The ISME Journal (2012) 6, 1558–1565

www.nature.com/ismej

ORIGINAL ARTICLE

Temperature responses of carbon monoxide and hydrogen uptake by vegetated and unvegetated volcanic cinders

Caitlin E King and Gary M King
Department of Biological Sciences, Louisiana State University, 202 Life Sciences Building, Baton Rouge, LA, USA

Ecosystem succession on a large deposit of volcanic cinders emplaced on Kilauea Volcano in 1959 has resulted in a mosaic of closed-canopy forested patches and contiguous unvegetated patches. Unvegetated and unshaded surface cinders (Bare) experience substantial diurnal temperature oscillations ranging from moderate (16 °C) to extreme (55 °C) conditions. The surface material of adjacent vegetated patches (Canopy) experiences much smaller fluctuations (14–25 °C) due to shading. To determine whether surface material from these sites showed adaptations by carbon monoxide (CO) and hydrogen (H_2) consumption to changes in ambient temperature regimes accompanying succession, we measured responses of CO and H_2 uptake to short-term variations in temperature and long-term incubations at elevated temperature. Based on its broader temperature optimum and lower activation energy, Canopy H_2 uptake was less sensitive than Bare H_2 uptake to temperature changes. In contrast, Bare and Canopy CO uptake responded similarly to temperature during short-term incubations, indicating no differences in temperature sensitivity. However, during extended incubations at 55 °C, CO uptake increased for Canopy but not Bare material, which indicated that the former was capable of thermal adaptation. H_2 uptake for material from both sites was completely inhibited at 55 °C throughout extended incubations. These results indicated that plant development during succession did not elicit differences in short-term temperature responses for Bare and Canopy CO uptake, in spite of previously reported differences in CO oxidizer community composition, and differences in average daily and extreme temperatures. Differences associated with vegetation due to succession did, however, lead to a notable capacity for thermophilic CO uptake by Canopy but not Bare material.
The ISME Journal (2012) **6,** 1558–1565; doi:10.1038/ismej.2011.206; published online 19 January 2012
Subject Category: microbial ecology and functional diversity of natural habitats
Keywords: carbon monoxide; hydrogen; temperature; volcanic; biogeochemistry

Introduction

Bacteria actively consume carbon monoxide (CO) and hydrogen (H_2) in both young, organic matter-poor volcanic deposits and in older, more mature deposits with well-developed plant communities (King, 2003a; King and Weber, 2008). Although changes in uptake rates and in the significance of the atmosphere as sources of these gases during ecosystem succession have been addressed previously (King, 2003a; King and Weber, 2008), specific responses of CO and H_2 uptake to environmental variables that change during succession, for example, organic carbon, soil texture, pH, and temperature, have not been documented (Weber and King, 2009). More generally, the responses of CO and H_2 uptake by soils to these and other variables have received limited attention, even though it is clear that soils have significant roles in the global budgets of both atmospheric CO and H_2 (Conrad, 1996; King and Weber, 2007).

The study presented here documents responses to temperature of CO and H_2 uptake by unvegetated (Bare) cinders and vegetated (Canopy) material that experience distinctly different temperature regimes due to plant community development during ecosystem succession. The two sites represent 'end members' in a mosaic of plant succession occurring on a single, large cinder deposit emplaced in 1959. Bare surface cinders, which are unshaded and uncolonized by plants, experience dramatic diurnal temperature fluctuations with maxima up to 55 °C. At a contiguous site supporting a closed canopy tree stand, surface material is shaded and experiences only moderate temperature changes (about 15 °C–25 °C). Nonetheless, Bare cinders actively consume atmospheric CO *in situ*, and previous studies have shown that the heated surface material

Correspondence: GM King, Louisiana State University, Department of Biological Sciences, 202 Life Sciences Building, Baton Rouge, LA 70803, USA.
E-mail: gking@lsu.edu
Received 19 September 2011; revised 2 December 2011; accepted 3 December 2011; published online 19 January 2012

(0–2 cm depth) consumes CO more rapidly than cooler sub-surface material (King and Weber, 2008).

Previous molecular ecological analyses have also shown that Bare cinder CO oxidizer communities consist primarily of taxa most closely related to *Ktedonobacteria* (Weber and King, 2010), a group of largely thermophilic or thermotolerant strains isolated from hot compost and geothermally-heated soils (Cavaletti *et al.*, 2006; Stott *et al.*, 2008; Yabe *et al.*, 2010a, b). The presence of *Ktedonobacteria*-like taxa in Bare cinders is consistent with results from Ranneklev and Bååth (2001), which indicate that fluctuating thermal regimes can select for and maintain thermophilic or thermotolerant communities simultaneously with mesophilic communities.

In contrast to Bare cinders, molecular ecological analyses have shown that Canopy surface material is dominated by proteobacterial CO-oxidizers with little or no indication of thermotolerant taxa (Weber and King, 2010). These differences in CO-oxidizer community composition have been attributed to patterns in organic matter accumulation and plant development (Weber and King, 2010), but the presence of *Ktedonobacteria*-like taxa in Bare cinders suggests that temperature regimes might also have a role.

