Effects of soil-surface microbial community phenotype upon physical and hydrological properties of an arable soil: a microcosm study

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Summary

The nature of the first few millimetres of the soil surface strongly affects water infiltration rates, generation of run-off, soil detachment and sediment transport. We hypothesized that the phenotypic community structure of the soil-surface microbiota affects the physical and hydrological properties of an arable soil. A range of contrasting microbial community phenotypes were established in microcosms by manipulating the wavelength of light reaching the soil surface, with the microcosms being incubated in the field for approximately 6 months. Phenotypes were characterized by phospholipid fatty acid (PLFA), ergosterol and chlorophyll analysis. The microcosms were then subjected to simulated rainfall at an intensity of 60 mm hour\(^{-1}\) for 20 minutes at a slope gradient of 9\(^{\circ}\). Water infiltration rates, run-off generation, soil loss (including a particle-size analysis of the sediment) and soil-surface shear strength were quantified.

Distinct microbial phenotypes developed on the soil surfaces with UV-A and restricted-UV treatments when compared with subsurface layers. There was significantly greater fungal biomass in the no-light treatment when compared with all other treatments, with approximately 4.5 times more ergosterol being extracted from the subsurface layer of the no-light treatment when compared with other treatments. The no-light treatment produced the greatest amount of run-off, which was approximately 15% greater than the restricted photosynthetically-active radiation (PAR) treatment. Significant differences between treatments were also found in shear strengths, with increasing strength being correlated with increasing ergosterol concentration. Water infiltration, erosion and the sediment concentrations in run-off were not significantly different between treatments. This work demonstrates that the quality of light reaching the soil surface affects the microbial phenotype, in turn producing functional consequences with regard to the physical and hydrological properties of arable soil surfaces.

Introduction

The characteristics of the first few millimetres of the soil surface strongly affect water infiltration rates, generation of run-off and soil erosion (Auzet et al., 2004). Whilst much is known about the physics and erosion properties of soil surfaces at the millimetre scale, little is known of their microbiology, particularly in temperate arable systems, although some preliminary work has been undertaken and reported by Jeffery et al. (2007) and Knapen et al. (2007). As microbes can affect both the physical and hydrological properties of soils, increased knowledge of the microbiology of the soil surface may lead to better understanding of the processes of soil erosion, water infiltration and run-off generation (Wright et al., 1999; Wright & Anderson, 2000), all of which have impacts on the sustainability of agricultural systems and surface water quality.

The soil surface can comprise two different types of crust: (i) microbiotic crusts, which are of biological origin, comprising a community of interacting microbes (St. Clair & Johansen, 1993) and (ii) physical crusts, which can form through slaking of soil aggregates, or after raindrops detach soil particles, which are carried in the splash jets and redeposited on the soil surface, sometimes forming a surface seal (Farres, 1978; Le Bissonnais,
When these seals dry they form crusts that can affect soil structural and hydrological properties, such as reduction in porosity at the soil surface (Le Bissonnais, 1990), reduced infiltration rates and concurrent increased generation of water runoff (Le Bissonnais et al., 1995).

Whilst much research has been done to investigate the physical soil properties that lead to a propensity to form crusts, erode soil and generate run-off (Le Bissonnais et al., 1995; Cattle et al., 2004), the majority of work investigating the effects of the microbiota on these properties has been conducted on microbiotic crusts (e.g. Loope & Gifford, 1972; St. Clair & Johansen, 1993; Belnap & Eldridge, 2001).

It is widely accepted that microbiotic crusts can affect a soil surface’s physical properties (McKenna-Neuman et al., 1996; Belnap & Eldridge, 2001). One of the most important roles of such crusts is the stabilization of the soil surface and commensurate reduction in the soil’s tendency to erode (St. Clair & Johansen, 1993).

