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The interaction of soil phototrophs and fungi with pH and their impact on soil CO_2, $CO^{18}O$ and OCS exchange

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ABSTRACT

The stable oxygen isotope composition of atmospheric CO_2 and the mixing ratio of carbonyl sulphide (OCS) are potential tracers of biospheric CO_2 fluxes at large scales. However, the use of these tracers hinges on our ability to understand and better predict the activity of the enzyme carbonic anhydrase (CA) in different soil microbial groups, including phototrophs. Because different classes of the CA family (α, β and γ) may have different affinities to CO_2 and OCS and their expression should also vary between different microbial groups, differences in the community structure could impact the 'community-integrated' CA activity differently for CO_2 and OCS. Four soils of different pH were incubated in the dark or with a diurnal cycle for forty days to vary the abundance of native phototrophs. Fluxes of CO_2, $CO^{18}O$ and OCS were measured to estimate CA activity alongside the abundance of bacteria, fungi and phototrophs. The abundance of soil phototrophs increased most at higher soil pH. In the light, the strength of the soil CO_2 sink and the CA-driven CO_2-H_2O isotopic exchange rates correlated with phototrophs abundance. OCS uptake rates were attributed to fungi whose abundance was positively enhanced in alkaline soils but only in the presence of increased phototrophs. Our findings demonstrate that soil-atmosphere CO_2, OCS and $CO^{18}O$ fluxes are strongly regulated by the microbial community structure in response to changes in soil pH and light availability and supports the idea that different members of the microbial community express different classes of CA, with different affinities to CO_2 and OCS.

1. Introduction

Changes in climate and land use could lead to a rapid release of terrestrial carbon (C) to the atmosphere in the near future, that may create a positive feedback of uncertain magnitude (Carvalhais et al., 2014; Heimann and Reichstein, 2008). In order to constrain some of the uncertainties surrounding the fate of the C sink provided by the terrestrial biosphere, it is necessary to improve the representation of soil processes in land surface models. For this the C cycle research community is developing novel tools and independent tracers that will enable the detection of changes in carbon emissions and soil community function at large scales.

The oxygen stable isotope composition of atmospheric CO_2 ($\delta^{18}O_a$) is one such tracer of biosphere fluxes at large scales (Cuntz, 2003; Francey and Tans, 1987; Welp et al., 2011; Wingate et al., 2009). This is because soil and leaf water pools carry very different isotopic compositions that are transferred to CO_2 fluxes during leaf photosynthesis and soil respiration under the action of a family of enzymes called carbonic anhydrase (CA), ubiquitous in plants and soil micro-organisms (Badger, 2003; Moroney et al., 2001; Smith and Ferry, 2000). However, the partitioning of leaf and soil CO_2 fluxes using $\delta^{18}O_a$ hinges on our understanding of how CA activity varies in different members of the soil community and across the land surface (Welp et al., 2011; Wingate et al., 2009). Wingate et al. (2009) demonstrated that the CA-catalysed oxygen isotope exchange rate in soils from different biomes was between 20 and 300 times faster than the un-catalysed rate. These rates of soil CA activity have recently been supported by another study modelling the hydrolysis of carbonyl sulphide (OCS) by CA and the net exchange of OCS between different soil types and the

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atmosphere (Ogée et al., 2016). This is an important and promising finding as OCS has emerged recently as another independent and promising tracer of gross CO_2 fluxes at large scales (Campbell et al., 2008; Montzka et al., 2004; Sandoval-Soto et al., 2005). However, it still remains unclear whether the diversity of CAs present in soils has an impact on the soil CA activity for OCS and CO_2, and to the same extent for both tracers. For example the dominant CAs in bacteria and fungi are those from the β class (Elleuche and Poggeler, 2010; Smith and Ferry, 2000; Smith et al., 1999) whilst algae and cyanobacteria express both α-CAs on their periplasmic membranes (Moroney et al., 2001) and β-CAs in their cytoplasm, chloroplasts and mitochondria. Furthermore, these different classes of CA can have different affinities to the substrates CO_2 and OCS (Haritos and Dojchinov, 2005; Kamezaki et al., 2016; Ogawa et al., 2013; Ogée et al., 2016) that may or may not change with soil pH (Notni et al., 2007; Rowlett et al., 2002). So far very little work has explored how the soil community structure influences the soil CA activity for OCS and CO_2.

Li et al. (2005) and subsequently Wingate et al. (2009) hypothesised that spatial variability in CA activity for CO_2 could be caused either by variations in the intrinsic activity of certain soil microbial groups and/or linked to shifts in soil community structure between biomes. In particular, soil eukaryote algae are generally much larger organisms (100 μm^3) than bacteria (1 μm^3) and are likely to contain higher concentrations of both intra- and extra-cellular CA (Coleman et al., 1984; Hopkinson et al., 2013; Moroney et al., 2001; Palmqvist and Badger, 1996; Sültemeyer, 1998). Algae are also most abundant at the soil surface (Bristol-Roach, 1927; John, 1942; Metting, 1981) where rapid equilibration of $\delta^{18}O_a$ with soil water also occurs (Wingate et al., 2010, 2009, 2008). On the other hand, the number of algae (10^6 g^{-1} dry soil) found at the soil surface is still generally out-numbered by bacterial and to a lesser extent fungal populations (typically 10^9 g^{-1} dry soil). In addition, soil pH is an important controlling factor of the abundance and diversity of algal (Lund, 1947; Shields and Durrell, 1964; Stokes, 1940), bacterial (Fierer and Jackson, 2006; Griffiths et al., 2011; Lauber et al., 2009) and fungal (Rousk et al., 2010; Tedersoo et al., 2014) communities, thus the variations in CA activity observed by Li et al. (2005) and Wingate et al. (2009) may also partially reflect pH-driven variations in the relative abundance of microbial groups at the soil surface as well as the activity of CA.

Irrespective of their role in the $\delta^{18}O_a$ signal, photoautotrophic micro-organisms (*i.e.* algae and cyanobacteria referred to hereon as phototrophs) are important players in the C and nitrogen (N) cycles, especially in dryland ecosystems (Belnap and Lange, 2003; Bowker et al., 2010; Castillo-Monroy et al., 2011). A number of studies focused on biological and microbiological soil crusts have pinpointed key roles of fungi and cyanobacteria in their function (Lan et al., 2015; Maestre et al., 2010). However there are very few studies that have investigated all of the photosynthetic micro-organisms present in soil biocrusts (*i.e.* cyanobacteria and algae, Schmidt et al., 2011) at the same time as bacteria and/or fungi (Bates and Garcia-Pichel, 2009; Lee et al., 2012; Nagy et al., 2005). This is also a similar situation for studies on temperate agricultural soils where there is a growing body of literature on fungal and bacterial community interactions but far fewer studies investigating the role of eukaryotic algae, despite evidence for their colonis on agricultural soil surfaces (Metting, 1981; Zancan et al., 2006). For example, it has been known for some time that variations in the abundance of phototrophs in soils can set-up 'ecological ripples' by improving soil fertility and crop productivity (Evans and Johansen, 1999; Shields and Durrell, 1964) at the same time as contributing an important functional role to the sequestration of soil C and N at the global scale (Castillo-Monroy et al., 2011; Elbert et al., 2012).

