Final Report

PhD project of the P-Campus graduate school

The relevance of biological soil crusts in the phosphorus cycle on sand dunes of the Baltic Sea coast

Sandra Kammann

Supervisors:	Prof. Dr. Ulf Karsten and Prof. Dr. Matthias Labrenz
Institutions:	University of Rostock and Leibniz Institute for Baltic Sea Research Warnemünde
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1 Summary and conclusion

The project results pointed to a conspicuous shift of the phototrophic biocrust community with the development of the dunes along each chronosequence, as reflected in different successional stages. Furthermore, the different geographical regions revealed a considerable impact on the biocrust species composition, which can be explained by habitat-specific factors. The enrichment of organic matter and nutrient contents, along with increased soil moisture and stability, are the key functions that originate from the metabolic activities in the different stages of biocrusts. The increase in total P in the biocrusts along both chronosequences could mainly be explained by the increased biomass formation. Consequently, biocrusts strongly shape dune development and contribute to geomorphological processes. In addition, the biocrust key functions offer opportunities for rehabilitation and restoration approaches, such as preventing sediment erosion in coastal dune areas.

2 Introduction and goals of the PhD project

The sand dunes along the Baltic Sea coast are mobile aeolian landforms under constant change. The dune geomorphology is based on initial geneses and on the following abrasion and accumulation processes due to wind, waves, and storm events. Besides the constant movement of the sand, extreme temperature fluctuation near the dune surface and drought make this area an extreme habitat (Martínez, Psuty and Lubke, 2004). The sand dunes of the Baltic Sea offer a unique habitat for the settlement of higher as well as cryptogamic vegetation like biological soil crusts (biocrusts). These particle-associated microbial communities, lichens, mosses, and their by-products, are one of the first colonization forms on temperate coastal sand dunes, forming the most productive micro-ecosystem in terrestrial drylands on Earth (Belnap, Büdel and Lange, 2001). Due to their relevance for primary production, nutrient enrichment of soils and the water cycle, and the stabilization of the top-soil layer, biocrusts are known as ˈecosystem engineersˈ (Evans and Johansen, 1999; Castillo-Monroy *et al.*, 2010; Chamizo *et al.*, 2016). Recent studies focused on the microbial-mediated processes of biocrusts in carbon (C) and nitrogen (N) cycling in drylands and temperate forests. The cycling of the growth-limiting element phosphorus (P) is less studied, especially in temperate regions (Schulz *et al.*, 2015; Baumann *et al.*, 2017; Glaser *et al.*, 2018). The results of previous studies already showed that the increase in the organic matter within the biocrust has a potential impact on the mechanisms of biogeochemical P cycling in the sediment. Inorganic bound P (e.g., Ca-phosphate minerals) can be solubilized from parent material either by the secretion of organic acids by microorganisms (Fox, 1995) or by an increase in the pH (Blume, Stahr and Leinweber, 2010). Phosphatases, produced by biocrust organisms, are known to hydrolyze organic phosphates releasing P (e.g., from dead cells) (Nannipieri *et al.*, 2011).

This study aims to characterize changes in the community structure of biocrust phototrophic organisms along dune chronosequences of the Baltic Sea coast. Moreover, it focuses on the ecological functions of biocrusts in P-cycling. Therefore, vegetation surveys followed by species determination and sediment analyses were conducted. The biocrust developmental patterns were linked with the dune successional stage along the chronosequences. In order to uncover a link between the biogeochemical cycles of N, C, and P and the biocrust biodiversity, correlations between species richness and nutrient status were investigated. Total P (P_t) analyses and analyses of various sequential fractions after (Hedley et al., 1982) provided a comprehensive picture of the distribution of P pools in the different successional stages of biocrust development. This method allowed quantifying the organic and inorganic bound P and the bioavailable P fraction. The results enhanced the fundamental understanding of biocrusts-related P-dynamics in the dune sand mediated by the community structure of biocrust phototrophic organisms. I hypothesize that i) along this marine-terrestrial gradient, the biocrusts will develop from thin aggregations of bacteria and algae to moss and lichen-dominated ˈmatureˈ communities. Consequently, ii) I assume that changes in biodiversity can be linked to increased biomass accumulation, representing potential organically bound P storages, and to mineralization and solubilization processes supporting P-bioavailability. Therefore, biocrusts are expected to fertilize the nutrient-poor sand, facilitating the growth of higher plants.

