

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Dew formation on the surface of biological soil crusts in central European sand ecosystems

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Received: 25 June 2012 – Accepted: 26 June 2012 – Published: 3 July 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Dew formation was investigated in three developmental stages of biological soil crusts (BSC), which were collected along a catena of an inland dune and in the initial substrate. The Penman equation, which was developed for saturated surfaces, was modified for unsaturated surfaces and used for prediction of dewfall rates. The levels of surface saturation required for this approach were predicted using the water retention functions and the thicknesses of the BSCs. During a single event, dewfall increased with crust development from 0.08 kg m^{-2} for the initial substrate to 0.10, 0.20 and 0.25 kg m^{-2} for crusts stages 1 to 3, respectively, which was well reflected by the model response. The suggested mechanism of dew formation involves a delay in water saturation in near-surface soil pores and EPS where the crusts were thicker and where the water capacity was high, resulting in elevated vapor flux towards the surface. The results also indicate that the amount of dewfall was too low to observe water flow into deeper soil. Analysis of the soil water retention curves revealed that, despite the sandy mineral matrix, moist crusts with clogged by swollen EPS pores exhibited a clay-like behavior. It is hypothesized that BSCs gain double benefit from suppressing their competitors by runoff generation and from improving their water supply by dew collection. Despite higher amounts of dew, the water availability to the crust community decreases with crust development, which may be compensated by ecophysiological adaptation of crust organisms, and which may further suppress higher vegetation or mosses.

1 Introduction

First colonizers of new land surfaces are cryptogams which often form biological soil crusts (BSC) covering the first millimeters of the top soil in many ecosystems from polar to desert environments. BSCs are assemblages of cyanobacteria, green algae, mosses, liverworts, fungi and/or lichens (Belnap and Lange, 2001) which stabilize the surface, redistribute water, accumulate organic matter, and which may predetermine

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appearance and succession of vascular plants. It has been demonstrated in this regard that water repellency, as well as reduced infiltration caused by swelling of exopolysaccharides upon rewetting result in higher run-off during rain events (Kidron et al., 1999; Yair, 2001; Lemmnitz et al., 2008; Fischer et al., 2010), which may run-on in depressions, may supply vascular plants and may influence vegetation patterns (Yair et al., 2011; Veste et al., 2011; Fischer et al., 2012). On the other hand, biological soil crusts built up by mosses limit water infiltration into deeper soil layers and reduce water availability to higher plants (Yair et al., 2011). Interaction with vascular vegetation may suppress BSCs, with shading by canopies or litter fall being possibly the most important factors for crust suppression. At the same time, availability of water to vascular plants largely depends on the form of precipitation: Rain infiltrating into the rooting zone of the soil supplies available water, while dew accumulating on leaves is – with few exceptions of desert succulents – not available to the plant metabolism. On the other hand, dew has been identified to be one of the major sources of BSC and lichen water supply under arid and semi-arid conditions (Kidron, 2000; Veste et al., 2001; Veste and Littmann, 2006). Hence, BSCs would benefit from repartitioning rain and from collecting dew.

Although the significance of dew for BSCs is emphasized in numerous studies, the influence of crust development on dew formation has received less attention. Lui et al. (2006) reported that dew deposition increased from sand and from a loamy physical crust, which they considered to be initial for crust growth, to an algal and to a moss crust. Zhang et al. (2009) described a similar pattern, where dew formation increased from bare sand to a cyanobacterial crust, to a lichen crust and to a moss crust.

We hypothesize that dew formation involves a delay in water saturation where the water capacity of the surface layer is high, resulting in elevated vapor flux towards the surface. The aim of this study is to identify the factors responsible for this delay in BSCs along a catena on an inland dune containing sandy substrate and three stages of crust development.

2 Material and methods

2.1 Biological soil crusts

The sampling site is located near Lieberose, Brandenburg, north-east Germany (51°55'49" N, 14°22'22" E). The climate is continental with an average annual rainfall of 569 mm a⁻¹ and an average annual temperature of 8.9°C measured at the nearest climatic station in Cottbus. Undisturbed samples of biological soil crusts were collected in May 2010 and in July 2011 on inland sand dunes along a catena from mobile active dune to dry acidic grassland with tussocks of *Corynephorus canescens*. The sandy substrate was used as control. The crusts were moistened during sampling to prevent surface disruption.

