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Carbon cycling of biological soil crusts mirrors ecological maturity along a Central European inland dune catena

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ABSTRACT

Photosynthesis and respiration of biological soil crusts (BSCs) sampled along a mobile inland dune catena were determined to evaluate the applicability of Odum's P/R ratio, determined under controlled conditions, for estimation of ecosystem maturity. The theory is that in the early stages of ecological succession, the total photosynthesis (P) exceeds the rate of community respiration (R), so that the P/R ratio is > 1, and that P/R approaches 1 as succession occurs. In the special case of organic pollution, the P/R ratio is typically < 1. Samples were collected in the deflation zone of the dune near the crest (BSC1, thickness 2–3 mm), at the lee side of grass tussocks at the slope (BSC2, thickness 2–4 mm) and near the base (BSC3, thickness 4–6 mm). Non-crusted sand was used as control (BSC0). Photosynthesis, respiration, crust biomass, as well as fossil and allochthonous pedogenic carbon entering the system with mineral substrate were determined. The respiration of the BSC1 was dominated by the degradation of allochthonous organic matter, leading to a diminished P/R ratio. The better developed BSC2 and BSC3 were less influenced by allochthonous organic matter, where BSC maturity increased downslope with biomass increase. No significant relation between the P/R ratio and soil water tension was found. Crust carbon pools increased and flows intensified, but mineralization constants decreased with system maturation. It was concluded that Odum's P/R ratio and accumulation of recalcitrant to biodegradation organic matter are indicative for biocrust maturity.

1. Introduction

Several key attributes have been defined to quantify ecosystem maturity, an overview of which was given by Christensen (1995) and Ludovisi et al. (2005). Due to methodological limitations for the determination of microbiotic species, of their abundance, their activity, their biomass, or their detritus, community structure based attributes seem to be less applicable for the purpose of maturity quantification in biological soil crusts (BSCs). Instead, overall ecosystem performance attributes seem to be more appropriate for micro-environments like BSCs.

Biological soil crusts possess unique combinations of model features that should be more widely exploited in community, landscape and ecosystem ecology. Being an especially useful model system that can enable researchers to see ecological principles more clearly and quickly, they are perhaps one of the best examples of micro-landscapes – real landscapes that are small in size (Bowker et al. 2014; Maestre et al. 2016). In this study, we used these unique model features of biocrusts to address the question of ecosystem maturity on its overall carbon cycling, which would be difficult to accomplish on the meso- or macroscale.

In the early stages of ecological succession, the rate of gross primary production, or gross photosynthesis (P) exceeds the rate of community respiration (R), so that the P/R ratio is > 1. In this case, community respiration should be regarded as summary respiration of photoautotrophic microphytes (R_p) and heterotrophic decomposers (R_d), similar to the concept proposed by Schlesinger and Bernhardt (2013) for the estimation of net ecosystem production. In the special case of organic pollution, the P/R ratio is typically < 1 in mature systems. In both cases, however, the theory is that P/R approaches 1 as succession occurs. The P/R ratio, therefore, should be an excellent functional index of the relative maturity of the system. As long as P exceeds R, organic matter and biomass will accumulate in the system (Odum 1969). While photosynthesis and respiration along successional stages from cyanobacterial to green algal, to moss, and finally to soil lichen crusts have been investigated earlier for arid conditions (Zaady et al. 2000), the maturity of BSC types dominated by the same species, *Zygogonium ericetorum* and *Klebsormidium crenulatum* as in our case, under temperate

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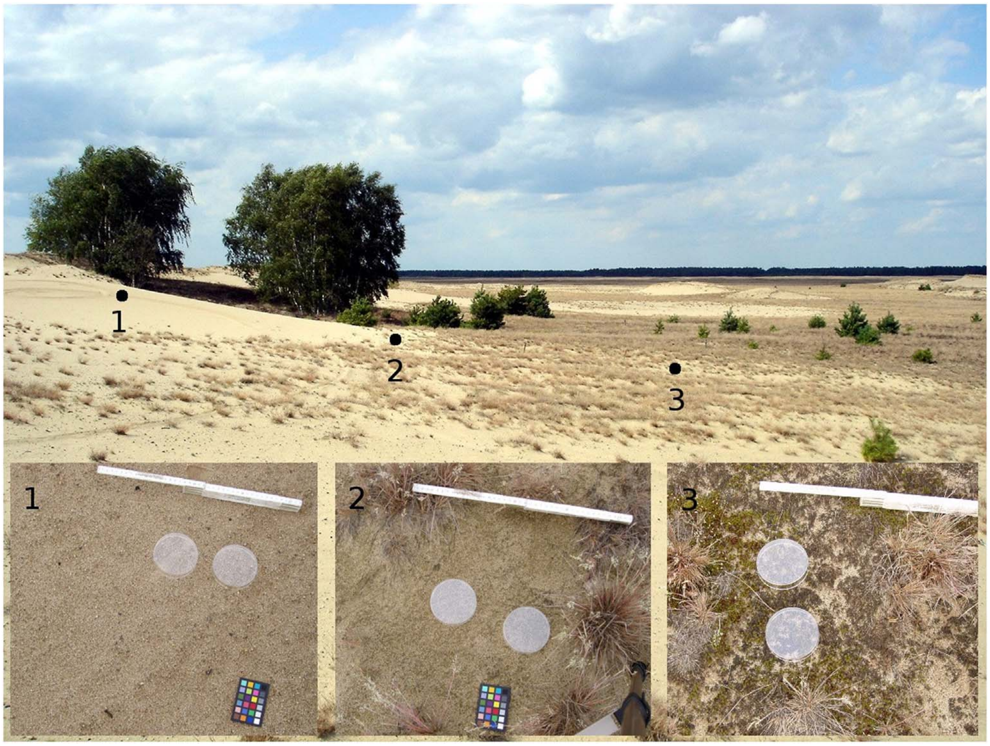