Erosion reduces soil productivity by removing the most fertile topsoil (Pimentel et al., 1987). As well as reducing fertility, where soils are shallow, this may lead to an irreversible loss of productive farmland. It has also been demonstrated that soil biota can also affect soil physical properties when microbiotic crusts are not present (Edgerton et al., 1995; Ritz & Young, 2004). Fungi have been shown to be particularly important in affecting soil physical properties that influence erosion (Medows et al., 1994).

Nisha et al. (2007) demonstrated that cyanobacterial populations within the soil can affect bulk density, water holding capacity and hydraulic conductivity. Falchini et al. (1996) found that when cyanobacteria from the genus Nostoc were inoculated onto the surface, porosity was maintained and the soil structure was protected from the damaging effects of water addition, such as slaking of aggregates or particle detachment. These are all pertinent functions for arable systems and hence warrant further investigation.

For undisturbed ground, studies of microbiotic crusts have been undertaken that investigate their effect on both erosion and hydrology (St. Clair & Johansen, 1993). However, there is currently a lack of data regarding the impact of the soil surface microbiota (at the millimetre scale) on erosion and hydrological processes in arable systems.

Arable soil surfaces are subject to relatively extreme environmental conditions when compared with deeper soil zones, and are capable of undergoing rapid changes with regard to temperature, water status and solar radiation (Robinson, 1966; Hillel, 1982; Strangeways, 2003). These relative extremes in environmental conditions have been shown to be sufficient to drive the formation of a distinct microbial community phenotype at the soil surface of arable systems, at a 1-mm scale, during periods of minimal disturbance as occurs between tillage operations (Jeffery et al., 2007), apparently driven by light (Jeffery et al., 2009).

Jeffery et al. (2007) demonstrated that a distinct soil-surface phenotype develops in arable systems that are undisturbed for sufficient periods of time. As many of the functions of microbiotic crusts, such as reduction in soil erodibility, are pertinent to soil structural dynamics in arable systems, we tested the hypothesis that such distinct soil-surface microbial phenotypes have different effects upon the physical and hydrological properties of an arable soil surface. This was done by quantifying the community-level phenotypes, the relative abundance of fungi, and the relative abundance of photoautotrophs in controlled experimental systems where surface communities were manipulated with modified light treatments. Hydrological and erosion processes were simulated through use of a rainfall simulator with run-off, infiltrate, sediment concentration and surface shear strength subsequently quantified and the data used to test the above-stated hypothesis.

Materials and methods

Materials: erosion trays

In order to measure soil physical and hydrological properties (run-off, infiltrate and soil loss), rectangular erosion trays (dimensions 60 × 110 × 200 mm) were constructed from steel and painted with Hammerite™ metal paint. Approximately 5 mm above the base of each erosion tray, a steel mesh, covered with a nylon mesh (gauge = 1 mm), was placed to allow infiltration of water, but not the passage of soil aggregates > 1 mm in size (Figure 1). A sandy loam soil (soil association, Bearsted 541A; Hodge et al., 1984) of pH 6.07 (determined in CaCl2 solution), organic carbon 10 g kg−1, total N 1.25 g kg−1; C:N 10.6, coarse sand 8.3%, medium sand 36.3%, fine sand 21.6%, silt 20.2 and clay 13.6% (determined by the pipette method) was collected from Silsoe Experimental Farm at Cranfield University, Silsoe, Bedfordshire (WGS84; 52°00′28.71″N, 000°26′04.21″W). The soil

Figure 1 Schematic figure showing a cross-section of the erosion tray and light baffle. The two pipes were used to attach plastic tubing to allow collection of run-off and infiltrate for analysis.

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was homogenized by first breaking up by hand, then passing through a 2-mm sieve, and subsequently thoroughly mixed. This was done when the soil was dry enough to crumble. Each erosion tray was then packed by adding the necessary quantity of soil in four parts. The first quarter of the soil was added and the erosion trays were shaken to settle the soil, which was then gently pressed down. This was repeated until all of the soil in each erosion tray was packed to a dry bulk density of 1.3 g cm$^{-3}$, deemed to be typical for an arable soil.

