. Rabbit density and atmospheric N deposition showed more or less similar patterns as blowout activity (Fig. 3). Rabbit density was significantly higher in Renodunal than in Wadden, especially in 2014. Also, atmospheric N deposition above the critical N load significantly decreased between 2000 and 2014 in both districts, but was generally higher in Wadden than in Renodunal.

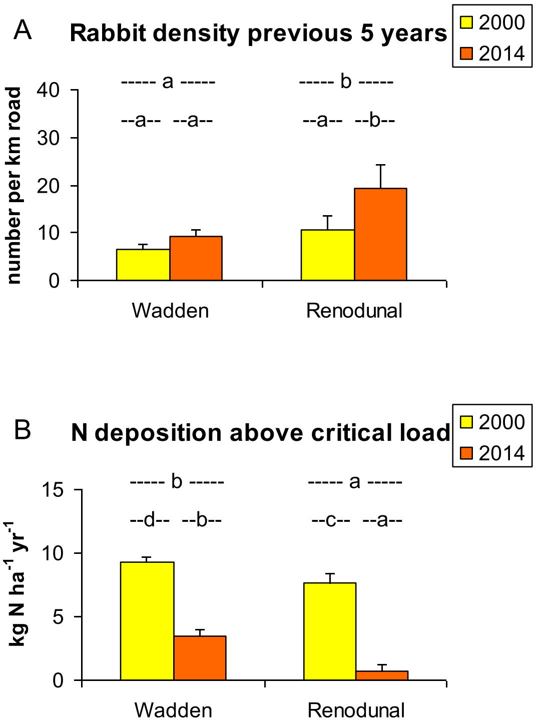

Fig. 3. Rabbit density and atmospheric N deposition in Wadden and Renodunal around 2000 and 2014. A. Rabbit density in the 5 years prior to the analysis of blowout activity ($n = 14–25$ for Wadden and 7–8 for Renodunal); B = N deposition above the critical N load ($n = 34$ for Wadden and 17 for Renodunal). Values are means and standard errors. Different letters indicate significant differences between individual mean values.

3.1.3. Blowout activity, pH and plant characteristics

As expected, pH in the blowouts was significantly higher in Renodunal than in Wadden, with mean values of 8.5 (±0.1) and 7.2 (±0.2) respectively. As a result, the Wadden and Renodunal districts clearly differed in plant species composition in the pioneer vegetation in and around the blowouts (Supporting materials Table S2). *Erodium lebelii* and *Hippophae rhamnoides* were significantly more common in Renodunal, and *Ammophila arenaria*, *Corynephorus canescens*, *Hypochaeris radicata* and *Jasione montana* in Wadden. The total number of vascular and arbuscular mycorrhizal (AM) plant species, which include many characteristic dune species, did not differ between districts. However, the number of non-AM plants was significantly higher in Wadden than in Renodunal. Blowout density and pH in the blowouts significantly correlated, and pH increased when blowout activity was higher, according to expectations (Fig. 4). However, this correlation may also mean that blowout activity increased when pH inside the blowout, which more or less represents the parent material, was higher. The positive correlation between blowout activity and pH was especially clear in the lime-poor Wadden, where some of the pH values were as high as in the lime-rich Renodunal, particularly in areas with high blowout density. The proportion of AM plant species did not differ between districts, but positively correlated with pH, especially in the lime-poor Wadden. The proportion of AM plant species also showed a positive correlation with blowout density, which indicates that high blowout activity may lead to an increase in characteristic dune plants and biodiversity.

3.1.4. Network analysis

In a correlation-based network analysis of blowout activity in 2014 and explanatory factors, blowout density significantly correlated with exposition to WSW wind and distance to the dune foot, even though they did not differ between districts (Fig. 5). Blowout density, the total active area and the area with high activity significantly correlated with pH in the blowouts. Critical N load also showed significant correlations with these blowout proxies, as well as with the area with low activity. Path density only correlated with the total active area and the area with low activity, and rabbit density only with the latter. In stepwise multiple linear regressions, most of the variance in blowout density, total active area and the area with high blowout activity was explained by pH (data not shown). For the area with low activity, critical N load was most important.

3.2. Plant and soil characteristics related to P nutrition

3.2.1. Soil characteristics

In accordance with the general survey, pH values significantly differed between districts in the more detailed plant-soil study (Supplementary materials Table S3). Lime content and pH were indeed higher in the lime-rich Renodunal than in the lime-poor Wadden (Table 2). However, like in the general survey, some pH values in Wadden were as high as in Renodunal, especially in pioneer stages (Fig. 6). This was especially the case in soils with at least some lime, with values of 0.2–0.4%. Soil organic C content and total N in the topsoil slightly differed between districts, but especially increased between pioneer and older stages of succession. In contrast, the fresh sand layer was thicker in pioneer than in older stages of succession.

As expected from differences in parent material, the amount of total, inorganic and organic amorphous Fe were significantly higher in the iron-rich Renodunal than in the iron-poor Wadden. Organic Fe also showed higher values in older than in pioneer stages. The proportion of organic Fe significantly increased from high to low pH (Fig. 6),