Fig. 1. Sampling site and points. 1 – BSC 1, 2 – BSC 2, 3 – BSC 3.

conditions has received less attention.

Biological soil crusts (BSCs) are assemblages of cyanobacteria, green algae, mosses, liverworts, lichens (Belnap and Lange 2001) and of a subsequently developing heterotrophic community which stabilize the surface, redistribute water, accumulate organic matter, and which may influence the succession of a vascular plant community. BSC patches develop on a small scale under specific topographic and microclimatic conditions, which include eolic deflation or water erosion of surface particles and particle sedimentation downslopes, protection from wind and from radiation in microdepressions and at the lee side of vegetational tussocks (Kidron and Zohar 2014). Further, the properties of the geological substrate and the BSCs themselves control water retention, infiltration and surface run-off (Kidron and Yair 1997; Yair 1990, 2001; Fischer et al. 2010, 2014). A general overview of the substrate development in the region was given by Hirsch et al. (2017). Biological soil crusts are the first colonizers of initial soils, playing an important role in soil formation and contribute to the further ecosystem development (Schaaf et al. 2011; Schulz et al. 2013). On mobile dunes microphytes often settle on continuously renewing surfaces, which are disturbed by either deflation or sedimentation of sand (Danin et al. 1989; Büdel and Veste 2008). Surface stabilization can be observed only at advanced stages of BSC development, when BSCs form a dense organic surface cover (Veste et al. 2011).

Successional growth of biological soil crusts can be influenced by physical components such as soil structure, by soil type, radiation budget, topographic attributes such as slope orientation, which may affect water availability or soil moisture (West 1990; Belnap 1995; Belnap and Gillette 1997; Lange et al. 1997; Kidron et al. 2000; Zaady et al. 2000; Veste et al. 2008; Yair et al. 2011; Kidron and Vonshak 2012; Fischer et al. 2014). In a situation where BSC growth and development are determined by microclimatic, as well as by geomorphodynamic factors, the question arises as to how BSC development and biomass correlates with ecological maturity. It seems to be well possible that, for example, low biomass may be specific to BSC communities in ecological equilibrium under dry environmental conditions with a stable soil surface (Veste et al. 2011). On the other hand, the same amount of low biomass might characterize a very initial system of settling cryptogames on a renewing surface under more favorable climatic conditions. Hence, it seems well possible that biomass does not coincide with ecological maturity.

The high significance of cryptogamic covers on the global carbon cycle was substantiated by the finding that the carbon turnover time, that is, the ratio between the carbon pool (C) and net primary production (NPP), was much shorter for cryptogamic covers (~1.2 years) than for terrestrial vegetation (~10 years, Elbert et al. 2012, Field et al. 1998), where NPP is defined as the amount of photosynthetically fixed carbon available to the first heterotrophic level in an ecosystem (Lindeman 1942). In immature biocrusts, which have not reached a close-to-equilibrium state yet, $R_{d.}$ lags behind NPP, and a decomposition community needs to be built up during biocrust development.

It is the aim of this study to demonstrate (I) that Odum's P/R is applicable for a comparison of BSC maturity within a wide range of water availability, (II) that BSC maturity increases as conditions of surface disturbance diminish, and (III) that accumulation and stabilization of organic matter in the biocrusts are benchmarks for ecosystem development. As poikilohydric organisms, BSC microphytes are adapted to frequent droughts. Hence, at least a proportion of the BSC carbon metabolism occurs at high soil water tension under conditions of drought stress. To address this aim, we determined the P/R ratio for different crusts along an inland dune catena at increasing drought stress under controlled light and temperature conditions until photosynthesis and respiration ceased, related these data to carbon fractions and quantified carbon pools and flows for given abiotic conditions.

2. Material and methods

2.1. Site description

The sampling site was located near Lieberose, Brandenburg in north-eastern Germany (N 51° 55′49″, E 14° 22′22″, 80 m a.s.l.). The climate is temperate continental with an average rainfall of 569 mm a^{-1}, an average potential evapotranspiration of ~780 mm a^{-1}, and an average annual temperature of 8.9 °C. Soil pH was 4.9 to 5.1 for all samples. Due to disturbances by former military