

Contribution of cryptogamic covers to the global cycles of carbon and nitrogen

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Many terrestrial surfaces, including soils, rocks and plants, are covered by photoautotrophic communities, capable of synthesizing their own food from inorganic substances using sunlight as an energy source^{1,2}. These communities, known as cryptogamic covers, comprise variable proportions of cyanobacteria, algae, fungi, lichens and bryophytes, and are able to fix carbon dioxide and nitrogen from the atmosphere³. However, their influence on global and regional biogeochemical cycling of carbon and nitrogen has not yet been assessed. Here, we analyse previously published data on the spatial coverage of cryptogamic communities, and the associated fluxes of carbon and nitrogen, in different types of ecosystem across the globe. We estimate that globally, cryptogamic covers take up around 3.9 Pg carbon per year, corresponding to around 7% of net primary production by terrestrial vegetation. We derive a nitrogen uptake by cryptogamic covers of around 49 Tg per year, suggesting that cryptogamic covers account for nearly half of the biological nitrogen fixation on land. We suggest that nitrogen fixation by cryptogamic covers may be crucial for carbon sequestration by plants.

Cryptogamic ground covers (CGC), including biological soil and rock crusts as well as bryophyte and lichen carpets, occur on many terrestrial ground surfaces. Cryptogamic plant covers (CPC), comprising epiphytic and epiphyllic crusts as well as foliose or fruticose lichens and bryophytes, spread over large portions of terrestrial plant surfaces, including stems, branches and leaves of trees and shrubs¹. As illustrated in Fig. 1, ground and plant covers occur in a variety of different types, colours and morphologies, and can be found in many different habitats and ecosystems².

The photoautotrophic communities can take up atmospheric CO₂, and many covers containing cyanobacteria can also fix atmospheric N₂ (ref. 3). They produce carbon- and nitrogen-containing organic compounds such as amino acids, carbohydrates and extracellular polymeric substances^{4,5}. These products, as well as cryptogamic biomass, are partly consumed by plants, animals and other organisms in the surrounding ecosystem or removed by erosion and runoff^{3,6,7} (Fig. 2). Thus, cryptogamic covers are able to fuel food webs by photosynthesis and nitrogen fixation, which is particularly important in arid regions and other terrestrial environments with low abundance of organic nutrients. The covers can also form biominerals and stabilize ground surfaces through the interaction of minerals, cellular filaments and organic polymers. Accordingly, they act as ecosystem engineers, promoting the rehabilitation of eroded soils in drylands^{8,9}. Their destruction by grazing and trampling enhances erosion and diminishes soil fertility

and water retention, and also the conversion of natural lands to human use (for example, agriculture and construction) can reduce the spread of cryptogamic covers¹⁰.

Fossil records suggest that covers similar to today's cyanobacterial soil and rock crusts formed the earliest terrestrial ecosystems in Earth's history between 2.6 and 2.7 billion years ago¹¹, long before land plants appeared about 500–700 million years ago¹². Thus, cryptogamic covers containing cyanobacteria were probably the only terrestrial biocenoses for a time span of about two billion years. Today, they are still pioneers in the colonization of bare grounds such as deglaciated rock surfaces, volcanic deposits and burnt areas^{13–15}.

The importance of cryptogamic covers for the functioning of ecosystems on local and regional scales has been addressed in a number of studies. In this study we investigate the carbon net uptake and the nitrogen fixation by cryptogamic covers in different types of ecosystem on continental and global scales. For this purpose, we processed and integrated experimental data and information from over 200 studies as detailed in the Supplementary Information. For each type of ecosystem and cryptogamic cover, we calculated best estimates and uncertainty ranges of the characteristic average fluxes of carbon net uptake and nitrogen fixation. Characteristic flux values and 90% confidence intervals are summarized in Supplementary Table S1, and the global geographic distribution is shown in Fig. 3.

