Atmospheric H_2 energetic fertilization to soil microorganisms in a forest ecosystem

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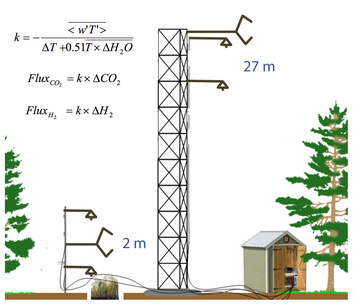
H_2 soil sink

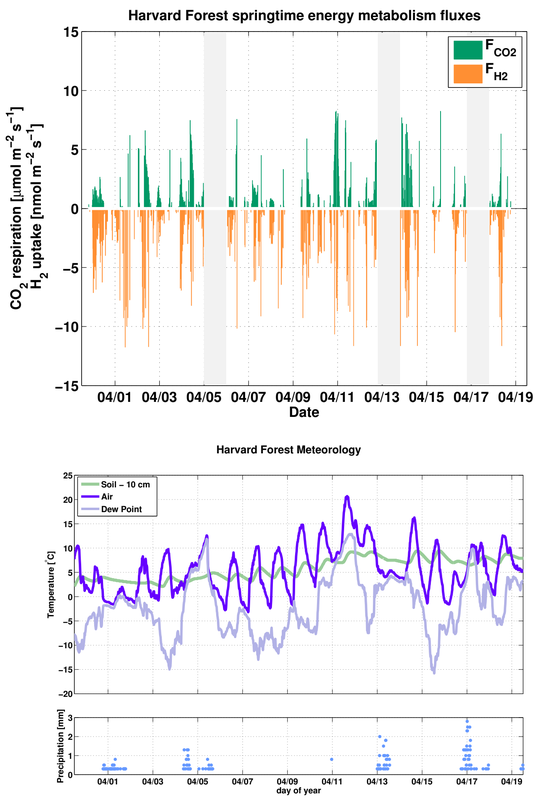
Soil microorganisms dominate the fate of atmospheric molecular hydrogen (H_2) and comprise an estimated 75-80% of its global sink. Recent work has linked atmospheric H_2 uptake to a novel high-affinity [NiFe]-hydrogenase expressed in active *Streptomyces sp.* cells [1], and is perhaps not driven by abiotic hydrogenases as was previously thought. Consequently, atmospheric hydrogen may be a 60-85 $Tg\,yr^{-1}$ energetic supplement to microbes in Earth's uppermost soil horizon. To understand the role of this supplement to the soil microbial ecology, this work explores the following questions:

1. What is the importance of atmospheric H_2 energy to soil microbial communities relative to carbon substrates?
2. How might this energetic supplement change with changes in anthropogenic H_2 emissions?

H_2 uptake in a forest ecosystem



A custom-built instrument to measure high-frequency H_2 fluxes, both above and below the canopy, has been deployed at the Environmental Measurement Site (EMS) tower at the Harvard Forest Long Term Ecological Research (LTER) site in Petersham, MA, USA. A modified bowen ratio approach is used to calculate chemical fluxes from a turbulent coefficient, k, derived from the sensible heat flux and gradient [2]. CO_2 **respiration fluxes and** H_2 **soil uptake fluxes** measured from a 2 m sub-canopy tower are shown below. Meteorological measurements from the nearby Fisher meteorological station (*http://harvardforest.fas.harvard.edu/*).



Role of spores

Is atmospheric H_2 really important to soil microbial communities?

This depends on **whether microorganisms actively utilize H_2 for energy**. Interestingly, H_2 oxidation in *Streptomyces* appears to occur during the sporulation phase of their complex life cycle [1].

Manganese oxidation by *Bacillus sp.* spores might be an analogue. During sporulation *Bacilli* require additional amounts of manganese and spores continue to bind and oxidize manganese even when mature and dormant [8]. It is **unclear whether manganese oxidation is coupled to spore metabolism or viability**.

If similar, H_2 oxidation in the environment might assist in the sporulation process, but then could largely be a passive process catalyzed by hydrogenases on the coat of dormant *Streptomyces* spores. If so, maximal H_2 uptake might occur during periods least favorable for the germination of spores to vegetative cells.

1) Importance of atmospheric H_2 to soil microbial community

How does energetic deposition via atmospheric H_2 impact soil microbial communities?

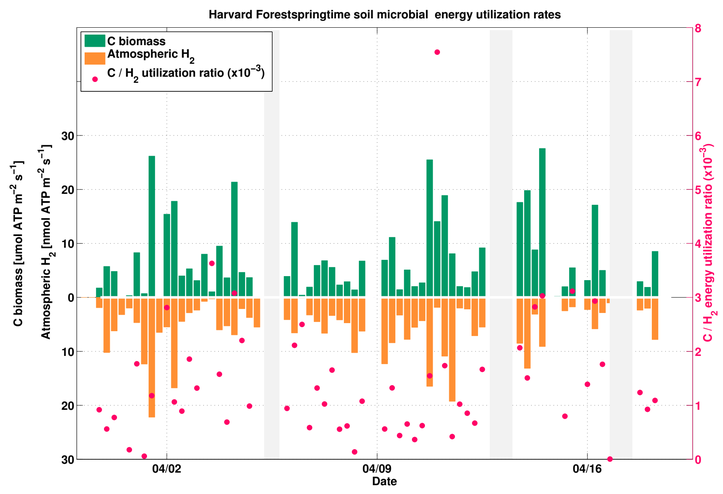
We consider the relative importance of energy derived from microbial oxidation of atmospheric H_2 versus carbon biomass oxidation.