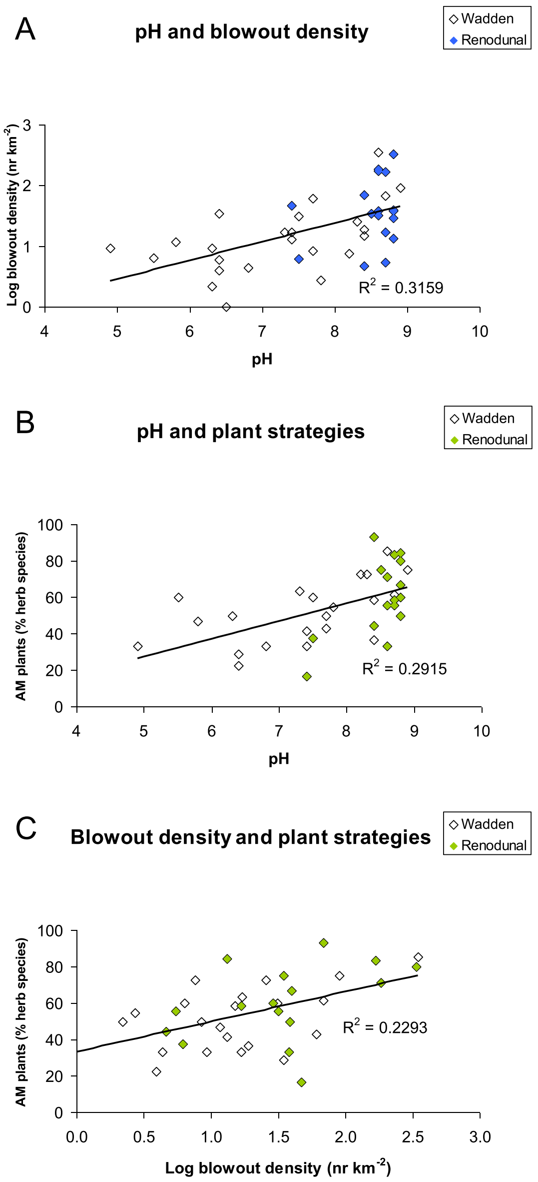

Fig. 4. Relationships between pH inside blowouts, blowout density and proportion of arbuscular mycorrhizal (AM) plant species in lime-poor Wadden and lime-rich Rendounal districts. A = pH and blowout density (n = 40); B = pH and the proportion of AM plant species (n = 37); C = blowout density and proportion of AM plant species (n = 37). All correlations were significant ($P < 0.05$).

especially within Wadden, which may lead to weaker P sorption. Total and inorganic P did not differ between succession stages, but were significantly higher in the lime-rich Renodunal than in the lime-poor Wadden district. Inorganic P also increased with pH, even in the P-poor Wadden. Organic P and weakly sorbed P increased from pioneer to older stages of succession. Both fractions also differed between districts, but organic P was higher in Renodunal, but weakly sorbed P in Wadden. The amount of weakly sorbed P significantly increased from high to low pH. Compared to pH 8, the amount of weakly sorbed P was approximately three times higher at pH 7, eight times higher at pH 6, and 17 times higher at pH 5. The correlation between weakly sorbed P and pH was even stronger when expressed as proportion of total P ($R^2 = 0.50$; data not shown), and the proportion of weakly sorbed P amounted from close to zero at pH > 8 to approximately 40% of total P at pH 5. In most sites, weakly sorbed P was lower than inorganic P, which means that at least part of the weakly sorbed P consisted of inorganic P. However, in Wadden sites with pH < 5.5, weakly sorbed P was higher than inorganic P, which shows that at least part of it consisted of organic P.

3.2.2. Plant characteristics

According to expectations, bare sand cover significantly decreased from pioneer to older stages of succession, although values were slightly higher in Renodunal than in Wadden (Supplementary materials Table S4, Table 3). Cover of the cryptogam and herb layer, aboveground vascular plant and root biomass increased from pioneer to older stages of succession. Root biomass also differed between dune districts, with significantly higher values in Wadden than in Renodunal. Root biomass significantly increased from high to low pH, more or less independent of dune district (Fig. 7). Compared to pH 8, root biomass was approximately three times higher at pH 7, six times higher at pH 6 and ten times higher at pH 5. Root biomass was also negatively correlated with the amount of inorganic P, and positively with the amount of weakly sorbed P.

Vascular plant species composition clearly differed between districts (Supplementary materials Table S5). Species such as *Hypochaeris radicata*, *Jasione montana*, *Rosa pimpinellifolia* and *Calluna vulgaris* were only found in Wadden, and *Cynoglossum officinale* and *Ligustrum vulgare* only in Renodunal. However, characteristic dune species which are normally absent from stabilized acidic dunes, such as *Galium verum*, *Viola curtisii* and *Ononis repens*, were found in and around the blowouts in both districts. The number of vascular plant species did not differ between districts, but significantly increased from pioneer to older stages of succession. In both Wadden and Renodunal, most plants were AM plants rather than non-AM plants, both in species and in cover, and the number of AM plant species and cover did not differ between districts or succession stages. However, the number and proportion of non-AM plant species was significantly higher in Wadden. The

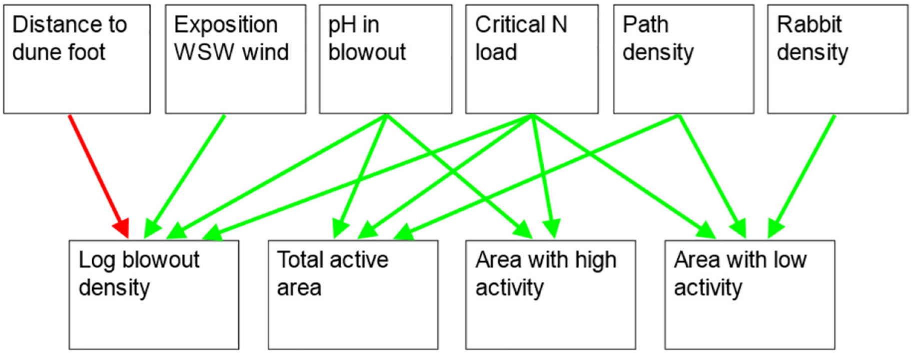

Fig. 5. Correlation-based network analysis of different proxies for blowout activity in 2014 and explanatory site factors. Only significant correlations ($P < 0.05$) are indicated. Positive correlations are given in green, and negative correlations in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Characteristics of the topsoil (0–10 cm) in different stages of succession in the lime-poor Wadden and lime-rich Renodunal dune district. Values given are mean values and standard deviation (n = 3–4, each based on 2–3 subreplicates).