To determine whether CO uptake responded to changes in temperature regimes resulting from the effects (for example, shading) of plant community development during succession, we measured short-term impacts of varied temperatures on uptake rates; we also assessed with an extended incubation (30 days) the capacity for adaption to elevated temperatures (55 °C) that might be favored by thermotolerant or thermophilic taxa maintained by fluctuating temperatures, especially at the Bare site. Although many CO-oxidizers also consume H_2 (Hudson *et al.*, 1988; King, 2003b), and as H_2 uptake by various material on Kilauea volcano has been previously attributed primarily to bacteria (King, 2003a), we also measured responses of H_2 consumption to varied temperature regimes and to an extended incubation at 55 °C.

Materials and methods

Site description

The Pu'u Puai volcanic deposit (GPS coordinates: 19°24′22.5″N × 155°15′18.2″W) in Hawaii National Volcanoes Park (Kilauea Volcano, Hawaii, USA) occurs downwind of an extensive 1959 lava fountain eruption. A mosaic of closed canopy forest patches (>10 m radius) containing *Meterosideros polymorpha* (Ohia lehua) and *Morella faya* (fire tree) is interspersed with unvegetated cinder patches. Canopy site surface material is characterized by an organic-rich peat-like material, while Bare site material consists of organic-poor cinders approximately 1 cm in diameter. Numerous details of this system have been described previously (King, 2003a; King and Weber, 2008; Weber and King, 2009). Temperature regimes for Bare and Canopy sites differ significantly. Unvegetated Bare site cinders experience substantial diurnal oscillations with maxima to 55 °C (average 24.6 ± 0.4), while the Canopy site experiences a more narrow temperature range with maxima up to 25 °C (average 18.1 ± 0.1; Figure 1). Average daily temperatures for surface material (0–2.5 cm) were determined over a 3 day period in August 2008, during which samples were collected using HOBO Data Loggers (Onset Computer Corp., Pocasset, MA, USA) with TMC 20 sensors. Surface temperatures monitored regularly for more than 18 months at both sites show similar results. Differences in temperature reflect the direct insolation received by Bare cinders and the shaded conditions at the Canopy site.

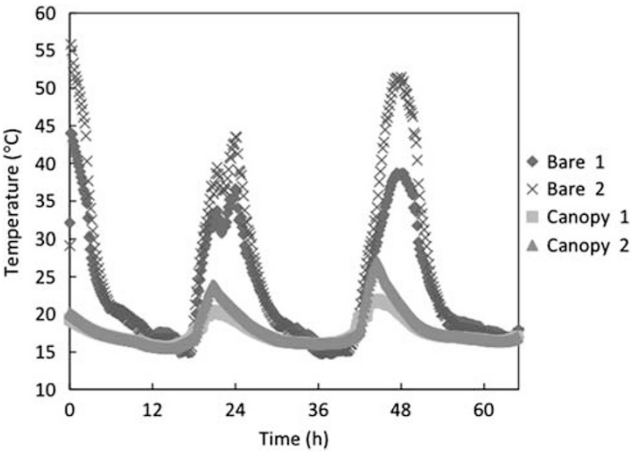

Figure 1 Surface (0–2.5 cm depth interval) temperature profiles of Canopy and Bare sites determined over a 3-day period in August 2008 during which samples were collected.

Sample collection

Bare cinders (0–2 cm depth) and the upper 2 cm of Canopy material beneath the litter layer were collected during August 2008 using ethanol-sterilized trowels and transferred to triplicate freezer storage bags. The samples were shipped to a laboratory at Louisiana State University at ambient temperature and processed upon arrival. Canopy material was homogenized by sifting through a sterile 2-mm sieve to remove fine roots and cinders, which do not contribute significantly to activity. Bare cinders were partially crushed to reduce the size range to about 5 mm. Samples were used immediately or stored in zip-top bags at ambient temperature (about 25 °C) in the dark until use. Material used to assay short-term responses of CO uptake to temperature was stored for 2 days before the analysis. Assays for H_2 uptake and for analysis of responses of CO uptake to long-term elevated temperatures were conducted over a period

of 4–12 weeks; prior observations have indicated that activity remains relatively stable during storage, but some changes in communities might occur.

Gas flux analyses

Maximum potential CO and H_2 uptake rates were determined by adding rate-saturating concentrations of CO and H_2 (100 p.p.m.) to samples in gastight containers (King, 1999b). Headspace sub-samples were obtained at intervals using a sterile needle and syringe and analyzed by gas chromatography (RGA, reduced gas analyzer; Trace Analytical Instruments, Columbia, MD, USA), as described previously (King, 1999b). All assays were conducted in triplicate; rates were expressed per gram dry weight (g.d.w.) of material based on water contents determined by drying samples at 100 °C.