The enrichment of the biotic and abiotic components suggests cryptogamic covers as key players in geochemical processes, supporting sediment moisture and stability. Moreover, it highlights these communities as ˈecosystem engineersˈ playing a valuable part in nature protection e.g., preventing sediment erosion in coastal dune areas.

3 Material und Methods

<u>Study sites:</u>

Biological soil crust samples were collected in 2020/21 along dune successional sequences on the peninsula Fischland-Darss-Zingst, the island Rügen (Mecklenburg Western Pomerania, Northern Germany), and an inland dune area (Lower Saxony, Northern Germany) (Fig. 1). Biocrust samples were taken along one transect at each study site. Each transect followed the natural, geomorphological succession (chronosequence) of the respective dune area. Along each transect, different successional dune stages were selected and further named dune subsites. At each subsite, a sampling plot of 1 m^2 was established and used for further vegetation analyses, biocrust, and sediment sampling.

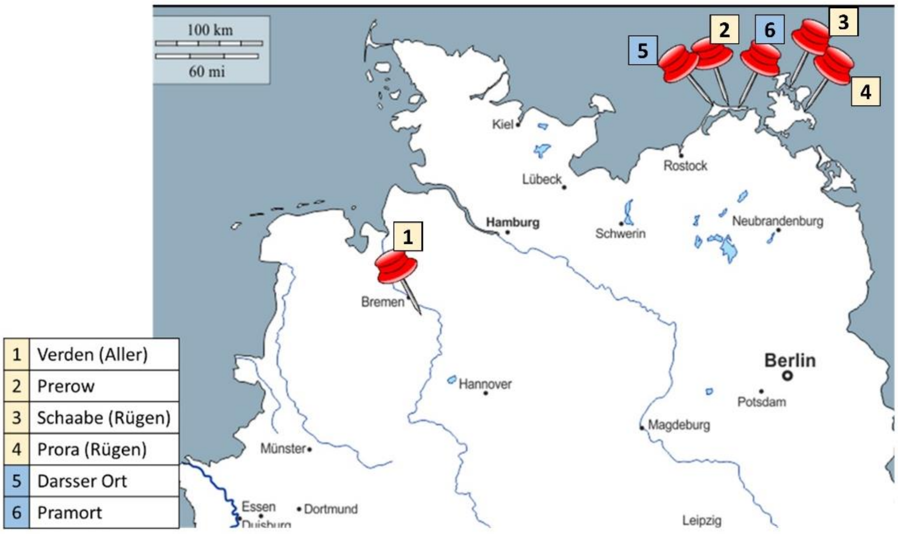

Figure 1. Overview of all six sampling sites in Northern Germany. Yellow shading indicates sampling in spring 2020 (1-4), blue shading indicates sampling in January 2021 (5-6).

<u>Sample collection and preparation:</u>

For biocrust sampling, Petri dishes (92 mm in diameter) were dropped and pushed gently into the respective biocrust. A metal spatula was then used to lift and further separate the biocrust from the underlying loose sediment. Since the distribution of the functional biocrust groups in each sampling plot (1 m^2) was varying, a randomized system was used for the biocrust selection. Further, a drill core (5 cm diameter; 30 cm length) was used for the analytical determination of sediment parameters. The drill was used three times randomly within the sampling plot. The samples were already visually divided in the field for the top- and sub-horizon. The sediment core samples were stored in plastic zip-lock bags and transported to the laboratory for further chemical analyses (Tab. 1).

Table 1: List of all measured parameters and the corresponding compartments (sediment and biocrust) they were measured in.