	Wadden pioneer stage	Wadden older stage	Renodunal pioneer stage	Renodunal older stage
pH topsoil[1]	7.0 (1.1)^{ab}	6.0 (1.0)^{a}	8.2 (0.1)^{b}	7.4 (0.0)^{b}
Lime content (%)[1]	0.1 (0.2)^{a}	0.2 (0.3)^{a}	1.9 (1.1)^{b}	1.1 (0.5)^{b}
Organic C in topsoil (g m^{-2})[1,2,3]	313 (293)^{a}	763 (278)^{b}	400 (132)^{a}	2017 (144)^{c}
N in topsoil (g m^{-2})[1,2,3]	20 (25)^{a}	62 (15)^{b}	17 (12)^{a}	161 (35)^{c}
Thickness fresh sand layer (cm)[2]	33 (2)^{b}	13 (11)^{a}	29 (5)^{b}	5 (3)^{a}
Total amorphous Fe topsoil (g m^{-2})[1]	17 (8)^{a}	19 (6)^{a}	53 (1)^{b}	51 (6)^{b}
Inorganic Fe (g m^{-2})[1]	14 (7)^{a}	1 (7)^{a}	49 (1)^{b}	39 (5)^{b}
Proportion inorganic Fe (% total)^{ns}	80 (13)^{a}	71 (27)^{a}	92 (1)^{a}	88 (2)^{a}
Organic Fe (g m^{-2})[1,2]	3 (2)^{a}	5 (4)^{a}	4 (0)^{a}	12 (2)^{b}
Proportion organic Fe (% total)^{ns}	20 (13)^{a}	29 (27)^{a}	8 (1)^{a}	12 (2)^{a}
Total P topsoil (g m^{-2})[1]	7.8 (2.7)^{a}	7.8 (2.7)^{a}	18.2 (5.6)^{b}	23.1 (1.5)^{b}
Inorganic P (g m^{-2})[1]	3.4 (2.7)^{a}	3.7 (3.0)^{a}	14.8 (2.6)^{b}	13.0 (3.7)^{b}
Proportion inorganic P (% total)[1]	39 (24)^{a}	42 (25)^{a}	83 (10)^{b}	56 (12)^{a}
Organic P (g m^{-2})[1,2,3]	4.4 (1.3)^{a}	4.0 (0.6)^{a}	3.4 (3.1)^{a}	10.1 (2.6)^{b}
Proportion organic P (% total)[1]	61 (24)^{b}	58 (25)^{b}	17 (10)^{a}	44 (12)^{b}
Weakly sorbed P (log mg m^{-2})[1,2,3]	3.1 (0.2)^{b}	3.2 (0.1)^{b}	1.3 (1.2)^{a}	3.5 (0.3)^{b}
Proportion weakly sorbed P (% total)[1]	22 (13)^{b}	20 (8)^{b}	0 (0)^{a}	14 (9)^{ab}

^{ns} = not significant. Different letters indicate significant differences between individual mean values.

[1] Significant differences between dune districts.

[2] Significant differences between succession stages.

[3] Significant interactions between dune districts and succession stages ($P < 0.05$).

proportion of AM plant species significantly increased with pH, especially in Wadden (Fig. 8). The proportion of AM plants was approximately 45% of all vascular plant species at pH 5, but 90% at pH 8. The proportion of AM plant species also significantly increased with inorganic P, for both the amount and proportion of total P. In contrast, the proportion of AM plant species showed a negative relationship with weakly sorbed P, although significantly so only when expressed as proportion of total P.

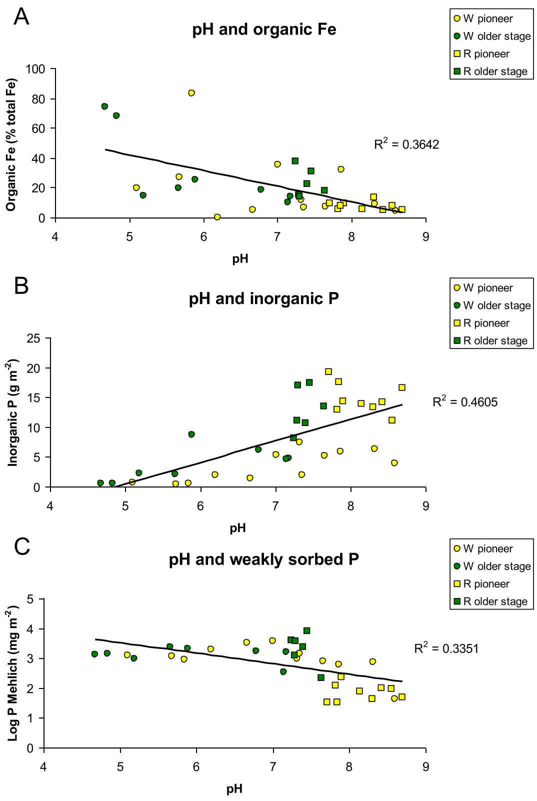

Fig. 6. Relationships between pH, organic Fe, inorganic P and weakly sorbed P in different stages of succession in lime-poor Wadden (W) and lime-rich Renodunal (R) dune districts. A = pH and the proportion of organic Fe; B = pH and the amount of inorganic P; C = pH and the amount of weakly sorbed P. All correlations were significant (n = 35; $P < 0.05$).

