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Climatic and soil texture threshold values for cryptogamic cover development: a meta analysis

Thomas Fischer[1]* & Maria Subbotina[2]

[1]*Brandenburg University of Technology Cottbus-Senftenberg, Central Analytical Laboratory, Konrad-Wachsmann-Allee 6, 03046 Cottbus, Germany; e-mail: thomas.fischer@tu-cottbus.de*
[2]*Permian State Agricultural Academy, 23 Petropavlovskaya str., Perm 614990, Russia; e-mail: subbotina@mail.ru*

Abstract: In a global meta study, which contained 157 biological soil crust (BSC) samples from all climatic regions worldwide, climatic and soil texture threshold values favoring BSC development were derived. Response variable was the "relative crust biomass", which was computed per literature source as the ratio between each individual crust biomass value of the given study to the study maximum value reported. Four crust types were distinguished: cyanobacterial, lichen, green algal and moss crusts. To quantify threshold conditions at which crust biomass responded to differences in texture and climate, we (I) determined correlations between bioclimatic variables, (II) calculated generalized linear models to determine the effect of typical climatic variables with soil clay content and with study site as a random effect. (III) Thresholds of climatic and texture effects were identified using a regression tree. Three mean annual temperature classes for texture dependent BSC growth limitation were identified: (1) <9 °C with a threshold value of 25% silt and clay (limited growth on coarser soils), (2) 9–19 °C, where texture did have no influence on relative crust biomass, and (3) >19 °C at soils with <4 or >17% silt and clay. Non of the precipitation related bioclimatic variables did influence the relative crust biomass significantly. Because biocrust development is limited under certain climatic and soil texture conditions, it is suggested to consider soil texture in biogeochemical modeling of cryptogamic ground covers.

Key words: algae; biogeography; cyanobacteria; crust biomass; lichens; mosses

Introduction

Cryptogamic covers, often referred to as biological soil crusts, result from an intimate association between soil particles and cyanobacteria, algae, microfungi, lichens and mosses (Belnap 2001) These crusts are known to stabilize surfaces, thus counteracting eolian deflation (Belnap 2001), enhancing water storage (Fischer et al. 2012) as well as soil fertility (Bowker 2007).

Attempts have been made to identify environmental factors that correlate with soil crust occurrence at a range of scales from micro- to regional scales (Concostrina-Zubiri et al 2013; Bowker et al. 2006). Soil texture, in particular, has been found to have significant influence on crust development (Concostrina-Zubiri et al 2013). Different crust types, in particular those dominated by mosses, have been found to be related to total annual rainfall, soil pH, calcium carbonate levels, plant cover, texture, organic carbon, and soil texture, whereas lichen crusts were related to annual rainfall, pH, calcium carbonate levels, plant cover, sheet erosion, organic carbon, and crust cover (Eldridge & Tozer 1997). Landscape type was reported to influence distribution and floristics of bryophytes (Eldridge & Tozer 1996), but to be a poor predictor of lichen floristics or crust cover (Eldridge 1996). Precipitation and temperature have further been identified as the most prominent factors influencing distribution and composition of North American biocrusts (Rosentreter & Belnap 2001), specific biocrust types were reported for specific climates in Africa (Ullmann & Büdel 2001a), and amount and distribution of rainfall were found to strongly influence the distribution of lichens (Rogers 1971) and bryophyte crusts (Downing & Selkirk 1993) in Australia.

Global change is projected to induce further expansion of arid regions and to promote desertification, which is accompanied by loss of vegetation cover and by an increase in the area covered by mobile sand (Geist 2005). Numerous studies reported on the response of biocrusts on global change, and there is large consent between researchers that land use change, invasive species, and increase of short-wave radiation (UVB) will decrease the abundance of biocrusts and alter their species composition. The physiological functions of biocrusts have been reported to be highly responsive to temperature, and changes in the amount or timing of precipitation may have profound consequences for their species composition and roles in ecosystems (Evens et al. 2001).

Along with afforestation, attempts have been made

* Corresponding author

Table 1. Literature sources used in this meta-study. Solely data published in peer reviewed scientific journals were used, duplicate datasets were removed.

Literature sources reporting:	
Surface area based chlorophyll a concentration	Fischer et al. (2012), Spröte et al. (2010), Kuske et al. (2012), Kidron et al. (2009, 2010). Pluis et al. (1994), Lan et al. (2012), Xiao et al. (2010)
Soil mhass based chlorophyll a concentration	Beraldi-Campesi et al. (2009), Herrick et al. (2010), Abed et al. (2010), Barger et al. (2006), Lan et al. (2011)
Surface coverage	Muscha & Hild (2006), Dougill & Thomas (2004), Dettweiler-Robinson et al. (2013), Thomas et al.. (2002), Breen & Lévesque (2008), Guo et al. (2008)
Algal biovolume	Kastovska et al. (2014)
Crust type, climatic and texture data used only	Concostrina-Zubiri et al. (2013), Chamizo et al. (2011)

to combat desertification by managing soil crusts, including promoting the development and restoration of areas of soil crust (Bowker 2007; Belnap & Eldridge 2001; Wang et al. 2009). Recovery rates of biocrusts are "dependent on many factors, including the type, severity, and extent of disturbance; structure of the vascular plant community; conditions of adjoining substrates; availability of inoculation material; and climate during and after disturbance" (Belnap & Eldridge 2001). Because biological soil crusts are known to be more stable on and to prefer fine substrates (Belnap 2001; Eldridge 2001), the question arises as to how successful crust management practices can be applied to sandy areas.