A number of recent studies have also indicated that soils from a range of biomes are capable of fixing CO_2 at different depths in the soil profile (Goyal, 1997; Hart et al., 2013; Nowak et al., 2015; Šantrůčková et al., 2005; Yuan et al., 2012). So far the attribution of CO_2 fixation in soils by phototrophic organisms is currently supported by observed changes in the abundance of marker genes encoding for RuBISCO (Nowak et al., 2015) but heterotrophic CO_2 fixation by bacteria and algae may also occur (Šantrůčková et al., 2005). Indeed complex relationships between phototrophs and other microbial partners often arise as phototrophs can excrete a large variety of substances including enzymes, organic acids and polysaccharides (Metting, 1981) into their surroundings that allow bacterial and fungal partners to grow. Phototrophs also contribute to the initiation of microbial mats that develop over time by recruiting other microbial partners (Flemming et al., 2016; Konopka et al., 2015; Thompson et al., 2015). However, as far as we are aware, no study to date has determined how changes in the net soil CO_2 efflux and other GHG tracers such as OCS are regulated by changes in the abundance of phototrophic (algae and cyanobacteria) and heterotrophic (bacteria and fungi) microbial groups in natural soils varying in pH. This is mainly because the tools to address these functional relationships are generally time-consuming (dilution counts) or indirect (pigment analysis). Furthermore, assessment of the soil photosynthetic microbial community often requires the implementation of different molecular tools (Schmidt et al., 2011). Consequently, soil microbial ecology often overlooks the entire phototrophic microbial community, despite growing evidence of their important ecological role in gas exchange, soil fertility and soil aggregation.

In this context we set out to investigate how the contribution of soil phototrophs and heterotrophs impacted the net exchange of atmospheric CO_2 and OCS with soils. We questioned how changes in the abundance of microbial groups altered the CA activity of soils for both tracers, and how changes in the soil community structure and function would be altered by soil pH. In particular, we set out to test the hypotheses that increasing soil pH would favour the development of soil phototrophs and that, as the abundance of phototrophs increased in soils, the sink strength for CO_2 and OCS as well as the associated CA activities would also increase. However, we hypothesised that the behaviour of the two trace gases across all soil types would diverge between light and dark periods as emissions of CO_2 would increase in the dark because of an increase in respiratory metabolism, whilst OCS exchange rates would remain unchanged as CA is considered to be a light-independent enzyme (Gimeno et al., 2017; Protoschill-Krebs et al., 1996).

2. Material and methods

2.1. Soil sampling and conditioning

Four soils were sampled from different field sites ensuring a wide range of pH values (4.6–8.1) (Table 1). According to the FAO World Reference Base for soil classification (IUSS Working Group WRB, 2006), Le Bray (LB) is a podzol with an organic, sandy A horizon sampled from a coniferous forest located 20 km from Bordeaux during February 2016. Lacage (LG) is a luvisol with a silty loam A horizon sampled from an INRA experimental field growing a wheat-alfalfa rotation located in Versailles during April 2016. Pierrelaye (DBZ) is a luvisol with a sandy A horizon sampled from an INRA experimental field growing a corn-wheat rotation located 30 km from Paris during December 2015. Finally Toulenne (TL) is a fluviosol sampled from an INRA experimental orchard growing cherry and peach trees located 50 km from Bordeaux during February 2016.

At each location three spatially-independent soil samples were

Table 1
Main characteristics of the different soils used for the study.

	Le Bray (LB)	La Cage (LG)	Pierrelaye (DBZ)	Toulenne (TL)
Land use	pine plantation	cropland	cropland	cropland
pH	4.6	6.3	7.0	8.1
Sand content (g kg^{-1})	947	184	822	167
Silt content (g kg^{-1})	26	647	87	523
Clay content (g kg^{-1})	27	169	91	310
C/N ratio	26.0	10.4	13.9	10.4

taken from the surface horizon 0–10 cm. Composite soil samples for each location were sieved with a 5 mm mesh and mixed to reconstitute one homogenised soil sample. For each soil the maximum water holding capacity (WHC) was estimated on three replicates following the method of Haney and Haney (2010). Thereafter for each soil, six microcosms were prepared, consisting of 350–400 g of fresh soil re-packed in a 0.825 dm^3 glass jar. Each soil was then weighed and maintained at 80% of its maximum WHC to encourage the development of native soil phototrophs. Each microcosm was sealed with Parafilm M© to minimise evaporation, and incubated in a climate-controlled room at 20 °C for forty days. At the start of the incubation three of the six microcosms were coated with aluminium foil (Dark Conditioning or DC) to inhibit the development of phototrophic organisms whilst the other three microcosms were conditioned under a day/night cycle (Light Conditioning or LC) consisting of a 16 h light/8 h dark photoperiod using LED lighting with an intensity of about 500 μmol(photons) m^{-2} s^{-1} in the visible range to promote the growth of the native phototrophic flora (Fig. 1). During the incubation period the jars were periodically opened two times a week to refresh the air in the microcosm headspace.

2.2. Gas exchange experimental setup

After forty days, the aluminium covers were removed from the three dark conditioned microcosms and a self-contained thermocouple datalogger (iButton, DS1923, Embedded Data Systems, Lawrenceburg, KY, US) was positioned at the top of each soil column to measure the humidity and temperature at the soil surface. Each microcosm was then sealed with a customised glass lid fitted with two stainless steel Swagelok® bulkhead fittings connected to 0.25 inch (3.175 mm) Teflon™ inlet and outlet lines to form a flow-through gas exchange chamber. The six soil microcosms were then placed in a customised climate-control chamber (MD1400, Snijders, Tillburg, NL) to acclimate at 25 °C with the lights on. An additional soil-free glass jar containing an iButton was also sealed and connected to a set of lines in the climate-control chamber in order to check that our setup was free of any OCS contamination.

During the gas exchange measurements, air was supplied to each of the microcosms using a compressor (FM2 Atlas Copto, Nacka, Sweden), coupled to a chemical scrub column (Ecodry K-MT6, Parker Hannifin, Cleveland, OH, US) that first removed water vapour, CO_2 and OCS from ambient air in the lab. Concentrations in the scrubbed airstream were typically less than 5 μmol(CO_2) mol^{-1}, 7 pmol(OCS) mol^{-1} and -40 °C dew point. A set of individual mass flow controllers (MFC, EL-Flow® Select, Bronkhorst, Ruurlo, NL) and stainless steel cylinders containing either pure CO_2 or CO_2-free dry air with 500 nmol(OCS) mol^{-1} (Linde, France) were then used to supply CO_2 and OCS to the air stream in a 4L aluminium buffer and reach concentrations around 420 μmol(CO_2) mol^{-1} (420 ppm) and 1000 pmol(OCS) mol^{-1} (1000 ppt). The (dry) air supplied to the inlet of each microcosm was taken from this buffer volume at a flow rate of 0.25 dm^3 min^{-1} (Fig. S1). The flow from the buffer volume to the microcosms was driven by a slight overpressure in the buffer of 20–30 mbar above atmosphere. Within a single flux measurement, the standard deviation on the inlet was less than 0.03 ppm(CO_2) and 1.5 ppt(OCS).

2.3. CO_2 mixing ratio and stable isotopes measurements (TDLAS)

The airstreams for a given microcosm were selected for CO_2 measurements by means of an 8-way solenoid (BX 758.8E1C312, 0–4 bar, Matrix, Italy). The airstream passed through a Nafion dryer (MD-40 Perma pure Inc., NJ, USA) before being analysed for its $^{12}C^{16}O_2$, $^{13}C^{16}O_2$ and $^{12}C^{18}O^{16}O$ concentrations (TGA100A, Campbell Scientific Inc., Logan Utah, USA). Laser emission on the absorption lines was maintained using a reference gas of 25% CO_2-in-air (Linde, France). Flow through the instrument was maintained with a diaphragm vacuum pump (KNF N940, Neuberger, UK Ltd, UK) connected to the TGA100A *via* a vacuum line and excess air was exhausted to the atmosphere (Fig. S1). Calibration was performed every 16 min using 3 aluminium calibration tanks containing CO_2-in-air (Deuste-Steininger, Germany) spanning a CO_2 concentration range (374.9 ± 1.9, 474.6 ± 2.4 and 687.1 ± 4.0 ppm) and similar $\delta^{18}O$ values (−14.68 ± 0.01, −14.70 ± 0.03 and −14.68 ± 0.03‰ VPDB-CO_2). Calibration tank gas was precisely characterised at the MPI for Biogeochemistry (Jena, Germany). A series of Allan variances indicated a standard deviation of 0.1 μmol(CO_2) mol^{-1} and 0.3‰ for $\delta^{13}C$ and $\delta^{18}O$ after 10s of averaging time. Calibration tank measurements were linearly interpolated in time and a calibration regression was performed as described in Wingate et al. (2010).