3.2.3. Network analysis

In a correlation-based network analysis of site factors, nutrients and plant characteristics, the amount of inorganic P positively correlated with lime content, pH of the topsoil and the amount of inorganic Fe (Fig. 9). In turn, inorganic P positively correlated with the proportion of AM plant species, which use inorganic P and benefit especially under P-limited conditions. However, inorganic P correlated negatively with the proportion of non-AM species, as well as root biomass. In contrast, the amount of weakly sorbed P negatively correlated with lime content, pH and the amount of inorganic Fe, but positively with the amount of organic Fe and soil organic C, which are associated with weaker P sorption. In turn, weakly sorbed P positively correlated with root biomass and aboveground biomass. Organic P and total N both positively correlated with organic Fe and soil organic matter, but organic P did not correlate with plant characteristics, and total N only with aboveground biomass.

4. Discussion

The goal of this study was to test whether natural blowout activity differs between lime-rich and lime-poor dunes, in order to evaluate suitability of blowout (re)activation as a restoration method in coastal dune grasslands. The study can be seen as a natural experiment with blowouts in lime-rich and lime-poor dunes, although explanatory variables are based on correlations rather than causal relationships. The study clearly shows that blowout activity was higher in lime-rich than in lime-poor dunes, and spontaneously increased between 2000 and 2014 in the first, but not in the latter. These differences could not be explained by wind velocity and rainfall, and only partly by position in the landscape. In contrast, blowout activity may be intrinsically linked to interactions between the geosphere, pedosphere and biosphere, especially through the effects of pH on P nutrition, plant strategies and root biomass.

4.1. Unimportant factors

Wind is important for the mobility of a dune system (Bagnold, 1941; Kawamura, 1951; Jungerius et al., 1981; Arens et al., 2004; Sherman and Li, 2012). We found higher blowout activity in lime-rich than in lime-

Table 3
Plant characteristics in different stages of succession in the lime-poor Wadden and lime-rich Renodunal dune district. Values given are mean values and standard deviation (n = 3–4, each based on 2 subreplicates).

	Wadden pioneer stage	Wadden older stage	Renodunal pioneer stage	Renodunal older stage
Bare sand (% cover)[1,2]	53 (23)^{b}	4 (5)^{a}	57 (23)^{b}	11 (10)^{a}
Cryptogam layer (% cover)[2]	3 (8)^{a}	26 (17)^{b}	1 (3)^{a}	39 (21)^{b}
Vascular plants (% cover)[2]	40 (10)^{a}	73 (10)^{b}	44 (5)^{a}	52 (20)^{ab}
Aboveground biomass (g m^{-2})[2]	109 (34)^{a}	305 (61)^{b}	91 (8)^{a}	258 (153)^{b}
Root biomass top 30 cm (log g m^{-2})[1,2]	3.3 (0.3)^{b}	3.8 (0.2)^{c}	2.7 (0.4)^{a}	3.2 (0.2)^{b}
Total vascular plant species (nr)[2]	13 (3)^{ab}	18 (6)^{b}	10 (2)^{a}	16 (1)^{ab}
AM plant species (nr)^{ns}	9 (5)^{a}	11 (6)^{a}	9 (2)^{a}	13 (1)^{a}
Proportion AM plant species (% total)[1]	65 (19)^{ab}	60 (18)^{a}	86 (6)^{b}	85 (4)^{b}
AM plant species (% cover)^{ns}	34 (14)^{a}	51 (3)^{a}	30 (12)^{a}	47 (19)^{a}
Proportion AM plant cover (% total)^{ns}	81 (19)^{a}	66 (36)^{a}	67 (22)^{a}	89 (2)^{a}
Non-AM vascular plant species (nr)[1]	4 (2)^{a}	7 (3)^{b}	1 (1)^{a}	2 (1)^{a}
Proportion non-AM plant species (% total)[1]	35 (19)^{ab}	40 (18)^{b}	14 (6)^{a}	15 (4)^{a}
Non-AM vascular plants (% cover)^{ns}	6 (5)^{a}	22 (21)^{a}	14 (8)^{a}	6 (2)^{a}
Proportion non-AM plant cover (% total)^{ns}	19 (19)^{a}	34 (36)^{a}	33 (22)^{a}	11 (2)^{a}

^{ns} = not significant. Different letters indicate significant differences between individual mean values.
[1] Significant differences between dune districts.
[2] Significant differences between succession stages ($P < 0.05$).

poor dunes, but average wind velocities were higher in lime-poor than in lime-rich dunes, instead of lower. Extreme wind velocities may be less important than expected, because heavy storms are often accompanied by rainfall, which increases soil moisture and reduces the actual sand transport (Lancaster and Helm, 2000; Arens et al., 2004). Jungerius et al. (1981) showed that wind velocities between 8.75 and 10 m s^{-1} were most effective for sand transport in blowouts, which is a common wind speed along the North Sea coast in winter (Clemmensen et al., 2014). Factors related to position in the landscape, which generally affect the actual sand transport (Arens et al., 2004; Kok et al., 2012), could only partially explain differences in blowout activity. Exposition of the dune area relative to the WSW wind, i.e., the main wind and net transport direction, and distance to the dune foot both showed significant correlations with blowout density, although differences between districts were not significant. However, factors such as exposure, height of the dune massif and grain size were unimportant. Differences in blowout activity could also not be explained by annual rainfall and the number of wet days. However, lime-rich dunes may