In order to generate different soil surface microbial communities, three different types of light filters plus a no-light control treatment, were used to establish four treatments (Table 1). The light filters were attached to varnished wood frames (dimensions 80 × 150 × 300 mm). Each frame stood 20 mm above, and parallel to, the surface of the erosion trays. On two opposite sides, the wood was 20 mm shorter, creating a gap between the ground and the frame, which provided a baffle that allowed the circulation of air, but ensured that no light reached the soil surface without passing through the light filter first (Figure 1).

**Experimental design**

Each erosion tray was randomly allocated to a light treatment (Table 1) and placed in the field in a randomized block design to produce eight replicates of each treatment. Blocks were aligned to run north to south to minimize any effects arising from shadows at sunrise and sunset. All erosion trays were left in the field for a period of approximately 6 months from November 2006 until May 2007. All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007). All were irrigated regularly (approximately weekly to a period of approximately 6 months from November 2006 until May 2007).

**Table 1** Properties of filters used to control quality of light reaching soil surfaces of the microcosms

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Filter</th>
<th>Filter properties</th>
</tr>
</thead>
<tbody>
<tr>
<td>Restricted photosynthetically-active radiation (PAR)</td>
<td>LEE filter: DS 124</td>
<td>&lt;5% transmission of wavelengths up to 460 nm</td>
</tr>
<tr>
<td></td>
<td>dark green</td>
<td>&lt;5% transmission of wavelengths between 610 and 700 nm, therefore</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;5% transmission of PAR</td>
</tr>
<tr>
<td>Restricted UV</td>
<td>LEE filter: DS 226</td>
<td>Ultraviolet 0% transmission of wavelengths below 380 nm, &gt;85% transmission of all wavelengths above 420 nm</td>
</tr>
<tr>
<td>No light</td>
<td>White opaque PVC</td>
<td>No wavelengths transmitted</td>
</tr>
<tr>
<td>With UV-A</td>
<td>LEE filter: DS 130</td>
<td>&gt;70% transmission of all wavelengths above 320 nm</td>
</tr>
</tbody>
</table>

Laboratory analyses

To confirm development of different soil-surface microbial community phenotypes under the different light treatments, and to allow interpretations of the causal relationships between different microbiological communities and soil-surface physical properties, three randomly chosen erosion tray replicates from each light treatment were used for the microbiological assays. All laboratory analyses were performed on the soil surface layer of the erosion trays, which was removed down to a depth of approximately 1 mm by scraping with a palette knife. The subsurface layer was then removed using the same technique down to a further depth of approximately 5 mm. Only these two depths, defined as the ‘surface’ and the ‘subsurface’, were investigated because work reported by Jeffery *et al.* (2007) demonstrated that the differences in soil-surface microbial phenotype diminished with depth, becoming not statistically significant by approximately 6-mm depth.

Chlorophyll *a* extraction and analysis were used to quantify photoautotrophs in the different treatments. The hot ethanol extraction method for quantification of chlorophyll *a* in soil was used (Metting, 1994) with 10-g aliquots of soil. Analysis of extracted chlorophyll *a* was undertaken with a SPECTRAmax 386 spectrophotometer (Molecular Devices Corporation, Sunnyvale, California, USA) and chlorophyll *a* concentration was calculated using the following equations:

\[
[\text{Chlorophyll } a] \text{ mg ml}^{-1} = \frac{(\text{OD at } 666 \text{ nm} - \text{OD at } 730) \times \text{ml of sample} \times 10}{890},
\]

and

\[
[\text{Chlorophyll } a] \text{ mg g}^{-1} \text{ soil} = \frac{[\text{Chlorophyll } a] \text{ mg ml}^{-1} \times \text{amount of petroleum ether (ml)}}{\text{amount of soil (10 g)}}.
\]

where OD = optical density.