The net uptake of carbon dioxide from the atmosphere (photosynthesis minus respiration) represents the net primary production (NPP) of cryptogamic covers¹⁶. With regard to different types of cover and ecosystem, the carbon uptake fluxes are largest for ground covers in extratropical forests (~103 g m⁻² yr⁻¹, Fig. 3a) and for plant covers in tropical forests (~10 g m⁻² yr⁻¹, Fig. 3c). For continental regions, the mean flux values are highest for Europe (~44 g m⁻² yr⁻¹) and lowest for Africa (~17 g m⁻² yr⁻¹); the relative proportions compared with the NPP of vegetation range from ~4% in Africa to ~10% in Europe and North America (Supplementary Table S2a). Globally integrated, the carbon net uptake of cryptogamic covers from the atmosphere amounts to ~3.9 Pg yr⁻¹ (2.1–7.4 Pg yr⁻¹; Supplementary Table S1a), which corresponds to ~7% of the NPP of terrestrial vegetation (~56 Pg yr⁻¹; ref. 17) and, for reference, is of a similar order of magnitude as the global annual carbon release due to biomass burning (~3.6 Pg yr⁻¹; ref. 18) and fossil-fuel combustion (~7.0 Pg yr⁻¹; ref. 19), respectively.

For the carbon content of cryptogamic covers we obtained a global estimate of ~4.9 Pg (3.0–8.2 Pg), which corresponds to ~1% of the carbon content of terrestrial vegetation (470–650 Pg; ref. 20).

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Figure 1 | Cryptogamic covers in different environments. **a**, Ground cover in the Namib lichen fields (*Teloschistes capensis*, *Xanthoparmelia walteri*, *Ramalina* spp.), Alexander Bay, South Africa. **b**, Soil crust with cyanobacteria (black) and chlorolichen (*Psora decipiens*), Nama Karoo semi-desert, Northern Cape, South Africa. **c**, Rock crust with chlorolichen (*Rhizocarpon geographicum* aggr.), Sadnig, Eastern Alps, Austria. **d**, Rock crust with chlorolichens (*Chrysothrix chlorina*, yellow, *Leproloma membranaceum*, whitish-grey) and mosses (*Dicranum scoparium*, *Hypnum cupressiforme* var. *filiforme*), Spessart, Germany. **e**, Plant cover with cyanolichen (*Physma byrsaeum*) on rainforest tree, northeast Queensland, Australia. **f**, Plant cover with chlorolichens (*Evernia prunastri*, *Parmelia sulcata*, *P. subrudecta* and others) and a bryophyte (*Orthotrichum affine*) on maple tree, Trier, Germany.

Accordingly, the carbon turnover time, that is, the ratio between carbon content and NPP (ref. 21), is shorter for cryptogamic covers (~ 1.2 years) than for terrestrial vegetation (~ 10 years), but it is still much longer than for oceanic phytoplankton (~ 2 – 20 days; ref. 22).

The flux of nitrogen fixation by cryptogamic covers is largest for ground covers in deserts ($\sim 0.76 \text{ g m}^{-2} \text{ yr}^{-1}$; Fig. 3b) and for plant covers in extratropical forests ($\sim 0.21 \text{ g m}^{-2} \text{ yr}^{-1}$; Fig. 3d). Accordingly, the mean flux for continental regions is highest in Australia and Oceania ($\sim 0.57 \text{ g m}^{-2} \text{ yr}^{-1}$) and lowest in Africa ($\sim 0.37 \text{ g m}^{-2} \text{ yr}^{-1}$). The relative contribution to total biological nitrogen fixation (BNF) ranges from $\sim 30\%$ in Europe and South

America to $\sim 80\%$ in Asia and North America, respectively (Supplementary Table S2b). Inventories of BNF and models of the nitrogen cycle that do not account for the contribution of cryptogamic covers, particularly plant covers in the boreal forests of North America and Asia, may be missing most of the BNF in those regions²³. Indeed, our results indicate that nitrogen fixation by cryptogamic covers is highest in ecosystems where fixation by plant symbionts is lowest (for example, extratropical forest). Globally integrated, the fixation of atmospheric nitrogen by cryptogamic covers amounts to $\sim 49 \text{ Tg yr}^{-1}$ (27 – 99 Tg yr^{-1} ; Supplementary Table S1b), corresponding to approximately $\sim 46\%$ of total BNF ($\sim 107 \text{ Tg yr}^{-1}$, 100 – 290 Tg yr^{-1} ; refs 24,25).