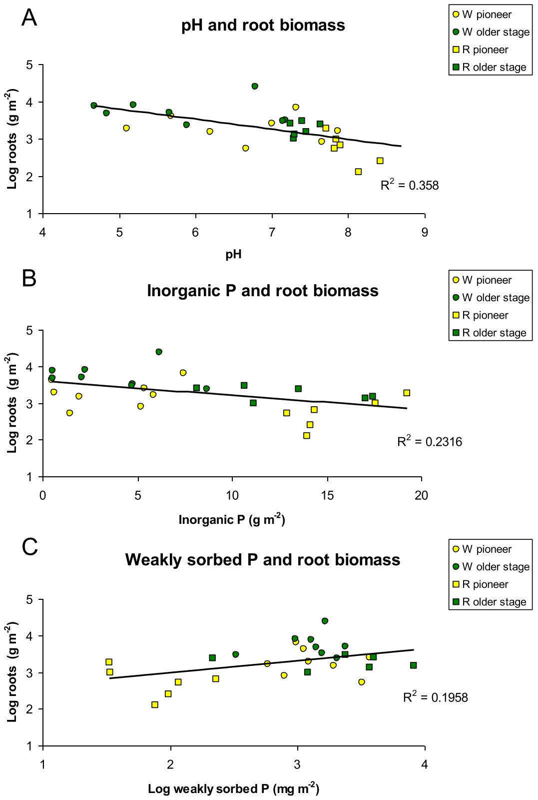

Fig. 7. Relationships between root biomass and pH, inorganic P and weakly sorbed P in different stages of succession in lime-poor Wadden (W) and lime-rich Renodunal (R) dune districts. A = pH and root biomass; B = amount of inorganic P and root biomass; C = amount of weakly sorbed P and root biomass. All correlations were significant (n = 28; $P < 0.05$).

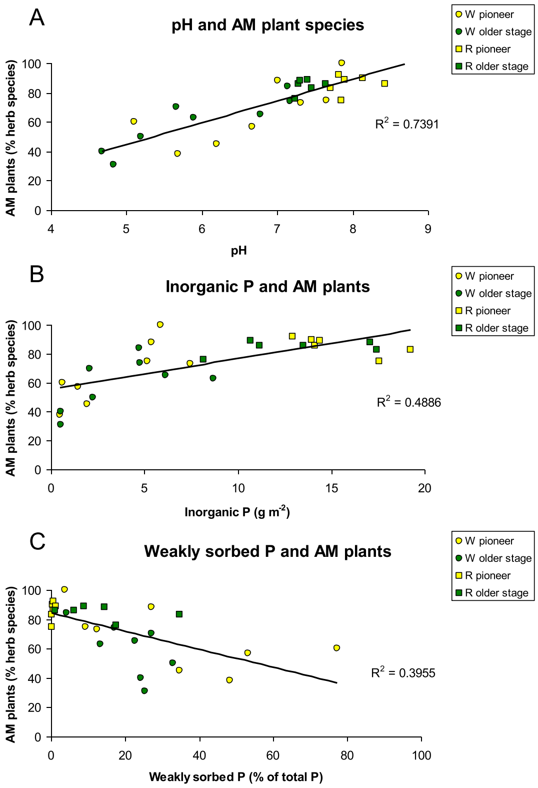

Fig. 8. Relationships between AM plant species and pH, inorganic P and weakly sorbed P in different stages of succession in lime-poor Wadden (W) and lime-rich Renodunal (R) dune districts. A = pH and proportion of AM plant species; B = amount of inorganic P and proportion of plant species; C = proportion of weakly sorbed P and proportion of AM plant species. All correlations were significant (n = 28; $P < 0.05$).

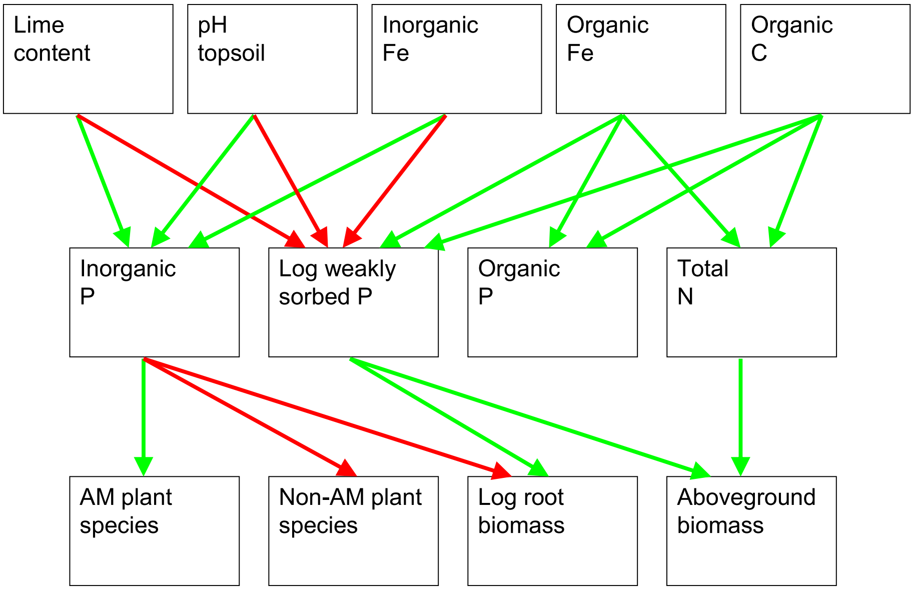

Fig. 9. Correlation-based network analysis of site factors, soil nutrients and characteristics of the vegetation. Values for topsoil and biomass variables are based on (m)g m^{-2}, and for AM and non-AM plant species on the proportion of total vascular plant species. Only significant correlations ($P < 0.05$) are indicated. Positive correlations are given in green, and negative correlations in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

be more sensitive to water erosion during heavy rain than lime-poor dunes, due to lower root biomass in both pioneer and older stages of succession. Grey sand with organic matter is water repellent in dry periods, and may be washed from the dune slopes when heavy rain follows a period of dry weather (Jungerius and Van der Meulen, 1988; Witter et al., 1991). Once the grey surface sand is removed, wind erosion may begin in the underlying yellow sand.

