Received: 8 December 2017 | Revised: 9 May 2018 | Accepted: 10 May 2018
DOI: 10.1002/eco.1991

SPECIAL ISSUE PAPER

WILEY

Effect of vegetation and its succession on water repellency in sandy soils

Lubomir Lichner[1] | Vincent J.M.N.L. Felde[2] | Burkhard Büdel[3] | Martin Leue[4] | Horst H. Gerke[4] | Ruth H. Ellerbrock[4] | Jozef Kollár[5] | Marek Rodný[1] | Peter Šurda[1] | Nándor Fodor[6] | Renáta Sándor[6]

[1] Institute of Hydrology, Slovak Academy of Sciences, Bratislava, Slovak Republic
[2] Department of Soil Science, Faculty of Organic Agricultural Sciences, University of Kassel, Witzenhausen, Germany
[3] Department of Plant Ecology & Systematics, Faculty of Biology, University of Kaiserslautern, Kaiserslautern, Germany
[4] Working Group "Hydropedology," Research Area 1 "Landscape Functioning", Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany
[5] Institute of Landscape Ecology, Slovak Academy of Sciences, Bratislava, Slovak Republic
[6] Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, Martonvásár, Hungary

Correspondence
Lubomir Lichner, Institute of Hydrology SAS, Dúbravská cesta 9, 841 04 Bratislava, Slovak Republic.
Email: lichner@uh.savba.sk

Funding information
Deutsche Forschungsgemeinschaft (DFG), Grant/Award Number: LE 3177/1-2; Hungarian Government, Grant/Award Number: GINOP-2.3.2-15-2016-00028; European Regional Development Fund, Grant/Award Number: ITMS 26220120062; Széchenyi 2020; Slovak Research and Development Agency, Grant/Award Number: APVV-15-0160; Slovak Scientific Grant Agency VEGA, Grant/Award Numbers: 2/0054/14 and 2/0118/18

Abstract

Vegetation and its succession can change the parameters of soil water repellency (SWR) due to the change in amount and composition of soil organic matter. This hypothesis was tested in natural and agricultural environments in Germany, Hungary, and Slovakia. The parameters investigated were the extent (determined by the repellency indices *RI*, RI_c, and RI_m) and persistence (determined by the water drop penetration time and water repellency cessation time) of SWR, as well as the potential wettability index of organic matter in sandy soils. The SWR parameters and soil organic carbon (SOC) content increased in the course of primary succession at Mehlinger Heide, Germany, and Sekule, Slovakia. Dye tracer experiments undertaken at Sekule revealed contrasting flow patterns: (a) preferential flow in water-repellent soil under biological soil crust and grass and (b) piston flow in wettable soil that consists almost of pure quartz sand. The effective flow cross section decreased, and the degree of preferential flow increased in the course of primary succession at Sekule. No consistent trend of the SWR parameters and SOC was observed in the course of secondary succession at Csólyospálos, Hungary. This is the first time that differences between trends in SWR parameters due to primary and secondary successions were observed and related to the composition of SOC and extracellular polymeric substances. It can be concluded that dynamics of soil organic matter composition during the succession controls SWR.

KEYWORDS

primary succession, secondary succession, soil properties, soil water repellency, vegetation, water flow

1 | INTRODUCTION

Soil water repellency (SWR) is a surface property of soil caused by hydrophobic compounds (SWR markers; Mao, Nierop, Rietkerk, Damsté, & Dekker, 2016) mainly originating from vegetation. SWR reduces or prevents water infiltration into the soil (Diehl, 2013; Orfánus et al., 2014; Orfánus, Stojkovová, Rajkai, Czachor, & Sándor, 2016). Reduced infiltration may lead to increased surface run-off and erosion, enhanced overland flow, and thus an increased risk of surface waters pollution (Leighton-Boyce, Doerr, Shakesby, & Walsh, 2007). Furthermore, SWR can form unstable wetting fronts and preferential flow paths (fingers), reducing the filter function of soil and increasing the risk of groundwater contamination (Ritsema & Dekker, 2000). Due to reduced soil water redistribution resulting in poor germination and plant growth, agricultural productivity can be reduced in water-repellent soils (Roper, 2005; Ward, Roper, Jongepier, & Micin, 2015). On the other hand, SWR can be a potential driver of vegetation dynamics in coastal dunes (Siteur et al., 2016) and has positive effects on the stability of soil aggregates (Fér, Leue, Kodešová, Gerke, & Ellerbrock, 2016; Goebel, Bachmann, Woche, & Fischer, 2005), thereby reducing evaporation (Bachmann, Horton, & van der Ploeg, 2001; Rye & Smettem, 2017). SWR can develop in soils of varied textural composition, but it is most common in sandy substrates (Lichner et al., 2010; Oostindie, Dekker, Wesseling, Geissen, & Ritsema, 2017; Wang, Zhao, & Horn, 2010; Woche et al., 2005).

The parameters investigated were the extent (determined by the repellency indices *RI*, RI_c, and RI_m) and persistence (determined by the water drop penetration time [WDPT] and water repellency cessation time [WRCT]) of SWR, as well as the potential wettability index (PWI) of the soil organic matter (SOM). WDPT determines how long water repellency persists in the contact area of a water droplet placed on a smoothed surface of soil (Doerr, Shakesby, & Walsh, 2000). WRCT is the time, in which the hydrophobic state of soil surface is changed to an almost wettable state during the infiltration measurement (Lichner et al., 2013). Estimation of repellency index *RI* is based on the intrinsic sorptivity method developed by Tillman, Scotter, Wallis, and Clothier (1989), where the sorptivity of water (influenced by repellency) is compared with the sorptivity of ethanol (not influenced by repellency). PWI was calculated as the ratio of the intensity of the absorption bands of hydrophobic and hydrophilic functional groups in the organic matter of bulk soil (Leue, Gerke, & Ellerbrock, 2013). It was found from the comparison of above-mentioned methods that the SWR characteristics are somewhat, but not always, well related among each other (Doerr, 1998; King, 1981; Moody & Schlossberg, 2010; Papierowska et al., 2018; Vogelmann, Reichert, Prevedello, Awe, & Reinert, 2015).

Succession is a process where vegetation progressively shifts towards the community typical for the prevailing climatic conditions (climax community) over time. This process is accompanied by changes in site conditions including continuous development of the soil. Primary succession occurs on an entirely new habitat that has never been colonized before, whereas secondary succession takes place on a previously colonized habitat. At each stage of succession (i.e., vegetation development), vegetation alters the soil and microclimate, allowing the establishment of new groups of species (Cammeraat, van Beek, & Kooijman, 2005; Csecserits et al., 2011; Duchicela, Sullivan, Bontti, & Bever, 2013). At the start of primary succession, no humus or organic matter is present in the sandy soil that may absorb, retain, or decelerate the percolating water, and therefore, any rainwater rapidly percolates down through the fairly coarse-grained sand resulting in piston-like flow (Lichner et al., 2011). During an initial stage of primary succession, bacteria, cyanobacteria, algae, mosses, lichens, fungi, and other organisms form biological soil crusts (BSCs; biocrusts) and alter their physical habitat (Belnap, Wilcox, Van Scoyoc, & Phillips, 2013). The hydrological behaviour of such crusts may determine water availability to higher plants (Kidron, 1999). SWR and/or pore clogging can cause run-off initiation on biocrust (Kidron, Yaalon, & Vonshak, 1999) and alter the piston-like flow of rainwater to preferential (fingered) flow (Homolák, Capuliak, Pichler, & Lichner, 2009; Lichner et al., 2012). Preferential flow persists in more advanced successional stages, when grass is the predominant vegetation cover (Lichner et al., 2011).

Biocrusts can cause local water redistribution by increasing surface run-off (Cantón, Domingo, Solé-Benet, & Puigdefábregas, 2001; Keck, Felde, Drahorad, & Felix-Henningsen, 2016) and protect the soil against water and wind erosion (Belnap, Phillips, Herrick, & Johansen, 2007; Kidron, 2001; Rodríguez-Caballero, Cantón, Chamizo, Lázaro, & Escudero, 2013). Bacteria can block smaller pores and reduce flow of water through soil due to adhesive or surface active compounds that can alter surface tension and affect water retention (Hallett, Karim, Bengough, & Otten, 2013). A lichen crust can protect the soil against the removal of soil soluble substances (Lázaro & Mora, 2014). Soil fungi enmesh particles with their network of hyphae, which along with excretion of proteins and other compounds (mainly polysaccharides—Flemming & Wingender, 2010; Kidron, Ying, Starinsky, & Herzberg, 2017) that bond soil particles, lead to increased soil stability protecting it from wind erosion (Tisdall, Nelson, Wilkinson, Smith, & McKenzie, 2012). Kidron et al. (2017) suggested that drought-induced changes in the polysaccharide content of the extracellular polymeric substance (EPS) matrix reduce crust elasticity, resulting in turn in higher susceptibility of the crust to rupture and flaking.

During their growth on soil, cyanobacteria excrete EPSs that glue trichomes to soil particles, in a three-dimensional EPS matrix (Mugnai et al., 2018). The tendency of EPSs having a higher level of gelification and being more tightly attached to cells and sediments (tightly bound EPSs) may be explained with the higher content in rhamnose, which is a deoxysugar having a hydrophobic character that favours the attachment to solid surfaces (Pereira et al., 2009). The results of Rossi, Potrafka, Pichel, and De Philippis (2012) suggested that the presence of EPSs can significantly enhance the hydraulic conductivity in BSCs, likely by conferring a spongy structure to a BSC thus increasing the number of waterways within it.