Short-term response of CO and H_2 uptake to temperature

Canopy material (0.5 g.f.w.) and Bare cinders (2 g.f.w.) were transferred into sterile 30 cm^3 tubes that were sealed with neoprene stoppers. Two sets of samples were incubated at temperatures from 5–65 °C (5 °C steps) using custom-built heating blocks. After a 10 min delay for temperature equilibration, gases were added to sample headspaces. CO and H_2 uptake were measured separately using triplicates for each temperature as described above. Sample dry weights were determined after the assays by drying samples overnight at 100 °C.

Response of CO and H_2 uptake to extended incubations at elevated temperature

Canopy material (25 g.f.w.) and Bare cinders (30 g.f.w.) were transferred into sterile 500 cm^3 jars with gastight lids fitted with a neoprene stopper. Triplicate samples with and without addition of a 0.05% yeast extract solution (50 μl [g sample]$^{-1}$) were incubated in the dark at 25 °C and 55 °C, respectively, for 30 days. The yeast extract solution was applied by uniformly distributing small droplets on the samples on day 0 and day 14 of the incubation, then air-drying the samples briefly in a laminar flow hood to maintain the original water contents. Samples were supplemented with yeast extract, as the decrease in readily available carbon at higher temperatures (Bárcenas-Moreno *et al.*, 2009) and the limited carbon availability at the Bare site might have prevented adaptation to elevated temperatures. During the 30 day incubation, a 22-gauge needle fitted with a sterile 25-mm syringe filter (0.22 μm pore size) was inserted through the neoprene stopper of each jar to allow atmospheric gas exchange, while preventing water loss. This vent was removed before uptake assays. Killed controls were created by autoclaving samples for 25 min.

CO and H_2 uptake rates were determined as previously described on day 0, after allowing an initial 25 min temperature equilibration, and on day 30. After the day 30 assay, samples previously incubated at 55 °C were incubated at 25 °C. Following a 1 h equilibration period, CO and H_2 assays were conducted on the samples to determine residual activity at 25 °C. After the assays, samples were dried for 2 days in an oven at 100 °C to determine dry weights.

Differences in net consumption rates among treatments were analyzed using a two-way analysis of variance with a general mixed model with multiple treatments and repeated measures using SAS software 9.2 (SAS Institute, Cary, NC, USA). Means were distinguished by Tukey's honest significant difference test ($\alpha = 0.05$). Differences in net production rates were determined using a two-tailed unpaired *t*-test ($\alpha = 0.05$).

Results

Short-term responses of CO and H_2 uptake to varied temperature

Mean Canopy material CO and H_2 uptake rates were approximately 23-fold and 17-fold greater than Bare cinder rates, respectively, over the temperature ranges examined. Canopy material H_2 uptake rates increased with temperature with a plateau from 30–50 °C followed by a sharp decline in activity at 55 °C (Figure 2a). H_2 uptake by Bare cinders also increased with temperature, rising to a distinct peak or optimum at 35 °C with a small decrease at 40 °C and a sharp decline at 55 °C (Figure 2b). The Canopy material H_2 uptake activation energy determined from an Arrhenius analysis (50.8 kJ mol^{-1}) was considerably lower than that for Bare cinders (82.9 kJ mol^{-1}; Figures 3a and b). CO uptake rates for both sites increased with temperature from 5–35 °C followed by a small decline at 40 °C (Figures 2a and b). At temperatures >45 °C, slight net CO production was observed. Activation energies for CO uptake were similar for Canopy material and Bare cinders (78.9 kJ mol^{-1} and 71.8 kJ mol^{-1}, respectively; Figures 3c and d).

Response of H_2 uptake to extended incubations at elevated temperature

During a 30 day incubation at 25 °C, Canopy material H_2 uptake was unchanged in controls ($P = 0.320$), but decreased significantly ($P = 0.003$) by about 50% in soils amended with yeast extract (Figure 4a). For Bare cinders incubated at 25 °C, H_2 uptake decreased significantly (about 74%; $P < 0.009$) in both untreated and yeast extract-amended samples (Figure 4b). After 30 day incubations at 55 °C, H_2 uptake was completely inhibited for both sites with or without added yeast extract (Figure 4). Neither Bare cinders nor Canopy material previously incubated at 55 °C consumed H_2 during recover assays at 25 °C. There was no evidence for H_2 uptake by killed controls.