4.2. Important factors

4.2.1. Rabbit density

Higher blowout activity in lime-rich than in lime-poor dunes may to some extent be explained by rabbit density, which was higher in Renodunal than in Wadden. This was especially the case in 2014, when blowout activity also increased. Rabbits are natural grazers in the European dunes, and may stimulate blowout activity with their grazing and digging activities (Van Damme and Ervynck, 1993; Van Dam, 2001; Isermann et al., 2010; Doody, 2013). In the past, high rabbit density has led to dune mobilization, as burroughs and underground galleries collapsed and formed starting points for new blowouts. Since the 1950s, rabbit numbers strongly decreased in NW Europe due to Myxomatosis and Rabbit haemorrhagic disease (Drees, 2003, 2007; Provoost et al., 2011; Arens et al., 2013). In Renodunal, rabbit populations generally recovered between 2000 and 2014, which may explain the increase of blowout activity here. Unfortunately, correlations between rabbit density and blowout activity were only significant for the area with low activity, probably due to lack of data, which were available for only 33 of the 51 dune areas. However, in a more detailed sister study, blowout activity in different years generally positively correlated with rabbit density, although one area showed high activity despite low rabbit numbers (Schouten, 2019).

4.2.2. Sensitivity to N deposition dependent on P

Higher blowout activity in lime-rich than in lime-poor dunes may also be explained by lower sensitivity to high atmospheric N deposition (Van Dobben and Van Hinsberg, 2008; Remke et al., 2010), as critical N load significantly correlated with blowout activity in 2014. Also, N deposition strongly decreased between 2000 and 2014 in both districts, but values declined to values close to the critical load in Renodunal only. Lime-rich dunes are less sensitive to high N deposition because P availability to the vegetation is generally lower than in lime-poor dunes (Kooijman et al., 1998, 2017, 2020). This was supported by the present study, although the actual pH values may be more important than lime richness of the parent material. Total and inorganic P increased from low to high pH even in lime-poor dunes, but inorganic P for a large part consists of calcium phosphates (Walker and Syers, 1976; Hinsinger, 2001; Pit et al., 2020), which are insoluble at pH 8 (Lindsay and Moreno, 1966). In theory, phosphate concentrations may increase at high pH if Ca precipitates as calcium or calcium-sodium carbonates (Toner and Catling, 2020). This brings down Ca concentrations in the soil solution, and may prevent precipitation of calcium phosphates. However, this process only takes place above pH 9, when carbonate is the dominant form of inorganic C. Even in the blowouts, pH values were below 9, and quickly dropped to lower values when pioneer plants established. Below pH 9, inorganic C is mainly present as bicarbonate, and Ca precipitates with P as calcium phosphates, which reduces P availability to the vegetation. Availability of P may be further reduced around pH 8 due to predominance of inorganic Fe, which points to strong sorption of P to amorphous Fe oxides (Kooijman et al., 2009; Gerke, 2010; Yan et al., 2016). However, P availability to the vegetation increased at low pH, due to dissolution of calcium phosphates below pH 6.5 (Lindsay and Moreno, 1966). Also, at low pH, part of the Fe oxides transformed into Fe-OM complexes when their OH-groups became protonated and were replaced by organic acids (Gu et al., 1994; Yan et al., 2016). This leads to weaker P sorption (Kooijman et al., 2009; Gerke, 2010), which was supported by the tenfold increase in weakly sorbed P between pH 8 and pH 5, even in the lime-poor Wadden.

4.2.3. pH more important than lime content

As indicated above, pH was more important to P nutrition than differences in lime content, as sites with high pH and low P availability to the vegetation were found even in lime-poor dunes. This probably also holds for blowout activity, as blowout density increased with pH even in the lime-poor Wadden, and pH was the most important explanatory factor for blowout density, total active area and the area with high blowout activity. Naturally, pH of the topsoil is influenced by blowout activity, and values were indeed higher in pioneer stages than in older stages of succession. In stabilized blowouts, the precipitation surplus of NW

Europe leads to dissolution and leaching of lime from the topsoil, and decrease in pH (Blume et al., 2016; Aggenbach et al., 2017). However, pH is also affected by the parent material, and high values generally occur in lime-rich dunes, but values around pH 8 were also found in and around the blowouts of lime-poor dunes with a little lime (0.2–0.4%).

4.2.4. Differences in root biomass

Differences in pH also affected root biomass, which is important as blowouts are stabilized by developing root systems in the unconsolidated substrate. High root biomass may also prevent development of new blowouts. In our study, root biomass showed a tenfold increase from pH 8 to pH 5, even though aboveground vascular plant biomass was not affected by pH. This is supported by Kooijman et al. (2005), who found higher root biomass in lime-poor than in lime-rich dunes in pioneer vegetation around reactivated blowouts. The increase in root biomass from high to low pH is probably associated with the increase in P availability over this gradient. It is however possible that the increase in root biomass at low pH is also related to the shift from AM to NM and ErM plant species. Root biomass negatively correlated with the proportion of AM plants ($R^2 = 0.22$), although this may reflect that both were affected by changes in P availability, rather than a causal relationship between them. Perhaps, AM plants need less roots than NM plants because part of the root function is taken over by the fungal network (Smith et al., 2011). Arbuscular mycorrhizal fungi may stabilize dune soils by themselves (Sutton and Sheppard, 1976; Koske et al., 2004), but roots are larger than fungal hyphae. However, in Unger et al. (2017), root biomass did not differ between (infected) AM and NM plants, although total root length was generally higher for NM plants. Also, root biomass was particularly high in sites with *Rosa pimpinellifolia*, which is probably an AM plant (Maryland-Quellhorst et al., 2012), but generally grows in slightly acidic dunes with higher P availability.