Belnap et al. (2013) used rainfall simulation to evaluate differences in infiltration, run-off, and erosion among biocrusts in the various levels of development (LODs) on fine sandy loams. They pointed out significant differences between the lowest (characterized by the lightest colour, indicating a low biomass of cyanobacteria, no lichens or mosses, and little if any surface roughness) and the highest (characterized by the darkest colour, indicating high cyanobacterial biomass, cover of lichens and mosses, and surface roughness) LODs, with run-off and erosion being the greatest from the biocrust with lowest LODs. However, the authors did not investigate even in dry antecedent conditions whether the changes in soil hydraulic properties resulted from SWR, and therefore, it is still not clear how the changes in SWR during initial successional stages are related to changes of soil properties. Thus, three hypotheses were tested in this study. Hypothesis 1 claims that for sandy soils, the SWR parameters increase with succession. Hypothesis 2 claims that during primary succession, the increase in SWR parameters is connected with an increase in soil organic carbon (SOC) content. Hypothesis 3 claims that during secondary succession, the increase in SWR parameters is connected with the transformation of organic compounds.

The objective of this study was to assess the influence of vegetation and its succession on the parameters of SWR and to explain SWR with a change in amount and composition of organic matter. The parameters investigated were the extent (determined by the repellency indices *RI*, RI_c, and RI_m) and persistence (determined by WDPT and WRCT) of SWR, as well as the PWI of organic matter in sandy soils. In order to include different vegetation compositions in Central Europe, the repellency studies were carried out in natural and cultivated areas along a gradient of increasing complexity of succession vegetation in 2016 and 2017. This field selection provided the opportunity for establishing the impact of primary succession (in Germany and Slovakia) and secondary succession (in Hungary) on SWR parameters.

2 | MATERIAL AND METHODS

2.1 | Study sites

The experimental sites MH1, MH2, and MH3 are located at Mehlinger Heide near Kaiserslautern, Germany (49°29′02″ N, 7°49′44″ E). The region has temperate oceanic climate with a mean annual temperature of 9.5 °C and mean annual precipitation of 610 mm. The soils at Mehlinger Heide are Regosols and Leptosols (World Reference Base, 2014) developed on Triassic sandstone and have a sandy texture (Soil Survey Division Staff, 1993). They were covered by BSCs and vascular plants (mainly *Calluna vulgaris*), or devoid of vegetation. The three sites MH1, MH2, and MH3 (separated by distance of about 160–170 m) were chosen to include different stages of succession. Site MH1 was a control trail, devoid of vegetation, and with a very high degree of disturbance by hiking tourists. Site MH2 was a pioneer site dominated by green microalgae. The most common alga is *Zygogonium ericetorum* occasionally accompanied by *Klebsormidum* sp. and few other unicellular green algae species. Cyanobacteria of the genus *Nostoc* were also observed. Site MH3 was an early successional stage dominated by lichens (*Cladonia coccifera*, *Cladonia chlorophaea*, and *Peltigera didactyla*) and few bryophytes (*Polytrichum piliferum*, *Lophozia bicrenata*, and *Jungermannia graciliana*).

The experimental sites S0, S1, S2, and S3 are located close to the village of Sekule (48°37′10″ N, 17°00′10″ E) in the Borská nížina lowland (southwest Slovakia). This region is positioned in the transition zone between temperate oceanic and continental climates with a mean annual temperature of 9 °C and mean annual precipitation of 550 mm, which mainly occurs during the summer months. Cyanobacteria (*Leptolyngbya* sp.) and algae (*Bracteacoccus* sp., *Choricystis minor*, *Eustigmatos* cf. *polyphem*, *Interfilum* sp., *Klebsormidium* sp. div., *Mychonastes zofingiensis*, *Stichococcus bacillaris*, *Tribonema minus*, and *Z. ericetorum*) were the first colonizers of the area, followed by an increase in lichens (*Cladonia* sp.) and mosses (*Dicranum polysetum*, *Ditrichum heteromallum*, *Hypnum cupressiforme*, *Polytrichastrum fumosum*, and *P. piliferum*; Drahorad, Steckenmesser, Felix-Henningsen, Lichner, & Rodný, 2013). Three almost adjacent study sites S1, S2, and S3 (separated by distance of about 10–20 m) were chosen to include different stages of vegetation development (succession). Their impact to SWR parameters was compared with the impact of control site S0 with limited impact of vegetation and organic matter and occurred at 50 cm depth beneath site S1. Site S1 was a pioneer site dominated by mosses *P. piliferum* and *Polytrichum juniperinum* and the lichen *Cladonia subulata*. Site S2 was in an early successional stage (more advanced compared with the previous site) dominated by mosses *P. piliferum* and *Ceratodon purpureus* and the lichen *C. subulata*, with a thin stand of the grass *Corynephorus canescens* and the herb *Thymus serpyllum* with an admixture of *Carex supina*, *Acetosella vulgaris*, *Eryngium campestre*, *Scleranthus annuus*, *Spergula morisonii*, and *Tithymalus cyparissias* (*Corynephorion* alliance). Site S3 was a more advanced successional stage treated as *Festucion vaginatae* alliance. It is richer in vascular plant species and with a higher vegetation cover. It was dominated by the grasses *Festuca rupicola* and *Festuca vaginata* that were accompanied by *C. supina*, *Potentilla arenaria*, *A. vulgaris*, *Armeria maritima*, *E. campestre*, *T. cyparissias*, *Veronica dillenii*, and *Teucrium chamaedrys*. Of cryptogams, the mosses *Bryum capillare*, *H. cupressiforme*, and *Brachythecium albicans* and the lichen *Cladonia furcata* were recorded. The soil microscopic fungi found in this locality were *Alternaria alternata*, *Aspergillus fisheri*, *Aspergillus glaucus*, *Aureobasidium pullulans*, *Chaetomium globosum*, *Humicola fuscoatra*, *Mortierella* sp., *Mycelia sterilia*, *Paecilomyces* sp., *Penicillium* sp., *Penicillium aspergiloides*, *koningii*, and *Trichoderma koningii* (Lichner et al., 2007). The soils of the Sekule sites are classified as Arenosols (World Reference Base, 2014) and have a sandy texture (Soil Survey Division Staff, 1993).

The experimental sites CSP1, CSP2, CSP3, and CSP4 are located at Csólyospálos (46°25′05″ N, 19°50′28″ E) at the Great Hungarian Plain. The region has continental climate with a mean annual temperature of 10 °C and mean annual rainfall of 530 mm (Dövényi, 2010). Site CSP1 was a cultivated agricultural area planted with carrot (*Daucus carota* subsp. *sativus*) in 2016 and with courgette (*Cucurbita pepo*) in 2017. Site CSP2, abandoned for 12 years, was at annual weed stage dominated by *Bromus tectorum* and *Polygonum aviculare*, but *Capsella bursa-pastoris*, *Asclepias syriaca*, and *Ambrosia artemisiifolia* were abundant too. Site CSP3, abandoned for 17 years, was covered by strongly synantropized species—poor grassland dominated by perennial weedy grass *Elymus repens* and annual grasses *B. tectorum* and *Bromus sterilis* with an admixture of *P. aviculare*, *Poa angustifolia*, *Silene latifolia* subsp. *alba*, *Hordeum murinum*, *Lamium purpureum*, and others. Site CSP4, abandoned for 44 years, was covered by successionally more advanced grassland dominated by perennial grasses (*F. vaginata*, *Festuca pseudovina*, *F. rupicola*, and *P. angustifolia*) with an admixture of some mostly weedy herbs (*Echium vulgare*, *S. latifolia* subsp. *alba*, *Erodium cicutarium*, and others). The soils of the Csólyospálos sites are classified as Arenosols (World Reference Base, 2014) and have sandy texture (Soil Survey Division Staff, 1993).

Determination of the sand, silt, clay, $CaCO_3$, and SOC contents, as well as pH and PWI, has been carried out in the laboratory with sieved (2-mm-mesh sieve), mixed, and air-dried (at 30 °C) samples collected from the topsoil (0–5 cm) horizon. The results of above-mentioned determination are presented in Tables 1 and 2.

2.2 | Field methods

All the field SWR measurements were carried out on the surface of the studied soils. Field water and ethanol infiltration measurements were performed with minidisk infiltrometer (Decagon, 2012) under a

TABLE 1 Physical and chemical properties of the top (0–5 cm) soils taken from the experimental sites MH1, MH2, and MH3 (Mehlinger Heide, Germany); S0, S1, S2, and S3 (Sekule, Slovakia); and CSP1, CSP2, CSP3, and CSP4 (Csólyospálos, Hungary)

Site	Cover type	Sand (%)	Silt (%)	Clay (%)	$CaCO_3$ (%)	SOC (%)	pH (H_2O)
MH1	Bare soil	97.20	0.03	2.77	0	0.37	4.48
MH2	Green microalgae	86.03	8.57	5.40	0	2.05	4.66
MH3	Lichens	77.06	13.44	9.49	0	5.84	4.49
S0	No cover	94.86	1.74	3.40	0	0.03	4.20
S1	Mosses	93.83	3.25	2.92	0	0.58	5.40
S2	Thin grassland with mosses	94.71	2.88	2.41	0	0.80	5.39
S3	Grassland	88.45	7.35	4.20	0	5.39	5.20
CSP1	Crops	94.93	3.15	1.92	3.43	0.64	8.13
CSP2	Annual weeds	95.0	2.6	2.4	3.15	0.94	8.10
CSP3	Grassland	95.22	3.09	1.69	2.69	0.70	7.74
CSP4	Grassland	88.14	9.53	2.34	2.87	2.09	7.81

Note. SOC: soil organic carbon.