2.4. OCS mixing ratio measurements (QCLS)

Microcosm airstreams were selected for OCS measurements by means of a 12-way rotary valve (EUTA-SD16WE VICI® 16 positions two way valve, Valco Instruments Co. Inc, Texas, USA). The airstream was pre-dried with a Nafion™ drier (MD-070-24-S-2, Perma Pure LLC, NJ, USA) before being measured (QCLS, Aerodyne Research Inc. Billerica, MA, USA). Flow was maintained with a TriScroll 600 pump (Agilent Technolgies, Santa Clara, CA, USA) connected to the QCLS *via* a vacuum line and excess air was exhausted to atmosphere. Instrument drift was corrected with frequent (every 16 min) background calibrations (with dry N_2) in all runs. After 12 min of measurements, a 4-min, two-point standard calibration was also implemented using the same dry N_2 bottle and compressed dry air from an Aculife®-treated cylinder with a known OCS concentration (524.8 ± 2.2 ppt) prepared and calibrated for OCS by the NOAA Global Monitoring Division. An Allan variance calculated from a 24 h continuous measurement on tank air indicated a standard deviation of 2.1 ppt(OCS) after 10 s averaging time.

2.5. Sampling sequence

Microcosm airstreams and calibration tanks were scanned at 1 Hz over 2 min and the last 20s used to compute the mean concentrations. In a sequence, seven chambers (the six soil-filled microcosms and a blank chamber) were scanned sequentially by the

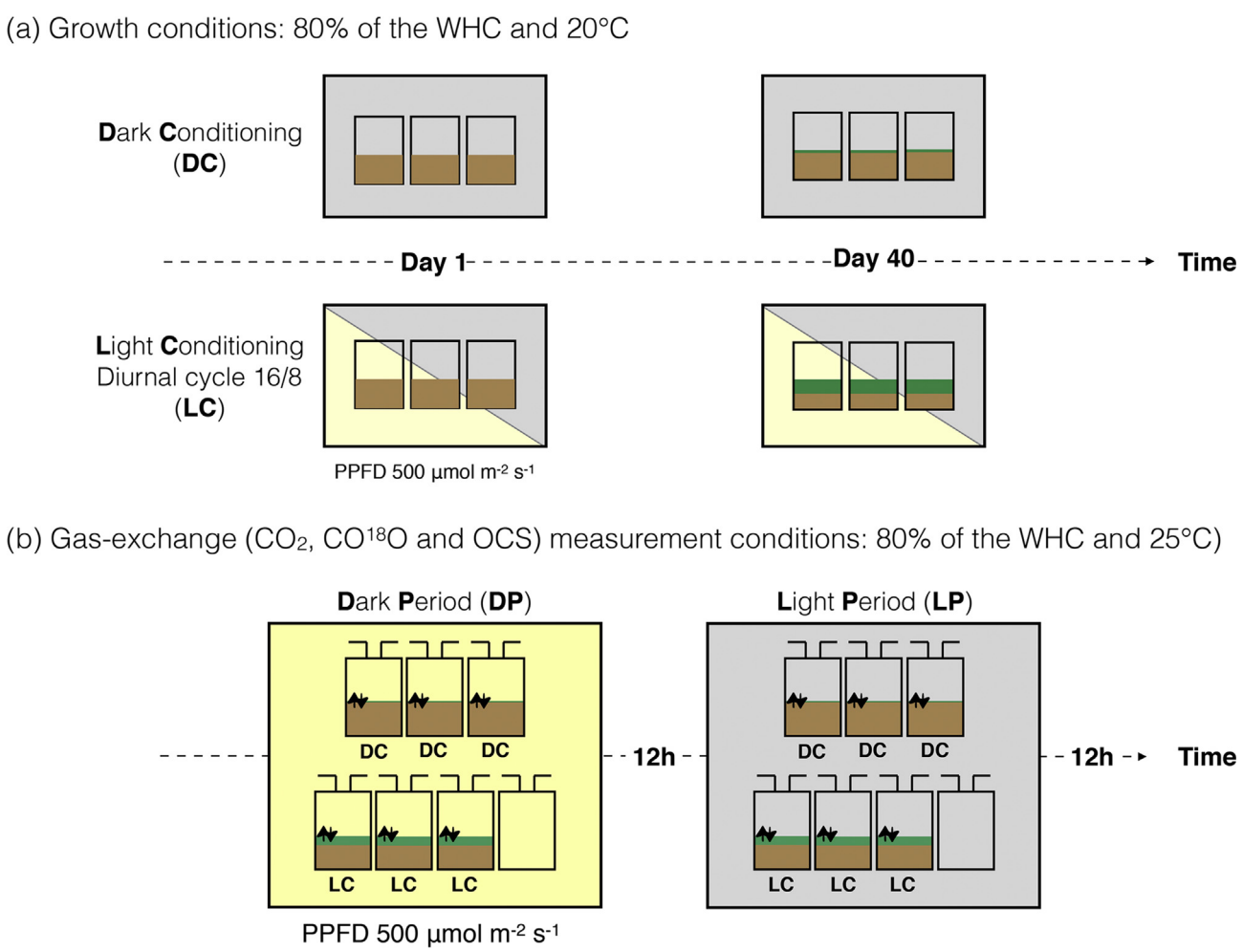

Fig. 1. Diagram illustrating the two-incubation treatments (applied from day 1 to day 40) and the two measurement treatments applied during the following 24 h of gas exchange measurements of the six microcosms from a given soil. DC: Dark Conditioning, LC: light conditioning, DP: dark period, LP: light period, WHC: water holding capacity, PPFD: photosynthetic photon flux density.

OCS and CO_2 isotope analysers and, when not measured, were continuously flushed at the same constant flow rate. The full sequence of gas exchange measurements lasted 24 h and combined light (LP) and dark (DP) periods and two different inlet CO_2 isotopic compositions (using two different pure CO_2 bottles, see Fig. S1). The first 12hrs of gas exchange were completed with the lights on (LP) providing a light intensity of 500 µmol(photons) m^{-2} s^{-1} in the visible range (Fig. 1). The subsequent 12hrs of gas exchange were then completed in the dark (DP).

2.6. Calculating fluxes and CA activity

The OCS and CO_2 fluxes were computed assuming steady-state conditions:

$$F = \frac{u_{in}}{S}(c_{out} - c_{in}) \quad (1)$$

where u_{in} is the flow rate of dry air through the chamber (mol s^{-1}), S is the soil surface (m^2) and c_{in} and c_{out} are the mixing ratios of OCS or total CO_2 (mol mol^{-1}) in the air entering and leaving the chamber respectively. Because these mixing ratios were determined on a dry air basis (because of Nafion dryer upstream of each analyser) only the flow of dry air on the inlet of the chamber was needed. For each microcosm, the three replicates of inlet/outlet pairs gave three individual values of the OCS and CO_2 fluxes from which a mean and standard deviation could be computed. The mean OCS flux from the blank (empty) chamber was always not significantly different from zero (Fig. S2), indicating that our experimental setup was free of any OCS contamination.