Parameters	Sediment core	Biocrust
pH	X	
Electrical conductivity	X	
$CaCO_3$	X	
Dithionite-citrate-bicarbonate extracted Fe (Fe_d)	X	
Oxalate extracted Fe (Fe_{ox})	X	
Water content (% FM)		X
Organic matter (% DM)		X
C_t, N_t, P_t	X	X
Sequential P fractionation	X	(X)
Phototrophic community		X
Chlorophyll *a* content		X

<u>Vegetation survey and species determination:</u>

A category system of seven predefined functional groups was designed to describe the overall surface coverage of each sampling plot. The set of functional groups was based on previous work conducted by Büdel *et al.*, 2009; Lan *et al.*, 2012; Williams *et al.*, 2017, but was slightly modified (Supplementary material Table 1). The point intercept method by Levy and Madden (1933) was used to record the predefined functional groups.

The air-dried biocrust material stored in the dark was further used for the identification of the most frequent and dominant algae species. Morphological identification of the biocrust organisms was based mainly on Ettl and Gärtner (2014) for green microalgae and on Komárek (2013) for cyanobacteria. Further, monographs and papers devoted to taxonomic revisions of the taxa of interest were used (Darienko and Pröschold, 2019).

Morphological identification of mosses was based on Frahm and Frey (2004) with taxonomical reference to Hodgetts *et al.* (2020). Lichens were determined according to Wirth, Hauck and Schultz (2013) and followed the nomenclature concept provided by Printzen *et al.* (2022). Some species of the genus *Cladonia* needed a deeper morphological analysis. Therefore, these samples were additionally analyzed by thin-layer chromatography according to Culberson and Ammann (1979).

4 Results

The results highlighted a varying phototrophic community composition within the biocrusts regarding the different successional stages of the dunes. A shift from algae-dominated to lichen- and moss-dominated biocrusts in later successional dune types was observed at all study sites (Fig. 2).

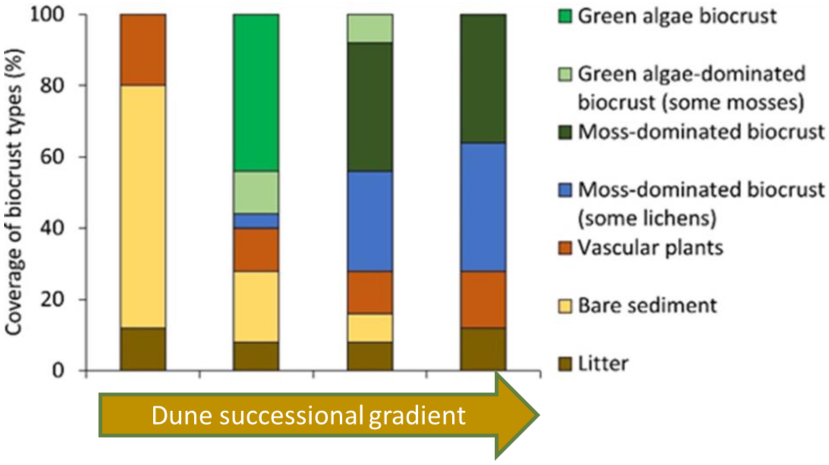

Figure 2. Summary of the vegetation survey. Percentage of the area covered by the different functional groups, as determined by the point intercept method.

Moreover, an increase in the organic matter and moisture content with advanced biocrust development was detected. The measured carbonate contents ($CaCO_3$ equivalents) were at all dune subsites very low. Higher carbonate contents in the younger dune stages represented the original, almost unweathered parent material. A decrease in the carbonate content with dune succession suggested an ongoing decalcification of the sandy sediment. Hereby, the top sediment layers had lower carbonate contents than the sub sediment. This observation indicated the metabolic activity of the biocrusts. Due to the CO_2 and H^+ produced during microbial soil respiration (Kuzyakov, 2006) and the excretion of organic acids, these potentially promoted a more rapid decalcification in the uppermost sediment layer (Fox, 1995; Belnap, 2011). The enrichment of carbon, nitrogen, and phosphorus in the different biocrust types showed a similar relationship. If the sediment core was divided into the top-horizon and sub-horizon, the nutrient concentrations in the top horizon were higher compared to the sub horizon. A (partly irregular) increase of the dithionite-citrate-bicarbonate extracted Fe (Fe_d) content along the successional gradients was recognizable, confirming the advanced weathering degree of the sediments inland.