TABLE 2 Mean value ± standard deviation of soil water repellency parameters (namely, the water drop penetration time [WDPT], water repellency cessation time [WRCT], potential wettability index [PWI], as well as standard [*RI*], combined [RI_c], and modified [RI_m] repellency indexes) of the top soils from the sites CSP1–CSP4 (Csólyospálos, Hungary), MH1–MH3 (Mehlinger Heide, Germany), and S1–S3 (Sekule, Slovakia)

Site	Cover type	WDPT (s)	WRCT (s)	PWI (–)	*RI* (–)	RI_c (–)	RI_m (–)
MH1	Bare soil	0.4 ± 0.2	n.d.	0.0037 ± 0.0013	1.1 ± 0.2	1.1 ± 0.2	n.d.
MH2	Green algae	1.7 ± 2.0	n.d.	0.045 ± 0.019	5.1 ± 2.6	5.1 ± 2.6	n.d.
MH3	Lichens	3,861 ± 1,572	n.d.	0.11 ± 0.033	13 ± 7	12 ± 6	n.d.
S0	No cover	1 ± 0	n.d.	n.d.	0.82 ± 0.17	n.d.	n.d.
S1	Mosses	67 ± 100	139 ± 136	0.021 ± 0.0047	18 ± 24	16 ± 19	3.6 ± 1.0
S2	Thin grassland with mosses	375 ± 132	277 ± 309	0.029 ± 0.011	25 ± 31	26 ± 32	7.9 ± 2.2
S3	Grassland	1,436 ± 513	1,679 ± 1,199	0.073 ± 0.035	138 ± 65	139 ± 64	14 ± 18
CSP1	Crops	3 ± 1	15 ± 5	0.024 ± 0.0071	1.8 ± 0.5	1.9 ± 0.4	n.d.
CSP2	Annual weeds	203 ± 324	547 ± 1,217	0.025 ± 0.0088	3.6 ± 3.8	3.2 ± 2.1	15.3 ± 28.8
CSP3	Grassland	3,607 ± 2,041	2,205 ± 1,258	0.020 ± 0.0027	142 ± 86	148 ± 123	30.5 ± 24.2
CSP4	Grassland	2,647 ± 3,672	1,047 ± 433	0.051 ± 0.015	79 ± 68	79 ± 78	10.1 ± 3.4

Note. n.d.: not determined.

pressure head value of h_0 = −2 cm. The sorptivity, *S*, was estimated from the cumulative infiltration, *I*, during early-time infiltration of water and ethanol (Clothier, Vogeler, & Magesan, 2000):

$$S(-2\ \text{cm}) = I/t^{0.5}. \quad (1)$$

Equation (1) was used to calculate both the water sorptivity (S_w) and ethanol sorptivity (S_e) from the cumulative infiltration versus time relationships taken from the minidisk infiltrometer measurements.

In the standard method of estimating the repellency index, S_e and S_w were measured in pairwise arrangements (Figure 1) and the standard repellency index *RI* was calculated as follows (Hallett, Baumgartl, & Young, 2001):

$$RI = 1.95\ S_e/S_w. \quad (2)$$

In the second method of estimating the repellency index, the combination of all the ethanol and water sorptivities was used to calculate a combined repellency index, RI_c, that is, $m \times n$ values of RI_c were calculated from *m* values of S_w and *n* values of S_e (Pekárová, Pekár, & Lichner, 2015).

In the third method of estimating the repellency index, the water sorptivity S_{wh} for water-repellent state of soil and the water sorptivity S_{ww} for nearly wettable state of soil were estimated, respectively, from the less steep and steeper parts of hockey-stick-like relationship (Figure 2) and used to calculate a modified repellency index RI_m (Alagna, Iovino, Bagarello, Mataix-Solera, & Lichner, 2017; Sepehrnia, Hajabbasi, Afyuni, & Lichner, 2016).

The persistence of SWR was assessed by both WDPT and WRCT (Lichner et al., 2013). The WDPT test involves placing a 50 ± 5-μL water drop from a standard medicine dropper or pipette on the soil surface and recording the time of its complete penetration (Doerr, 1998). A standard droplet release height of approximately 10 mm above the soil surface was used to minimize the cratering effect on the soil surface. WRCT was estimated from the intersection of two straight lines, representing the two stages of infiltration (Figure 2; Lichner et al., 2013).

The tracer experiments at the biocrust and grassland sites at Sekule were carried out at the 100 cm × 100 cm plots, and experiment at the pure sand site at the 50 cm × 100 cm plot, using the method similar to Bachmair, Weiler, and Nutzmann (2009) and Homolák et al. (2009). Brilliant Blue dye was added at a concentration of

FIGURE 1 The pairwise arrangement of minidisk infiltrometers for measurements of water (right) and ethanol (left) infiltration at Mehlinger Heide, Germany

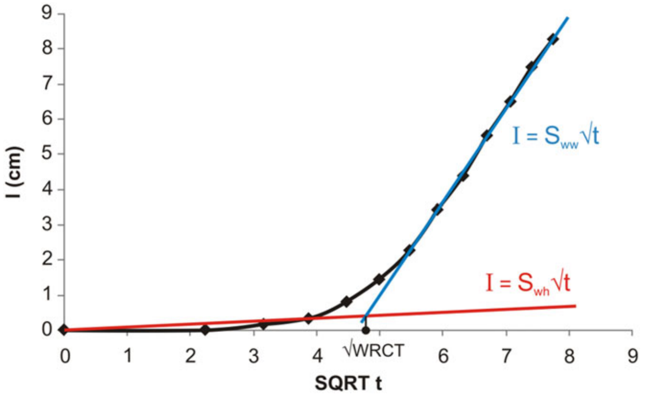

FIGURE 2 The hockey-stick-like relationship of the cumulative infiltration of water (I) against the square root of time (SQRT t) for sandy soil from Csólyospálos site. The water sorptivity S_{wh} for water-repellent state of soil and the water sorptivity S_{ww} for nearly wettable state of soil were estimated, respectively, from the less steep and steeper parts of hockey-stick-like relationship. The water repellency cessation time (WRCT) was estimated from the point of intersection of two straight lines, representing the I = f (SQRT t) relationships for water-repellent and nearly wettable states of the soil

10 g L^{-1} to the water used to simulate rainfall, and the dyed water was applied at a rate of about 1 mm min^{-1}. The tracer application was conducted manually with a watering can. One hundred millimetres of dyed water were applied at the biocrust and grassland sites and 50 mm at the pure sand site. The above-mentioned irrigation rates were chosen to represent increased rainfalls expected as a consequence of the climate change. Thirty minutes after sprinkling, vertical sections were excavated at distances of 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 cm from the edge of the plot at the biocrust and grassland sites and 10, 20, 30, 40, and 50 cm from the edge of the plot at the pure sand site. Clean soil profiles were photographed with a digital camera, and the photographs have been digitally corrected and georeferenced using standard GIS software.

The effective cross section (ECS; Täumer, Stoffregen, & Wessolek, 2006) and the degree of preferential flow (DPF; Lichner et al., 2011) were used to quantify the heterogeneity of water flow in soils. The fraction of total water content change was determined from the stained area. The picture of each vertical section was divided into 10 vertical bands with a width of 10 cm, and the numbers n_j of stained 5 cm × 5 cm pixels were calculated in each band j (Figure 3a). It was supposed that the water content change in the band is proportional to the number of stained pixels. The number of stained pixels is not an integer if the whole area of pixels is not stained. The fraction of total water content change f_j (the ratio between the water content change in band j and the total water content change in the vertical profile) for each band was calculated using

$$f_j = n_j / \sum_{j=1}^{10} n_j \text{ with } \sum_{j=1}^{10} f_j = 1. \tag{3}$$

The fractions f_j were ranked in descending order and presented against the fraction of cross-sectional area (11 dots in Figure 3b). A beta distribution

$$p(x;\alpha,\beta) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{(\alpha-1)} (1-x)^{\beta-1} \quad (\alpha>0, \beta>0, 0\le x\le 1), \tag{4}$$

(where Γ is the Gamma function [or Euler's integral of the second kind] and α and β are the parameters) was fitted to the data and the Levenberg–Marquardt algorithm was used to optimize the parameters α and β. The ECS was then estimated according to the definition in Täumer et al. (2006) as the fraction of the total area that corresponds to the 90% of water content change in vertical section (Figure 3b). ECS equals to 0.9 for piston flow, and it decreases with an increase in the impact of preferential flow in the soil.

The DPF, equal to the area between the beta distribution curve and the 1:1 line (representing the distribution of fraction of total water content change vs. fraction of cross-sectional area for a piston flow—Figure 3b), was calculated from

$$\mathrm{DPF} = \int_{x=0}^{1} p(x;\alpha,\beta)\, dx - 0.5. \tag{5}$$

DPF increases with an increase of the impact of preferential flow in the soil from 0 for piston flow to almost 0.5 for the case when all the flow in the soil is realized through a narrow preferential path (e.g., a crack in heavy clay soil).

