



## Synergistic effects of diffusion and microbial physiology reproduce the Birch effect in a micro-scale model



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### ARTICLE INFO

#### Article history:

Received 20 July 2015

Received in revised form

22 September 2015

Accepted 24 October 2015

Available online 7 November 2015

#### Keywords:

Dry/wet cycles

Birch effect

Microbial communities

Spatial dynamics

Individual-based model

Carbon cycling

Rainfall timing

### ABSTRACT

Large rainfall events following drought cause pulses of CO<sub>2</sub> flux that are higher than models predict. This phenomenon, named the “Birch effect” after its discoverer, has been observed for decades, and will influence carbon-climate feedbacks as drying–rewetting (DRW) cycles become more common under intensified climates. Yet, the many interacting factors that determine how soil DRW cycles affect C balance have been difficult to separate empirically. Here we use a spatially explicit biogeochemical–microbial model to examine the mechanisms underlying CO<sub>2</sub> dynamics under DRW. We independently model physiological activity and diffusion based on how they vary with (constant) moisture levels in nature, and subject the model to DRW to test the importance of different mechanisms in models with one or two microbial functional groups (cheaters and producers). Our model reproduces respiration patterns similar to empirical observations of the Birch effect when we include mechanisms that link water content to microbial growth and to diffusion rate, whereas inclusion of either mechanism alone produces significantly lower pulses upon rewetting. Diffusion limitation under drought increases substrate availability under rewetting, a process mediated by biogeochemical hotspots and continued enzyme activity under drought. At the same time, high microbial growth under rewetting is needed to replenish enzyme pools and to sustain the biomass required to generate respiration pulses under repeated DRW. Inclusion of cheaters in the model dampens the size of the rewetting pulse and the cumulative amount of CO<sub>2</sub> release, as cheaters outcompete producers and reduce overall biomass. Our results provide several novel hypotheses regarding the microbial, biogeochemical, and spatial processes that mediate the Birch effect, which will contribute to a better mechanistic understanding of this important deviation from model predictions.

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### 1. Introduction

Pulses of carbon dioxide (CO<sub>2</sub>) emitted when dry soils are rewet were first observed by H. F. Birch in 1958 (Birch, 1958). Numerous studies since then have shown that soil respiration is consistently elevated when preceded by an extended dry period, and can release more carbon (C) when exposed to drying–rewetting (DRW) cycles than when held at constant moisture (Austin et al., 2004; Borken

and Matzner, 2009). The mechanisms that explain this pattern remain elusive. This continues to limit our ability to predict the magnitude of these pulses, which can make up 90% of the C mineralized from some systems (Jacobson and Jacobson, 1998; Huxman et al., 2004). Most ecosystem models currently underestimate CO<sub>2</sub> releases under DRW events, suggesting that the mechanisms that contribute to soil respiration under DRW may differ from those at play under constant moisture (Whitford et al., 1981; Throop and Archer, 2009; Collins et al., 2014). Because DRW cycles will become more common as the earth's hydrologic cycle intensifies, understanding how these rainfall patterns influence C balance is critical (IPCC, 2007).

It has been challenging to precisely describe what gives rise to the Birch effect because the effect is mediated by biological and

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physical factors operating on a micro-scale. This makes the involved mechanisms both highly interactive and methodologically challenging to study. Physical and biological mechanisms influence the Birch effect by altering microbial performance, but the former act through substrate limitation, while the latter impose osmotic stress. Physical factors can exert major control on CO<sub>2</sub> patterns as moisture varies. When soils are dry, water-soluble substrates have reduced rates of diffusion and mass transport. Microbes rely on these substrates for energy and biomass, so when their diffusion is limited in the absence of water films, microbial activity is inhibited (Skopp et al., 1990; Stark and Firestone, 1995). Some enzyme activity may persist during this time, further increasing dissolved substrates under drought (Lawrence et al., 2009; Manzoni et al., 2014). Thus, one cause of the Birch effect is the accumulation of these diffusion-limited substrates under drought and the sudden availability of resources under rewetting. Physical destabilization of soil aggregates under rewetting could further add to this increased carbon availability of rewetting, and subsequent CO<sub>2</sub> pulse (Navarro-García et al., 2012).