4.2.5. Differences in plant strategies

Whether plant strategies affect blowout activity through differences in root biomass remains to be studied, but blowout activity probably affects plant strategies through pH and P nutrition. In our study, the proportion of AM plant species increased from 25 to 40% at pH 5 to 60–90% at pH 8, in accord with Kooijman et al. (2020). We did not measure actual fungal infection in the field, but for AM plants, the AM status is almost always natural (Smith et al., 2011). As many AM plants belong to the most characteristic dune species, their predominance at high pH is associated with an increase in biodiversity and conservation status of these dune habitats. Arbuscular mycorrhizal plants are suitable colonizers of open sandy habitats (Koske et al., 2004), and are supported by their fungal partners in uptake of water and N (Johansen et al., 1994). Colonizers such as *Ammophila arenaria* indeed performed better when infected with AM fungi (Koske and Polson, 1984). Arbuscular mycorrhizal plant species may also be abundant at high pH because of the high amounts, but low availability of inorganic P (Kooijman et al., 2020). For AM plants, inorganic P is their main P resource (Read and Perez-Moreno, 2003; Smith and Smith, 2011), but the P uptake benefits for the host plant will outweigh the costs of carbon supply to the fungus mainly when P is a limiting factor (Johnson et al., 1997; Smith and Read, 2008; Hoeksema et al., 2010). At low pH, however, P is no longer a limiting factor, due to the high amounts of weakly sorbed P. Also, many AM fungi are sensitive to low pH (Van Aarle et al., 2002). At low pH, NM and ErM plant species became more abundant, which may be due to the increase in weakly sorbed (organic) P. Weakly sorbed P is a suitable P resource for NM plants, which exudate small organic acids such as citrate and oxalate, and release P from the sorption complex by ligand exchange (Lambers et al., 2008; Gerke, 2015). Also, at low pH, weakly sorbed P at least partly consisted of organic P. Besides organic acids, NM plants exudate phosphatase enzymes, which especially disintegrate labile forms of organic P (Güsewell, 2017). For ErM plants, organic P even is their main P resource (Emmerton et al., 2001; Cairney and Meharg, 2003).

4.3. Blowout activity in lime-rich dune grasslands

Along the Dutch coast, blowout activity was higher in lime-rich than in lime-poor dunes. We have no data on blowouts in other European countries, which are often stabilized to prevent erosion. However, a quick scan of satellite images on Google Earth showed that many active dunes are located in lime-rich dunes along the coasts of northern France, Belgium and northern Denmark. As mentioned, blowout activity may be stimulated in lime-rich dunes by high pH, low P availability, high amount of AM plant species and/or low root biomass. Also, low P availability makes lime-rich dunes less sensitive to high N deposition. Due to high lime content, pH will remain high for a long time even in stabilized blowout areas, and predominance of AM plants and low root biomass were found even in older stages of succession. This makes it easier to reverse the stabilization process, which was supported by the increase in blowout activity in Renodunal between 2000 and 2014, which mainly occurred in areas with low activity in 2000. The spontaneous reactivation of the blowouts between 2000 and 2014 was likely partly due to the decrease in N deposition to values closer to the critical load, but may have been further stimulated by rabbit activity, which clearly increased in this period. Rabbits may even profit from high pH and predominance of AM plants, as these are more nutritious and have higher N and P content than NM plants (Kooijman et al., 2020). In lime-rich dunes, the stabilization potential of the vegetation may thus be relatively low. This may be a problem in areas with high erosion, but (re)activation of blowouts may only be needed in areas where blowouts do not keep active by themselves. Also, for species-rich grasslands, blowout activity should not be too high, as only a slight cover of sand is needed to replenish the buffer capacity.

4.4. Blowout activity in lime-poor dune grasslands

4.4.1. Lime-poor dunes with some lime

In lime-poor dunes, slight differences in lime content may lead to large differences in pH, P availability, plant strategies and root biomass. In Wadden, pH values comparable with lime-rich Renodunal dunes were found especially in sites with some lime (0.2–0.4%). High pH Wadden sites were located in the border zone between Wadden and Renodunal district, which geochemically belonged to Wadden, but were also found on Wadden islands. In such sites, plant diversity may be very high, because both calcicole and calcifuge species grow together (Aggenbach et al., 2018). However, the soil is vulnerable to acidification because lime content and buffer capacity are low, and ongoing blowout activity is needed to keep the pH high enough. This happened in a natural way on the main coast with clear western exposition, although human activity around coastal villages probably also played a role, with overexploitation in the past, and nowadays trampling by tourists (Slings, 1994). In less exposed areas such as on the Wadden islands, (re)activation of blowouts may be a good method to improve conservation status of dune grasslands, especially when the parent material contains at least some lime, or when the dunes are located right behind dynamic fore dunes, through which shell fragments can be blown in from the beach.

4.4.2. Extremely lime-poor dunes

In most lime-poor dune sites, pH in and around the blowouts was lower than in lime-rich dunes, due to very low lime content of the parent material (Eisma, 1968). In these sites, stabilization potential of the vegetation was high, due to high P availability and root biomass, and possibly a lower proportion of AM plant species. The Google earth survey of satellite images suggested that blowout activity was also very low in the lime-poor dunes of Germany and Denmark, except for the German island Norderney, which has large rabbit populations (Isermann et al., 2010), and Sylt, which is extremely exposed and located in an area with lower N deposition than the Netherlands (Erisman et al., 2015). In more populated parts of Europe, high N deposition is a large problem in lime-poor dunes, especially at low pH when