Under steady-state conditions, the fluxes of $^{12}C^{16}O_2$ (^{16}F) and $^{12}CO^{18}O$ (^{18}F) can also be computed using Eq. (1), and the oxygen isotopic signature of the soil CO_2 flux ($^{18}\delta_F = 0.5\,^{18}F/^{16}F/R_{std}$ - 1, expressed relative to the isotope ratio R_{std} of the VPDB-CO_2 standard) can thus be calculated from the $^{12}C^{16}O_2$ mixing ratios and $\delta^{18}O$ of the inlet ($^{16}c_{in}$, $^{18}\delta_{in}$) and outlet ($^{16}c_{out}$, $^{18}\delta_{out}$) air:

$$^{18}\delta_F = \frac{^{16}C_{out}\,^{18}\delta_{out} - {}^{16}C_{in}\,^{18}\delta_{in}}{^{16}C_{out} - {}^{16}C_{in}} \quad (2)$$

For each steady state three replicates of the inlet and outlet were obtained leading to three individual values of $^{18}\delta_F$ from which a mean and standard deviation could be computed.

Soil carbonic anhydrase activity was then calculated, either in the form of OCS hydrolysis rate (k_h) or CO_2-H_2O isotopic exchange rate (k_{iso}). The OCS hydrolysis rate k_h was estimated following Ogée et al. (2016). According to their Eq. (16b), and assuming no OCS source from the soil microcosm, the OCS flux F_S estimated with Eq. (1) is directly related to k_h:

$$F_s = \sqrt{k_h B_s \theta D_s} C_s \tanh\left(\frac{z_s}{2z_{max}}\right) \quad (3)$$

where B_S, D_S, C_S represent respectively the OCS solubility in soil water (m^3 $m\text{-}^{-3}$), the OCS effective diffusivity through the soil column (m^2 s^{-1}) and the gaseous OCS concentration at the soil-air interface (mol m^{-3}), z_{max} is maximum soil depth and z_S is a characteristic depth above which diffusion of OCS out of the soil becomes faster than OCS hydrolysis: $z_s = (D_s/k_h\ B_s\ \theta)^{1/2}$ (Ogée et al., 2016). The solubility B_S is only a function of temperature while D_S is a function of temperature, soil moisture and porosity, and the formulation of Moldrup et al. (2003) for repacked soils was used. Assuming well-mixed conditions in the chamber we have $C_s = c_{out}\ p/8.31441/T$ where p (Pa) and T (K) are the air pressure and temperature inside the headspace. Equation (3) was then solved iteratively for the OCS hydrolysis rate k_h.

Using a similar approach as in Tans (1998) or Wingate et al. (2010) but accounting for the finite depth z_{max} of our soil microcosms, we were also able to relate the CO_2-H_2O isotopic exchange rate k_{iso} (s^{-1}) to $^{18}\delta_F$:

$$^{18}\delta_F = \delta_{eq} + \varepsilon_D\left(1 - \frac{z_c}{z_{max}}\tanh\left(\frac{z_{max}}{z_c}\right)\right) + \frac{k_{iso} B_c \theta D_c C_c}{F_c}(\delta_{eq} - \delta_a)\tanh\left(\frac{z_{max}}{z_c}\right) \quad (4)$$

where B_C, D_C, C_C, F_C and z_C are the counterparts of B_S, D_S, C_S, F_S and z_S for CO_2, δ_a is the $\delta^{18}O$ of CO_2 at the soil-air interface (assumed equal to $^{18}\delta_{out}$) and δ_{eq} is the CO_2 isotopic composition of CO_2 in equilibrium with soil water. The latter was measured after each gas exchange measurement (see below) so that Eq. (4) could be solved iteratively to retrieve k_{iso} from $^{18}\delta_F$ measurements. Note that Eq. (4) is not strictly valid in our case because it assumes uniformity of CO_2 production, soil moisture, porosity, temperature, k_{iso} and δ_{eq} throughout the soil column, and no CO_2 consumption. Care was taken to homogenise the soil microcosms prior to their incubation and to maintain a constant soil water content during the incubation but the day/night cycle imposed on half of them helped developed soil phototrophs at the soil surface that clearly challenged the validity of Eq. (4). Theoretically we could account for their presence and derive another equation but, in practice, this would introduce extra parameters that would be difficult to estimate. We thus preferred to use Eq. (4) for all our microcosms and the retrieved k_{iso} will be considered below as an apparent CO_2-H_2O isotopic exchange rate, related to some extent to soil CA activity for CO_2.

2.7. Soil community analyses

Immediately after gas exchange measurements, material from the soil surface (0–2 cm) was sampled from each microcosm and stored in the dark at −80 °C before being freeze-dried. Microbial DNA was extracted from 1 g of soil from each triplicate microcosm of each treatment as previously described (Plassart et al., 2012; Terrat et al., 2012). DNA concentrations of crude extracts were determined by electrophoresis in a 1% agarose gel using a calf thymus DNA standard curve, and used as estimates of microbial molecular biomass (Dequiedt et al., 2011). After quantification, DNA was purified using a PVPP column (Sigma Aldrich, Saint-Louis, USA) and GENECLEAN turbo kit (MpBIO, Illkirch, France). Bacterial, fungal and phototroph (algae and cyanobacteria) abundances were estimated using the number of copies measured for 16S-, 18S- and plastidial 23S-rDNA genes, respectively, by qPCR using a StepOne® Real-Time PCR System (Applied Biosystems, Courtaboeuf, France) with a SYBRGreen® detection system and primer sets defined previously (Chemidlin Prévost-Bouré et al., 2011; Plassart et al., 2012; Sherwood and Presting, 2007).

2.8. Soil water oxygen isotope composition

Immediately after the gas exchange measurements material from different soil depths (0–2, 2–4 and 4–6 cm depth) was sampled from each microcosm and stored at 5 °C before cryogenic vacuum distillation. Distilled waters were then analysed for $\delta^{18}O$ composition (LWIA-45EP, Los Gatos Research Inc., San Jose, California, USA).

2.9. Statistical analyses

All statistical analyses were performed with the R software package (R3.1.3, R Core Team, 2015). Mixed effect linear models (lme in nlme package, Pinheiro et al., 2015) allowed to assess how soil conditioning (DC or LC) and physicochemical properties (texture and pH) influenced the bacterial, fungal and phototroph abundances. Soil conditioning (DC or LC) and measurement type (DP or LP), soil type (LB, LG, DBZ, TL) and their interactions were taken as fixed effects and replicates as a random effect. Mixed effects linear models were also used to test whether the CO_2 and OCS fluxes as well as their associated CA activity (k_{iso} and k_h) were related to the abundance of photosynthetic microorganisms.

3. Results

3.1. Effect of conditioning on the abundances of microbial groups

The development of green mats in the microcosms incubated under a diurnal cycle (LC treatment) were observed by the naked eye after forty days on three of our soils (LG, DBZ and TL), but not on the most acidic soil (LB) or any soil that had been incubated in the dark (DC treatment). The qualitative indications of the visual observations were supported by the qPCR data (Fig. 2). An overall increase in the number of 23S rDNA gene copies, a proxy for the abundance of photosynthetic microorganisms, was found in all the LC-incubated microcosms relative to the DC-incubated microcosms, but not significantly in the most acidic soil (LB). The largest increases in phototrophs abundance were observed on the high pH soils (DBZ and TL), whereas the smallest change in abundance occurred on the acidic, and less green, soil (LB). In all soils where phototrophs abundance increased significantly (*i.e.* all soils except LB), an increase in the number of bacterial and fungal gene copies was also found using LME analysis, indicating that the LC treatment also promoted bacterial and fungal growth (Fig. 2). Interestingly, although increases in bacterial and fungal gene copies were also observed with LC in these soils, there was an overall shift in the community structure, with phototroph gene copies increasing in relative abundance to the bacterial and fungal members (Fig. 2). Such a shift was also found in the LB soil, because of a decrease of bacterial and fungal gene copies induced by the LC treatment (Fig. 2).