However, a reduction in the ratio of the pedogenic Fe-compounds Fe_{ox}/Fe_{d} was not confirmed in the chronosequences on the peninsula Fischland-Darss-Zingst, probably due to very young dune ages and low iron contents. A decrease in this ratio was expected, which would indicate soil development (Cornell and Schwertmann, 2003).

With increasing dune age and soil development, the distribution of the P fractions showed the same trends at all sites. The P concentrations of the labile or moderately labile fractions increased, while the Ca-bound P concentrations and proportions in the stable P fraction decreased (Fig. 3). For biocrusts of coastal dunes, an average threefold higher P content was determined compared to the sediment cores. Similar to the sediment cores, an absolute enrichment of labile and easily soluble P was recognizable here. Again, this happened at the expense of Ca-bound P (H_2SO_4 fraction).

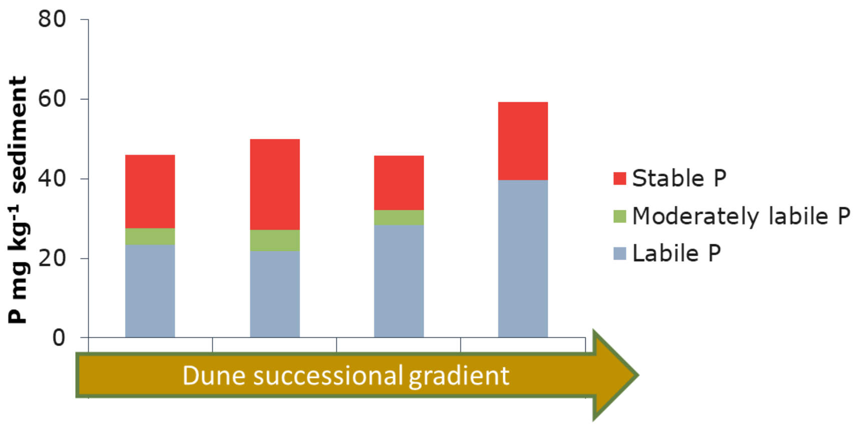

Figure 3. Visualization of the dynamics of P-pools in dune sediments covered with biocrusts.

The biocrust community composition and the related sediment characteristics revealed that the community composition of moss, lichen, and algae in the biocrusts differed between the sampling sites and along the transects. Statistical analyses using PerMANOVA verified that the community composition was significantly shaped by the sampling site and developmental stage of the dunes. The biocrust's gravimetric water content and Chl *a* content tended to correlate with the change in the community composition between the sampling sites and plots. The phototrophic species richness showed the trend to influence especially the total phosphorus content within the biocrust, even though this trend could not be statistically verified as significant. Looking at the phototrophic groups separately, the moss richness tended to be likely influencing the phosphorus content within the biocrust.

5 Discussion

Coastal dunes are characterized by strong winds resulting in a highly mobile substrate. Additionally, nearshore, higher sediment salinity, and air-borne salt spray cause harsh environmental conditions. Along with a scarcity of nutrients, only thin algae-dominated biocrusts can colonize dunes of an early successional stage (García Novo *et al.*, 2004; Lane *et al.*, 2008). Consequently, precipitation will easily infiltrate into the loose sandy sediment (Gypser *et al.*, 2016). However, the mature biocrust establishment was hardly observed in younger dunes due to the frequent disturbance by erosive wind forces leading to sand mobility (Martínez, Vázquez and Sánchez Colón, 2001) or due to water limitation caused by the low water-holding capacity of the sand (Chamizo *et al.*, 2016).