On the surface of crust 1, dominating sand grains were physically stabilized in their contact zones by accumulated organic matter and by few green algae (*Zygodonium eritecorum*, *Klebsormidium crenulatum*). The pore space was dominated by the mineral matrix. On the surface of crust 2, the algae partially filled in the matrix pores and enmeshed sand grains. Crust 3 was characterized by intense growth of filamentous and coccoid algae, by few mosses (*Polytrichum piliferum*), which covered less than 5% of the surface and by fungi associated with mosses. Crust organisms completely occupied the matrix pores here. A detailed description of the crusts was given by Fischer et al. (2010). The substrate was classified as carbonate-free aeolian sand with less than 4% of particles below 63 µm diameter. The geometric mean particle diameter d_g was 140 µm. The thicknesses of crusts 1, 2 and 3 were 1.5 ± 0.5 , 4.0 ± 1.0 and 4.5 ± 1.0 mm, respectively.

2.2 Water retention functions

Water retention curves, representing both BSC and the underlying substrate, were recorded consecutively in sand (suction pressure 0 to -0.01 MPa) and kaolin beds (suction pressure -0.01 to -0.05 MPa, Eijkelkamp apparatus, The Netherlands)

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using 8.13 cm^3 ($l_{\text{core}} = 11.5 \text{ mm}$, $2r = 30.0 \text{ mm}$) steel rings, which were prepared from 250 cm^3 undisturbed soil samples taken in the field. At the end of the kaolin bed experiment, the samples were air dried to constant weight at 65 % Relative Humidity (RH) and 20°C (suction pressure -58 MPa) and at 105°C , which was considered to be absolute dryness. Non crusted substrate was used as a control.

In order to retrieve corrected water retention functions of solely the BSCs, the volumetric proportion of the underlying substrate was subtracted from the total for each suction level using the water retention function of the control and the BSC thicknesses (Eq. 1).

$$\Theta_{\text{BSC}}(\Psi_i) = \frac{\Theta_{\text{total}}(\Psi_i)V_{\text{core}} - \frac{l_{\text{core}} - l_{\text{BSC}}}{l_{\text{core}}} \Theta_{\text{Control}}(\Psi_i)V_{\text{core}}}{V_{\text{BSC}}} \quad (1)$$

where $\Theta_{\text{BSC}}(\Psi_i)$, $\Theta_{\text{total}}(\Psi_i)$ and $\Theta_{\text{Control}}(\Psi_i)$ are the volumetric water contents of the BSC, of the soil core containing both BSC and the substrate below and of the control substrate at each suction level Ψ_i , respectively, V_{core} , l_{core} , V_{BSC} and l_{BSC} are volumes and thicknesses of the soil core and the BSCs, respectively. V_{BSC} was calculated using $\pi r^2 l_{\text{BSC}}$ and amounted to 1.06, 2.83 and 3.18 cm^3 for crusts 1, 2 and 3, respectively. The van Genuchten function (Eq. 4) was numerically fitted to these BSC water retention data.

2.3 Dewfall

For the determination of dewfall the Petri dishes containing air-dry initial substrate and crusts were pushed into the ground so that their edges were close to the flat surface of the soil. Dew was measured by weighing the Petri dishes with an accuracy of $\pm 0.01 \text{ g}$ (Sartorius, Germany) before the onset of dewfall (2 August 2011, 15:00 CEST) and at dawn (3 August 2011, 05:00 CEST). Air temperatures and relative humidities were recorded hourly at 5 and 200 cm above the ground, the soil temperature was recorded 5 cm below the surface using mercury thermometers, RH sensors (Hama, Germany),

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hair hygrometers and a temperature sensor (Amarell, Germany), respectively. The surface temperature of the samples was determined using an IR thermometer (Testo, Germany), where the emissivity was set to 0.95 for all samples. Wind data of a neighboring climatic station with a recording interval of 5 min were used for determination of aerodynamic resistances r_a (Allen et al., 1988). Because BSCs, which are considered to be the location for water phase transition in this study, reside on mineral soil and higher vegetation is absent, no boundary layer resistance r_t for vapor flow was considered.