The number of fungal gene copies was always relatively smaller than the phototroph and bacterial gene copies across all soil treatments (Fig. 2). In soils conditioned in the dark (DC treatment), the highest abundance of fungal gene copies was found in the most acidic soil, but the trend was opposite in soils conditioned to a day-night cycle (LC treatment). However, in terms of relative abundance their overall contribution within the community generally decreased with the LC treatment (Fig. 2).

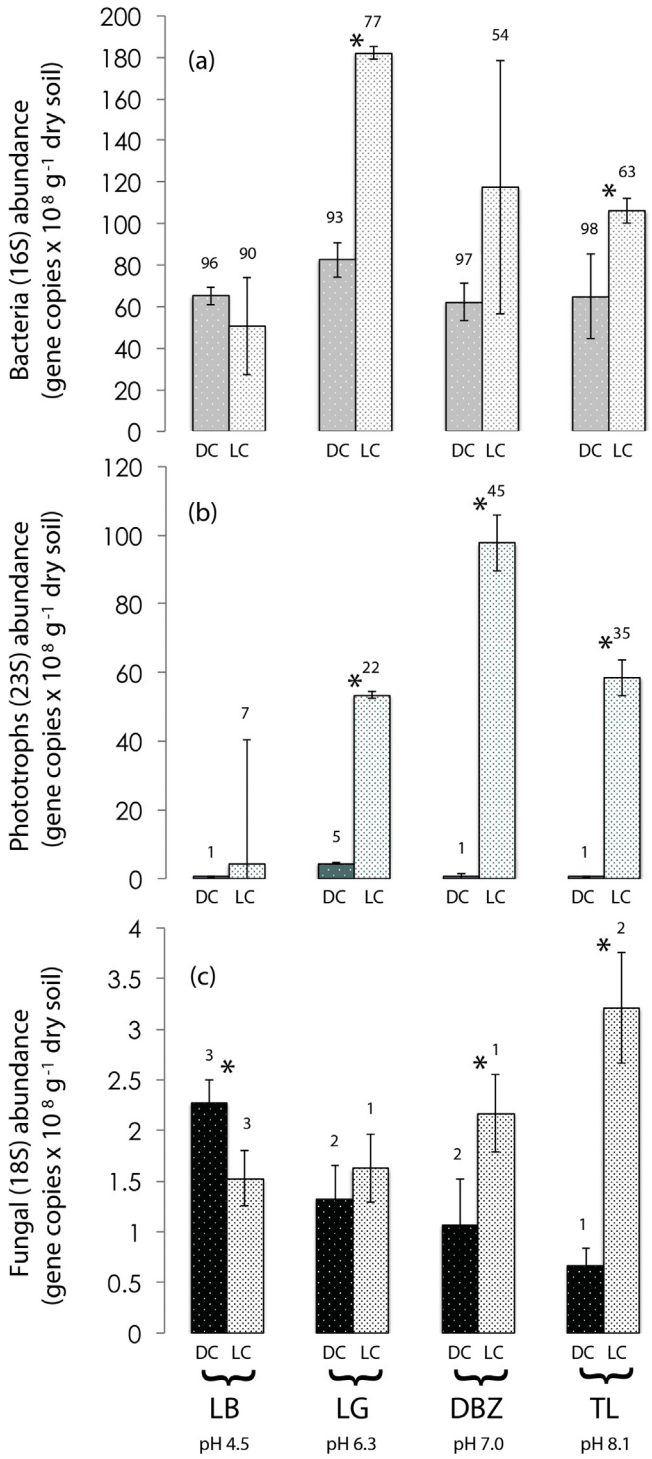

Fig. 2. Relative number of bacterial (16S), fungal (18S) and phototroph (23S) gene copies (±SD, n = 3) for the four soils (LB, LG, DBZ & TL) incubated in the dark (DC) and light (LC) after 40 days. Asterisks indicate soils incubation treatment (DC/LC) effect were significant ($p < 0.01$). Numbers above each bar plot indicate the relative abundance of the given microbial group in the given soil.

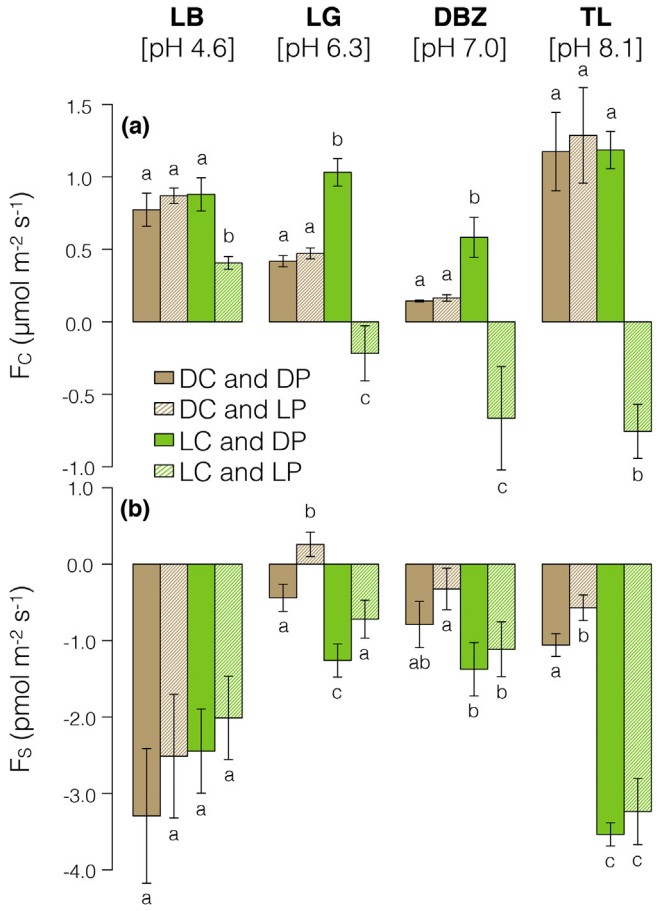

Fig. 3. Mean variations (±SD, n = 3) in the net soil (a) CO_2 and (b) OCS fluxes for four different soils measured in the light (LP) and the dark (DP) after incubation for 40 days in the light (LC) or the dark (DC). a, b and c indicate significant effects of both treatment within soils ($p < 0.05$).

3.2. CO_2 flux

In all soils that had been conditioned to darkness (DC treatment) there was no significant change in net observed CO_2 fluxes with light availability (Fig. 3a, compare DC-DP and DC-LP). In addition, these dark-conditioned soils were always a source of CO_2 to the atmosphere irrespective of whether they were measured in the light or in the dark. In contrast, the net CO_2 fluxes from soil microcosms conditioned to a day-night cycle (LC treatment) always differed significantly between the dark and light measurement periods, with reduced CO_2 emissions to the atmosphere or even CO_2 uptake in the light (Fig. 3a, compare LC-DP and LC-LP). The strength of this light response, characterised by the difference in the net CO_2 fluxes measured between light and dark periods ($\Delta F_{C,light-dark}$), partly reflected the changes in the abundance of 23S gene copies g^{-1} of dry soil in the LC treatments (Fig. 2) but was best captured by differences in soil pH, with the largest light response occurring in the most alkaline soil (Fig. 4a).