Soil moisture can positively affect carbon and nitrogen fixation by microorganisms, as was observed for biocrusts in arid regions (Belnap and Eldridge, 2001). The accumulation of organic carbon by microbial biomass formation plays an essential role in early pedogenesis (Kaviya *et al.*, 2019). Organic carbon accumulation is controlled by the turnover rates of the soil organic matter (Šourková *et al.*, 2005). The organic matter accumulation, especially detected in later dune successional stages colonized by mature biocrust covers, was assumed to be based on faster biomass formation and litter input than decomposition within the studied dune areas.

The observed increase in the organic matter content within the biocrusts potentially impacts the mechanisms of biogeochemical P-cycling in the sediment. Inorganic bound P (e.g., Ca-phosphate minerals) can be solubilized from parent material either by the microbial secretion of organic acids (Fox, 1995) or by an increase in the pH (Blume, Stahr and Leinweber, 2010). Phosphatases, produced by biocrust organisms, are known to hydrolyze organic phosphates, releasing P (e.g., from dead cells) (Nannipieri *et al.*, 2011). Therefore, the increase in total P in the top sediment layers along the studied dune chronosequences can mainly be explained by the increased biomass formation and hence biological activity.

Moss-dominated biocrusts were most abundant in later successional (mature) dune stages. These biocrust types formed a denser and more coherent layer on the sediment surface. The growth of lichens increased significantly. The percentage coverage by vascular plants was highest in older grey dune areas, dominated by Poaceae. The development of grey dunes was characterized by increased sand stabilization due to less sand accumulation (Martin, 1959). Therefore, vegetation cover could expand and support the formation of an organic matter layer on the sediment surface (Isermann, 2011). Such a layer was composed of dead plant material along with living phototrophic and heterotrophic biomass originating from the biocrusts. Biocrusts of mature dunes, as the latest phase of dune succession, represented a high organic matter content as an indicator of early soil formation (Dümig *et al.*, 2014).

Such mature biocrusts absorb water into the cellular mucilage using morphological adaptations, such as lamellae and filaments, and thus exhibit a higher water-holding capacity (Chamizo *et al.*, 2012; Belnap *et al.*, 2013), thereby stimulating sediment water retention and increasing water availability (Sun, Xiao and Kidron, 2022), at least in the top layer. Chamizo et al. (2016) additionally highlighted the later stages of biocrust succession, as dominated by lichens and mosses by their higher infiltration capability and water retention, finally leading to higher soil moisture.

Species composition of biocrusts

At all studied dune sites, the phylum Chlorophyta exhibited the highest species richness in biocrusts, which is well-known from humid terrestrial habitats (Hoffmann, 1989; Glaser *et al.*, 2018). These algae can act as pioneer colonizers of the mobile sand, facilitating further stabilization and colonization. Representatives of the filamentous genus *Klebsormidium* (Streptophyta) were almost omnipresent in all sampled biocrusts. *Klebsormidium* species exhibit as terrestrial taxa a wide tolerance to temperature, irradiance, and water availability, and are known for their stickiness to bind soil particles together (Karsten and Rindi, 2010; Holzinger and Karsten, 2013). With this broad ecological tolerance and traits, this genus can cope with the harsh conditions in the dunes near the water's edge and coexist in competition with other cryptogamic species, such as mosses and lichens in the biocrusts.

Cyanobacteria, which predominated in biocrusts on the peninsula Fischland-Darss-Zingst, also contribute to sediment stability by producing exopolysaccharides, which leads to enhanced soil particle aggregation and the prevention of dune erosion (Büdel *et al.*, 2016). In general, it has to be considered that cyanobacteria play a crucial role in the enrichment of sandy sediment with nutrients, especially in this nitrogen-poor habitat, because of the capability for fixation of atmospheric nitrogen (Langhans, Storm and Schwabe, 2009; Zhang *et al.*, 2009).

Moss- and lichen-dominated biocrusts were distinctive of older stages of dune development. *Ceratodon purpureus*, to name one key species, was found in transitional stages of dune succession. This moss species is typical for mobile dune types due to its high tolerance to sand deposition (Martínez and Maun, 1999). Another moss species only found on the dunes of the inland dune is *Syntrichia ruraliformis*. This species is highly desiccation-tolerant (Mishler and Oliver, 1991; Stark, Greenwood and Brinda, 2017). This trait favors moss growing on dune types under constant abiotic stress, such as high irradiation and low water-holding capacity.