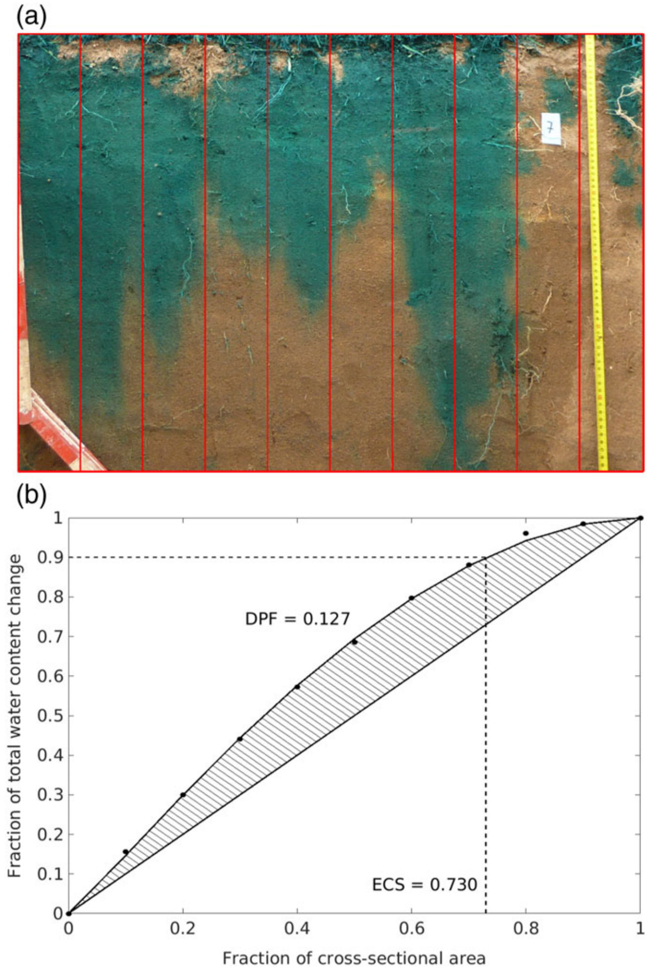

FIGURE 3 Estimation of effective cross section (ECS) and degree of preferential flow (DPF) from the image of a vertical section of dyed soil, taken in the grassland soil at site S3. (a) The image of the vertical section with ten 10-cm-wide vertical bands (red lines) used for an estimation of the fractions of total water content change against the fractions of total cross-sectional area. (b) The plot of the cumulative water content changes against the cumulative cross-sectional area (black dots), with ECS estimated as the fraction of the total cross-sectional area that corresponds to the 90% of total water content change, and DPF presented as the shaded area between beta function fitted to the data and straight line representing the piston flow

2.3 | Laboratory methods

For the diffuse reflectance infrared Fourier transform spectral analyses, the soil material was carefully crushed with an agate mortar leaving the mineral soil particles intact. The undiluted soil material was poured into standard cylindrical cups (five repetitions) and measured with a Fourier transform infrared spectrometer (Bio-Rad FTS 135) using a diffuse reflectance infrared Fourier transform device (e.g., Ellerbrock & Gerke, 2013). For each spectrum, 16 coadded scans between wave number (WN) 4,000 and 400 cm^{-1} were taken at a spectral resolution of 4 cm^{-1} and corrected for ambient air using a background spectrum of a gold target (99%; Infragold). The spectra were converted to Kubelka–Munk units, corrected for CO_2 absorption (WN 2,400–2,280 cm^{-1}), smoothed (boxcar, factor 15), and corrected for baseline shifts using the software WIN-IR Pro 3.4 (Digilab, MA, USA; e.g., Ellerbrock, Gerke, & Böhm, 2009).

The PWI (Leue et al., 2013) of the SOM at the intact structural surfaces was calculated as the ratio of infrared signal intensities of the C—H stretching vibrations of the hydrophobic alkyl groups (WN 2,948–2,920 cm^{-1} and 2,864–2,849 cm^{-1}) and those of the hydrophilic C=O groups (WN 1,720–1,700 cm^{-1} and 1,625–1,600 cm^{-1}) according to Ellerbrock, Gerke, Bachmann, and Goebel (2005). The C—H band intensities were measured as the vertical distance (i.e., the height) from a local baseline plotted between tangential points, whereas the C—O band intensities were measured as height from the total baseline of the spectra. The PWI value is a reciprocal of the wettability; larger PWI values indicate a smaller wettability of the SOM.

3 | RESULTS

The values of SWR parameters (namely, the WDPT, WRCT, PWI, as well as standard [*RI*], combined [RI_c], and modified [RI_m] repellency indexes) of the top soils from the sites CSP1–CSP4 (Csólyospálos, Hungary), MH1–MH3 (Mehlinger Heide, Germany), and S1–S3 (Sekule, Slovakia), estimated in situ and in the laboratory with five to 10 replicates, were processed statistically and presented in Table 2 in the form of mean value ± standard deviation. It should be noted that *RI* data are similar to the RI_c data for all the sites studied, and therefore, *RI* data only were presented in Figures 4–6. The values of parameters of the heterogeneity of water flow in soils, namely, the ECS and DPF estimated in situ with five (pure sand) to 10 (biocrust and grass cover) replicates, were statistically analysed and presented in Table 3 in the form of mean value ± standard deviation. The values ECS = 0.730 and DPF = 0.127 are one of 10 pairs of values estimated from 10 images of vertical sections of dyed soil, taken in the grassland soil at site S3.

3.1 | Effect of primary succession on soil properties

Effect of primary succession on soil properties was studied at Mehlinger Heide and Sekule. Field measurements (of *RI*, RI_c, RI_m, WDPT, and WRCT) at Mehlinger Heide and Sekule were conducted during hot and dry spells in 2016, and laboratory measurements of PWI of topsoil samples were conducted at ZALF Müncheberg in 2017. All SWR parameters increased with SOC content in the course of succession (Figures 4 and 5), which confirms Hypotheses 1 and 2. WDPT increased about 9,650 times, *RI* and RI_c about 12 times and 11 times, respectively, and SOC about 16 times at Mehlinger Heide, Germany. On the other hand, WDPT increased about 1,440 times, *RI* about 170 times, and SOC about 180 times at Sekule, Slovakia. Mean values of ECS decreased, and the mean values of DPF increased in the course of succession at Sekule, Slovakia (Table 3), which means that the heterogeneity of water flow increased in the soil. It can be seen at the images of vertical sections of dyed soil, taken in pure sand at site S0 (Figure 7a), sandy soil covered with biocrusts at site S1 (Figure 7b), and sandy soil covered with grass

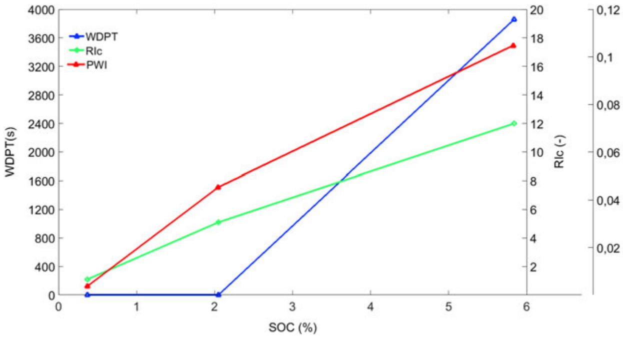

FIGURE 4 Soil water repellency parameters (water drop penetration time [WDPT], combined repellency index [RI_c], and potential wettability index [PWI] of the soil organic matter) versus soil organic carbon (SOC) content relationships for Mehlinger Heide, Germany, sites

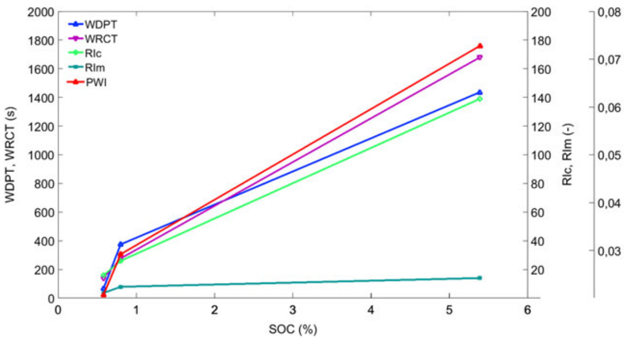

FIGURE 5 Soil water repellency parameters (water drop penetration time [WDPT], water repellency cessation time [WRCT], combined repellency index [RI_c], modified repellency index [RI_m], and potential wettability index [PWI] of the soil organic matter) versus soil organic carbon (SOC) content relationships for Sekule, Slovakia, sites

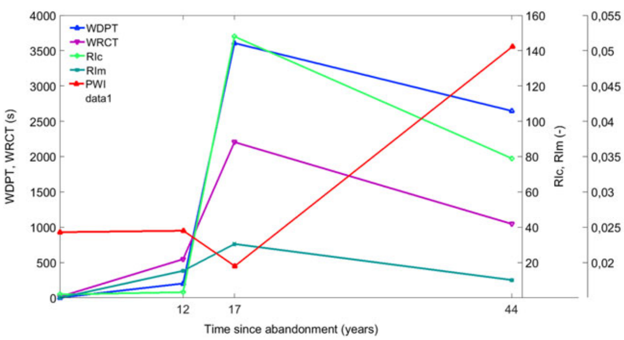

FIGURE 6 Soil water repellency parameters (water drop penetration time [WDPT], water repellency cessation time [WRCT], combined repellency index [RI_c], modified repellency index [RI_m], and potential wettability index [PWI] of the soil organic matter) versus time since abandonment relationships for Csólyospálos, Hungary, sites

TABLE 3 Mean value ± standard deviation of effective cross section (ECS) and degree of preferential flow (DPF) of the top soils from the sites S0, S1, and S3 (Sekule, Slovakia)