Dark respiration rates from LC-incubated soils were generally the same or larger than DC-incubated soils (Fig. 3a, compare LC-DP and DC-DP). This difference was qualitatively reflected by the changes in the number of phototroph, fungal and bacterial gene copies caused by the conditioning treatment (Fig. 2), except in the most alkaline soil where the increase in gene copies did not translate into larger dark respiration rates.

3.3. OCS flux

Nearly all soil types and treatments were sinks for OCS (Fig. 3b). Only the dark conditioned soil from Lacage (LG) emitted OCS to the atmosphere when measured in the light. In both the DC- and LC-incubated soils there was an overall trend for the net OCS flux to

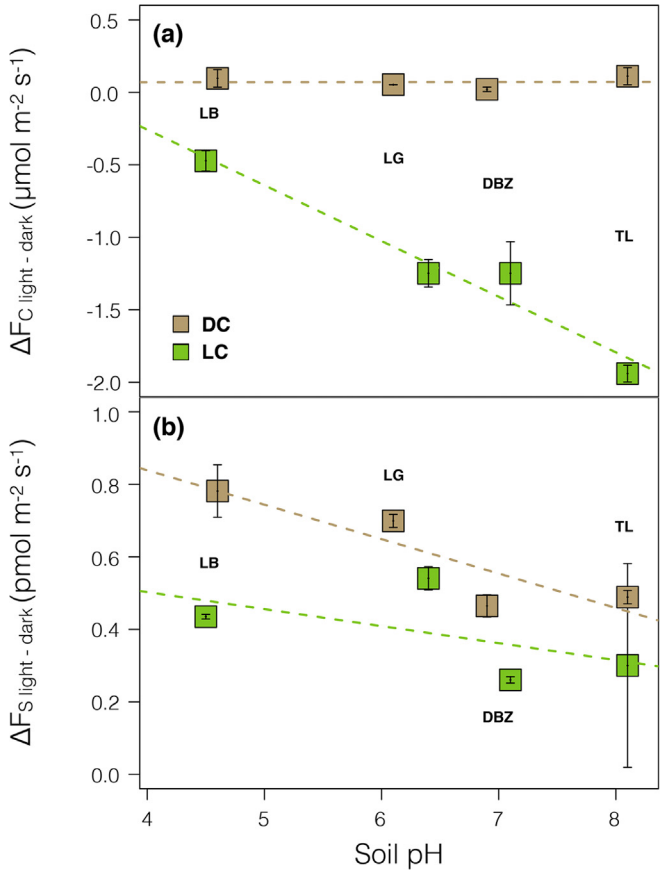

Fig. 4. Mean differences (±SD, n = 3) in the net soil (a) CO_2 and (b) OCS fluxes measured during the light (LP) and the dark (DP) period for four soils of different pH incubated in the light (LC) or the dark (DC) for ~40 days.

decrease when measured in light and thus become a weaker OCS sink (Fig. 3b). However, this difference in sink strength ($\Delta F_{S,light-dark}$) was not statistically significant from zero for the majority of soils (Fig. 4b).

Apart from the most acidic soil (LB), the effect of the incubation treatment was statistically significant, with light-conditioned soil microcosms acting as larger OCS sinks than dark-conditioned ones (Fig. 3b). This effect of the incubation treatment on the soil OCS fluxes seems to follow changes in the number of fungal gene copies between the two treatments (Fig. 2).

3.4. Relationship between fluxes and CA activity

To assess more quantitatively the link between soil microbial groups and gas exchange rates, we performed different tests on the DC- and LC-incubated datasets. We found that the net soil CO_2 flux was only correlated with the number of phototroph gene copies g^{-1} of dry soil and only during the light measurement periods (Fig. 5c). This correlation was negative and consistent with an increase in light-induced CO_2 uptake from the atmosphere as the number of phototroph gene copies increased. In contrast, we found that the net soil OCS flux was only correlated with the number of soil fungal 18S gene copies g^{-1} of dry soil with almost similar responses between light and dark measurements (Fig. 5e). Thus although the number of fungal gene copies was extremely low compared with either the bacterial or phototroph gene copies, even a small increase in the number of fungal gene copies within the community significantly increased the OCS sink strength.

Estimations of microcosm carbonic anhydrase activity were made using either the enzyme-catalysed rate of CO_2-H_2O isotope exchange (k_{iso}) or the enzyme-catalysed OCS hydrolysis rate (k_h). Generally we found that k_{iso} varied between 0.01 and 0.75 s^{-1}, and was higher in the LC treatments compared to DC treatment (Fig. 6a), although not significantly on the acidic soil (LB) that exhibited very little difference in phototroph abundance (Fig. 5a). We also found that k_{iso} was positively correlated to the abundance of soil phototroph gene copies irrespective of the measurement period (LP or DP) (Fig. 6a). The shift in k_{iso} between DC and LC treatments on the different soils was however more directly related to differences in soil pH than algal and cyanobacterial DNA counts (Fig. 6b), with a clear monotonic increase of k_{iso} in LC treatments with more alkaline conditions. Estimated k_h varied between 0.002 and 0.028 s^{-1} and was positively correlated to fungal abundance across all soil treatments, but not other variables such as phototroph or bacterial counts or soil pH. As a consequence, and contrary to what we expected, no significant relationship was found between k_{iso} and k_h in this dataset.

4. Discussion

4.1. Light and pH as drivers of soil community structure

Major progress has been made describing how bacterial and fungal abundance and diversity varies with pH, land management and climate (Dequiedt et al., 2011; Griffiths et al., 2011; Lauber et al., 2008; Leff et al., 2015; Tedersoo et al., 2014) using a suite of novel molecular techniques (Bardgett & Van Der Putten, 2014). In contrast, these advances have not been widely implemented to characterise variations in soil phototroph communities, and as far as we are aware, no study using molecular tools has been used to explore the interactions of both the bacterial (16S) and eukaryotic algal (23S) phototroph communities alongside heterotrophic microbial groups in soils. Most studies to date, especially those focussing on dryland ecosystems and biocrusts, have tended to focus efforts on characterising the diversity and abundance of bacterial members of the biocrusts, notably the contribution of cyanobacteria (Couradeau et al., 2016; Steven et al., 2012, 2013, 2015a) and fungal communities (Bates et al., 2010; Steven et al., 2014, 2015b; Xiao and Veste, 2017) using 16S and 18S qPCR approaches. In addition, a combination of 16S and 18S genes have previously been used with other tools such as microscopy to assess algal diversity in high elevation and high-latitude drylands (Schmidt et al., 2011). However, most other studies on the ecology of soil algae and bacteria have used manual and time-consuming approaches such as soil slurry dilutions combined with identification and count techniques (Lund, 1947; Shields and Durrell, 1964; Stokes, 1940; Zancan et al., 2006). Nonetheless, from these early studies it was shown that the number of soil algae varies strongly with soil pH (Lukešová and Hoffmann, 1996; Lund, 1947; Metting, 1981; Shields and Durrell, 1964; Starks and Shubert, 1982; Stokes, 1940) and that the presence of soil algae could even change soil pH (Budel et al., 2004). These findings are consistent with the results of our study using a novel 23S approach on soils showing that phototroph abundance increased positively on alkaline soils when incubated in the light and at optimum water content.

