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LETTER

What is the relationship between soil methane oxidation and other C compounds?

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We measured potential rates of methane (CH_4) oxidation in semiarid soil and observed greater rates of CH_4 oxidation in the wet season than the dry season (Sullivan *et al.*, 2013). Importantly, we demonstrated that common mechanisms (soil water, soil texture), thought to control methane (CH_4) oxidation in upland soil did not explain seasonal patterns in potential CH_4 oxidation in semiarid soil. Instead, dissolved organic carbon (DOC) was the chemical characteristic that best predicted CH_4 oxidation. We then used a series of laboratory studies to attribute this trend to the ability of CH_4 oxidizers in dry ecosystems to metabolize both DOC and CH_4. Such mixotrophic activity by CH_4 oxidizing bacteria (MOB) has been found in other studies (e.g., Conrad, 2009; Dunfield *et al.*, 2010; Dedysh & Dunfield, 2011; Fender *et al.*, 2012). On the basis of the correlation between DOC and CH_4 oxidation rates, we speculated that facultative use of DOC by MOB increased CH_4 oxidation in the wet season. In their Letter to the Editor, Zhou *et al.* (2013) proposed an alternative hypothesis that explains lower rates of CH_4 oxidation in dry seasons than wet seasons: ethylene produced by water-stressed plants inhibits CH_4 oxidation during dry seasons. This intriguing hypothesis, which thus far is unsupported by data, warrants thorough investigation, but we desire to respond to several issues raised by their commentary on our manuscript.

We absolutely agree with Zhou *et al.* (2013) that 'more specific experimental work is needed' before definitively linking DOC and CH_4 oxidation. With this in mind, we posed the title of our manuscript as a question and repeatedly encouraged further investigation. Our results were unexpected and novel because they demonstrated soil CH_4 oxidation rates in semiarid ecosystems to be independent of soil physical conditions but related to DOC concentration. Here, we consider the hypothesis (that inhibition of CH_4 oxidation by plant-derived ethylene explains our seasonal patterns of CH_4 oxidation) proposed by Zhou *et al.* (2013) in light of our original manuscript and other data, we have gathered from the same study system.

Conclusive evidence for CH_4 inhibition by other substrates is generally elusive. A meta-analysis of ammonium (NH_4) inhibition of CH_4 oxidation, probably the most well-studied example of CH_4 oxidation inhibition, demonstrated equivocal effects of NH_4 (whether alone or in combination with other N forms) on CH_4 oxidation (Aronson & Helliker, 2010). Is there a stronger case for ethylene inhibition of CH_4 oxidation? A study cited as evidence for ethylene inhibition of CH_4 oxidation by Zhou *et al.* (2013) observed ethylene production from anaerobic decomposition of organic matter in wet periods (Xu & Inubushi, 2009) rather than ethylene production from water-stressed plants during dry periods. Yet, we measured the highest rate of CH_4 oxidation in the wet season, and it occurred in fine textured soils with greater possibility of anaerobic conditions than other coarser-textured soils we measured. Because the concentration of ethylene required to inhibit CH_4 oxidation varies substantially (Xu & Inubushi, 2009), the effect of ethylene on CH_4 oxidation, if it exists at all, is likely variable as well. Unfortunately, at this time, no direct evidence exists to suggest that water-stressed plant roots emit sufficient ethylene to inhibit CH_4 oxidation.

We can also reconsider another study (Sullivan *et al.*, 2012) in light of the proposed relationship between CH_4 oxidation rates and ethylene. Ethylene has been shown to inhibit NH_4 oxidation (McCarty & Bremner, 1991; Xu & Inubushi, 2009) as well as CH_4 oxidation. In a parallel but separately published experiment from the same study sites and using soil from the same cores as the CH_4 measurements in Sullivan *et al.* (2013), Sullivan *et al.* (2012) demonstrated that potential NH_4 oxidation (potential nitrification) in dry soils was equal to or greater than NH_4 oxidation in wet soils. Based on the hypothesis proposed by Zhou *et al.* (2013), we would expect dry season ethylene production to suppress NH_4 oxidation as well as CH_4 oxidation, but this was not the case.

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Finally, the stimulation of CH_4 oxidation by DOC and the inhibition of CH_4 oxidation by ethylene are not mutually exclusive hypotheses. If it is ultimately shown that stressed plants inhibit CH_4 oxidation via ethylene production, stressed plants may also exude less oxidized C belowground in dry seasons. However, in the wet season, facultative use of DOC by CH_4 oxidizers AND reduced ethylene inhibition may increase CH_4 oxidation.

Smith (1976) described ethylene thus: 'Important, far-reaching claims have been made about its role in soil biology.' Unfortunately, the link between plant stress, ethylene production, and CH_4 oxidation is still largely conceptual. We recommend future investigators experimentally manipulate soil DOC with compounds that mimic root exudates and microbially derived solutes and measure responses of soil CH_4 oxidation. Ideally, such a study will have both field (observational) and laboratory-based (mechanistic) components. We encourage the future research endeavors described by Zhou *et al.* (2013) and others designed to elucidate the relative effects of DOC and ethylene on CH_4 oxidation.

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