2.4 Theory

The Penman equation was developed for evaporation from saturated surfaces. Dry soils, however, behave differently, because they represent an unsaturated porous surface, which means that water is bound to the soil matrix or to EPS by capillary or osmotic forces. Heusinkveld (2008) modified the standard Penman equation for unsaturated surfaces by introducing the relative humidity h_s of the soil pores.

$$L_v E = \frac{h_s s (Q^* - G) + \frac{\rho C_p}{r_{at}} (h_s e_w(T) - e)}{h_s s + \gamma} \quad (2)$$

where $L_v E$ is the latent heat flux ($W m^{-2}$, or $J m^{-2} s^{-1}$), h_s is the relative humidity of the soil pores, s is the derivative of the saturated vapor pressure ($Pa K^{-1}$), Q^* is the net radiation and G is the soil heat flux ($W m^{-2}$), ρ is the density of air ($kg m^{-3}$), C_p is the specific heat of air at constant pressure ($J kg^{-1} K^{-1}$), r_{at} is the sum of the aerodynamic plus the boundary layer resistances ($s m^{-1}$), $e_w(T)$ is the saturated vapor pressure at reference height (Pa), e is the vapor pressure at reference height (Pa) and where γ is the psychrometric constant ($66 Pa K^{-1}$).

The Penman equation can also be used to describe the process reverse to evaporation: surface condensation, or dewfall. In contrast to the standard Penman equation,

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where dew formation on a free water surface is reduced by the second term of Eq. (2), under dry soil conditions the dew formation will be enhanced, because the saturation deficit of the atmospheric surface layer rarely approaches zero (Heusinkveld, 2008). In addition, soil pores fill with water as dew enters the surface, resulting in an increase of h_s over time. Assuming increasing water capacity with crust development, we hypothesize that dew formation increases, because water saturation in pores will be reached later in time when the soil water capacity is high, which will prolongate the vapor flux towards the surface. The question arises as to what factors control dew formation in porous layers, as in BSCs in particular, when considering this kinetic component during dewfall.

To determine the dewfall rate dD/dt in $\text{kg m}^{-2} \text{s}^{-1}$, Eq. (2) was rewritten to Eq. (3).

$$\frac{M_{\text{H}_2\text{O}}L_vE}{\Delta H_{\text{vap}}} = \frac{dD}{dt} = \frac{h_s s (Q^* - G) + \frac{\rho C_p}{r_a} (1 - h_s) e_w(T)}{h_s s + \gamma} \cdot \frac{M_{\text{H}_2\text{O}}}{\Delta H_{\text{vap}}} \quad (3)$$

where $1 - h_s$ is the water saturation deficit in the soil pores, $M_{\text{H}_2\text{O}}$ is the molecular weight ($0.018 \text{ kg mol}^{-1}$) and ΔH_{vap} is the condensation heat of water (44 kJ mol^{-1} at 20°C). Q^* was assumed to equal 0 (nighttime), G was assumed to be -2 W m^{-2} . For simplicity, it was also assumed that 1 m^3 water equals 1000 kg.

The van Genuchten function was used for water retention curve fit (van Genuchten, 1980; Eq. 4).

$$\Theta(\Psi_M) = \Theta_r + \frac{\Theta_s - \Theta_r}{[1 + (\alpha \Psi_M)^n]^{1-n^{-1}}} \quad (4)$$

where Ψ_M is the soil water potential (hPa), Θ_r and Θ_s are the residual and saturated volumetric water contents ($\text{m}^3 \text{ m}^{-3}$) of the crust, respectively, and where the parameters α (in cm^{-1}) and n are related to the inverse of the air entry suction as well as the pore size distribution, respectively. Ψ_M is related to h_s in Eq. (5) (Lal and Shukla,

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2004).

$$h_s = \exp\left(\Psi_M \frac{M_{\text{H}_2\text{O}}}{RT}\right) \quad (5)$$

where R is the specific gas constant ($462 \text{ J kg}^{-1} \text{ K}^{-1}$) and T is the surface temperature (K).

We predicted dewfall D (in $\text{m}^3 \text{ m}^{-2}$) in 1 h intervals ($t_0 = 23:00$ CEST) by numerically integrating Eq. (3) over time, which was then used to calculate the increase of the volumetric water content $\Theta(t_i + 1)$ using Eq. (6), and which resulted in a crust specific response in Ψ_M (using Eq. 4) and in h_s (using Eq. 5).

$$\Theta(t_i + 1) = \Theta(t_i) + \frac{D_i}{l_{\text{BSC}}} \quad (6)$$

where l_{BSC} is the BSC thickness in m.

This algorithm was repeated for the following 1 h intervals by consecutively using h_s predicted with Eq. (5) as well as the meteorological data recorded in the field in Eq. (3). The R software suite was used for the calculations. We used 1 h time steps because it is well acknowledged that the Penman equation generates some overall error for shorter time intervals when the assumption of a constant soil heat flux is made (Davie, 2008).