Phospholipid fatty acid (PLFA) extraction and analysis were undertaken as outlined by Bligh & Dyer (1959) and extended by Zelles (1999), using 5-g aliquots of soil for each sample. Extracted PLFAs were analysed by gas chromatography using an HP 5 column on a G2070AA Chemstation, Model 6890N, gas chromatography appliance (Agilent Technologies, Santa Clara, California, USA) and compared with known retention times to identify individual PLFAs on the basis of a Supelco 26 peak standard (Sigma-Aldrich company Ltd, Poole, Dorset, UK). The fungal:bacterial
ratio was calculated using 18:2ω6 (fungal biomarker) divided by the summed %mol of biomarkers i15:0, ai15:0, 15:0, i16:0, 16:1ω7t, i17:0, 17:0, 18:1ω7 and 19:0c as an expression of total bacterial abundance (Frostegård & Bååth, 1996).

Ergosterol was extracted by the rapid ultrasonication method described by Ruzicka et al. (1995) using 5-g aliquots of soil for each sample. All samples were then ultrasonicated at 150 W with a sonic probe (VirSonic 600, model s3000-210; VirTis, New York, USA) for 200 s while kept on ice. Analysis was performed with a Waters HPLC system (Milford, Massachusetts, USA). Each sample (20 μl) was injected into a 150-mm (4.6 mm i.d.) Phenomenex (Torrance, California, USA) Luna 5-μm silica column preceded by a Phenomenex security guard column and eluted with n-hexane-propan-2-ol (98.2 v/v) at 1.5 ml minute⁻¹. A UV absorbance detector was used to measure the absorbance at 282 nm.

Rainfall simulation

Five randomly selected replicate erosion trays from each light treatment were selected. These erosion trays were then subjected to simulated rainfall, generated by a gravity-fed, hypodermic needle rainfall simulator at a rate of 60 mm hour⁻¹ for 20 minutes. This storm intensity and duration were chosen to be representative of a typically erosive rainfall event in the UK, with a return period of approximately one in 15 years (NERC, 1975). The erosion trays were placed on a table approximately 8 m below the drop fromers of the rainfall simulator so that the raindrops reached their terminal velocity. The erosion trays were inclined at a 9° slope (representing a relatively steep arable field in the UK) and ensured that surface run-off was generated. The rainfall intensity and texture of the soil used were also chosen to encourage the formation of a surface seal (Farres, 1978; Le Bissonnais, 1990). Infiltrate was also collected and measured as described below.

Throughout the simulated rainstorm, run-off and infiltrate were collected from the erosion trays via plastic tubing, which carried the water to 1-litre collection bottles. Volumes of total run-off and infiltrate were quantified with measuring cylinders at the end of the simulated rainfall. The run-off generated during the storm was filtered through pre-dried (55°C) and tared Whatman No 1 filter papers. After the run-off had been filtered, the filter papers were again dried overnight (at 55°C) and weighed. The difference in filter paper mass was taken to be the sediment that had been eroded by the run-off from the soil surface of the erosion trays.

Shear strength at the soil surface was measured using a Torvane (Soiltest, ELE International, Loveland Colorado, USA). After exposure to simulated rainfall, the erosion trays were placed in an oven overnight at 105°C to allow drying of any seals in order to create a crust. Moreover, drying also ensured that all replicates were at the same moisture content prior to the measurement of shear strength. After leaving the microcosms to cool for several hours, the Torvane (diameter 25 mm) was used to measure the soil shear strength at three randomly chosen, discrete locations on the soil surface of each erosion tray, giving 15 replicate measurements of shear strength for each treatment. Following the standard methodology, the Torvane was gently pushed into the soil surface to a depth of 5 mm and rotated at a slow and steady rate until the shear properties of the soil failed and then a reading was taken.

Data analysis

Data analysis was undertaken by using Statistica 7.1 (Statsoft Inc., Tulsa, Oklahoma, USA) with the exception of correlation matrix determination, which was undertaken with Microsoft Excel (Microsoft, Redmond, Washington, USA). Post-hoc ANOVA, using Fisher’s least significant difference (LSD) was used to test differences in chlorophyll a, ergosterol concentrations, fungal-to-bacterial PLFA biomarker ratios, run-off, infiltrate, soil loss and soil shear strength. PLFAs were examined with principal components (PC) analysis of %mol data, by using covariance with post-hoc ANOVA.