The majority of the identified lichen species belong to the genus *Cladonia*. Those prefer growing on the sand under acidophilic habitat conditions, as they mainly occurred in the later dune stages. In transitional dune stages like grey dunes, lichen species primarily grew on plant litter, such as *Athallia cerinella, Lecania cyrtella, Myriolecis hagenii, Myriolecis persimilis, Physcia tenella*, and *Xanthoria parietina*. Those prefer to grow on trees (Wirth, Hauck and Schultz, 2013). In the transitional dune stages, tree debris, such as bark or branchlet, was overgrown by these lichen species and provided the favored habitat.

6 Outlook

From the knowledge gained from the fieldwork, further questions arise about the influence of the biocrust community on the P-cycle of coastal dunes. It is important to clarify which other P sources are available to the biocrusts in addition to the P bound in the parent rock material. In particular, the input from atmospheric deposition must be considered. Furthermore, it must be clarified which microbial organisms are the key players involved in the phosphate mobilization. Getting a deeper insight into the driving microorganisms in the P-cycling and their functions within, key genes involved have to be investigated. Using metagenomic approaches would reveal the relative abundance of P-cycling genes in different stages of biocrust development and further they could be assigned to functional groups. These include, for example, phosphorus degradation, solubilizing, and transporter genes. A taxonomic assignment of microbial genes coding for enzymes involved in the sand dune P-cycle reveals changes in gene abundances between different biocrusts successional stages. To reach from gene potential to gene expression metatranscriptomic are necessary. This method will allow me to identify differences in the P-gene expression under, for example, changing environmental conditions or phosphorus depletion.

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Supplementary Material

Table 1: Overview of all defined functional biotic and abiotic groups used to determine the dune surface coverage. Abbreviations of these groups, a short description, a color code, and visual examples of each functional group are given.

Category	Short	Description	Code	
Vascular plants	VP	Tracheophyta		
Bare sediment/ sand	Ba	No vegetation or biocrust visible, loose sand layer		
Litter	Li	Litter layer i.e. needles, leaves, branches		
Biocrust				
Green algae	GA	Early successional stage, slightly brittle, <3 mm thick, greenish-shimmering		
Green algae-dominated /mosses	GA/M	Stable green crust, occasionally mosses		
Moss-dominated	MD	biocrust dominated by mosses, partly many algae species (mostly green algae), several cm thick/high		
Moss-dominated /lichens	MD/L	MD-type, occasionally lichens (mostly chlorolichens), many algae species (mostly green algae), several cm thick/high		

List of: Research stays outside of supervising institutions, presentations or posters at conferences, public outreach, and/or publications

Conference contribution	**Public outreach**	**Publications**
P-Symposium 2019 → Poster	P-Campus 2020, Year-end meeting with ministry representatives → Presentation	Kammann S, et al. *Successional Development of the Phototrophic Community in Biological Soil Crusts on Coastal and Inland Dunes*. Biology. 2023; 12(1):58. https://doi.org/10.3390/biology12010058
P-Symposium 2020 → Poster	P-Lecture series 2021 → Presentation	
P-Symposium 2021 → Poster	„Lange Nacht der Wissenschaft“ 2022 → Biocrust Exhibition	
P-Symposium 2022 → Presentation	Press release 2023 https://www.uni-rostock.de/universitaet/kommunikation-und-aktuelles/medieninformationen/detailansicht-1/n/rostocker-forscherin-untersucht-ostseeduenen-und-findet-kleine-startups/	
GSB Conference, Dublin, Ireland 2023 → Presentation	Article Ostseezeitung 2023 https://www.ostsee-zeitung.de/lokales/rostock/forscherin-der-uni-rostock-arbeitet-an-bodenkrusten-der-ostsee-duenen-JSBRFS5KZFEZZCEELHVZ4ZP7KE.html	