The majority of studies had been conducted from micro- to regional or continental scales, and global approaches to the influence of environmental factors on biocrust development are rare. We conducted a global meta-analysis of data on biological soil crusts to determine threshold values of soil texture, climatic variables and crust biomass for crust development using data from all climatic except tropical and high alpine regions. Fischer et al. (2012) observed similar crust biomasses on finer soils under arid and on coarser soils under temperate conditions, and it was our motivation to prove this finding on a larger scale. We hypothesized that the higher water holding capacity of finer substrates would favor crust development, and that the amount of silt and clay in the substrate that is required for enhanced crust development would vary with changes in climatic conditions.

While examining literature sources, it became evident that the amount of studies to be incorporated into this meta analysis was reversely related to the amount of common environmental parameters they share. Hence, the attempt to generalize previous findings quantitatively in a global meta analysis would require reduction of the environmental factors considered, which inevitably would result in an increase of the statistical error, which then would include all factors taken out of consideration.

Material and methods

We survey the literature to obtain data on soil crust development, assessed as crust surface area, chlorophyll a concentration, adjusted for soil mass, or algal biovolume (Table 1). To account for differences in methodology, relative crust biomass was computed per literature source as the ratio between each individual crust biomass value of the given study to the maximum value reported in that study. We distinguished between four crust types: cyanobacterial, lichen, green algal and moss crusts.

The following presuppositions were made for a study to be included into this meta analysis.

(I) The study should provide geographical coordinates, a quantitative crust biomass indicator (like, for example, area related amount of chlorophyll), as well as a quantitative measure of soil texture (like, for example, per cent silt and clay). Climatic data were taken from the WorldClim database.

(II) The study design should contain a variety of climatic or soil texture conditions, where all biocrusts were investigated using identical methods. This condition was necessary to achieve comparability between the studies by calculating "relative crust biomass".

(III) The study should report on at least one of the following crust types: cyanobacterial, green algal, lichen, or moss crusts.

An overview of the literature sources used in this study is given in Table 1, remarks on data assessment are listed in Table 2. Unless stated otherwise, data were taken from the text of the Material and Methods sections, and all samples reported were used. Data from published figures were collected by importing the digital (usually pdf) version of the literature sources into the UTHSCSA ImageTool v. 3.0 (UTHSCSA 2014) and by calibrating the image coordinates of the data points against the coordinates of the image axes. A general description of the dataset is given in Table 3.

To identify preferential climatic and soil texture conditions for different crust types, relative abundances of cyanobacterial, lichen, green algal and moss crusts for different annual precipitation versus mean annual temperature and versus soil texture were estimated using the levelplot function of the lattice package of the R software suite. Principal component ordination analysis of the dataset after z-transformation of variables was conducted to give a general overview of the dataset.

To quantify threshold conditions at which crust biomass responded to differences in texture and climate, we firstly used the correlation analysis to examine correlations between suites of climatic variables. Variables that were correlated with $|r| > 0.7$ were grouped using the ward algorithm of the corrplot function of R (Friendly 2002). We also included the aridity index of the Global Aridity Index (Global-Aridity) Geo-Database (Trabucco et al. 2009) into the set of variables. Considering intercorrelation of variables (Fig. 4, Table 4), we selected mean annual temperature (BIO1), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), annual precipitation

Table 2. Remarks on data assessment.

Source	Comment
Fischer et al. (2012)	Data from Fig. 9, samples "Lieberose Crest", "Lieberose Slope", "Lieberose Base", "Nizzana Crest", "Nizzana Slope", "Nizzana Base"
Concostrina-Zubiri et al. (2013)	Data from Table 4, samples "EX", "LI", "MI", "HI"
Chamizo et al. (2011)	Data from Table 2, samples "El Cautivo P", "El Cautivo IC", "El Cautivo C", "El Cautivo L", "Las Amoladeras C", "Las Amoladeras L", "Las Amoladeras M"
Beraldi-Campesi et al. (2009)	Data from Table 1, samples "CP1", "CP2", "CP3", "SD8, "SD9", "SD18"
Spröte et al. (2010)	Data from Figures 7 and 10, samples "H1", "H2", "H3", "L1", "L2", "L3" (L – Lugteich, H – Huehnerwasser)
Kuske et al. (2012)	Data from Table 1 and Figure 1b, samples "Arches untrampled", "Arches trampled", "ISKY-1 untrampled", "ISKY-1 trampled", "ISKY-2 untrampled", "ISKY-2 trampled"
Herrick et al. (2010)	Data from Table 2, samples "H1", "H2", "H3", "L1", "L2", "L3" (L – Low, H – High)
Muscha & Hild (2006)	Location coordinates from Figure 1 using Google Earth, Textures from Table 1, Biomass and crust types from Figure 3, samples "BigTrails in", "PoisonSpider in", "Donlin in", "Powder-Rim in", "LanderAnt in", "WorlandCattle in", "SandCreek in", "RankinBasin in", "Red-Wash2 in"
Dougill & Thomas (2004)	Location coordinates from Figure 1 using Google Earth, data from Table 1, samples "Makoba", "Molopo", "Omaheke rangelands", "Omaheke ranch", "Berry Bush"
Kidron et al. (2010)	Data from Figure 5, samples "A", "B", "C", "D", "E"
Kidron et al. (2009)	Data from Figure 8. According to Fig. 5, all crusts with >20 mg m^{-2} were classified as moss crusts
Pluis (1994)	Data from Figure 4, location coordinates from Figure 1 using Google Maps, samples "upper", "lower", "left", "right", chlorophyll A concentrations are mean values from fig. 4B and C
Lan et al. (2010)	Data from Figure 8, samples "Shifting sand", "Algae crust", "Lichen crust", "Moss crust"
Xiao et al. (2010)	Data from Tables 1 and 2, samples "uncrusted sand", "moss crusted sand", "uncrusted sandy loam", "moss crusted sandy loam"
Dettweiler-Robinson et al. (2013)	Data from Table 2, samples "Early succession", "Late succession"
Thomas et al. (2002)	Location coordinates from Figure 1 using Google Earth, data from Table 1 and Table 3, samples Kalahari "Sands Bio 1", "Kalahari Sands Bio 2", "Ironstone Ridge Bio 1", "Ironstone Ridge Bio 2", "Ironstone Ridge Bio 3", "Ironstone Colluvium Bio 1", "Ironstone Colluvium Bio 2", "Ironstone Colluvium Bio 3", "Valley Alluvium Bio 1", "Valley Alluvium Bio 2", "Valley Alluvium Bio 3", "Calcrete Colluvium Bio 1", "Calcrete Colluvium Bio 2", "Calcrete Colluvium Bio 3", "Calcrete Ridge Bio 1", "Calcrete Ridge Bio 2", "Calcrete Ridge Bio 3"
Abed et al. (2010)	Location coordinates from Figure 1 using Google Earth, data from Tables 1 and Figure 5, samples "WK", "SD", "AD"
Barger et al. (2006)	Location coordinates from[16], Data from Table 1, samples "Dark crust intact", "Light crust", "Dark crust trampled", "Scraped" removed due to disturbance
Lan et al. (2011)	Data from Table 1 and Figure 1, samples "Man made Dalateqi", "Algae Dalateqi", "Moss Dalateqi", "Algae Shapotou", "Lichen Shapotou", "Moss Shapotou", arithmetic mean of all extraction methods
Breen & Lévesque (2008)	Location coordinates from Figure 1 using Google Earth, data from Table 2 and Figure 8, samples "CG2", "CG3", CG4", CG5", "CG6", "CG1" excluded: too close to glacier.
Guo et al. (2008)	Data from Table 2, samples "Physical Crust", "Algal Crust", "Moss Crust"
Kastovska et al. (2014)	Location coordinates from Figure 1 using Google Earth, data from Figure 3, samples "sub-glacial sediment", "barren", "cryoconite holes", "vegetated soil", Crust type defined from cyanobacterial and green algal abundances in Table 2