3 Results

3.1 BSC water retention

The corrected water retention functions of the BSCs and the corresponding van Genuchten fitting parameters are shown in Fig. 1 and in Table 1, respectively.

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3.2 Dewfall

Dewfall increased with crust development from 0.08 kg m^{-2} for the initial sandy substrate to 0.10 , 0.20 and 0.25 kg m^{-2} for crusts 1 to 3, respectively (Fig. 2). The surface temperatures during sampling were 11.9°C for the substrate and 12.0 , 12.5 and 12.6°C for crusts 1 to 3, respectively. The relative humidity 5 cm above ground reached 100% at 23:30 CEST and remained at saturation until dawn. We did not observe soil water discharge into depth in this study. Instead, the BSCs formed a moist layer over dry sand when dewfall ceased in the morning, even at higher precipitation (Fig. 3).

Dawning suction pressures amounted to -0.005 (pF = 1.71), -0.631 (pF = 3.80), -2.00 (pF = 4.30) and -1.58 MPa (pF = 4.20) in the initial substrate and in crusts 1 to 3, respectively, where the moistened layer of the substrate was assumed to be 0.5 mm thick.

4 Discussion

Although the sandy mineral matrix did not differ between the crusts, the van Genuchten parameter n decreased from the control substrate to the moist crusts 1, 2 and 3 (Table 1), thereby exhibiting a clay like behavior. Moistening of the crusts for water retention measurements obviously lead to clogging of soil pores through swelling of EPS (Fischer et al., 2010).

The saturated volumetric water content Θ_s amounted to a typical for sand value of 0.34, but increased to atypically high for mineral soils values of 0.67, 0.73 and 0.85 for crusts 1, 2 and 3, respectively (Table 1). This increase in water holding capacity reflects the progressing occupation of the surface substrate with organic matter: The initial substrate did not significantly contain organic components, which gained in importance as the matrix pores became occupied by crust organisms and by EPS. The data reported by Chenu (1993) for sand-polysaccharide mixtures support our approach of using the

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van Genuchten function, which have been demonstrated to be comparable with BSCs (Fischer et al., 2010).

The main sources of moisture for dew formation on the soil surface are the free atmosphere and moist deeper soil (Garrett and Segal, 1988; Littmann and Veste, 2008).

By placing the BSCs into petri dishes in this study, the crust surface was exposed to the free atmosphere only, while the influence of deep soil moisture on dew formation was excluded. Hence, only above ground atmospheric conditions are relevant for dew formation here. Dewfall values predicted by the proposed model corresponded well with the field data, however, some bias could be observed for crust 3. Because the water potentials of crusts 2 and 3 never exceeded -1.5 MPa during the dewfall event, the water retention function is considerably influenced by the residual volumetric water content Θ_r at suction levels below this value (Fig. 1). Hence, some underestimation of Θ_r for crust 3 may be assumed.

Lui et al. (2006) and Zhang et al. (2009) reported increasing dewfall with crust development, which can be confirmed by our data. Because in our set of equations used for dewfall prediction BSCs differ between each other in Eqs. (4) and (6), it can be deduced that under constant further conditions dew formation depends on their water retention properties, which are dominated by accumulation of EPS, that it decreases with an increase of the initial water content $\Theta(t_0)$, and that it increases with BSC thickness (Fig. 2).

The dawning water potentials decreased with BSC thickness, ranging between -2 MPa in crust 2 and -0.005 MPa in the substrate. Swift et al. (1979) reported that bacteria are inactive below -1.0 to -1.5 MPa in soils, whereas soil fungi are active down to -15 MPa, and that some *Aspergillus* and *Penicillium* are active to -40 MPa and below. Fischer (2009) reported that soil respiration amounted to approx. 5–8 % of maximal respiration at -1.5 MPa, indicating still ongoing microbial activity under conditions of plant wilting. Moore (1986) found for leaf and needle litter that decomposition will cease at -38 MPa. Palmer and Friedman (1990) reported soil water potential tolerances of cryptoendolithic lichens that begin to photosynthesize at a matric water

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potential > -46.4 MPa. Cyano-lichens and free-living cyanobacteria need liquid water for the activation of photosynthesis (Lange et al., 1993, 1998). Contrarily, the photosynthesis metabolism of green-algae and green algae soil lichens as well as of dry *Microcolues sociatus* is reactivated solely by hydration in equilibrium with high air humidity (Lange et al., 1994; Lange 2001). Lange et al. (1992) and Veste et al. (2001) estimated that BSCs are photosynthetically active at precipitation amounts > 0.1 mm, which is similar to the dewfall amounts reported in our field experiment (Fig. 2).