Results

Moisture content

The soil erosion trays had different moisture contents following a 6-month field incubation and before exposure to the simulated rainfall. These were by treatment: restricted UV, mean = 11.2% (SE 1.3%); with UV-A, mean = 12.9% (SE 1.2%); no light, mean = 14.6% (SE 0.5%); and restricted PAR, mean = 12.3% (SE 0.4%). However, statistical analysis of these data showed that the variation in moisture contents of different erosion trays was not caused by treatment effects (P = 0.18). Therefore, these differences did not introduce any bias into the final analysis of treatment effects on the hydrology of the erosion trays.

Microbial analyses

The soil surface layers for both the ‘with UV-A’ and ‘restricted-UV’ treatments were differentiated from other soil depths in Principal Component 1 (PC1; Figure 2a). The PLFA 16:0 accounted for much of the discrimination seen in PC1 between these two soil depths. The PLFA 18:1ω9c was also responsible for much of the discrimination seen between depths in PC1 as well as in PC2. The subsurface layer of the ‘with UV-A’ treatment was significantly different from all other treatments and depths. The PLFA 18:2ω6 was primarily responsible for much of the discrimination seen in the ‘with UV-A’ subsurface layer (Figure 2b).

Significant differences were found between light treatments with respect to fungal to bacterial PLFA biomarker ratios (P < 0.01; Figure 3). The only treatment that showed significant differences between depths was the restricted-UV treatment, which supported a significantly greater fungal to bacterial ratio in the subsurface layer when compared with the subsurface layer (P = 0.02; Figure 3). No significant difference was found in relation to fungal to bacterial ratios with regard to the interaction between treatment and depth (P = 0.15; Figure 3). There was no significant difference between depths in the ‘with UV-A’ treatment, and both depths had a significantly larger ratio of fungal to bacterial
Figure 2 Effect of different wavelengths of light upon phenotypic community structure of surface- and near-surface soil. (a) First and second principal component (PC) plots derived from PLFA profiles originating from surface layers of erosion trays from all treatments. Points show means (n = 3), bars show standard error. Percentage variation accounted for by PC is shown in parenthesis on each axis. Mean depth of each sample (mm) is denoted by numerals within symbols. One of the values for the surface layer of the restricted-UV treatment was excluded from the principal component analysis as an outlier because of contamination in the chromatogram. For this reason the two remaining values have been plotted individually instead of as a mean. (b) Loading plots with those PLFAs contributing most to the variance seen in the PC plots shown as filled symbols and named.
biomarkers when compared with the other treatments, except for the restricted-UV surface treatment \((P < 0.01; \text{Figure 3})\). For the restricted-PAR and no-light treatment, there were no significant differences in the fungal to bacterial PLFA biomarker ratio at either depth \((P = 0.4; \text{Figure 3})\).

There were no significant differences in chlorophyll \(a\) concentrations between the light treatments \((P = 0.08; \text{data not shown})\). There was also no significant difference between depths \((P = 0.3)\) or in the interactions between depth and treatment \((P = 0.8)\). However, there were significant differences in ergosterol concentration between treatments \((P < 0.01)\), between depths \((P = 0.02)\) and in the interactions between treatments and depths \((P < 0.01; \text{Figure 4})\). The ergosterol concentrations in the no-light treatment were significantly greater than for the other treatments at both investigated depths \((P < 0.01; \text{Figure 4})\). The mean ergosterol concentration in the no-light, subsurface samples was also significantly greater than that observed in the no-light, surface samples \((P < 0.01; \text{Figure 4})\). No other significant differences were found between light treatments at the two depths. Ergosterol concentrations were greatest in the no-light treatment (Figure 4).