(BIO12), precipitation of driest quarter (BIO17) and precipitation of coldest quarter (BIO19) for regression analysis to identify the variables which had a significant influence on relative crust biomass. In addition, the sum of silt and clay and the region of study were included as random effects.

We then used generalized linear models to examine the effect of a range of climatic variables of each of these groups of intercorrelated variables with soil clay content. Study site was used as a random effect. Apart from the feature of generalized linear models to allow for response variables that have error distribution models other than a normal distribution, we used the default "gaussian" family for our regression analysis, because the data were normally distributed when excluding response values of 1 (which had higher frequency by implication) and 0 (substrate, no crust). Shapiro-Wilk normality test gave $p = 0.111$. We found that both identification of significant variables using glm regression, as well as calculation of a regression tree were justified.

Potential thresholds of significant climatic, texture or climatic x texture effects were identified with regression trees using the rpart package in R (Breiman et al. 1984). Threshold values were computed for the partitioning of relative biomass using mean annual temperature (℃, denoted as "temperature") as well as the sum of silt and clay (per cent, denoted as "fines") for classification.

Finally, we used the WorldClim (2014) and the Harmonized World Soil databases (2014) to generate combined maps where, on a global scale, soil texture and climatic conditions for biocrust growth limitations apply.

Results

An ordination analysis of the entire dataset is presented in Figure 1. The Central European study sites located in the Netherlands (Pluis 1994) and Germany (Spröte

Table 3. General overview of the dataset: Numbers of observations per geographical region and crust type, empty fields – no data reported.

	BSC type					
	Algal	Cyano-bacterial	Lichen	Moss	Bare soil	Sum
USA/Mexico		19	29	8	10	66
Central Europe	12			1		13
Mediterranean		16	2	8	1	27
Southern Africa		22				22
Arctic		9				9
Asia/Arab Peninsula	1	8	1	6	4	20
Sum	13	74	32	23	15	157