Due to water retention by EPS the onset of the phase transition from vapor to liquid water more resembles vapor adsorption rather than surface condensation. Hence, rapid adsorption of freshly condensed water by dry EPS prevents the formation of free surface water films, which are, for example, necessary for cyanobacterial activity. Because delayed water saturation of thicker crusts most likely affects the metabolic activity of crust organisms, it can be assumed that some adaptation of the crust community is likely to occur. Furthermore, the water holding capacity of the BSCs may also influence the duration of BSC wetting and of the photosynthetic activity during daytime. In combination with micro-scale differences of the microclimate (Kidron et al., 2000; Veste et al., 2006) these are important feedback mechanisms for the development of the different crust stages.

The proposed mechanism of dew formation involves later water saturation in near-surface soil pores and EPS where the crusts are thicker and where the water capacity is high, resulting in elevated vapor flux towards the surface. This applies to both the free atmosphere as well as to the deeper soil, possibly also resulting in some extraction of moisture from the rooting zone of higher plants and its capture in BSCs.

5 Conclusions

The results support the hypothesis that BSCs redistribute rain, which can be utilized by vascular plants after infiltration into the rooting zone, and promote formation of dew, which is less available to vascular plants. It can be hypothesized that BSCs gain double

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benefit from suppressing their competitors by runoff generation and from improving their water supply by dew collection. Despite higher amounts of dew, the water availability to the crust community decreases with crust development, which may be compensated by ecophysiological adaptation of microorganisms, and which may further suppress higher vegetation or hinder mosses from taking over. It can be concluded that under constant further conditions organic matter accumulation and crust thickness were the main factors of dew formation.

Acknowledgements. This study is part of the Transregional Collaborative Research Centre 38 (SFB/TR 38), which is financially supported by the Deutsche Forschungsgemeinschaft (DFG, Bonn) and the Brandenburg Ministry of Science, Research and Culture (MWFK, Potsdam). The authors thank Horst Gerke (ZALF Müncheberg), Xiao Bo (BTU Cottbus) for their kind review of the manuscript, Wolfgang Wieprecht, Uwe Zehner, Philipp Lange (BTU Cottbus) and Matthieu Lae (Ecole des Mines Douai, France) for technical assistance.

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Table 1. van Genuchten fitting parameters of the corrected BSC water retention functions, Θ in $\text{m}^3 \text{m}^{-3}$, unit of $-\Psi$ in regression analysis was hPa.

	Θ_r	Θ_s	α	n
Substrate	0.006	0.34	0.0380	2.48
Crust 1	0.000	0.67	0.0036	1.97
Crust 2	0.030	0.73	0.0012	1.80
Crust 3	0.005	0.85	0.0060	1.64

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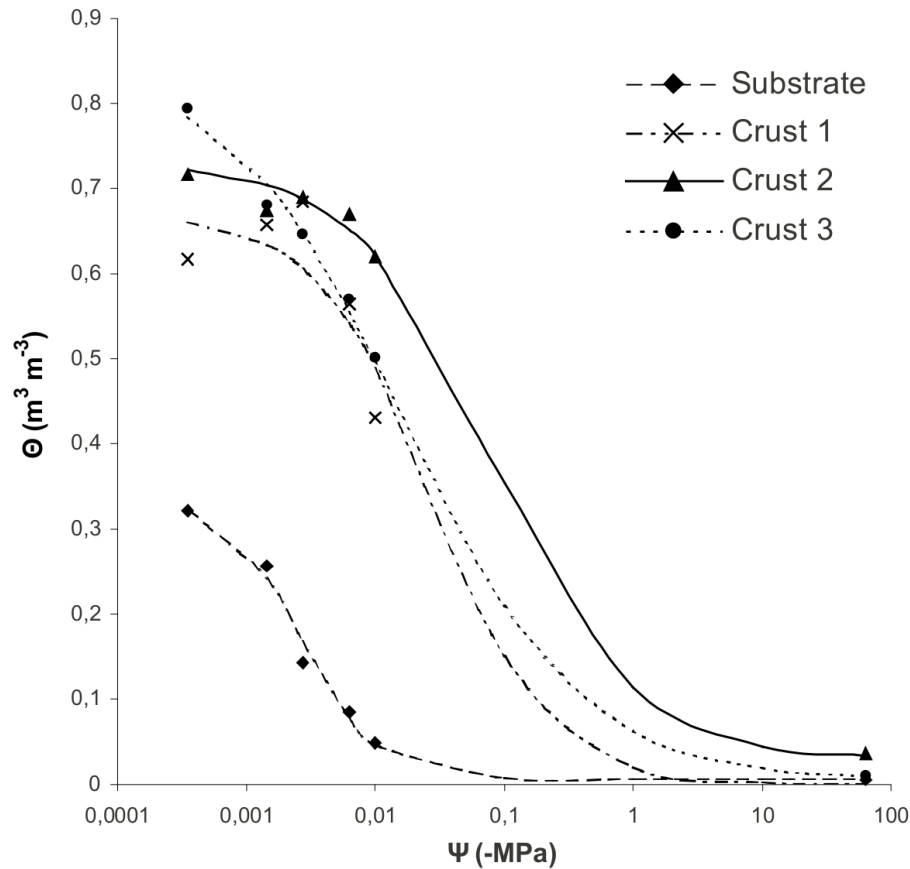