Previous studies have also shown that the growth of soil algal populations is often accompanied by increases in bacterial populations (Ramanan et al., 2016; Stokes, 1940). In the case of our study if we infer that changes in the number of 16S and 23S gene copies represent a proxy for putative changes in the size of the respective communities we can also infer a similar pattern. In our study this might be partially explained by an increase in the cyanobacterial community in response to light and pH. For example,

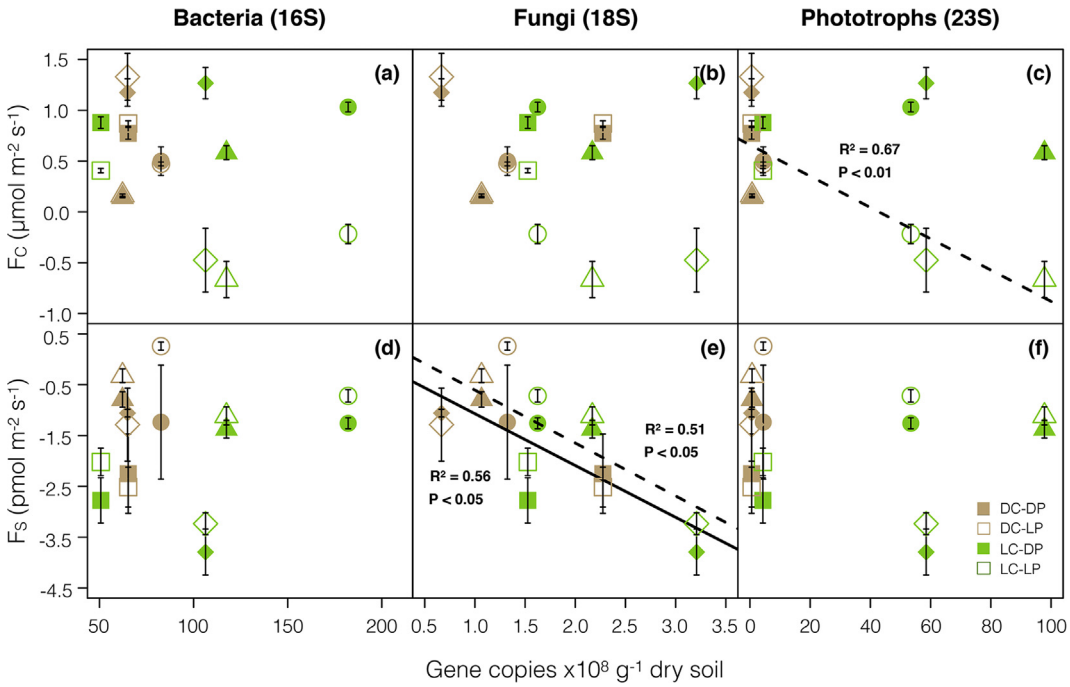

Fig. 5. Relationship between the net soil CO_2 and OCS fluxes for four soils (LB: squares, LG: circles, DBZ: triangles, TL: diamonds) as a function of the number of gene copies per gram of dry soil for bacteria (16S), fungi (18S) and phototrophs (23S) measured in the light (LP) and the dark (DP) after incubation for ~40 days in the light (LC) or the dark (DC). Significant linear model results are also displayed (solid lines for dark periods and dashed lines for light periods).

previous studies have shown that alkaline soils tend to promote the development of diatom and cyanobacterial species whilst acidic soils tend to favour green alga species from the chlorophyta (Metting, 1981; Shields and Durrell, 1964; Starks and Shubert, 1982). It has also been hypothesised that the development of algal communities may also be tracked by an increase in the number of nitrogen-fixing bacteria such as the *Azotobacter* (Stokes, 1940; Reay, 2015). These bacteria have evolved to grow rapidly in aerobic conditions and fix nitrogen from the atmosphere at optimal pH values of 7–7.5 (Garrity et al., 2005). It is also widely known that many soil microbes benefit from the soluble organic compounds secreted into the soil by phototrophs (Brock and Clyne, 1984; Cole et al., 1982; Larsson and Hagström, 1982). Indeed, the number of fungal gene copies was also positively related with the number of phototroph gene copies and pH but only in the light conditioned treatments. In contrast, microcosms incubated in the dark showed a decrease in fungal gene copies with increasing pH, demonstrating that a strong positive interaction between phototrophs and fungal communities exists. This is in some respects consistent with other studies that have found variations in fungal gene copies and diversity with pH (Tedersoo et al., 2014), and with other study findings that plant community composition (Leff et al., 2015) or soil C:N ratios (Lauber et al., 2008) may be better predictors of fungal community composition than pH. Our results indicate that the relationships between different members of the microbial groups and pH may be conditional on the presence of certain phototrophs. Investigating these differences in community member interactions were beyond the scope of our present study. However, on-going development of our molecular method should enable us to explore and better understand these finer scale relationships within the soil community groups in the near future.

4.2. The influence of soil community structure on CO_2 uptake

Most soils in the world emit CO_2 to the atmosphere (Bond-Lamberty and Thomson, 2010; Raich and Schlesinger, 1992). However, there are a number of studies showing that some alkaline soils act as sinks for CO_2 (Elbert et al., 2012; Jasoni et al., 2005; Schlesinger et al., 2009; Wohlfahrt et al., 2008). This is typically explained by abiotic mechanisms such as thermally-induced pressure pumping or carbonate dissolution and CO_2 transport to groundwater (Schlesinger et al., 2009; Schlesinger, 2017). Recent studies have also shown that the process of carbonate formation is often microbially-induced and linked to CA activity (Benzerara et al., 2014; Couradeau et al., 2012; Kupriyanova et al., 2007; Li et al., 2005; Thaler et al., 2017), highlighting the potential of microbial communities in calcareous soils to enhance CO_2 uptake. Our study demonstrated that soil phototrophs have the potential to respond rapidly to seasonal changes in light. It also highlighted that the extent of the community response to light is strongly controlled by soil pH as discussed above. We showed that an increase in the putative abundance of native phototrophs has the potential to rapidly convert soils from being a net source to becoming a net sink of CO_2 during daylight hours. However, we also observed that soils containing more 23S gene copies generally respired more CO_2 than dark-conditioned soils during the dark period. Thus, on balance over a 24hr period with a 12 h/12 h day/night cycle, most soils (with the exception of DBZ at pH 7) remained a net source of CO_2 to the atmosphere.

Interestingly it is worth noting that variations in the putative abundance of soil phototrophs may introduce noise in diurnal and seasonal measurements of soil CO_2 respiration. For example, an important parameter in land surface models is the Q_{10} that describes how the sensitivity of the soil CO_2 efflux is driven by soil temperature (Lloyd and Taylor, 1994; Mahecha et al., 2010). There is a general tendency to have a higher Q_{10} in winter than in summer and macro-molecular rate theory has been evoked to help explain this pattern (Alster et al., 2016; Schipper et al., 2014). However, the presence of phototrophs could also lower estimates of Q_{10} by reducing the CO_2 efflux during the day when temperatures are high

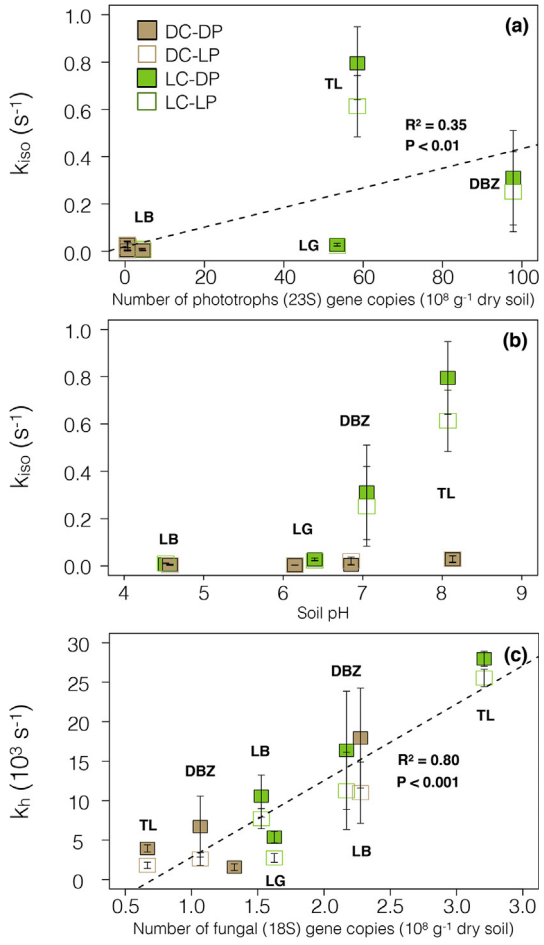

Fig. 6. Significant relationship found between CA-catalysed activity and (a) the number of phototroph gene copies per gram of dry soil using the oxygen isotopic exchange, (b) soil pH also using the oxygen isotopic exchange and (c) the number of fungal gene copies per gram of dry soil using the OCS hydrolysis rates for the four different soils measured in the light (open symbols; LP) and the dark (close symbols; DP) after ~40 days of incubation in the dark (brown symbols; DC) or the light (green symbols; LC). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and increasing it at night when temperatures are lower. Future studies exploring the link between phototroph abundance for different biomes and soil CO_2 efflux could help explain some of the emergent patterns observed in key C cycle model parameters and improve our ability to predict how they interplay with climate, soil and vegetation composition.