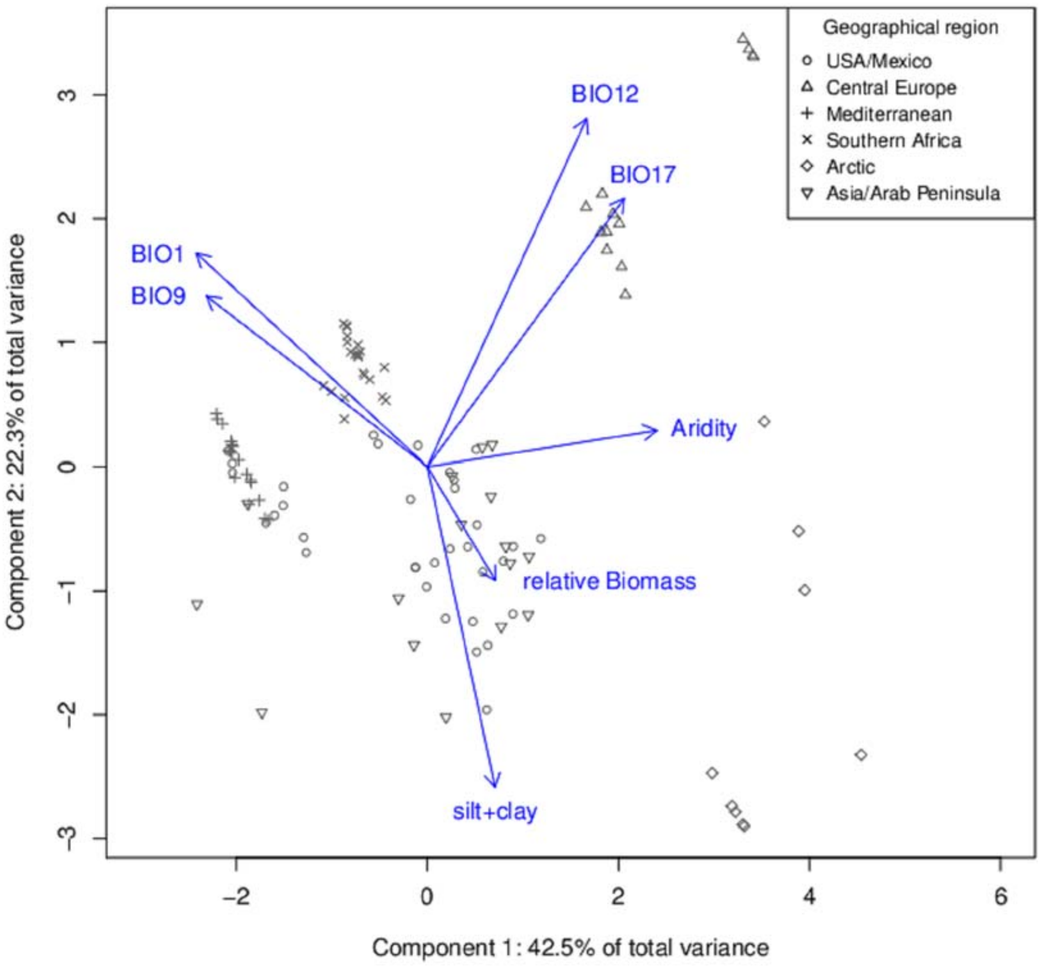

Fig. 1. Principal component ordination biplot of the dataset after z-transformation by geographical region. Denomination of bioclimatic variables: see Table 4.

et al. 2010; Fischer et al. 2012) received highest precipitation in this meta-study. Together with the studies conducted at arctic sites (Breen & Lévesque 2008; Kastovska et al. 2014), they represent the least arid conditions (aridity index increases with decreasing aridity), whereas studies from the Negev Desert (Fischer et al. 2012; Kidron et al. 2009, 2010), Oman (Abed et al. 2010) and the Colorado Plateau (Beraldi-Campesi et al. 2009) represented the most arid conditions in this meta analysis.

Cyanobacterial crusts were the most abundant crust type in this meta analysis, and dominated at an annual precipitation between 200 and 600 mm, on coarser textured soils (Fig. 2, Table 3), and at mean annual temperatures < 5 and > 15 °C. Lichens were found to prefer finer soils and to avoid annual precipitation > 400 mm, whereas green algae in soil crusts have been reported on sandy substrate and with annual precipitation > 500 mm. Moss crusts were the most diverse type reported in this meta analysis (Table 3, Figs 2 and 3).

A correlation plot of the bioclimatic variables considered is shown in Figure 4. Groups of variables in-

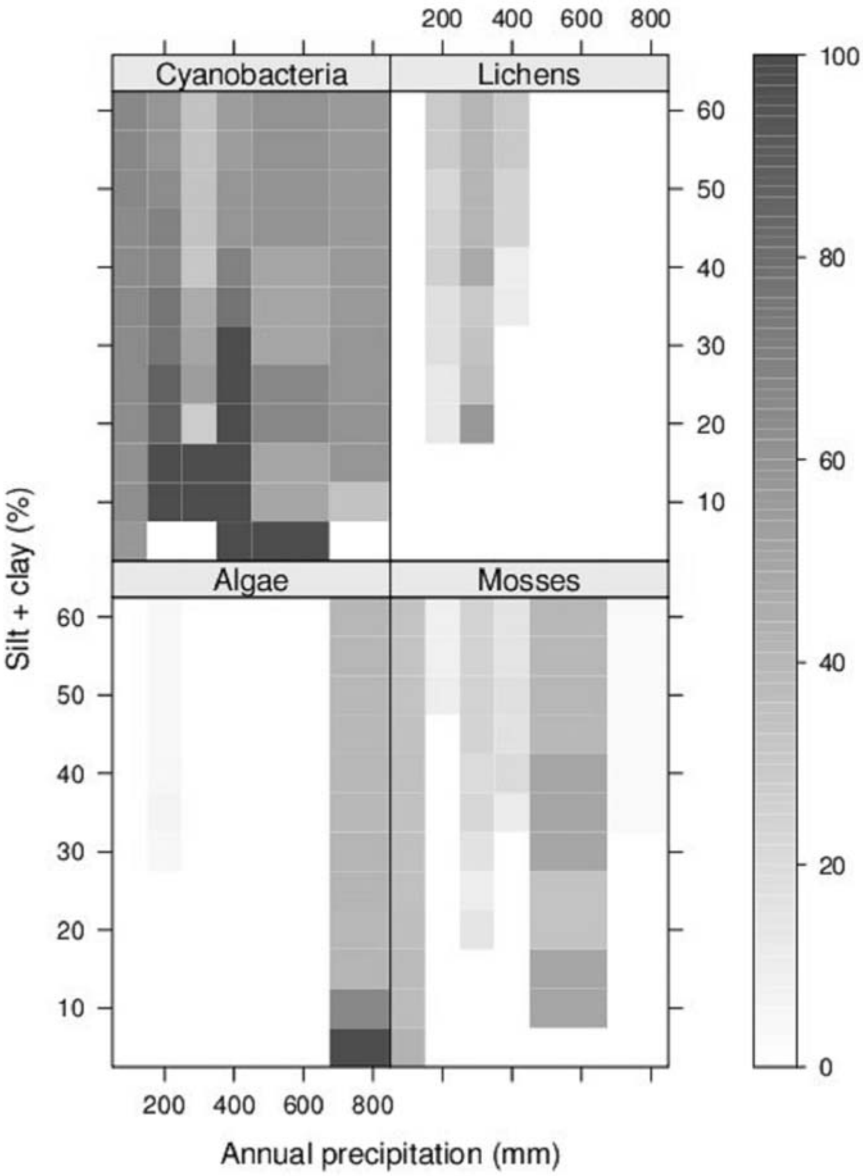

Fig. 2. Relative abundances (in %) of cyanobacterial, lichen, green algal and moss crusts for different annual precipitation and soil texture conditions.

tercorrelated with $|r| > 0.7$ are listed in Table 4. It should be noted that mean annual temperature (BIO1) and annual precipitation (BIO12) were not correlated significantly (Pearson's product-moment correlation – 0.12, p = 0.19, Fig. 1).