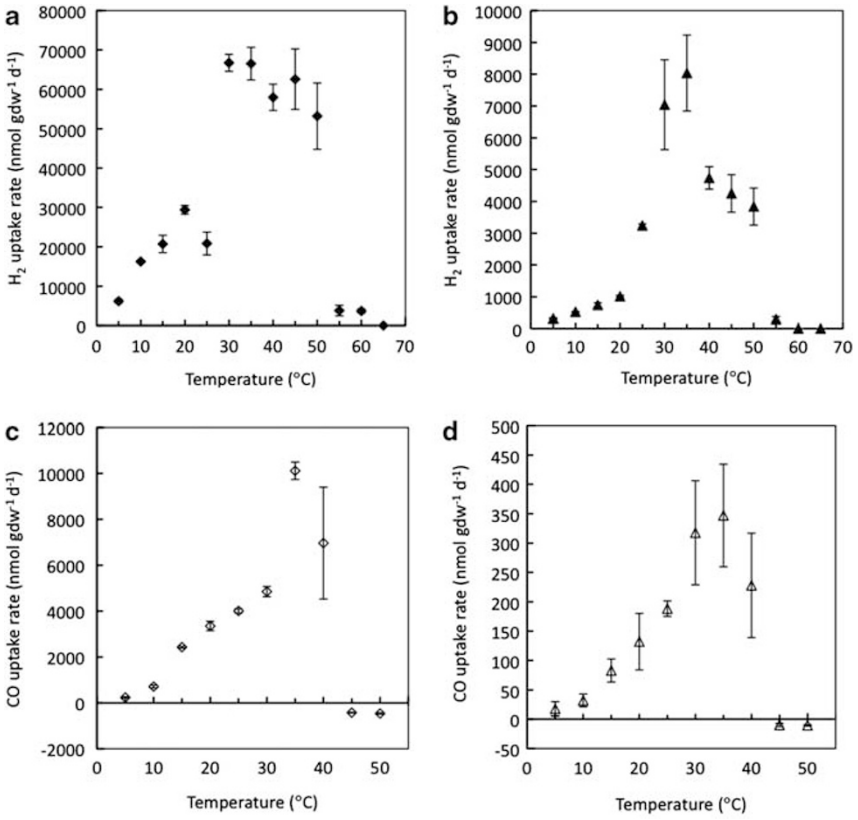

Figure 2 Maximum potential uptake rates as a function of temperature for (**a**) Canopy H_2 uptake (**b**) Bare H_2 uptake (**c**) Canopy CO uptake and (**d**) Bare CO uptake. All data are means of triplicates ± 1 standard error (s.e.). Values less than zero indicate net CO production.

Response of CO uptake to extended incubations at elevated temperature

For Canopy material incubated at 25 °C, CO uptake rates after 30 days were not significantly different for samples with and without yeast extract ($P > 0.170$, Figure 5a). For Bare cinders incubated at 25 °C, CO uptake rates after 30 days decreased significantly ($P < 0.0001$) relative to initial values for material with or without yeast extract (Figure 5b). The extent of the decreases, 73% and 58%, respectively, were similar to those observed for H_2 uptake (74%, Figure 4b). At 55 °C, CO was initially produced by Canopy material, with no net uptake observed; CO production rates were equivalent in the absence and presence of yeast extract (two-tailed unpaired *t*-test, $P = 0.735$, Figure 5a). After 30 days at 55 °C, CO was consumed rather than produced at similar rates in the absence and presence of yeast extract ($P = 0.986$), and activity was equivalent to about 45% and 55%, respectively, of the levels observed at 25 °C. For Bare cinders incubated at 55 °C, slight CO production occurred in the absence of yeast extract; CO was neither produced nor consumed initially in the presence of yeast extract (Figure 5b). After 30 days, no significant net CO consumption or production occurred in the absence or presence of yeast extract. CO uptake was not recovered at 25 °C for samples previously incubated at 55 °C for either site. CO was not consumed in any killed controls, but CO production was observed for killed Canopy material incubated at 55 °C.

Two additional analyses of CO and H_2 uptake after incubation for 30 days at 25 °C and 55 °C, respectively, were conducted using material collected in December 2008. Results were comparable to those presented here (Supplementary Figure S1, Supplementary Figure S2).

Discussion

Responses to temperature by CO and H_2 uptake offer a number of insights about each process, and the impacts of plant development on them. We show, for example, that H_2 uptake activation energies for Bare cinders and Canopy material (82.9 kJ mol^{-1} and 50.8 kJ mol^{-1}, respectively; Figure 2) fall within ranges reported for bacterial activity (about 50–140 kJ mol^{-1}), and markedly exceed values for exoenzymatic activity (10–30 kJ mol^{-1}; Schuler and Conrad, 1991). This is consistent with the outcome of a previous inhibitor study (King, 2003a), which demonstrated that H_2 uptake was largely bacterial rather than exoenzymatic (Conrad, 1996). Thus, the relative importance of bacteria versus exoenzymes as a H_2 sink does not appear to be greatly affected by