First, we compare the **annual global turnover** of the relevant H_2 and carbon biomass energy pools. For H_2, we assume a global average 530 ppb mixing ratio and a conservative ATP generation cost of 80 $kJ/mol\,ATP$. For CO_2, we assume that ATP generation from the oxygenic oxidation of the carbon biomass pool proceeds as if through glucose oxidation yielding 29 - 38 $mol\,ATP/mol\,glucose$.

	annual chemical energy pool	ATP equivalent	source
H_2 Soil Sink	59 - 84 $Tg\,H_2\,yr^{-1}$	16 - 22 $nmol\,ATP\,m^{-2}\,s^{-1}$	[10][11]
microbial C oxidation	68.6 $Gt\,C\,yr^{-1}$	6000 - 7800 $nmol\,ATP\,m^{-2}\,s^{-1}$	[a]

We find the relative importance of carbon biomass oxidation to H_2 oxidation to for energy generation is therefore about 200:1 to 500:1. In other words, H_2 **energy could be just as important as carbon biomass for about 0.2 - 0.6% of cells in the soil microbial community**. In general, about 1 to 0.1% of colony forming units (cfu) per gram of soil are *Streptomyces sp.*; for those able to utilize atmospheric H_2, its energy supplement could be just as important as energy of carbon origin [1].

Second, we use two weeks of H_2 and CO_2 **flux measurements from Harvard Forest** to calculate the relative importance of energy sources in a springtime forest ecosystem. The figure shows ATP generation rate, where ATP generation timeseries are mirrored for ease of viewing.



The relative importance of carbon biomass oxidation at Harvard Forest is variable and is centered on 1300:1 C:H_2, which is **similar, but slightly higher than the above estimate**. These CO_2 fluxes include both heterotrophic microbial respiration and autotrophic root respiration. This calculation likely overestimates the C respiration yielding energy to the microbial community, and is thus **a lower estimate** of the importance of H_2 energy to the microbial ecosystem, which again should be significant for strains able to oxidize atmospheric H_2.

[a] values from R. Thauer and W. Metcalf lectures, 2010 MBL Microbial Diversity Course, Woods Hole, MA, USA

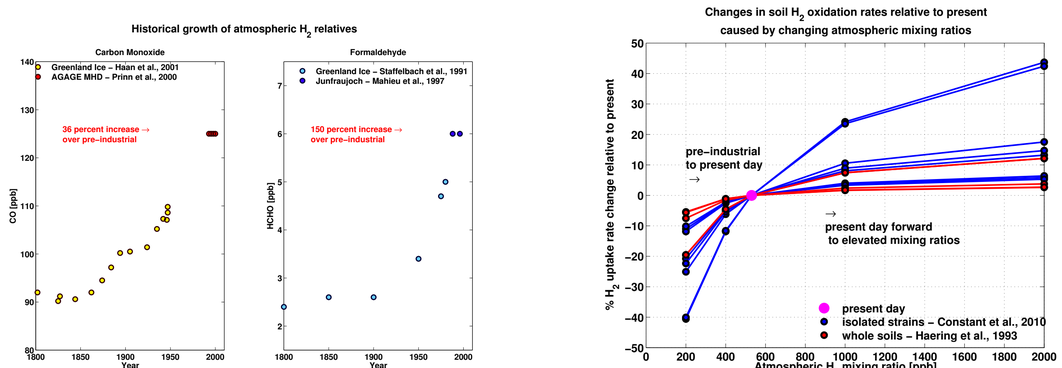
2) Impact of historical and future changes in atmospheric H_2

How does microbial consumption of atmospheric H_2 change in response to changing concentrations?

Emissions of atmospheric H_2 have likely increased since the industrial revolution. Today they are about 50% anthropogenic, and increases in fossil fuel use, biomass burning, or use of H_2 as an energy carrier could increase H_2 mixing ratios in the atmosphere. **We explore past and future scenarios to understand potential changes in energetic deposition to soil microbial communities.** Microbial H_2 uptake (v_0) is modeled with Michaelis-Menten enzyme kinetics by using max reaction rates v_{max} and enzyme affinities K_m^{-1} that have been reported for both whole soil samples and microbial isolates with the following equation: $v_0 = v_{max} \times [H_2]/(K_M + [H_2])$ $[nmol\,min^{-1}\,g_{dw}^{-1}]$ [4] [1].

Pre-Industrial to Present : Instrumental records of atmospheric H_2 show no significant growth rate; however, measurements from Greenland firn air suggest that **mixing ratios increased markedly from 1960 to the early 1980s** before flattening [6]. A similar pattern has been observed for two related gases, carbon monoxide (CO) and formaldehyde ($HCHO$), where the mixing ratios of those gases have increased by about 40% and 150 % over preindustrial levels, respectively [3] [7] [9] [5]. We assume H_2 mixing ratios may have increased by similar relative amounts from preindustrial levels of 200 or 400 ppbv to 530 ppbv today.

We find, that as atmospheric H_2 mixing ratios increased over the industrial revolution, **soil microbial uptake must have increased**; using this simple approach, uptake may have increased from rates 5 to 20% below today. The strong microbial H_2 sink for may have attenuated increases in atmospheric mixing ratios, whereas gases like CO and $HCHO$ lack a strong microbial buffer.



Present to Future : We explore a hypothetical doubling and quadrupling of atmospheric H_2 mixing ratios from present to the future.

We find that the **whole soil** uptake rate may have limited capacity to increase H_2 uptake as the rate only increases by 2-7 and 3-12% for a doubling or quadrupling of H_2 mixing ratios; however, some **isolated strains** exhibit a relatively larger increase (up to 25 - 40%). The actual response of the H_2 soil sink likely depends on the interplay of H_2 mixing ratios and the fitness of microbial strains exhibiting a continuum of uptake kinetics [1].

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