Mean annual temperature (BIO1), annual temperature range (BIO7) and mean temperature of the wettest quarter (BIO8) had a marginal influence ($p < 0.1$), whereas the sum of silt and clay had significant influence ($p < 0.05$) on relative crust biomass. There was no significant interaction between these climatic variables and the sum of silt and clay ($p > 0.1$). The influence of the study site on the linear model was always significant ($p < 0.01$). For simplification, mean annual temperature (BIO1) and the sum of silt and clay were used for further analysis.

The terminal nodes of the regression tree (Fig. 5) were distributed bimodally forming two significantly differing classes ($p < 0.01$) with relative biomasses ranging from 0.3 to 0.4, and from 0.6 to 0.7, respectively. Relative crust biomass was < 0.4 at mean annual temperatures > 19 ℃ and when the percentage of silt and clay was < 4 or > 17% (left branch of the regression tree), or at mean annual temperatures < 9 ℃ when the sum of silt and clay was < 25% (right branch of the regression tree). At conditions differing from these, relative crust biomass was > 0.6 (Fig. 5). Figure 6 maps land areas where conditions of biocrust growth limitation apply.

Discussion

There were three main results of our study: First, we classified soil texture and climatic conditions according to their influence on biocrust growth limitation. Second, we determined soil texture and climatic preferences of the four biocrust types identified. Finally, we generated global maps where these conditions of biocrust growth

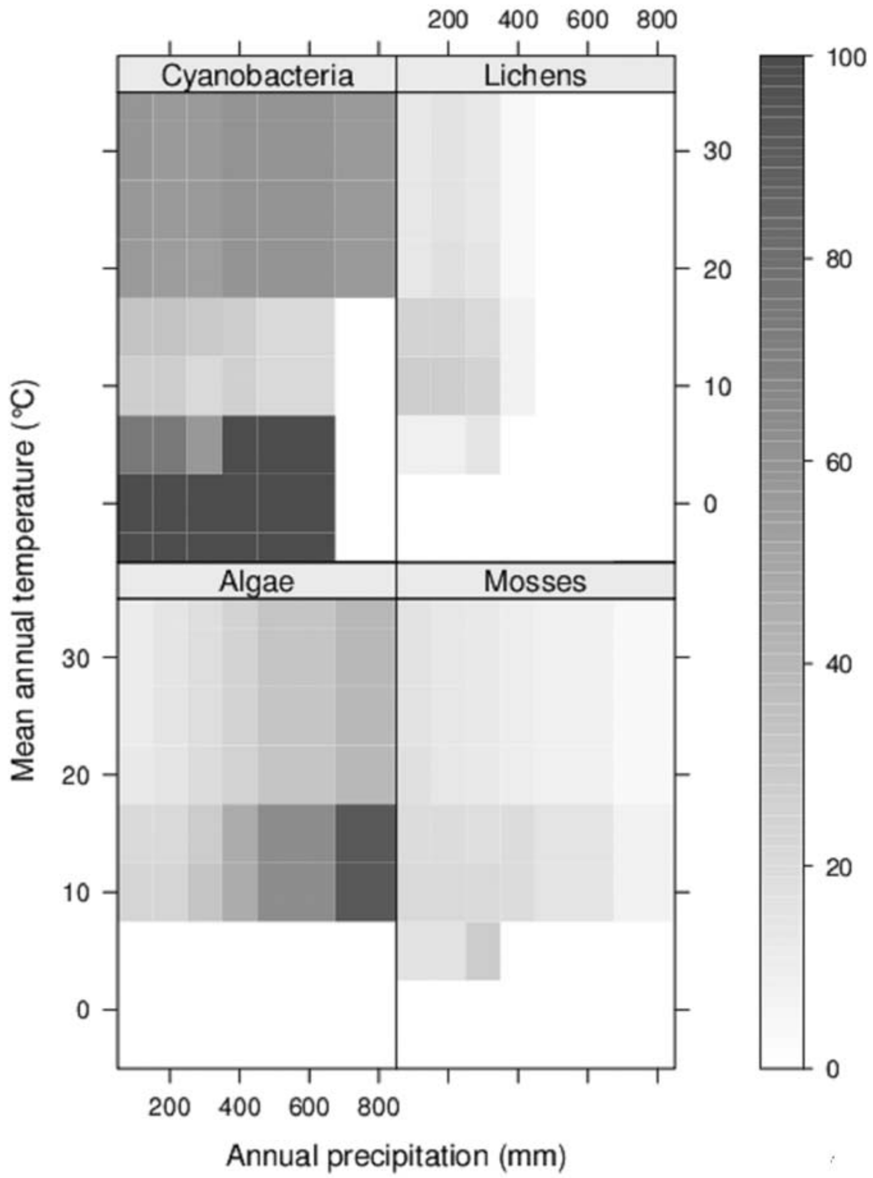

Fig. 3. Relative abundances (in %) of cyanobacterial, lichen, green algal and moss crusts for different annual precipitation and mean annual temperature conditions.

limitation apply.

We identified three mean annual temperature classes for texture dependent BSC growth limitation:

1) < 9℃ with a threshold value of 25% silt and clay (limited growth on coarser soils),

2) 9–19℃, where texture did have no influence on relative crust biomass, and

3) > 19℃ at soils with <4 or > 17% silt and clay.