**Simulated rainfall experiment**

The difference in run-off generated from the erosion trays was found to be marginally significant between treatments \((P = 0.07)\). A post hoc analysis showed that significantly more run-off was generated from the erosion trays in the no-light treatment when compared with the restricted-PAR treatment \((P = 0.01; \text{Figure 5})\). No significant differences were found in the amount of run-off generated by the other three treatments \((P > 0.05; \text{Figure 5})\). There were no significant differences in infiltrate from the erosion trays under the different light treatments \((P = 0.48; \text{data not shown})\). There were also no significant differences in either soil loss from the erosion trays under the four different light treatments \((P = 0.86; \text{Figure 5})\) or the sediment concentration in the run-off generated by the erosion trays under each light treatment \((P = 0.53; \text{Figure 5})\).

There was no significant interaction (factorial ANOVA) between light treatment and the particle size distribution of the sediment from the run-off \((P = 0.4; \text{Figure 6})\). However, a much greater variability was seen in the particle size distribution of the eroded soil in the restricted-UV treatment when compared with the other treatments. This was especially true for the silt fraction, where there was a five-fold increase in the variation compared with the other treatments.

Analysis via nested ANOVA with a post hoc LSD test found that the shear strength at the soil surface of the no-light treatment was significantly larger than in the other light treatments \((P < 0.01; \text{Figure 7})\). No statistically significant difference could be observed between the other three light treatments \((P > 0.05; \text{Figure 7})\).

**Discussion**

The different light treatments were sufficient to drive the formation of different microbial community phenotypes at the surface of the
Effects of microbial phenotype on surface soil physics

Figure 5 The effect of different wavelengths of light on the hydrology and erodibility of soil from erosion trays as analysed by (a) amount of run-off generated, (b) soil losses and (c) sediment concentrations in run-off. Simulated rainfall was applied for 20 minutes at a rate of 60 mm hour$^{-1}$. The slope gradient was $9^\circ$ ($n=5$; bars show standard error).

This result is not in agreement with the ergosterol data shown in Figure 5, which showed the total fungal biomass to be greatest in the no-light treatment. This apparent discrepancy in the results may be because of an overall reduction in microbial biomass in the ‘with UV-A’ treatment. This allowed for the fungal portion of the microbial community to be relatively large when compared with other treatments, even though the total fungal biomass was smaller than in other treatments. The total fungal biomass in the ‘with UV-A’ treatment was not significantly different from the restricted-PAR and restricted-UV treatments (Figure 5). This implies that, whilst UV reduces the microbial biomass in the soil surface layers, fungi may better withstand the effects of the UV and so become relatively dominant within the soil surface microbial communities.

As the same homogenized soil was used to pack the erosion trays, and differences in other variables such as watering regime were minimized, any differences that became apparent upon statistical analysis of either soil surface shear strength or hydrological properties must have resulted from differences in the soil surface microbial communities. This is because, as previously mentioned, while there was some variation between initial soil moisture contents of erosion trays, this did not vary significantly between treatments, and so while it is possible that this difference increased the variability of the results, post-analysis, it is not possible that it introduced a bias into the results leading to a Type 1 error.

Microorganisms are known to produce a wide variety of extracellular exudates, many of which are hydrophobic, including various polysaccharides and glycoproteins (Medows et al., 1994; McKenna-Neuman et al., 1996; Wright & Anderson, 2000). Any difference in the composition of hydrophobic extracellular exudates as a result of different microbial community phenotypes within the soil surface may affect the soil surface’s hydrological properties (White et al., 2006). It is also possible that changes in the physical nature of the soil surface (e.g. changes in soil porosity) occurred under the influence of the microbial communities. For example, Falchini et al. (1996) reported that the presence of cyanobacteria protected porosity from the damaging effects of water. Fungal hyphae are also thought to physically bind soil particles together (Trsdall, 1991; Medows et al., 1994).

While there were significant differences in run-off generated from the soil surfaces exposed to the different light treatments, there was no significant difference in the amount of infiltrate collected from each treatment. In terms of a simple water balance, this implies that more water must be stored within the soil matrix of those treatments with less run-off (i.e. their water holding capacities were increased). Larger amounts of run-off were generated by the no-light treatment and less water would have entered the soil matrix of this treatment. However, as there was no significant difference with regard to amount of water infiltration between treatments, less water must have remained in the pores of the soil of the no-light treatment (i.e. it had a reduced water holding capacity). Because the soil was homogenized and the same packing density was used for all erosion trays, this reduced water-holding capacity must have been an effect of the microbial community of the no-light treatment.