4.3. The influence of soil pH and community structure on CA activity

The enzyme carbonic anhydrase catalyses both the reversible hydration of CO_2 and the irreversible hydrolysis of OCS in algae (Gries et al., 1994; Protoschill-Krebs and Kesselmeier, 1992), bacteria (Kamezaki et al., 2016; Kesselmeier et al., 1999; Ogawa et al., 2013) and fungi (Elleuche and Poggeler, 2010; Masaki et al., 2016). The activity of this enzyme is essential for the homeostatic regulation of intra-cellular pH in organisms (Smith and Ferry, 2000). Most organisms strive to maintain a physiologically optimal pH of around 7 (Krulwich et al., 2011). However many organisms and indeed many bacterial and fungal genus have developed metabolic traits for surviving in extreme acidic and alkaline environments (Hesse et al., 2002; Krulwich et al., 2011; Mortensen et al., 2008; Slonczewski et al., 2009), and the enzyme CA seems to play a central role in this survival. The results from our study confirmed that soil pH not only had a strong influence on the putative abundance of phototrophs but also on the strength of the photosynthetic CO_2 sink and associated CA activity (k_{iso}). This result was unsurprising as it is well known that unicellular green algae, such *as Chlamydomonas,* typically exhibit CA activities as high as those found in animals or higher plants and can express different classes of CA in a range of organelles including the periplasmic membrane (Moroney et al., 2001; Palmqvist and Badger, 1996). It has also been shown for β-CA, the most abundant class of CA in soil bacteria and fungi, that the catalysed CO_2 hydration is maximal in the pH range above 8 (Rowlett et al., 2002).

More surprisingly our CA activity estimates for CO_2 and OCS did not co-vary between the different light treatments. The rate of enzyme-catalysed OCS hydrolysis (k_h) was surprisingly not significantly related to the putative abundance of phototrophs or soil pH but was only explained by changes in the number of fungal gene copies (Fig. 6c). This was even more surprising given that the relative number of fungal gene copies to the total number of gene copies g^{-1} of soil was so small (Fig. 2), especially if we consider that the genomes of some fungal species can have several copies of the 18S operon (Fournier et al., 1986; Garber et al., 1988; Herrera et al., 2009; Howlett et al., 1997) potentially indicating that our 18S inferred estimates of putative fungal abundance could be overestimated. Most fungi, including the Basidiomycetes and Hemiascomycetes, contain only β-CAs, although some filamentous Ascomycetes and 'basal fungi' such as the Chytridiomycota, and Blastocladiomycota, also contain genes for encoding α-CAs (Elleuche and Poggeler, 2010; Elleuche, 2011). In contrast, all three classes of CA seem rather common in bacteria (Smith et al., 1999) and algae (Moroney et al., 2001), although α-CA seem more abundant in algae whilst γ-CA are often found in bacteria. Thus a relative increase in fungal populations could be accompanied by a relative increase in β-CA expression. Little is currently known about the affinity of these different CA classes to OCS but a few studies seem to indicate that β-CAs have a much higher affinity to OCS than α-CA, leading to OCS hydrolysis rates up to 1000 times faster (Haritos & Dojchinov, 2005; Ogawa et al., 2013, 2016; Ogée et al., 2016). If γ-CAs have a similar affinity to OCS as α-CAs, then OCS uptake by soils should be mostly responsive to changes in β-CA expression. This may indicate that the relationship we found between k_h and the number of fungal gene copies is possibly dominated by the expression of β-CAs in fungi. This would be consistent with a recent study on forest soil fungal isolates that demonstrated that a number of species exhibited a strong uptake of OCS (Masaki et al., 2016). These species included *Scytalidium* sp. THIF03, *Trichoderma* spp. THIF08, THIF17, THIF21, THIF23 and THIF26 with *Trichoderma* species known to contain only β-CAs (Elleuche and Poggeler, 2010). Next generation sequencing (NGS) on our experimental soils will allow us to investigate whether changes in OCS flux can be associated to changes in the presence of these key fungal OCS degraders.

Alternatively, changes in OCS flux could have also been driven by a shift in the community structure towards fungal species that emit OCS, such as *Umbelopsis* and *Mortierella* spp. THIF09 and THIF13 (Masaki et al., 2016), especially in soils with a lower number of fungal gene copies. This particular hypothesis should definitely be tested in future studies using NGS. Nonetheless, with our current experimental approach it was clearly demonstrated, that when light and moisture were not limiting, phototrophs bloomed. This increase in phototroph gene copies also caused fungal gene copies, and to a lesser extent, bacterial gene copies to increase at the same time leading to a greater OCS uptake rate (and an exactly opposite response in the most acidic soil). Thus the presence of the

phototrophs conferred some benefit to the fungal population in non-acidic soils. This may have resulted either from the transfer (or leakage) of organic compounds to the fungi in a manner similar to the situation in lichens or by constituting prey to the fungi. For example many fungi in the *Chytridiomycota* are parasites of algae and are known to contain two β-CAs and one α-CA in secretions (Elleuche, 2011), that could putatively hydrolyse OCS. This hypothesis should also be tested in the future using NGS. This would help characterise the importance of OCS consuming and producing metabolic pathways in soil organisms and improve our ability to model the exchange of OCS from soils at larger scales.

5. Conclusion

Using molecular tools our study could reveal the interplay between soil pH and light in determining changes in the relative abundance of soil algal, bacterial and fungal gene copies. This additional information helped us interpret the fluxes of two key tracers in the global C cycle. Interestingly, our study showed for the first time that the magnitude of each of these fluxes was regulated differently. Soil pH and phototroph gene copies strongly drove the soil CO_2 efflux as well as the CO_2-H_2O isotopic exchange rate, emphasising the need to account for the variability of these environmental parameters to correctly use stable oxygen isotopes as a proxy of biospheric CO_2 fluxes. Our study also showed that changes in fungal gene copies exhibited a strong relationship with the rate of net OCS exchange. Finally our study demonstrates that, by combining such molecular tools with soil gas exchange measurements, it will soon be possible to assess the impact of both prokaryote and eukaryote phototroph activity and diversity on the ability to sequester C, N and S in soils and predict how soil community structure regulates CO_2 and OCS soil-atmosphere exchange.

Author contributions

JS, PAM, OC, JO and LW conceived and designed the experiment. JS, SW and SJ designed and conducted the gas-exchange and water isotope measurements. PAM, OC and VN designed and made the qPCR database and analysis. JS, JO, PAM, OC, AK and LW analysed the data. JS, LW JO and OC wrote the manuscript. All authors commented and contributed to the final version.

Competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.09.009.

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