BSC growth was suppressed by soil texture in relative harsh climates only – either when it was relatively cold (< 9℃), or hot (> 19℃). It further can be concluded that biocrust development was optimal when mean annual temperatures ranged from 9 to 19℃ irrespective of soil texture (Fig. 5). Hence, soil texture outside optimal ranges may suppress biocrust growth under certain climatic conditions. Soil texture is closely related to environmental factors which may affect biocrust development, in particular with water holding capacity. Being poikilohydric, the metabolism of cryptogams highly depends on the availability of water in their environment: It is not surprising that finer substrates, possessing higher water holding capacities as can be assumed from general properties of water retention curves for coarser and finer soils, promoted biocrust growth in colder climates (temperature class 1). On the other hand, elevated amounts of fine particles, resulting in higher water availability had a negative influence in hot climates (temperature class 3). This is in good accordance with the findings of Eldridge et al. (2011) who reported that high temperatures combined with high humidity reduce the photosynthetic ability of the phycobiont, which limits the distribution of lichens.

None of the precipitation related bioclimatic variables did influence the relative crust biomass significantly. Rosentreter & Belnap (2001) concluded that

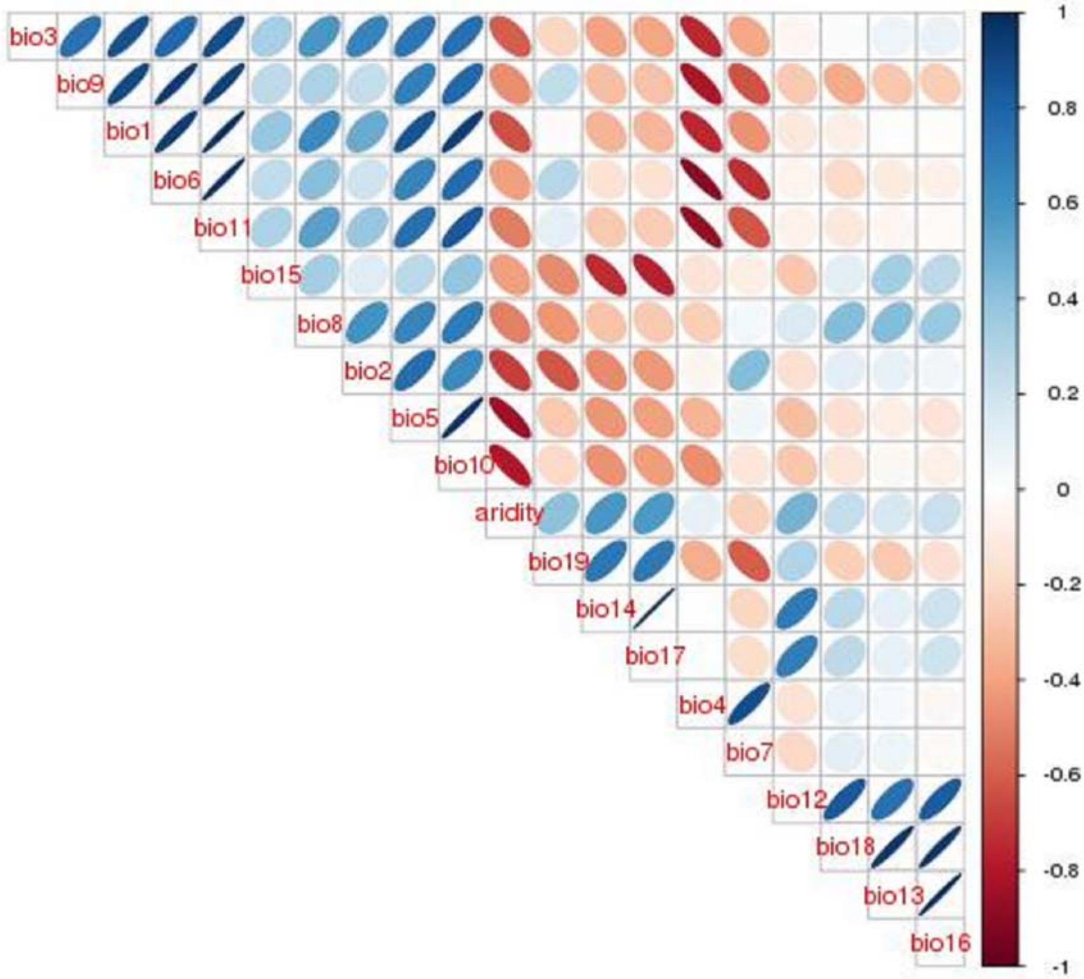

Fig. 4. Correlation plot of bioclimatic variables and the aridity index, variables were grouped using the ward clustering algorithm of the corrplot function of R.

Table 4. Groups of Intercorrelated bioclimatic variables, which are denominated as follows (Worldclim 2014: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp – min temp)), BIO3 = Isothermality (BIO2/BIO7) (* 100), BIO4 = Temperature Seasonality (standard deviation *100), BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 (omitted due to redundancy) = Temperature Annual Range (BIO5-BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter. Unless indicated otherwise, $|r| > 0.7$; [1] $|r| > 0.4$ with bio1, bio2, bio9, bio11, [2] $|r| > 0.5$ with aridity index, bio1, bio10, [3] $|r| > 0.5$ with bio1, bio2; Variables marked in bold were considered to be most common within each group and were used for further analysis.