Site	Cover type	ECS (m^2 m^{-2})	DPF (–)
S0	No cover	0.869 ± 0.00780	0.0364 ± 0.00592
S1	Mosses	0.819 ± 0.0200	0.0701 ± 0.0142
S3	Grassland	0.795 ± 0.0204	0.0996 ± 0.0151

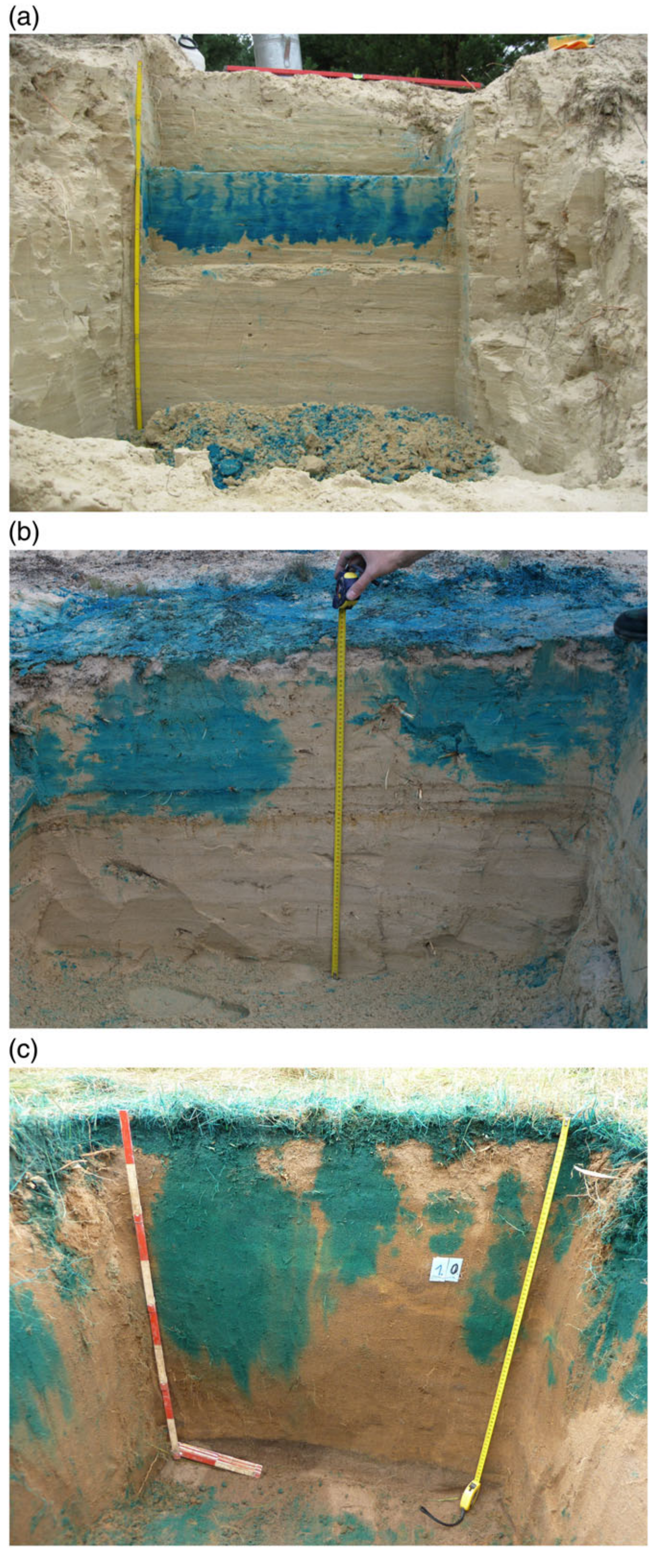

FIGURE 7 The image of vertical sections of dyed soil, taken in (a) pure sand with a negligible impact of vegetation or organic matter at site S0; (b) sandy soil covered with biological soil crust at site S1; and (c) sandy soil covered with grass at site S3

at site S3 (Figure 7c) that in contrast to the piston flow in wettable pure sand (with a negligible impact of vegetation or organic matter), preferential flow occurred in the water-repellent soils under the biocrusts and grass.

3.2 | Effect of secondary succession on soil properties

Both field measurements (of *RI*, RI_c, RI_m, WDPT, and WRCT) during hot and dry spells at Csólyospálos and laboratory measurements of PWI of topsoil samples at ZALF Müncheberg were conducted in 2017. At Csólyospálos sites CSP1–CSP3, the SWR parameters estimated in situ increased in the course of secondary succession. The smaller WDPT and WRCT data (SWR parameters) for CSP4 as compared with CSP3 (Table 2) can be explained by a higher soil water content, *w*, at CSP4 site (w = 4.45% vol.) as compared with CSP3 site (w = 3.95% vol.). The SWR parameters showed a moderate increase between CSP1 and CSP2 sites (Figure 6), similar to an increase between S1 and S2 sites (Figure 5). The PWI increased between sites CSP1 and CSP2, as well as CSP3 and CSP4, and decreased between sites CSP2 and CSP3 where a decrease in SOC (from 0.94% to 0.7%) occurred. Mean values of water drop penetration time, $WDPT_p$ (with index "p" to indicate that these data are a measure for the potential SWR), measured on dried soil samples (with 10 replicates) in the laboratory were 1.8 s at both CSP1 and CSP2 soils, 479.5 s at CSP3, and 137.9 s at CSP4 soils. They showed similar dependence on the time since abandonment as WDPT measured in situ (the measure of actual SWR).

4 | DISCUSSION

At the Mehlinger Heide site in the temperate climate of central Europe, biocrusts are mainly formed by the filamentous green alga *Z. ericetorum*, whereas other algal or cyanobacterial species follow later on, but in any case remain rare. The observed decreasing effect of biocrust on infiltration due to an increase in SWR parameters at site MH2 is in accordance with prior findings that cyanobacterial and green microalgal EPSs do affect the hydrophysical properties of the soil via various mechanisms, such as increasing water repellency (Fischer, Veste, Wiehe, & Lange, 2010). It has to be noted that not all EPSs are hydrophobic. Rather, the degree to which they can induce SWR depends on their composition, namely, the contents of ester-linked acetyl groups, peptidic moieties, and deoxysugars (Pereira et al., 2009). Although a recent study did not find differences in the pore characteristics between biocrusts before and after the non-invasive extraction of EPSs (Felde et al., 2016), this still leaves open the possibility of EPSs, changing the properties of the pore system and hence water retention when they are wetted (Colica et al., 2014; Or, Phutane, & Dechesne, 2007).

It was found in this study that lichens at site MH3 showed lower infiltration in sandy soil than the other components of biocrusts due to an increase in SWR parameters. This observation is in line with the findings of Chamizo, Cantón, Lázaro, Solé-Benet, and Domingo (2012), who showed that lichens exhibited lower infiltration than the other biocrusts in sandy loam and silty loam soils. The study by Berdugo, Soliveres, and Maestre (2014) also pointed out a strong effect of plants and biocrusts on wetting and drying events in Central Spain and attributed the effect of biocrusts on wetting to hydrophobic lichen exudates. In accordance with the results of this study, a study on the effects of surface crusts on water infiltration in an arid desert region of NW China also found a negative effect of SOM content on water infiltration, although they did not address the influence of SWR (Yang et al., 2016). The study by Li et al. (2016) also found that the effect of biocrusts on water infiltration became stronger with crust succession in the order cyanobacterial crusts, lichen crusts, moss crusts.

Chamizo, Cantón, Miralles, and Domingo (2012) found that soil water content, and organic carbon and nitrogen contents significantly increased in the crust and its underlying soil with crust development, especially in the first centimetre of soil underneath the crust. Water repellency is not a static property but can strongly depend on the season (Dekker, Ritsema, Oostindie, Moore, & Wesseling, 2009). During prolonged hot and dry periods, the entire topsoil can dry out and become water repellent. Rainfall events can then cause incomplete wetting, with the ECS being reduced to 20% to 40% of the total cross-sectional area (Täumer et al., 2006). Preferential flow paths—once created—can persist over time from the beginning of summer till the end of autumn (Wessolek, Stoffregen, & Täumer, 2009). This process can save some carbon and nitrogen pools from leaching during the hot half of year. However, during winter time, the spatial arrangement of preferential flow paths can change completely, as the area share of the water-repellent spots can be smaller than 10% (Täumer et al., 2006).

As the biocrust community becomes more complex in the course of succession, it is also likely that an increased abundance of fungi will strongly affect SWR (Rillig, 2005; Young, Feeney, O'Donnell, & Goulding, 2012). The effectiveness of SOM on increasing SWR was impressively demonstrated by Lamparter, Bachmann, Woche, and Goebel (2014), who could show that increasing the SOC content by less than 0.1 g C kg^{-1} resulted in an increase of the contact angle from 30° to 70°. Therefore, the increase of SWR with vegetation succession has important implications for SOM decomposition and hence C sequestration (Goebel, Bachmann, Reichstein, Janssens, & Guggenberger, 2011), which is of major importance in the context of climate change.