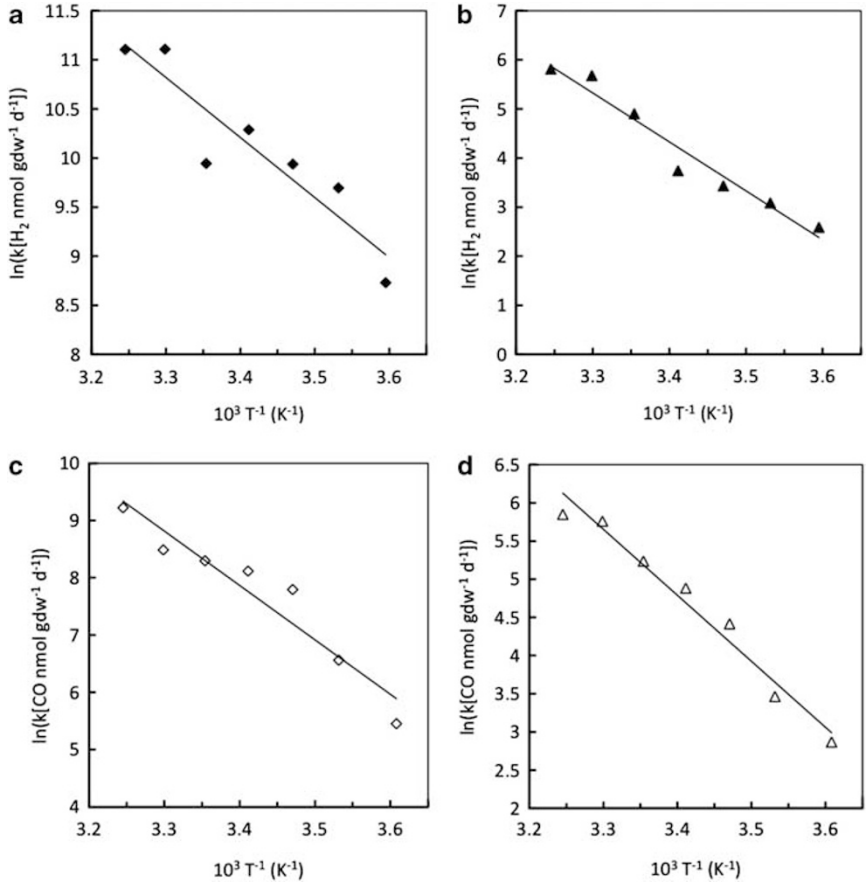

Figure 3 Arrhenius plots for determining activation energy for (**a**) Canopy H_2 uptake ($y=-6.11x+31.0$, $r^2=0.857$; $E_a=50.8\,kJ\,mol^{-1}$); (**b**) Bare H_2 uptake ($y=-9.97x+38.2$, $r^2=0.955$; $E_a=82.9\,kJ\,mol^{-1}$); (**c**) Canopy CO uptake ($y=-9.49x+40.1$, $r^2=0.918$; $E_a=78.9\,kJ\,mol^{-1}$); and (**d**) Bare CO uptake ($y=-8.63x+34.2$, $r^2=0.970$; $E_a=71.8\,kJ\,mol^{-1}$).

vegetation due to ecosystem succession, at least over the short term (that is, decades).

The difference in activation energies between Bare and Canopy sites also indicates that Bare cinder H_2 uptake is quite more temperature sensitive than that for Canopy material. Indeed, Canopy material, which experiences lower average temperatures and is not subjected to daily extremes, shows greater thermal tolerance through a broader temperature optimum (30–50 °C for Canopy versus 30–35 °C for Bare cinders). Nonetheless, these results indicate that succession does not lead to a lower temperature optimum for Canopy H_2 uptake as an adaptive response to lower temperatures.

The lack of adaptive responses for H_2 uptake is also evident in results from 30 days incubations of Bare cinders and Canopy material with and without yeast extract at 25 °C and 55 °C (Figure 4). At 25 °C, Canopy H_2 uptake remained unchanged in the absence of yeast extract and decreased when yeast extract was added, possibly due to substrate-induced repression of hydrogenase production. At 25 °C, Bare cinder H_2 uptake declined regardless of yeast extract treatment, which suggests that even though Bare and Canopy systems are capable of active H_2 consumption, the process is regulated differently at the two sites. Incubation at 55 °C for 30 days resulted in complete inhibition of H_2 uptake for both sites regardless of yeast extract availability. Additionally, heated samples were not able to recover H_2 uptake at 25 °C, which indicates that the original H_2-oxidizers had been effectively lost. This agrees with results of Chowdhury and Conrad (2010), who showed that temperatures of 50 °C or even less rapidly deactivated H_2 uptake by a variety of soils, including desert sands. Recovery apparently required synthesis of new enzymes, which appears to have not occurred for Bare cinders or Canopy material incubated at 55 °C over a 30-day period.

The short-term responses of CO uptake to temperature differ little between Bare cinders and Canopy material (Figures 2c and d). Activity for both rises to an optimum of 30–35 °C, and then declines sharply with net CO production at temperatures $\geqslant$45 °C. Activation energies for both sets of samples are also equivalent (71.8 kJ mol^{-1} and 78.9 kJ mol^{-1} for Bare cinders and Canopy material, respectively; Figures 3c and d), indicating similar sensitivities to temperature change. These results