Changes in water-holding capacity between treatments possibly occurred because of changes in the pore structure of the soil as a...
result of biological activity. An increase in the proportion of larger pores would make the soil less able to hold water at lower tensions (Brady, 1990). Alternatively, differences in the make-up of extracellular exudates may have occurred, specifically differences in the ratio of hydrophobic to hydrophilic compounds within the pore structure, because this could potentially affect both the hydraulic conductivity and water-holding capacity of the soil (White et al., 2006; Urbanek et al., 2007). An increase in the proportion of hydrophobic compounds would mean that water would generally be flushed more easily through the pore network, decreasing the water holding capacity of the soil. The decrease in water-holding capacity in soil under the no-light treatment may have occurred for either of these reasons, or a combination of the two. Further work to analyse the organic compounds within the soil pore space and the porosity and pore-size distribution would need to be carried out to investigate the principal causes of the observed effects.

Another factor that may have influenced the infiltration of water through the soil in each microcosm is the presence or absence of areas of preferential flow (Flury & Flühler, 1994). For example, variation in the initial packing of the erosion trays may have led to localized variability in bulk density within each erosion tray, which could affect water flow. However, the packing methodology used should have minimized this effect and as the erosion trays were randomly assigned to treatments, the effects of any differences in packing on treatment effects would have been homogenized and have only affected the error term in the ANOVA.

Biological activity has been shown to affect the pore structure of soils over time-scales of a few weeks (Feeney et al., 2006). As light has been shown to affect the communities only within approximately the top millimetre of the soil, it is possible that different community effects, not dependent on the light treatments, may have occurred in the deeper soil levels. These may then have affected soil infiltration rates and water holding capacities in a way not directly dependent on the light treatment. The relatively large variance within treatments as shown by the standard error bars in Figure 5 implies that variation in the soil hydrological properties between replicates within treatments did occur, probably because of the above-mentioned factors.

No differences were observed in either the amount of soil eroded, the sediment concentration in the run-off, or the particle-size distribution of the eroded sediment from the erosion trays. This implies that the different soil-surface microbial phenotypes resulting from the different light treatments did not affect the soil surface’s structural integrity as influenced by particle detachment by rainfall. This result disagrees with other results concerning microbiotic crusts, which have shown repeatedly that, in arid systems at least, microbiotic crusts increase soil surface stability and reduce erodibility (Loope & Gifford, 1972; Johansen, 1993; Knapen et al., 2007). However, microbiotic crusts take many years to reach maturity, where they achieve their full effects on soil erodibility (St. Clair & Johansen, 1993), and they form under very different conditions to the temperate arable soils used in our experiment. It may be that the soil-surface microbial communities in this experiment would change further as they matured, into communities that may affect the erodibility of the soil surface. However, arable systems are generally not left undisturbed for
extended periods, so it is unlikely that sufficient time would be available in arable systems for surface communities to mature any further than those used in this experiment.

Nisha et al. (2007) reported that cyanobacteria can have a significant impact on the soil surface by improving the structural stability of the surface in organically-poor soils. This may also be true for soils that have more organic matter, such as that used in this study, although further work is required to test this hypothesis. Chlorophyll a levels were very small compared with those reported by Jeffery et al. (2009). This is possibly because photoautotrophs come from an aerial source and so were unable to reach the soil surface because they were obstructed by the light filters and frames. Again, further work is required to test whether increased levels of photoautotrophs in the soil surface layers in arable systems would affect the erodibility of the soil surface.