The observed decreasing effect of biocrust on infiltration due to an increase in SWR parameters at Sekule site S1 is in accordance with the findings of Kidron et al. (1999) and Warren (2003) who pointed out that biocrusts dominated by cyanobacteria have a tendency to impede infiltration in sandy soils. Reduced infiltration rates were also observed in these soils due to pore clogging by cross-linking of sand particles with green algal filaments and hydrophobicity that was linked to the microbial EPSs (Fischer et al., 2010; Pereira et al., 2009). However, at later successional stages, the dense linkage of soil particles by green algae decreased, but the growth of moss plants and lichen thalli increased (Gypser, Veste, Fischer, & Lange, 2016), but these changes may have different effects on infiltration. Although Kidron, Yair, Vonshak, and Abeliovich (2003) and Warren (2003) concluded that moss-dominated crusts appear to enhance infiltration and reduce run-off in sandy soils (as the moss plants could have increased infiltration along their rhizoids; Felde, Peth, Uteau-Puschmann, Drahorad, & Felix-Henningsen, 2014; Spröte et al., 2010), Gypser et al. (2016) observed a decrease in steady-state water flow of the biocrust samples in the course of succession from green algal crust to moss–lichen crust.

The images of vertical sections of dyed soil with fingered flow paths, taken in sandy soil covered with biocrust (Figure 7b) and grass (Figure 7c), are similar to those taken in sandy soil covered with grass near Ouddorp, the Netherlands (Dekker, Doerr, Oostindie, Ziogas, & Ritsema, 2001; Dekker & Ritsema, 1994). The observed decrease in ECS in the course of succession (due to an increase in SWR) is in accordance with the findings of Täumer et al. (2006) who found about 2 times greater ECS during the October–January measurements compared with July measurements.

The secondary succession at Csólyospálos site showed a different trend than the primary succession; however, in the beginning, both the changes in SWR parameters and the SOC increase were similar. CSP1 cropland site was not water repellent, as the cultivation modifies the water infiltration and ceases the water repellency (Hallett et al., 2001). After 12 years of abandonment, CSP2 site was still dominated by annual forbs. Generally, the cover is rapidly establishing in the initial stage, which is affected by the previous cultivated crops, seed sources, method of cultivation (Johnson, 1945), and climatic factors. CSP2 was characterized by mixed stands, which contributed to a 32% increase in SOC because of the increased amount of above- and below-ground biomass production over years. During the revegetation process, the SWR also increased, which might be caused by the large quantity of nondegraded organic compounds of the local vegetation (Sándor et al., 2015) as the humic acid to fulvic acid ratio (<0.001% to 0.30%, respectively) did not prove the transformation of organic compounds at CSP2. The dense cover of annual forbs (mostly weeds) plays a significant role in soil fertility increase (see SOC) that favours the germination and development of perennial species. The mixed grass and weed stage, such as CSP3, is effected by the invasion of perennial species, but total densities are usually much reduced (Johnson, 1945). The changes in vegetation cover and density may contribute to the significant decrease (26%) in SOC at the top layer (1–6 cm) and increase in SWR parameters. Possible reason of SOC reduction would be the increased ecosystem respiration of CSP3 site during dry spells. For instance, Ciais et al. (2005) and Sousana et al. (2007) showed that the magnitude of the CO_2 activity is sensitive to drought and heat spells, which affect both gross photosynthesis and ecosystem respiration. As CSP3 site was covered by less dense vegetation, thus, the heat waves can have more severe effect mainly on forbs. The vegetation period in 2017 was afflicted with heat waves and small precipitation amounts, having an effect on SWR (Doerr & Thomas, 2000). The greatest values of SWR parameters were measured at CSP3 site, where the WDPT values were comparable with those of MH3 site and the *RI* values were comparable with those of S3 site. However, the PWI and OC values showed the opposite trend, with a decrease between CSP2 and CSP3 sites. As the in situ measured soil water content was below 4% vol., the dry condition could result in an increase in SWR; meanwhile, the C might be released from the soil layers through plant and soil respiration. Gilmanov et al. (2007) investigated 20 European grasslands and found that some years with frequent drought events could turn a grassland system into C source. Thus, the effects of climate and natural vegetation changes cannot be easily separated. The grassland vegetation at CSP4 site was characterized by much higher SOC and PWI; however, the in situ measured SWR parameters at CSP4 site were smaller than those measured at CSP3 site. At CSP4 site, a higher level of infiltration of the soil was observed. The higher silt and clay content of the soil at this site may explain the observed root density of perennial grasses, which provides favourable conditions for plant growth, which is likely to contribute to C sequestration.

This is the first time that differences between SWR parameter trends due to primary and secondary successions were observed, and these findings were confirmed by a range of in-situ and laboratory measurements. However, it is difficult to identify the complex soil chemical properties responsible for the development of SWR (Dekker et al., 2009). Generally, particulate organic matter that accumulates on and between soil particles plays significant role. Therefore, the difference in SWR due to primary and secondary successions may be associated with differences in the composition of SOC and EPSs (Pereira et al., 2009), which are abundant in the biosphere (Dekker et al., 2009). A more detailed investigation of the dynamics, persistence, and stability of SWR under primary and secondary succession is needed to

- identify the complex soil chemical properties responsible for the development of SWR,
- distinguish effects of climate from those of natural vegetation changes, and
- improve modelling of changes in SWR with the focus on the future performance of grasslands.

5 | CONCLUSION

Continuous increase in the SWR parameters of sandy soils was observed during primary succession associated with an increase in SOC content. Considering the soil C sink potential, the most improved stage of primary succession is more beneficial for the natural ecosystem, providing better soil fertility and more sequestered atmospheric CO_2. No continuous trend of the SWR parameters of sandy soil was observed in the course of secondary succession at abandoned fields. During the early stages of secondary succession of around 12 years at Csólyospálos site, the SWR increase can be caused by the greater amount of net biome production of annual forb species, which also contributes to the increase in SOC content. Extreme weather events, such as dry spells and drought, could turn a grassland system (~17 years of abandonment) into C source associated with a dynamic change in vegetation. Therefore, the effects of climate and changes in natural vegetation (such as the dominance of perennial grass species after annual forbs) due to succession cannot easily be separated from each other. The effect of severe water deficit periods can contribute to the loss of soil fertility and also to a delay in the natural vegetation transformation to its climax community. The most favourable properties with respect to soil fertility were represented under the most mature grassland site during the progressive stages of secondary succession. These soil properties could be associated with the area's original subclimax grassland community and also with the transformation of SOM compounds. As the changing climatic conditions result in more frequent and more extreme weather events, SWR may play a role of increasing importance in practically every soil processes through the gradually changing water infiltration characteristics. Consequently, the modelling of the phenomenon may become a significant issue in climate change impact studies that focus on the future performance of grasslands.

ACKNOWLEDGEMENTS

The authors thank Prof. Smettem and two anonymous reviewers for their wise comments and suggestions, which helped to improve the paper. This work was supported by the Slovak Scientific Grant Agency VEGA Projects 2/0054/14 and 2/0118/18, the Slovak Research and Development Agency Project APVV-15-0160, the Széchenyi 2020 programme, the European Regional Development Fund, the Hungarian Government (GINOP-2.3.2-15-2016-00028), and the Deutsche Forschungsgemeinschaft (DFG), Bonn, Germany, under Grant LE 3177/1-2: "Quantification of small-scale physicochemical and microbiological properties of intact macropore surfaces in structured soils." This publication is a result of the project implementation ITMS 26220120062 Centre of Excellence for the Integrated River Basin Management in the Changing Environmental Conditions, supported by the Research & Development Operational Programme funded by the ERDF.

ORCID

Lubomir Lichner http://orcid.org/0000-0001-6057-1903
Vincent J.M.N.L. Felde http://orcid.org/0000-0002-1018-2376
Burkhard Büdel http://orcid.org/0000-0002-1257-260X
Horst H. Gerke http://orcid.org/0000-0002-6232-7688
Jozef Kollár http://orcid.org/0000-0002-0069-4220
Marek Rodný http://orcid.org/0000-0001-9065-8188
Peter Šurda http://orcid.org/0000-0002-1367-9820
Nándor Fodor http://orcid.org/0000-0002-6460-1767
Renáta Sándor http://orcid.org/0000-0001-5132-1945

REFERENCES

Alagna, V., Iovino, M., Bagarello, V., Mataix-Solera, J., & Lichner, L. (2017). Application of minidisk infiltrometer to estimate water repellency in Mediterranean pine forest soils. *Journal of Hydrology and Hydromechanics*, *65*, 254–263.

Bachmair, S., Weiler, M., & Nutzmann, G. (2009). Controls of land use and soil structure on water movement: Lessons for pollutant transfer through the unsaturated zone. *Journal of Hydrology*, *369*, 241–252.

Bachmann, J., Horton, R., & van der Ploeg, R. R. (2001). Isothermal and nonisothermal evaporation from four sandy soils of different water repellency. *Soil Science Society of America Journal*, *65*, 1599–1607.

Belnap, J., Phillips, S. L., Herrick, J. E., & Johansen, J. R. (2007). Wind erodibility of soils at Fort Irwin, California (Mojave Desert), USA, before and after trampling disturbance: Implications for land management. *Earth Surface Processes and Landforms*, *32*, 75–84.

Belnap, J., Wilcox, B. P., Van Scoyoc, M. W., & Phillips, S. L. (2013). Successional stage of biological soil crusts: An accurate indicator of ecohydrological condition. *Ecohydrology*, *6*, 474–482.

Berdugo, M., Soliveres, S., & Maestre, F. T. (2014). Vascular plants and biocrusts modulate how abiotic factors affect wetting and drying events in drylands. *Ecosystems*, *17*, 1242–1256.

Cammeraat, E., van Beek, R., & Kooijman, A. (2005). Vegetation succession and its consequences for slope stability in SE Spain. *Plant and Soil*, *278*, 135–147.

Cantón, Y., Domingo, F., Solé-Benet, A., & Puigdefábregas, J. (2001). Hydrological and erosion response of a badlands system in semiarid SE Spain. *Journal of Hydrology*, *252*, 65–84.