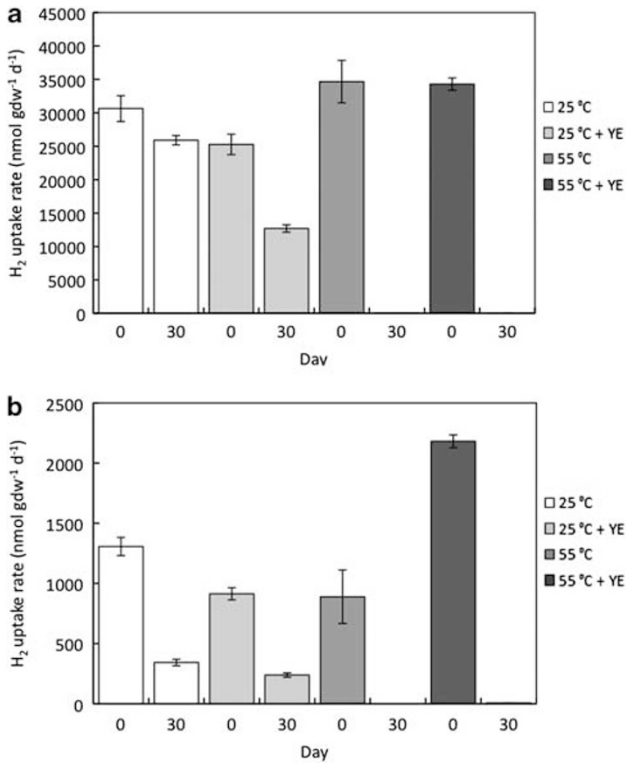

Figure 4 Mean maximum potential H_2 uptake rates for (**a**) Canopy and (**b**) Bare samples incubated at either 25 °C or 55 °C with or without added yeast extract (YE) for 30 days. All data are means of triplicates ± 1s.e.

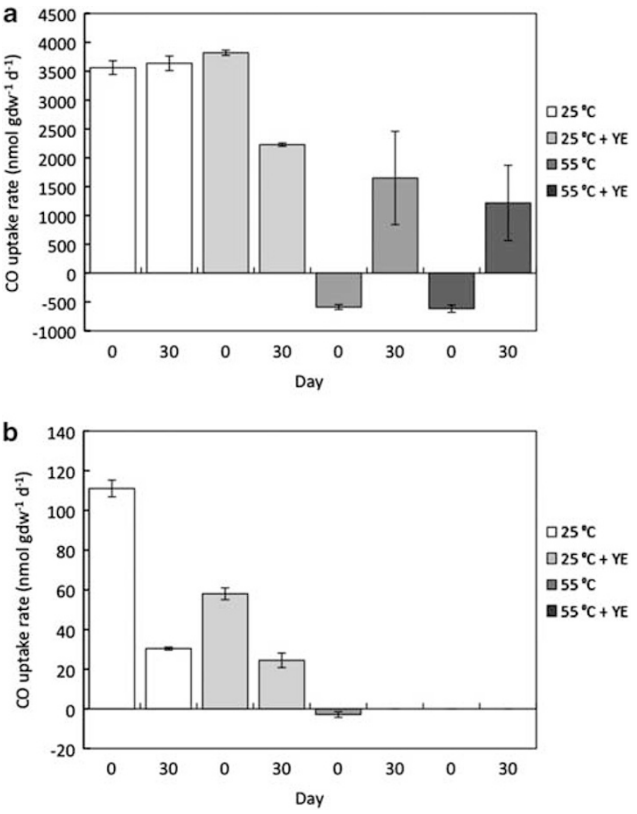

Figure 5 Mean maximum potential CO uptake rates for (**a**) Canopy and (**b**) Bare samples incubated at either 25 °C or 55 °C with or without added yeast extract (YE) for 30 days. All data are means of triplicates ± 1s.e. Values less than zero indicate net CO production.

suggest little, if any, adaptation by Canopy material CO uptake to lower temperature regimes, an observation consistent with results for H_2 uptake.

Interestingly, Bare cinder and Canopy material temperature optima and activation energies both exceed values measured for atmospheric CO uptake by a temperate continental forest soil (Maine, USA; King, 1999a). The lower temperature optima and temperature sensitivity observed for a continental soil might reflect adaptations to the generally colder climate at the site. This suggests that adaptations to lower temperature regimes resulting from plant community development on Hawaiian volcanic deposits might occur, but require longer time spans than represented by the sites in this study (about 50 years).

However, results from extended incubations of Bare cinders and Canopy material at 55 °C indicate that succession may also expand temperature response capacities (Figure 5). In particular, after 30 days incubation at 55 °C, CO uptake by Bare cinders remains undetectable with or without yeast extract (Figure 5b). In contrast, CO uptake by Canopy material increased dramatically, with a change from initial net CO production to net CO consumption (Figure 5a). As CO production is largely an abiological process (in this case resulting from thermal degradation of organic matter), whereas CO uptake is a microbial process (Conrad and Seiler, 1985; King and Weber, 2007), the observed shift from production to consumption indicates that the Canopy site harbors thermophilic CO-oxidizers that are either activated (for example, spore germination) or capable of significant growth and CO uptake when temperature regimes are suitable. As yeast extract did not enhance activity after 30 days relative to no additions (Figure 5), endogenous substrates appear sufficient to fuel activation or growth.