(I)	**bio1**, bio3, bio4, bio6, bio7[1], bio9, bio11
(II)	**bio1**, bio2[2], bio5, bio10, aridity index[3]
(III)	**bio12,** bio13, bio16, bio18
(IV)	bio4, **bio7**
(V)	bio14, bio15, **bio17**
(VI)	**bio8**
(VII)	**bio19**

crust cover is positively correlated with increasing precipitation, and that his relationship holds until precipitation is high enough for vascular plant cover to preclude the presence of biocrusts. Garcia-Pichel et al. (2013) reported a marginal importance of precipitation and emphasized mean annual temperature as driving factor for the continental-scale distribution of key microbes, for the crust type and for chlorophyll yields of biocrust relevant microbial strains in topsoil communities. Apart from that, it is well possible in our study that the power of regression was weak due to the necessary disregard of some driving factors of biocrust development, such like soil chemical properties, plant cover, or landscape type (Eldridge & Tozer 1996, 1997), which then would contribute to the statistical error. Differing between countries soil texture classification systems, in particular the distinction between fine sand and silt, may further introduce some variation. In the global approach presented by this meta-study, these circumstances were treated as additional source of residual variation, which further may blur texture and climatic effects, but which, on the other hand, allow globalization of the findings.

We further showed that **cyanobacterial crusts**

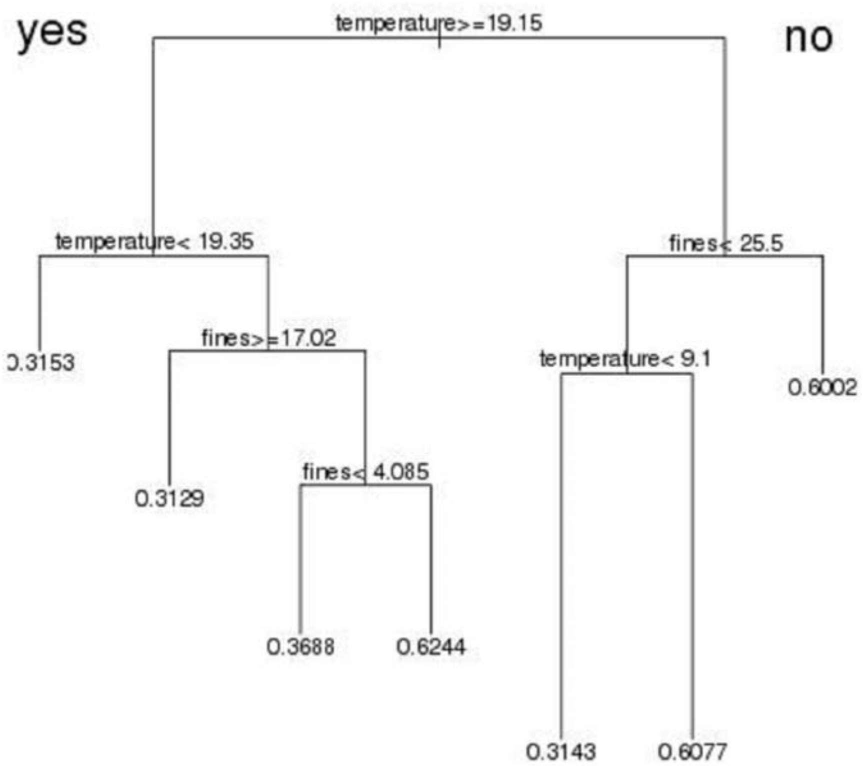

Fig. 5. Regression tree of relative crust biomasses with mean annual temperature (℃, denoted as "temperature") as well as the sum of silt and clay (per cent, denoted as "fines") used for partitioning.

dominated on coarser texture in a 200–600 mm precipitation range (Fig. 2, Table 3), where the majority of the literature sources reported high abundances of the genus *Microcoleus*, which may respond to temperature change on the genus level (Garcia-Pichel et al. 2013).

Our results indicate that **lichens** prefer finer soil and avoid annual precipitation >400 mm, which is in good accordance with literature findings that BSCs tend to bind fine particles (Belnap & Eldridge 2001; Chamizo et al. 2011), and that lichens generally characterize late stages of BSC development (Eldridge & Greene 1994; Belnap & Eldridge 2001).

Green algae in soil crusts have been reported worldwide (Büdel 2001). This study included reports on *Zygogonium* spec. and *Klebsormidium* spec. from sandy costal (Pluis 1994) and inland dunes (Spröte et al. 2010; Fischer et al. 2012) in central Europe, where annual precipitation was > 500 mm.

Mosses seem to be too diverse on the genus or species level to derive general texture or climatic conditions which they prefer. For example, *Gigaspermum repens* (Hook.) Müll. Hal. (Eldridge & Greene 1994) or *Polytrichum piliferum* Schreb. ex. Hedw. (Fischer et al. 2010b) are able to grow on loose sands, while species diversity increased with clay content (Eldridge & Greene 1994). With respect to soil texture and climate, moss crusts were the most diverse BSC type reported in this meta-study (Figs 2 and 3).

Biological soil crusts are known to bind fine material (Belnap & Eldridge 2001) and their elemental composition differs from the underlying soil (Beraldi-Campesi et al. 2009; Fischer et al. 2010a). Finer texture and the presence of extracellular polymeric substances, improve the hydrological regime for crust biota (Fischer et al. 2010b, 2012). Collection of fine material and improvement of growth conditions can therefore induce positive feedback mechanisms for crust development. There is no support for the notion, therefore, that fine texture is a cause or effect of crust succession, and this meta-study evaluates soil textures as reported for the crust layers. Belnap & Eldridge (2001) reported the following successional sequence: Large filamentous cyanobacteria, small cyanobacteria and green algae, very early successional lichens, early successional lichens/mosses, mid successional lichens/mosses and late successional lichens/mosses. Ullmann & Büdel (2001b) found that the transition from cyanobacteria-dominated to lichen-dominated crusts was highly correlated with substrate characteristics. The literature data summarized in the present study support these findings: Green algae, which typically characterize early stages of crust development, occurred on coarse textured soils, and with increasing percentages of fine particles the abundances of cyanobacteria, mosses and lichens also increased (Fig. 2). BSCs are further known to respond to conditions apart form soil texture and climate, for example to succession after various sources of disturbance (Belnap & Eldridge 2001; Concostrina-Zubiri et al. 2013; Spröte et al. 2010; Kuske et al. 2012; Herrick et al. 2010; Muscha & Hild 2006; Dougill & Thomas 2004), to geomorphic characteristics like slope exposition (Kidron et al. 2001, 2010; Yair 2001), or to meteorological conditions during sampling.