Chamizo, S., Cantón, Y., Lázaro, R., Solé-Benet, A., & Domingo, F. (2012). Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. *Ecosystems*, *15*, 148–161.

Chamizo, S., Cantón, Y., Miralles, I., & Domingo, F. (2012). Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. *Soil Biology & Biochemistry*, *49*, 96–105.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., … Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*, 529–533.

Clothier, B. E., Vogeler, I., & Magesan, G. N. (2000). The breakdown of water repellency and solute transport through a hydrophobic soil. *Journal of Hydrology*, *231–232*, 255–264.

Colica, G., Li, H., Rossi, F., Li, D. H., Liu, Y. D., & De Philippis, R. (2014). Microbial secreted exopolysaccharides affect the hydrological behavior of induced biological soil crusts in desert sandy soils. *Soil Biology and Biochemistry*, *68*, 62–70.

Csecserits, A., Czucz, B., Halassy, M., Kröel-Dulay, G., Rédei, T., Szabó, R., … Török, K. (2011). Regeneration of sandy old-fields in the forest steppe region of Hungary. *Plant Biosystems*, *145*, 715–729.

Decagon (2012). *Mini disk infiltrometer user's manual, version 10*. (p. 18). Pullman: Decagon Devices, Inc.

Dekker, L. W., Doerr, S. H., Oostindie, K., Ziogas, A. K., & Ritsema, C. J. (2001). Water repellency and critical soil water content in a dune sand. *Soil Science Society of America Journal*, *65*, 1667–1674.

Dekker, L. W., & Ritsema, C. J. (1994). How water moves in a water-repellent sandy soil: 1. Potential and actual water-repellency. *Water Resources Research*, *30*, 2507–2517.

Dekker, L. W., Ritsema, C. J., Oostindie, K., Moore, D., & Wesseling, J. A. (2009). Methods for determining soil water repellency on field-moist samples. *Water Resources Research*, *45*, W00D33.

Diehl, D. (2013). Soil water repellency: Dynamics of heterogeneous surfaces. *Colloids and Surfaces A: Physicochemical and Engineering Aspects*, *432*, 8–18.

Doerr, S. H. (1998). On standardizing the "water drop penetration time" and the "molarity of an ethanol droplet" techniques to classify soil hydrophobicity: A case study using medium textured soils. *Earth Surface Processes and Landforms*, *23*, 663–668.

Doerr, S. H., Shakesby, R. A., & Walsh, R. P. D. (2000). Soil water repellency: Its causes, characteristics and hydro-geomorphological significance. *Earth Science Reviews*, *51*, 33–65.

Doerr, S. H., & Thomas, A. D. (2000). The role of soil moisture in controlling water repellency: New evidence from forest soils in Portugal. *Journal of Hydrology*, *231–232*, 134–147.

Dövényi, Z. (2010). *Microregions in Hungary*. (p. 876). Budapest: Hungarian Academy of Science. (In Hungarian.)

Drahorad, S., Steckenmesser, D., Felix-Henningsen, P., Lichner, L., & Rodný, M. (2013). Changes in hydrophysical soil parameters and penetration resistance during the process of early-stage succession in dune sand in Sekule, Slovakia. *Biologia*, *68*, 1089–1093.

Duchicela, J., Sullivan, T. S., Bontti, E., & Bever, J. D. (2013). Soil aggregate stability increase is strongly related to fungal community succession along an abandoned agricultural field chronosequence in the Bolivian Altiplano. *Journal of Applied Ecology*, *50*, 1266–1273.

Ellerbrock, R. H., & Gerke, H. H. (2013). Characterization of organic matter composition of soil and flow path surfaces based on physicochemical principles: A review. *Advances in Agronomy*, *121*, 117–177.

Ellerbrock, R. H., Gerke, H. H., Bachmann, J., & Goebel, M.-O. (2005). Composition of organic matter fractions for explaining wettability of three forest soils. *Soil Science Society of America Journal*, *69*, 57–66.

Ellerbrock, R. H., Gerke, H. H., & Böhm, C. (2009). In situ DRIFT characterization of organic matter compositions on soil structural surfaces. *Soil Science Society of America Journal*, *73*, 531–540.

Felde, V. J. M. N. L., Peth, S., Uteau-Puschmann, D., Drahorad, S., & Felix-Henningsen, P. (2014). Soil microstructure as an under-explored feature of biological soil crust hydrological properties. *Biodiversity and Conservation*, *23*, 1687–1708.

Felde, V. J. M. N. L., Rossi, F., Colesie, C., Uteau-Puschmann, D., Horn, R., Felix-Henningsen, P., … Peth, S. (2016). Pore characteristics in biological soil crusts are independent of extracellular polymeric substances. *Soil Biology and Biochemistry*, *103*, 294–299.

Fér, M., Leue, M., Kodešová, R., Gerke, H. H., & Ellerbrock, R. H. (2016). Droplet infiltration dynamics and soil wettability related to soil organic matter of soil aggregate coatings. *Journal of Hydrology and Hydromechanics*, *64*, 111–120.

Fischer, T., Veste, M., Wiehe, W., & Lange, P. (2010). Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. *Catena*, *80*, 47–52.

Flemming, H.-C., & Wingender, J. (2010). The biofilm matrix. *Nature Reviews Microbiology*, *8*, 623–633.

Gilmanov, T., Soussana, J.-F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., … Wohlfahrt, G. (2007). Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agriculture, Ecosystems & Environment*, *121*, 93–120.

Goebel, M.-O., Bachmann, J., Reichstein, M., Janssens, I. A., & Guggenberger, G. (2011). Soil water repellency and its implications for organic matter decomposition—Is there a link to extreme climatic events? *Global Change Biology*, *17*, 2640–2656.

Goebel, M.-O., Bachmann, J., Woche, S. K., & Fischer, W. R. (2005). Soil wettability, aggregate stability, and the decomposition of soil organic matter. *Geoderma*, *128*, 80–93.

Gypser, S., Veste, M., Fischer, T., & Lange, P. (2016). Infiltration and water retention of biological soil crusts on reclaimed soils of former open-cast lignite mining sites in Brandenburg, north-east Germany. *Journal of Hydrology and Hydromechanics*, *64*, 1–11.

Hallett, P. D., Baumgartl, T., & Young, I. M. (2001). Subcritical water repellency of aggregates from a range of soil management practices. *Soil Science Society of America Journal*, *65*, 184–190.

Hallett, P. D., Karim, K. H., Bengough, A. G., & Otten, W. (2013). Biophysics of the vadose zone: From reality to model systems and back again. *Vadose Zone Journal*, *12*. https://doi.org/10.2136/vzj2013.05.0090

Homolák, M., Capuliak, J., Pichler, V., & Lichner, Ľ. (2009). Estimating hydraulic conductivity of a sandy soil under different plant covers using minidisk infiltrometer and a dye tracer experiment. *Biologia*, *64*, 600–604.

Johnson, W. M. (1945). Natural revegetation of abandoned crop land in the Ponderosa pine zone of the Pike's Peak region in Colorado. *Ecology*, *26*, 363–374.

Keck, H., Felde, V. J. M. N. L., Drahorad, S. L., & Felix-Henningsen, P. (2016). Biological soil crusts cause subcritical water repellency in a sand dune ecosystem located along a rainfall gradient in the NW Negev desert, Israel. *Journal of Hydrology and Hydromechanics*, *64*, 133–140.

Kidron, G. J. (1999). Differential water distribution over dune slopes as affected by slope position and microbiotic crust, Negev Desert, Israel. *Hydrological Processes*, *13*, 1665–1682.

Kidron, G. J. (2001). Runoff-induced sediment yield over dune slopes in the Negev desert. 2: Texture, carbonate and organic matter. *Earth Surface Processes and Landforms*, *26*, 583–599.

Kidron, G. J., Yaalon, D. H., & Vonshak, A. (1999). Two causes for runoff initiation on microbiotic crusts: Hydrophobicity and pore clogging. *Soil Science*, *164*, 18–27.

Kidron, G. J., Yair, A., Vonshak, A., & Abeliovich, A. (2003). Microbiotic crust control of runoff generation on sand dunes in the Negev Desert. *Water Resources Research*, *39*, 1108.

Kidron, G. J., Ying, W., Starinsky, A., & Herzberg, M. (2017). Drought effect on biocrust resilience: High-speed winds result in crust burial and crust rupture and flaking. *Science of the Total Environment*, *579*, 848–859.

King, P. M. (1981). Comparison of methods for measuring severity of water repellence of sandy soils and assessment of some factors that affect its measurement. *Australian Journal of Soil Research*, *19*, 275–285.

Lamparter, A., Bachmann, J., Woche, S. K., & Goebel, M.-O. (2014). Biogeochemical interface formation: Wettability affected by organic matter sorption and microbial activity. *Vadose Zone Journal*, *13*(7). https://doi.org/10.2136/vzj2013.10.0175

Lázaro, R., & Mora, J. L. (2014). Sediment content and chemical properties of water runoff on biocrusts in drylands. *Biologia*, *69*, 1539–1554.

Leighton-Boyce, G., Doerr, S. H., Shakesby, R. A., & Walsh, R. P. D. (2007). Quantifying the impact of soil water repellency on overland flow generation and erosion: A new approach using rainfall simulation and wetting agent on in situ soil. *Hydrological Processes*, *21*, 2337–2345.