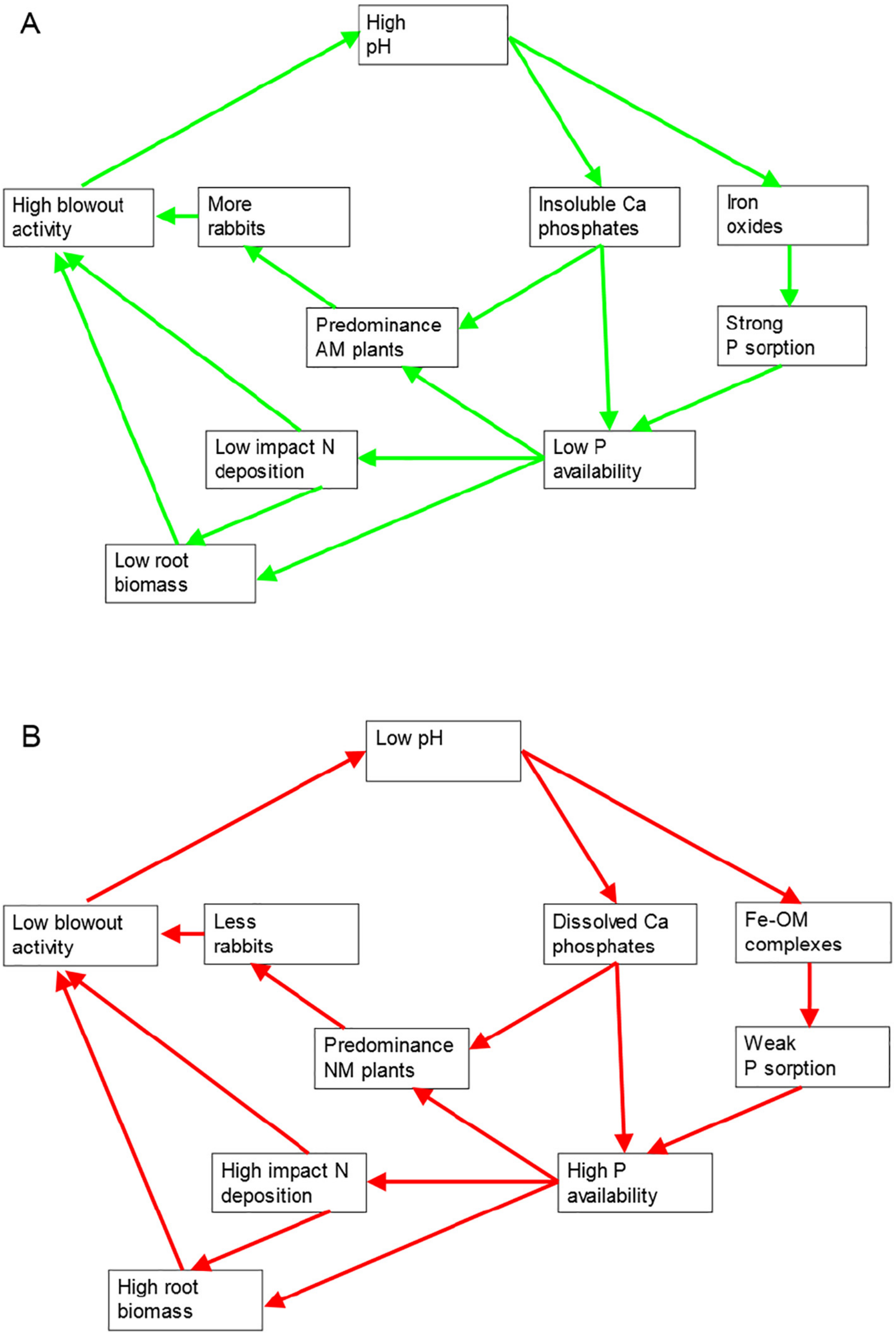

Fig. 10. Conceptual model of the impact of pH on P nutrition, plant strategies, sensitivity to high atmospheric N deposition, root biomass and blowout activity in coastal dune grasslands. A = high pH system associated with high blowout activity; B = low pH system associated with low blowout activity.

P availability is also high (Remke et al., 2010; Kooijman et al., 2017). Normally, N is a limiting nutrient to the vegetation in lime-poor dunes, and in areas with low N deposition, open sandy places may persist for long periods. In the beginning of last century, when N deposition was still very low, blowout activity in Wadden was much higher than today. However, Wadden dunes with low pH are currently threatened by high availability of both P and N, which stimulates plant growth and makes it more difficult to keep the blowouts active. In a reactivation experiment, such blowouts quickly stabilized, and the deposition area became densely covered with *Empetrum nigrum* within a few years (Aggenbach et al., 2018). In extremely lime-poor dunes, it may be better to not (re)activate blowouts at all, but allow further succession of Grey dunes (H2130) towards Dune heathland with *Empetrum nigrum* (H2140) or *Calluna vulgaris* (H2150), which are priority habitats for the European Union as well.

5. Conclusions

Blowout activity is a complex process regulated by many factors, which operate on different spatial and temporal scales. This study shows that blowout activity was higher in lime-rich than in lime-poor dunes. This result could not be explained by differences in wind velocity and rainfall, and only partly by location of the dunes. Rabbit density, which highly fluctuate due to viral diseases, played at least some role. Probably most important were differences in pH and P nutrition, through their effects on plant strategies, root biomass, sensitivity to high N deposition and possibly even food quality for rabbits (Fig. 10). Actual pH values may be even more important than lime content, as high pH led to low P availability and root biomass and predominance of AM plants even in lime-poor dunes. This study further supports that P nutrition, which is often treated secondary to soil organic matter and N, is actually a key factor in coastal dune grasslands. (Re)activation of blowouts may be a suitable method to increase resilience of coastal dune grasslands, especially in lime-poor dunes with a little lime. In lime-rich dunes, (re)activation of blowouts may also help, but may not be necessary because many keep active on their own. In extremely lime-poor dunes, (re)activated blowouts probably rapidly stabilize, and it may be more sustainable to let dune grasslands develop towards dune heathlands, which are Natura 2000 priority habitats as well.

CRediT authorship contribution statement

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

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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