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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 (CH₄) oxidation in semiarid soil and observed greater rates of CH₄ 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 (CH₄) oxidation in upland soil did not explain seasonal patterns in potential CH₄ oxidation in semiarid soil. Instead, dissolved organic carbon (DOC) was the chemical characteristic that best predicted CH₄ oxidation. We then used a series of laboratory studies to attribute this trend to the ability of CH₄ oxidizers in dry ecosystems to metabolize both DOC and CH₄. Such mixotrophic activity by CH₄ 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 CH₄ oxidation rates, we speculated that facultative use of DOC by MOB increased CH₄ oxidation in the wet season. In their Letter to the Editor, Zhou *et al.* (2013) proposed an alternative hypothesis that explains lower rates of CH₄ oxidation in dry seasons than wet seasons: ethylene produced by water-stressed plants inhibits CH₄ 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 CH₄ 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 CH₄ 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 CH₄ oxidation by

plant-derived ethylene explains our seasonal patterns of CH₄ 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 CH₄ inhibition by other substrates is generally elusive. A meta-analysis of ammonium (NH₄) inhibition of CH₄ oxidation, probably the most well-studied example of CH₄ oxidation inhibition, demonstrated equivocal effects of NH₄ (whether alone or in combination with other N forms) on CH₄ oxidation (Aronson & Helliker, 2010). Is there a stronger case for ethylene inhibition of CH₄ oxidation? A study cited as evidence for ethylene inhibition of CH₄ 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 CH₄ 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 CH₄ oxidation varies substantially (Xu & Inubushi, 2009), the effect of ethylene on CH₄ 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 CH₄ oxidation.

We can also reconsider another study (Sullivan *et al.*, 2012) in light of the proposed relationship between CH₄ oxidation rates and ethylene. Ethylene has been shown to inhibit NH₄ oxidation (McCarty & Bremner, 1991; Xu & Inubushi, 2009) as well as CH₄ oxidation. In a parallel but separately published experiment from the same study sites and using soil from the same cores as the CH₄ measurements in Sullivan *et al.* (2013), Sullivan *et al.* (2012) demonstrated that potential NH₄ oxidation (potential nitrification) in dry soils was equal to or greater than NH₄ oxidation in wet soils. Based on the hypothesis proposed by Zhou *et al.* (2013), we would expect dry season ethylene production to suppress NH₄ oxidation as well as CH₄ oxidation, but this was not the case.

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Finally, the stimulation of CH₄ oxidation by DOC and the inhibition of CH₄ oxidation by ethylene are not mutually exclusive hypotheses. If it is ultimately shown that stressed plants inhibit CH₄ 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 CH₄ oxidizers AND reduced ethylene inhibition may increase CH₄ 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 CH₄ 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 CH₄ 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 CH₄ oxidation.

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