Several previous studies (Ranneklev and Bååth, 2001; Pettersson and Bååth, 2003; Hartley and Hopkins, 2008; Bárcenas-Moreno *et al.*, 2009) have demonstrated that soil microbial communities can adapt to elevated temperature regimes. For example, using growth rate as a variable, Ranneklev and Bååth (2001) have shown that heating peat soil from 25–55 °C resulted in community adaptation with optimal growth at 55 °C in only 3 days. Heating resulted in rapid growth of thermophiles due to limited substrate competition and additional resources from mesophilic bacterial necromass (Bárcenas-Moreno *et al.*, 2009). Although bulk heterotrophic communities at Bare and Canopy sites might have adapted similarly to elevated temperature, H_2-oxidizers at both sites were either inactivated or killed, while only Canopy CO-oxidizers

were capable of thermal adaptation. These results show that responses to temperature changes vary between processes (for example, H_2 versus CO uptake) and for the same process at different sites (for example, Bare versus Canopy).

The results of extended incubations at 55 °C are surprising in at least two respects. H_2 oxidation occurs in many bacterial taxa, including thermophiles (Friedrich and Schwartz, 1993). Some thermophiles, for example, *Bacillus schlegelii*, also oxidize both CO and H_2 (Hudson *et al.*, 1988). Thus, the absence of an adaptive response for H_2 uptake is enigmatic when a response is observed for CO. The development of a thermophilic CO uptake capacity by Canopy material suggests that incubation conditions *per se* did not preclude activation or growth of facultative lithotrophs in general. Whether or not H_2 uptake by other soils and volcanic substrates lacks an adaptive response to elevated temperatures is currently unknown.

Development of a thermophilic CO uptake capacity in Canopy material but not Bare cinders is also surprising. Bare cinders support populations of *Ktedonobacteria*-like CO-oxidizers based on analyses of *coxL* and 16S rRNA gene sequences (Weber and King, 2010). Indeed, *Ktedonobacteria*-like sequences dominate Bare cinder *coxL* libraries (Weber and King, 2010). These sequences, which are most closely related to a class of bacteria consisting of a majority of thermophiles, have not been observed in Canopy site *coxL* or 16S rRNA gene sequence libraries. Thus, one could anticipate an adaptive response to elevated temperature for Bare cinder CO uptake even though some *Ktedonobacteria* are mesophilic (Cavaletti *et al.*, 2006).

The absence of a Bare cinder response might indicate that incubation conditions were unsuitable for activation or growth of *Ktedonobacteria*-like populations. The fact that successful enrichments of thermophilic *Ktedonobacteria* from Bare cinders have required multiple efforts (King and King, unpublished) supports this possibility. Development of thermophilic CO uptake in Canopy material but not Bare cinders might also reflect differences in CO oxidizer diversity, population sizes and resource availability for growth and metabolism, all of which increase from Bare cinders to Canopy material (King and Weber, 2008; Weber and King, 2010). Although thermophiles occur as dormant forms in many soils (Marchant *et al.*, 2002, 2008; Rahman *et al.*, 2003), higher total microbial and CO-oxidizer diversity and population sizes in Canopy material might increase the likelihood that one or more thermophiles becomes active with elevated temperature. Similarly, higher organic matter and nitrogen contents of Canopy material might facilitate activation or growth. The ease of enrichment and isolation of a thermophilic CO-oxidizing *Alicyclobacillus* from heated Canopy material is consistent with this possibility (King and King, unpublished).

Responses of CO and H_2 uptake to temperature also offer additional insights about the communities involved in these processes. The similarities of short-term and long-term responses of CO and H_2 uptake in Bare cinders suggest that the two processes might be carried out, in part, by the same bacteria or at least physiologically similar populations. In contrast, different responses by CO and H_2 uptake in Canopy material suggest that distinct populations carry out the two processes, with little overlap between them.

Although Canopy material and Bare cinders support distinctly different CO-oxidizing communities (Weber and King, 2010) and respond differently to long-term elevated temperatures, differences in temperature regimes between sites, including extremes and mean values, do not result in different temperature optima or temperature sensitivity. Temperature responses and adaptation of Canopy material and Bare cinder H_2 uptake also appear unaffected by differences between the sites in ambient temperature regimes. A comparison of Bare cinder and Canopy material responses to water stress has revealed a similar pattern, with no difference in the impact of imposed water stress on CO oxidation, in spite of dramatic differences between the sites in water regimes *in situ* (Weber and King, 2009). These results collectively suggest that during succession, changes in edaphic factors, for example, temperature and water potential, affect rates of bacterial activities, but do not have a primary role in establishing the ecophysiological properties of bacterial communities on young volcanic systems. Other factors, such as the specific phylogenetic composition of colonists arriving at these sites, their physiological characteristics and survival, and the development of plant communities, likely have more determinative roles over short time periods (perhaps decades).

Acknowledgements

We acknowledge support from National Science Foundation Microbial Observatory Grant (NSF-MCB-0348100).

References

Bárcenas-Moreno G, Gómez-Brandón M, Rousk J, Bååth E. (2009). Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. *Global Change Biol* **15**: 2950–2957.

Cavaletti L, Monciardini P, Bamonte R, Schumann P, Rohde M, Sosio M *et al.* (2006). New lineage of filamentous, spore-forming, Gram-positive bacteria from soil. *Appl Environ Microbiol* **72**: 4360–4369.

