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Review

Soil extracellular enzyme dynamics in a changing climate

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ABSTRACT

Assays for extracellular enzyme activity (EEA) have become a common tool for studying soil microbial responses in climate change experiments. Nevertheless, measures of potential EEA, which are conducted under controlled conditions, often do not account for the direct effects of climate change on EEA that occur as a result of the temperature and moisture dependence of enzyme activity in situ. Likewise, the indirect effects of climate on EEA in the field, that occur via effects on microbial enzyme producers, must be assessed in the context of potential changes in plant and soil faunal communities. Here, EEA responses to warming and altered precipitation in field studies are reviewed, with the goal of evaluating the role of EEA in enhancing our understanding of soil and ecosystem responses to climate change. Seasonal and interannual variation in EEA responses to climate change treatments are examined, and potential interactions with elevated atmospheric CO_2, increased atmospheric N deposition and changes in disturbance regimes are also explored. It is demonstrated that in general, soil moisture manipulations in field studies have had a much greater influence on potential EEA than warming treatments. However, these results may simply reflect the low magnitude of soil warming achieved in many field experiments. In addition, changes in plant species composition over the longer term in response to warming could strongly affect EEA. Future challenges involve extending studies of potential EEA to address EEA responses to climate change in situ, and gaining further insights into the mechanisms, such as enzyme production, stabilization and turnover, that underlie EEA responses.

1. Introduction

Over the last decade, assays for extracellular enzyme activity (EEA) have become an increasingly common tool for examining soil microbial responses in climate change experiments (Weedon et al., 2011). Coupled with these assays being relatively easy to perform and inexpensive, they provide a useful integrative measure of microbial activity that complements other soil carbon and nutrient analyses (Allison et al., 2007). Such measures are critical for exploring the mechanisms whereby soil organic matter decomposition may respond to climate change, driving feedbacks between climate, ecosystems and atmospheric CO_2 concentrations (Bengtson and Bengtsson, 2007). Extracellular enzymes are the “proximate agents of organic matter decomposition,” and key enzymatic reactions include those involved in the degradation of cellulose and lignin, those that hydrolyze reservoirs of organic N such as proteins, chitin and peptidoglycan, and those that mineralize P from nucleic acids, phospholipids and other ester phosphates (Sinsabaugh et al., 2008). When these suites of enzymes are examined simultaneously, EEA can be used to infer shifts in microbial demand for carbon (including labile versus recalcitrant forms), nitrogen and phosphorus (Sinsabaugh and Moorhead, 1994). Despite these potential advantages, when shifts in EEA occur in response to climate change treatments, the underlying mechanisms can be unclear, with the direct effects of climate change treatments confounded with possible indirect effects (Kardol et al., 2010; Weedon et al., 2011). Specifically, measures of potential EEA, which are conducted under controlled conditions in the laboratory, often do not account for the direct effects of climate on enzyme activity in situ (Fig. 1 – solid line) (Wallenstein and Weintraub, 2008). Moreover, with respect to the indirect effects of climate on EEA, the direct effects of climate on enzyme production that occur via changes in microbial activity and community composition (Fig. 1 – dashed lines) are potentially confounded with or fail to properly account for the indirect effects of climate on soil microorganisms that occur via changes in plant and soil faunal communities (Fig. 1 – dotted lines). The goal of this paper is to explore trends in EEA responses to warming and altered precipitation in the context of climate change experiments. Furthermore, it will examine studies of interactions between EEA responses to climate change and other important global change factors, such as elevated atmospheric CO_2, increased atmospheric N

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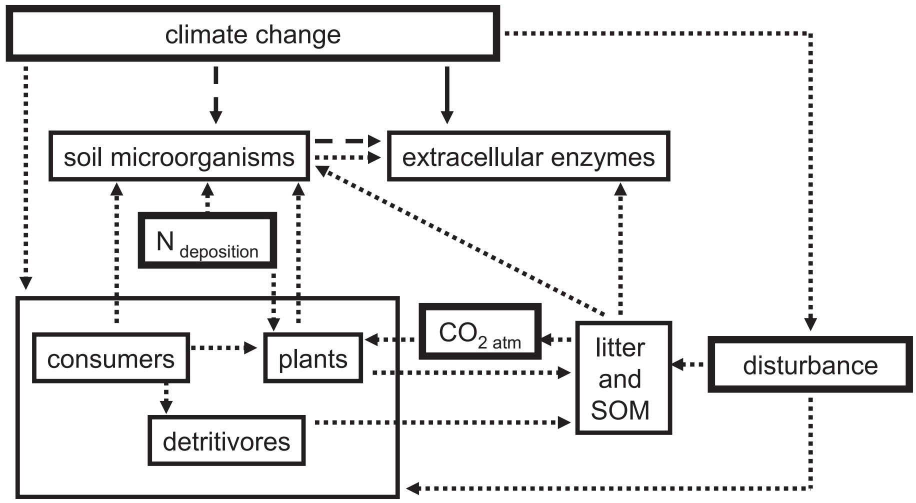