Fig. 1. Water retention curves of the initial substrate and the BSCs. Ψ is the soil water potential, Θ is the volumetric water content. Arithmetic mean values with $n = 3$.

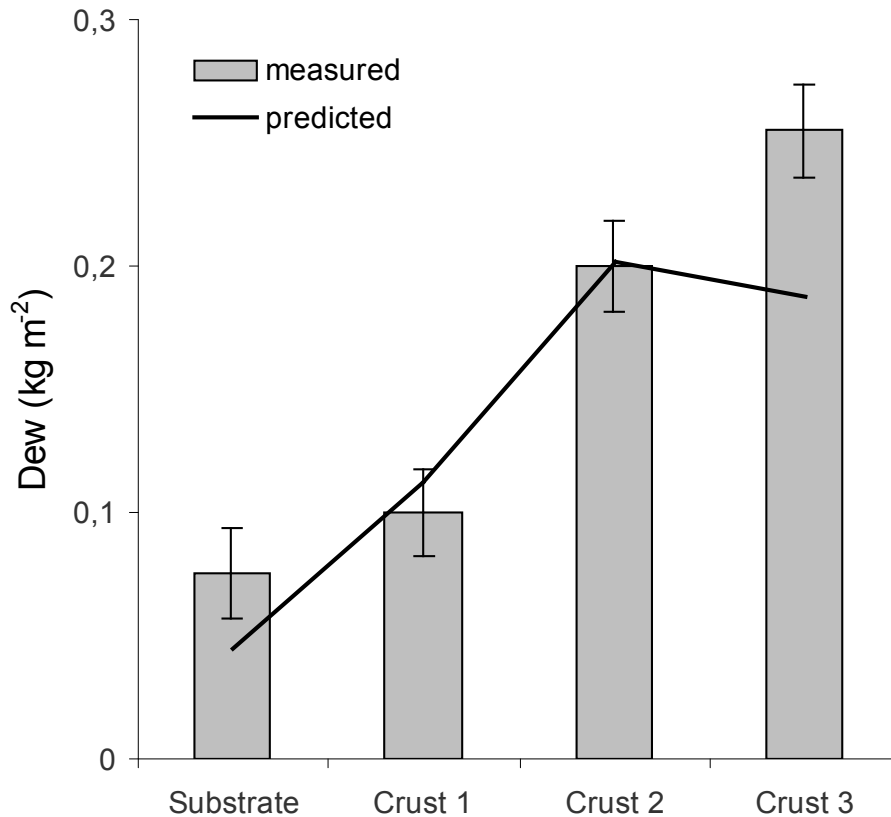


Fig. 2. Measured (columns) and predicted (solid line) amounts of dew in the initial substrate and in the crusts 1, 2 and 3; 2 August 2011, 15:00 CEST (installation) to 3 August 2011, 05:00 CEST (at dawn). Arithmetic mean values with $n = 3$, bars indicate standard deviation.

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Fig. 3. Crust 2 after drizzling rain in the morning. BSCs formed a moist layer over loose dry sand, so that no water flow into deeper soil could be observed. Image: Maik Veste, 21 May 2008.

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