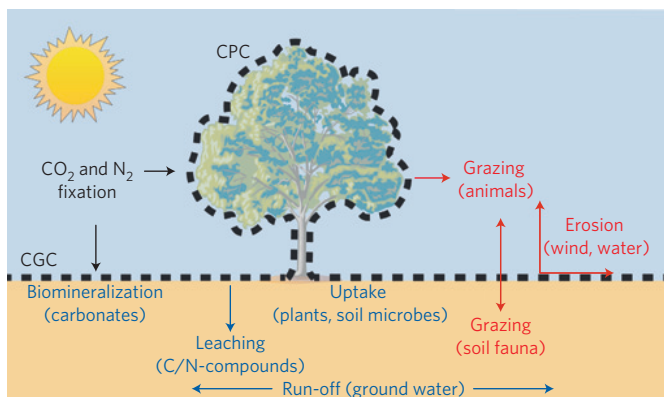


Figure 2 | Biogeochemical activity and life cycle of cryptogamic covers on ground surfaces (CGC) and plant surfaces (CPC).

The large contribution to BNF on regional and global scales suggests that cryptogamic covers are likely to have an impact on the sequestration of CO₂ by terrestrial plants, because this process is often constrained by the availability of fixed nitrogen^{26,27}. Thus, the effects of CO₂ fertilization on the development of terrestrial vegetation may be influenced by changes in the abundance and activity of cryptogamic covers, which are sensitive to

land-use changes and climate parameters such as temperature and precipitation²⁸. We suggest that the role of cryptogamic covers in the nitrogen cycle should be considered in assessments of the CO₂ fertilization effects and related climate feedback mechanisms.

Whereas the fixation of nitrogen by plant symbionts usually occurs in bulk soil, cryptogamic covers fix nitrogen at the surface of soil, rocks and plants. The difference between surface and bulk fixation is potentially relevant to the bioavailability of the fixed nitrogen as well as for multiphase chemical reactions and exchange of nitrogen with the atmosphere. Recent studies show that chemical conversion of reactive nitrogen at the Earth's surface can lead to a release of nitrous acid, which is a major source of OH radicals and influences the oxidizing power and self-cleaning capacity of the atmosphere^{29,30}.

Overall, our results suggest that cryptogamic covers on ground and plant surfaces are major players in the global biogeochemical cycles of carbon and nitrogen and should thus be explicitly considered in climate and Earth system models. Land-use and climate change are likely to influence the geographic distribution and metabolic activity of cryptogamic covers, which may in turn affect their role in the climate system and represent a previously unrecognized feedback cycle. Regional and seasonal patterns as well as long-term trends in biodiversity, abundance and metabolic activity need to be better characterized for a full understanding of the role of cryptogamic covers in the Earth's history and future climate.