Fig. 1. Conceptual framework outlining the distinctions among direct effects of climate on enzyme activity in situ (solid line), the effects of climate on enzyme production that occur via changes in microbial activity and community composition (dashed lines) and the indirect effects of climate on soil microorganisms (dotted lines). Global change drivers (climate, atmospheric N deposition, elevated atmospheric CO_2 and disturbance) are indicated by the thick-bordered boxes. The box containing plants, consumers and detritivores is used to indicate that each of these groups is directly affected by climate and disturbance. For simplicity, the contributions of plant enzymes to the soil extracellular enzyme pool have been omitted.

deposition and changes in disturbance regimes, including fire cycles and extreme climate events. EEA responses to climate change will be interpreted in the context of the conceptual framework illustrated in Fig. 1, in order to evaluate the potential role of EEA in enhancing our understanding of soil and ecosystem responses to climate change.

2. EEA responses to climate warming

2.1. Critical review of approaches used in warming experiments

Numerous techniques have been developed for administering warming treatments, ranging from controlled environment experiments to field experiments involving open top chambers, greenhouses, retractable passive warming curtains, snow removal, heated coils/fluid filled tubes inserted into soil or overhead infrared heaters (see review by Shen and Harte, 2000). While often dictated by financial, logistical or spatial constraints, the selection of a given warming technique has important implications for the interpretation of EEA responses. For example, while the small size and rapid growth of microorganisms allows for meaningful microbial community level warming responses to be obtained from soil microcosms under controlled conditions in growth chambers, in these experiments it is difficult to examine potential interactions of EEA with other important ecosystem components (e.g. plants) over long time scales. In other words, as with controlled environment experiments in general (Newman et al., 2011), while these soil temperature manipulations are useful for providing a clear examination of specific mechanisms, the tradeoff is that they lack a high degree of realism or external validity. In contrast, in field experiments, the tradeoff of increased realism is generally one of decreased mechanistic understanding of EEA responses. Nevertheless, field experiments are also frequently challenged by shortcomings in spatial and temporal scale when assessing EEA responses to climate change. For example, in mature forests, there are no viable options for warming tree canopies. Likewise, given the high cost of running infrastructure such as electric heaters in the field (Kimball et al., 2008), multiple treatment levels have been uncommon in these experiments, reducing the ability to assess possible non-linearities in EEA responses to variation in the magnitude of warming. When plots are warmed in the field, mobile organisms such as herbivores can also choose to feed preferentially in either warmed plots or the surrounding matrix, biasing plant warming responses (Moise and Henry, 2010), and potentially affecting EEA.

Comparing among field warming techniques, passive warming using open top chambers and greenhouses is limited with respect to the maximum effect size on soil warming, and these methods can introduce artifacts by blocking rain, wind or animals (Marion et al., 1997). In addition, this infrastructure does not provide a simulation of warming over winter in snow-covered regions, where soil microorganisms may be vulnerable to increased soil frost in a warmer climate as a result of decreased snow cover (i.e. decreased insulation of soil from air) and subsequent exposure to cold air temperatures at night or during cold spells (Groffman et al., 2001). Alternatives that have been used to simulate climate warming over winter include snow removal, heated soil wires, fluid-filled pipes and overhead heaters. Snow removal (which simulates increased snow melt in a warmer climate) and heated wires are frequently used in forest systems, although these methods decouple soil warming from possible aboveground warming responses, such as changes in plant litter quality, that could affect EEA. The effects of snow removal experiments on microbial activity and EEA must also be interpreted with caution, given that extreme soil freezing can occur when snow removal coincides with extremely cold air temperatures, potentially exaggerating frost effects; thus, snow removal may best simulate reduced precipitation rather than warming (Henry, 2007). The installation of heating wires can disturb soil over the short term (Shen and Harte, 2000), and a source of electricity is required. Likewise, infrared overhead heaters require access to electricity, and the high running costs potentially limit the continuation of warming over the long term, such that the cumulative effects of warming on EEA responses that occur via long term changes in plant species composition and soil organic matter cannot be addressed.

2.2. Effects of warming on potential and in situ EEA in field experiments

A main focus of EEA assays in the context of climate warming studies has been the potential contribution of warming to changes