Leue, M., Gerke, H. H., & Ellerbrock, R. H. (2013). Millimetre-scale distribution of organic matter composition at intact biopore and crack surfaces. *European Journal of Soil Science*, *64*, 757–769.

Li, B., Gao, J., Wang, X., Maa, L., Cui, Q., & Veste, M. (2016). Effects of biological soil crusts on water infiltration and evaporation Yanchi Ningxia, Maowusu Desert, China. *International Journal of Sediment Research*, *31*, 311–323.

Lichner, L., Eldridge, D. J., Schacht, K., Zhukova, N., Holko, L., Šír, M., & Pecho, J. (2011). Grass cover influences hydrophysical parameters and heterogeneity of water flow in a sandy soil. *Pedosphere*, *21*, 719–729.

Lichner, L., Hallett, P. D., Drongová, Z., Czachor, H., Kovacik, L., Mataix-Solera, J., & Homolák, M. (2013). Algae influence hydrophysical parameters of a sandy soil. *Catena*, *108*, 58–68.

Lichner, L., Hallett, P. D., Feeney, D., Ďugová, O., Šír, M., & Tesař, M. (2007). Field measurement of the impact of hydrophobicity on soil water transport under different vegetation over time. *Biologia*, *62*, 537–541.

Lichner, L., Hallett, P. D., Orfanus, T., Czachor, H., Rajkai, K., Šír, M., & Tesař, M. (2010). Vegetation impact on the hydrology of an aeolian sandy soil in a continental climate. *Ecohydrology*, *3*, 413–420.

Lichner, L., Holko, L., Zhukova, N., Schacht, K., Rajkai, K., Fodor, N., & Sándor, R. (2012). Plants and biological soil crust influence the hydrophysical parameters and water flow in an aeolian sandy soil. *Journal of Hydrology and Hydromechanics*, *60*, 309–318.

Mao, J. F., Nierop, K. G. J., Rietkerk, M., Damsté, J. S. S., & Dekker, S. C. (2016). The influence of vegetation on soil water repellency-markers and soil hydrophobicity. *Science of the Total Environment*, *566–567*, 608–620.

Moody, D. R., & Schlossberg, M. J. (2010). Soil water repellency index prediction on using the molarity of ethanol droplet test. *Vadose Zone Journal*, *9*, 1046–1051.

Mugnai, G., Rossi, F., Felde, V. J. M. N. L., Colesie, C., Büdel, B., Peth, S., … De Philippis, R. (2018). Development of the polysaccharidic matrix in biocrusts induced by a cyanobacterium inoculated in sand microcosms. *Biology and Fertility of Soils*, *54*, 27–40.

Oostindie, K., Dekker, L. W., Wesseling, J. G., Geissen, V., & Ritsema, C. J. (2017). Impacts of grass removal on wetting and actual water repellency in a sandy soil. *Journal of Hydrology and Hydromechanics*, *65*, 88–98.

Or, D., Phutane, S., & Dechesne, A. (2007). Extracellular polymeric substances affecting pore-scale hydrologic conditions for bacterial activity in unsaturated soils. *Vadose Zone Journal*, *6*, 298–305.

Orfánus, T., Dlapa, P., Fodor, N., Rajkai, K., Sándor, R., & Nováková, K. (2014). How severe and subcritical water repellency determines the seasonal infiltration in natural and cultivated sandy soils. *Soil & Tillage Research*, *135*, 49–59.

Orfánus, T., Stojkovová, D., Rajkai, K., Czachor, H., & Sándor, R. (2016). Spatial patterns of wetting characteristics in grassland sandy soil. *Journal of Hydrology and Hydromechanics*, *64*, 167–175.

Papierowska, E., Matysiak, W., Szatyłowicz, J., Debaene, G., Urbanek, E., Kalisz, B., & Łachacz, A. (2018). Compatibility of methods used for soil water repellency determination for organic and organo-mineral soils. *Geoderma*, *314*, 221–231.

Pekárová, P., Pekár, J., & Lichner, L. (2015). A new method for estimating soil water repellency index. *Biologia*, *70*, 1450–1455.

Pereira, S., Zille, A., Micheletti, E., Moradas-Ferreira, P., De Philippis, R., & Tamagnini, P. (2009). Complexity of cyanobacterial exopolysaccharides: Composition, structures, inducing factors and putative genes involved in their biosynthesis and assembly. *FEMS Microbiology Reviews*, *33*, 917–941.

Rillig, M. C. (2005). A connection between fungal hydrophobins and soil water repellency? *Pedobiologia*, *49*, 395–399.

Ritsema, C. J., & Dekker, L. W. (2000). Preferential flow in water repellent sandy soils: Principles and modeling implications. *Journal of Hydrology*, *231–232*, 308–319.

Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R., & Escudero, A. (2013). Soil loss and runoff in semiarid ecosystems: A complex interaction between biological soil crusts, micro-topography, and hydrological drivers. *Ecosystems*, *16*, 529–546.

Roper, M. M. (2005). Managing soils to enhance the potential for bioremediation of water repellency. *Australian Journal of Soil Research*, *43*, 803–810.

Rossi, F., Potrafka, R. M., Pichel, F. G., & De Philippis, R. (2012). The role of the exopolysaccharides in enhancing hydraulic conductivity of biological soil crusts. *Soil Biology & Biochemistry*, *46*, 33–40.

Rye, C. F., & Smettem, K. R. J. (2017). The effect of water repellent soil surface layers on preferential flow and bare soil evaporation. *Geoderma*, *289*, 142–149.

Sándor, R., Lichner, L., Filep, T., Balog, K., Lehoczky, E., & Fodor, N. (2015). Spatial variability of hydrophysical properties of fallow sandy soils. *Biologia*, *70*, 1468–1473.

Sepehrnia, N., Hajabbasi, M. A., Afyuni, M., & Lichner, L. (2016). Extent and persistence of water repellency in two Iranian soils. *Biologia*, *71*, 1137–1143.

Siteur, K., Mao, J. F., Nierop, K. G. J., Rietkerk, M., Dekker, S. C., & Eppinga, M. B. (2016). Soil water repellency: A potential driver of vegetation dynamics in coastal dunes. *Ecosystems*, *19*, 1210–1224.

Soil Survey Division Staff. (1993). Soil survey manual. Soil Conservation Service. U.S. Department of Agriculture Handbook 18**:** 437.

Sousana, J.-F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., … Valentini, R. (2007). Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. *Agriculture, Ecosystems & Environment*, *121*, 121–134.

Spröte, R., Fischer, T., Veste, M., Raab, T., Wiehe, W., Lange, P., … Hüttl, R. F. (2010). Biological topsoil crusts at early successional stages on Quaternary substrates dumped by mining in Brandenburg, NE Germany. *Géomorphologie: Relief, Processus, Environnement*, *16*, 359–370.

Täumer, K., Stoffregen, H., & Wessolek, G. (2006). Seasonal dynamics of preferential flow in a water repellent soil. *Vadose Zone Journal*, *5*, 405–411.

Tillman, R. W., Scotter, D. R., Wallis, M. G., & Clothier, B. E. (1989). Water-repellency and its measurement by using intrinsic sorptivity. *Australian Journal of Soil Research*, *27*, 637–644.

Tisdall, J. M., Nelson, S. E., Wilkinson, K. G., Smith, S. E., & McKenzie, B. M. (2012). Stabilisation of soil against wind erosion by six saprotrophic fungi. *Soil Biology and Biochemistry*, *50*, 134–141.

Vogelmann, E. S., Reichert, J. M., Prevedello, J., Awe, G. O., & Reinert, D. J. (2015). Soil hydrophobicity: Comparative study of usual determination methods. *Ciencia Rural*, *45*, 260–266.

Wang, X. Y., Zhao, Y., & Horn, R. (2010). Soil wettability as affected by soil characteristics and land use. *Pedosphere*, *20*, 43–54.

Ward, P. R., Roper, M. M., Jongepier, R., & Micin, S. F. (2015). Impact of crop residue retention and tillage on water infiltration into a water-repellent soil. *Biologia*, *70*, 1480–1484.

Warren, S. D. (2003). Biological soil crusts and hydrology in North American deserts. In J. Belnap, & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (2nd ed.) (pp. 327–337). Berlin: Springer-Verlag.

Wessolek, G., Stoffregen, H., & Täumer, K. (2009). Persistency of flow patterns in a water repellent sandy soil—Conclusions of TDR readings and a time-delayed double tracer experiment. *Journal of Hydrology*, *375*, 524–535.

Woche, S. K., Goebel, M.-O., Kirkham, M. B., Horton, R., Van der Ploeg, R. R., & Bachmann, J. (2005). Contact angle of soils as affected by depth, texture, and land management. *European Journal of Soil Science*, *56*, 239–251.

World Reference Base. (2014). World reference base for soil resources 2014. World Soil Resources Reports No. 106. Rome; 192.

Yang, J.-L., Zhang, G.-L., Yang, F., Yang, R.-M., Yi, C., Li, D.-C., … Liu, F. (2016). Controlling effects of surface crusts on water infiltration in an arid desert area of Northwest China. *Journal of Soils and Sediments*, *16*, 2408–2418.

Young, I. M., Feeney, D. S., O'Donnell, A. G., & Goulding, K. W. T. (2012). Fungi in century old managed soils could hold key to the development of soil water repellency. *Soil Biology and Biochemistry*, *45*, 125–127.

How to cite this article: Lichner L, Felde VJMNL, Büdel B, et al. Effect of vegetation and its succession on water repellency in sandy soils. *Ecohydrology*. 2018;11:e1991. https://doi.org/10.1002/eco.1991