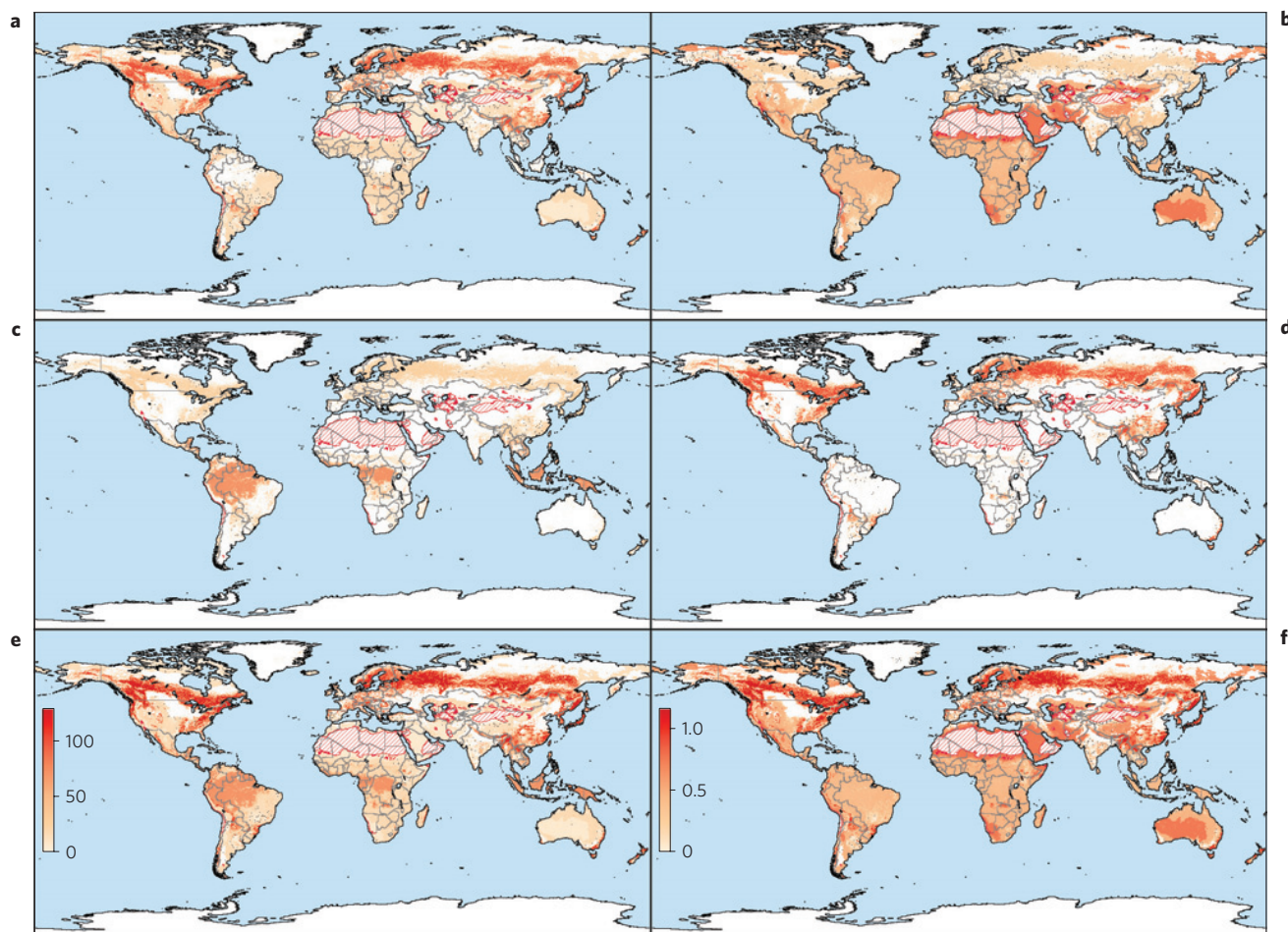


Figure 3 | Geographic distribution of CO₂ uptake and N₂ fixation by cryptogamic covers. a–f, The colour coding indicates the flux intensity of carbon net uptake (a,c,e) and nitrogen fixation (b,d,f) by CGC (a,b), CPC (c,d) and their sum (CGC + CPC, e,f). The flux units are g m⁻² yr⁻¹; note that the scale bars for carbon (e) and nitrogen (f) differ by two orders of magnitude. White areas indicate ecosystems for which no data are available; hashed areas were excluded from global budget calculations (annual mean precipitation <75 mm yr⁻¹ and desert areas designated as dune sand/shifting sands and rock outcrops).

Received 12 January 2012; accepted 2 May 2012; published online 3 June 2012

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Acknowledgements

This work has been supported by the Max Planck Society, the German Research Foundation (BU 666/3, 4, 5, 11, WE2393/2-1, 2-2), the Geocycles Cluster Mainz (LEC Rheinland-Pfalz) and the European Commission (PEGASOS, grant no. 265148). We gratefully acknowledge E. Falge for support in the determination of leaf area indices and O. L. Lange for helpful comments.

Author contributions

W.E., B.W., B.B. and U.P. conceived the study. W.E. and B.W. collected flux and coverage data. S.B. and J.S. contributed ecosystem classifications. B.B. and B.W. provided photographs. W.E., B.W., S.B., J.S., B.B., M.O.A. and U.P. wrote the paper.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to B.W. or U.P.