The ecological amplitude of individual species re-

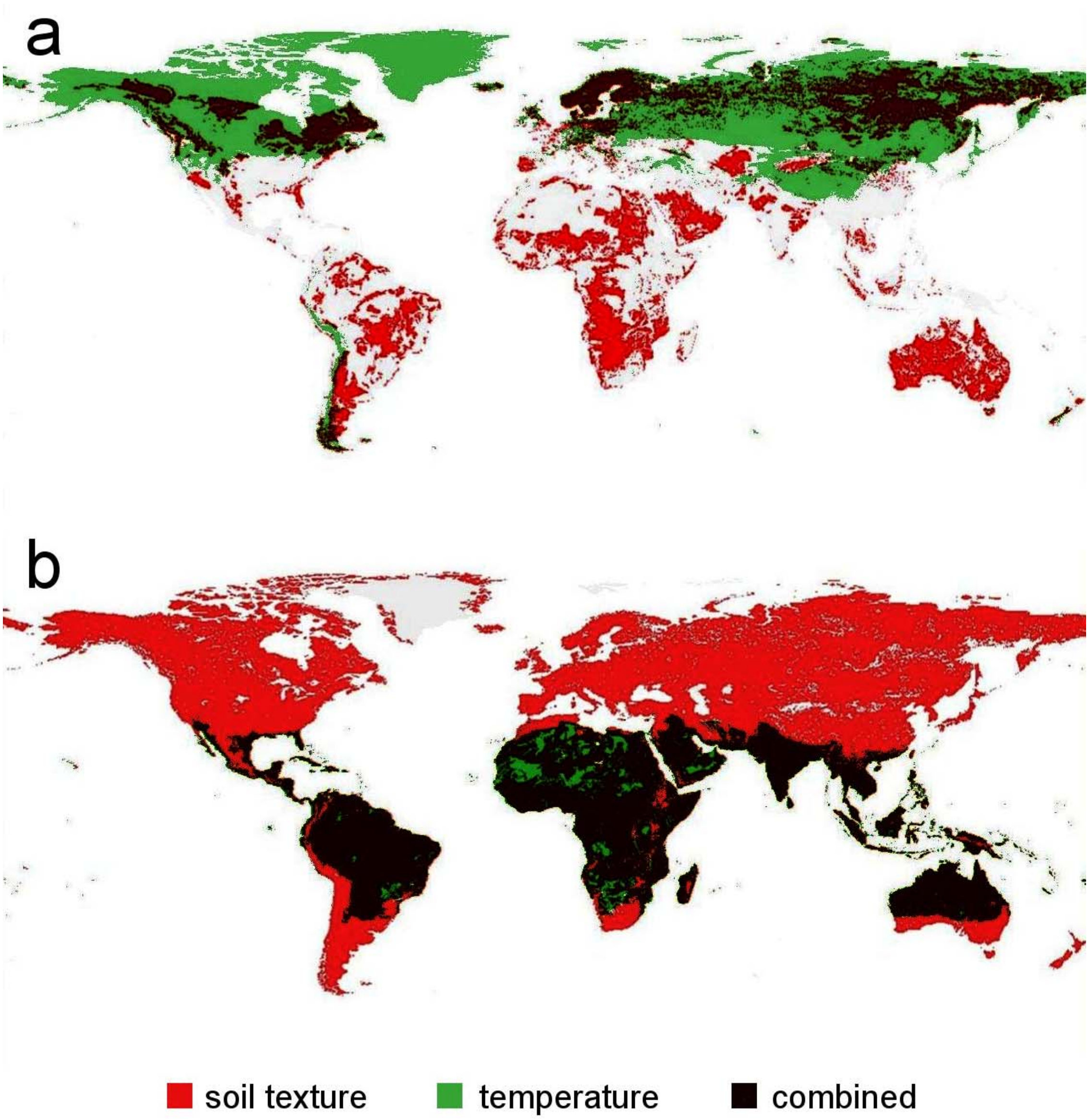

Fig. 6. Combined maps of global distribution of (a) soil texture with <25% silt and clay (red) and annual mean temperature < 9 °C (green); (b) soil texture below 4% and above 17% silt and clay (red) and annual mean temperature > 19 °C (green); Overlapping signifies areas where conditions of texture related biocrust growth limitation apply.

ported in the literature sources definitely exceeds the soil texture or climatic conditions for BSC occurrence found here. Many of these species have been described to reside on soil surfaces as individuals but not forming biological soil crusts as defined by Belnap (2001) *in sensu stricto*. Hence, this meta-study represents BSCs as specific natural entities, which occupy specific ecological niches and which support specific ecosystem functions in open lands apart from occasional occurrence of individual specimen.

On a global scale, a considerable land areas are affected by texture related biocrust growth limitation (Fig. 6). It should be considered here that the Harmonized World Soil Database (2014) provides soil texture data from the (presumably mostly biocrust free) topsoil, which in conjunction with the findings that biocrusts tend to collect fine particles may introduce some bias. However, the results of this study have implications for the biogeochemical modeling of cryptogamic ground covers. Though recently proposed models consider the water storage capacity of the thalli (Porada et al. 2013) or apply scaling factors for given ecosystem categories (Elbert et al. 2012), soil texture was not parameterized explicitly. We suggest to consider soil texture in biogeochemical modeling of biological soil crusts.

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