The sediment collected from the run-off from all treatments had a tendency to contain a greater proportion of silt than was recorded for the in situ soil (Figure 7). This is in accordance with the erosion literature, which shows that the silt fraction is the most susceptible to detachment and transport, as it has less cohesion than the clay fraction and a relatively low mass compared with the sand fraction (Hjulstrom, 1935; Poesen, 1985). The restricted-UV treatment showed the greatest variation between replicates and appeared to be subject to greater loss of silt by the run-off. However, these data were highly variable between replicates and, consequently, differences were not statistically significant.

The erosion trays were oven-dried in order to encourage surface crust formation from any seals that had been formed by raindrop impact. It was hypothesized that soil-surface shear strength would then give an indication of crust formation because of the increased dry bulk density of crusts increasing shear strength (Brady, 1990; Zhang et al., 2001). Crust formation occurs as a result of the destruction and dispersal of soil-surface aggregates, which are then deposited over the soil surface (Brady, 1990). Soil aggregates can disintegrate during the process of slaking (where air within the pore spaces of an aggregate is pressurized by the rapid dissipation of water through the aggregate; Morgan, 1995). It would therefore be expected that soils with a relatively large fungal biomass would have an increase in aggregate stability and hence a reduction in aggregate breakdown from raindrop impact and slaking. This would therefore mean less seal and physical crust formation. This is because fungi normally function to bind soil aggregates together (Tisdall, 1991).

Soil shear strength was significantly greater in the no-light treatment when compared with the other treatments. Ergosterol concentrations were positively correlated with shear strength across treatments ($r^2 = 0.49$ for the surface layer and $r^2 = 0.75$ for the subsurface layer). This is likely to be a result of hyphal enmeshment as discussed above and adhesion arising from fungal metabolites (Wright et al., 1999; Wright & Anderson, 2000) and is suggestive of the increased shear strength being the result of changes in fungal abundance as opposed to a physical soil crust formation. However, with the methods used in this study, it was not possible to distinguish whether the increased fungal biomass was in the form of hyphal fungi, which can physically bind soil aggregates, or yeasts, which cannot. As such, it is not possible to conclude whether the increased shear strength of the no-light treatment was a result of increased bulk density as a result of the formation of a physical crust, or was a result of a form of biological crust where the fungi were binding the soil particles together, so increasing the soil shear strength.

Fungal biomass has previously been shown to be greater in the soil surface layers, as fungi grow preferentially over surfaces compared with through the pore space (Otten & Gilligan, 1998). In our experiment, there was a general trend for the largest concentration of ergosterol to come from the soil surface layers, except for the no-light treatment, although the differences were not statistically significant.

The fungal biomass was greatest in the no-light treatment, and within the no-light treatment, greatest in the subsurface layer. This demonstrates that changes in community structure occur when light is removed from the soil surface, favouring the growth of fungi. It is possible that the development of some elements of the microbial community that would compete with fungi was restricted by the removal of light (e.g. photoautotrophs), or the removal of photoautotrophs from the system by the elimination of light may have reduced an antibiosis effect occurring between the photoautotrophs and the fungi. Alternatively, it may be that the fungal proportion of the soil surface microbial community is better adapted to growing in the dark. Further work would need to be undertaken to discover the mechanism(s) that led to this result.

The data collected from the PLFA analysis agree with Jeffery et al. (2009) and provide further evidence that light, and specifically PAR, is an important driving factor responsible for the development of distinct soil-surface microbial community phenotypes and this in turn can affect soil hydrological and physical properties.

Conclusions

Altering the incident wavelength of light changes the community level microbial phenotype at the soil surface. These differences are manifest in different quantities of photoautotroph and fungi within the soil-surface communities brought about by the influence of differences in wavelength of light on the soil-surface community. These differences in soil surface microbial community are capable of inducing changes in the soil surface structural and hydrological properties and processes. These changes included a marginally significant effect on run-off generation, and increased shear strength, implying seal generation, both occurring in the no-light treatment. Whilst some of the mechanisms of these effects remain unclear, functional consequences of surface microbial communities were apparent and demonstrate that the microbiota can have consequential effects upon soil physical and hydrological properties in arable systems.
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