Chowdhury SP, Conrad R. (2010). Thermal deactivation of high-affinity H_2 uptake activity in soils. *Soil Biol Biochem* **42**: 1574–1580.

Conrad R. (1996). Soil microorganisms as controllers of atmospheric traces gases (H_2, CO, CH_4, OCS, N_2O and NO). *Microbiol Rev* **60**: 609–640.

Conrad R, Seiler W. (1985). Characteristics of abiological carbon-monoxide formation from soil organic matter, humic acids, and phenolic-compounds. *Environ Sci Tech* **19**: 1165–1169.

Friedrich B, Schwartz E. (1993). Molecular biology of hydrogen utilization in aerobic chemolithotrophs. *Annul Rev Microbiol* **47**: 351–383.

Hartley IP, Hopkins D. (2008). Soil microbial respiration in arctic soil does not acclimate to temperature. *Ecol Lett* **11**: 1092–1100.

Hudson JA, Daniel RM, Morgan HW. (1988). Isolation of a strain of *Bacillus schlegelii* from geothermally heated antarctic soil. *FEMS Microbiol Lett* **51**: 57–60.

King GM. (1999a). Attributes of atmospheric carbon monoxide oxidation by Maine forest foils. *Appl Environ Microbiol* **65**: 5257–5264.

King GM. (1999b). Characteristics and significance of atmospheric carbon monoxide consumption by soils. *Chemosphere Glob Change Sci* **1**: 53–63.

King GM. (2003a). Contributions of atmospheric CO and hydrogen uptake to microbial dynamics on recent Hawaiian volcanic deposits. *Appl Environ Microbiol* **69**: 4067–4075.

King GM. (2003b). Uptake of carbon monoxide and hydrogen at environmentally relevant concentrations by mycobacteria. *Appl Environ Microbiol* **69**: 7266–7272.

King GM, Weber CF. (2007). Distribution, diversity and ecology of aerobic CO-oxidizing bacteria. *Nat Microbiol Rev* **5**: 107–118.

King GM, Weber CF. (2008). Interactions between bacterial carbon monoxide and hydrogen consumption and plant development on recent volcanic deposits. *ISME J* **2**: 195–203.

Marchant R, Banat IM, Rahman TJ, Berzano M. (2002). The frequency and characteristics of highly thermophilic bacteria in cool soil environments. *Environ Microbiol* **4**: 595–602.

Marchant R, Franzetti A, Pavlostathis SG, Tas DO, Erdbrugger I, Unyayar A *et al.* (2008). Thermophilic bacteria in cool temperate soils: are they metabolically active or continually added by global atmospheric transport? *Appl Microbiol Biotechnol* **78**: 841–852.

Pettersson M, Bååth E. (2003). Temperature-dependent changes in the soil bacterial community in limed and unlimed soil. *FEMS Microbiol Ecol* **45**: 13–21.

Rahman TJ, Marchant R, Banat IM. (2003). Distribution and molecular investigation of highly thermophilic bacteria associated with cool soil environments. *Thermophiles* **32**: 209–213.

Ranneklev SB, Bååth E. (2001). Temperature-driven adaptation of the bacterial community in peat measured by using thymidine and leucine incorporation. *Appl Environ Microbiol* **67**: 1116–1122.

Schuler S, Conrad R. (1991). Hydrogen oxidation activities in soil as influenced by pH, temperature, moisture, and season. *Biol Fertil Soils* **12**: 127–130.

Stott MB, Crowe MA, Mountain BW, Smirnova AV, Hou S, Alam M *et al.* (2008). Isolation of novel bacteria, including a candidate division, from geothermal soils in New Zealand. *Environ Microbiol* **10**: 2030–2041.

Weber CF, King GM. (2009). Water stress impacts on bacterial carbon monoxide oxidation on recent volcanic deposits. *ISME J* **3**: 1325–1334.

Weber CF, King GM. (2010). Distribution and diversity of carbon monoxide-oxidizing bacteria and bulk bacterial communities across a succession gradient on a Hawaiian volcanic deposit. *Environ Microbiol* **12**: 1855–1867.

Yabe S, Aiba Y, Sakai Y, Hazaka M, Yokota A. (2010a). *Thermosporothrix hazakensis* gen. nov., sp. nov., isolated from compost, description of *Thermosporotrichaceae* fam. nov. within the class *Ktedonobacteria* Cavaletti *et al.* 2007 and emended description of the class *Ktedonobacteria*. *Int J Syst Evol Microbiol* **60**: 1794–1801.

Yabe S, Aiba Y, Sakai Y, Hazaka M, Yokota A. (2010b). *Thermogemmatispora onikobensis* gen. nov., sp. nov. and *Thermogemmatispora foliorum* sp. nov., isolated from geothermal fallen leaves and a description of *Thermogemmatisporaceae* fam. nov. and *Thermogemmatisporales* ord. nov. within the class *Ktedonobacteria*. *Int J Syst Evol Microbiol* **61**: 903–910.

Supplementary Information accompanies the paper on The ISME Journal website (http://www.nature.com/ismej)