Because microorganisms are osmotically regulated, fluctuations in moisture level also impose a direct physiological stress on microbial performance. For instance, when moisture is limited, microbes must allocate more resources toward maintenance and stress tolerance, and less to growth (Schimel et al., 2007). This variation in microbial activity, biomass, and resource allocation can also alter respiration patterns under fluctuating water potentials. At the most extreme, microbial death from osmotic stress under either drought or a sudden rewetting can reduce biotic potential and increase resource (necromass) availability. But susceptibility to these outcomes may vary among taxa, making the traits that characterize a microbial community important for its overall response to water variability. In particular, certain traits or life-history strategies can increase the tolerance of microbial communities to drought or to rewetting stress (Van Gestel et al., 1993; Halverson et al., 2000; Evans and Wallenstein, 2014). Since these traits are involved in tradeoffs, often related to C allocation, changes in the relative abundance of organisms with these traits can alter predictive relationships between C efflux and soil moisture (Evans and Wallenstein, 2012).

While it is generally accepted that both biological and physical mechanisms can contribute to the Birch effect, their relative roles and influences on biogeochemical dynamics have been difficult to identify empirically, due to the scales on which they occur. Using a model, Lawrence et al. (2009) found that bio-available substrate could accumulate through persistent enzyme activity (despite decreased metabolic activity), mediating the Birch effect. This suggests that the greater availability of additional substrate under rewetting is what stimulates a large CO<sub>2</sub> pulse. Other studies have found that adding labile C under rewetting amplifies CO<sub>2</sub> release (Xiang et al., 2008; Jenerette and Chatterjee, 2012), supporting the idea that microbes are substrate-limited under rewetting, and that additional dry days would cause substrate accumulation and increasingly large rewetting pulses. There is also empirical support for the role of biological processes in mediating the Birch effect. Respiration rates can correlate with microbial biomass and soil C:N ratio (Borken and Matzner, 2009; Jenerette and Chatterjee, 2012), suggesting biotic potential constrains (and possibly controls) pulse size. Carbon dynamics under DRW can also be influenced by microbial community composition (Fierer et al., 2003; Evans and Wallenstein, 2012), presumably because taxa employ different life-history strategies that influence their response to rewetting (Evans and Wallenstein, 2014). Without the ability to measure all processes simultaneously and manipulate them on the (micro-) scale on which they occur, it is difficult to understand their interactions or quantify their individual contributions to respiration.

Individual-based models have been used to link local interactions – like those between microbes and their immediate soil habitat – to emergent properties or functions they mediate. Thus, such models are well suited to address questions in a soil environment, where primary controls on processes are occurring on a vastly different scale than our measurements of the processes (Wang and Or, 2010; Moyano et al., 2013). In this study, we examine the biogeochemical and microbial dynamics that occur under DRW, and study the relative effects of different mechanisms mediating the production of CO<sub>2</sub> on fine spatial and temporal scales. We use a spatially explicit individual-based model previously developed by Kaiser et al. (2014), in which microorganisms and the biogeochemical dynamics they mediate are simulated on a 1 mm × 1 mm soil grid containing 10,000 soil microsites in 1-h time steps. By linking diffusion of labile substrates and microbial physiology to moisture level, we address the following three questions:

- 1) What processes contribute to high rates of CO<sub>2</sub> flux after rewetting dry soils?
- 2) What are the relative roles of biological and physical mechanisms in respiration patterns under DRW?
- 3) Does microbial functional diversity alter the mechanisms that explain the Birch effect?

## 2. Methods

### 2.1. Model structure

The model used in this study builds upon the individual-based microbial community model described in detail in Kaiser et al. (2014). The model operates on a grid of 100 × 100 microsites that each have a size of 10 μm × 10 μm × 10 μm, resulting in a total grid size of 1 mm × 1 mm. The grid boundaries are cyclic, with each grid edge connecting to its opposite edge, forming a torus. Microorganisms distributed in grid cells produce extracellular enzymes that catalyze organic matter into dissolved organic matter (DOM), which they use for enzyme production and growth. Microbial respiration consists of maintenance respiration (a fixed fraction of biomass) and respiration required for enzyme production and growth (a fraction of C used for biomass/enzyme buildup). Additional microbial “overflow” respiration occurs when the C:N ratio of available DOM exceeds the ratio of the microbes' C:N demand (Schimel and Weintraub, 2003). Microbial cells reproduce and randomly colonize a neighboring microsite when they reach a given maximum cell size. While both microbes and enzymes are immobile in the model (except for microbial dispersal in the course of reproduction), DOM moves between neighboring microsites via diffusion. Microbial community dynamics emerge from competition for resources and space.

We model microorganisms belonging to one of two functional groups that primarily differ in whether they produce extracellular enzymes (producers) or do not produce enzymes (cheaters). Producers also possess a larger cell size (dictating the size they are required to reach before they can replicate) and a higher C:N ratio (9.0), whereas cheaters possess a smaller cell size and a lower C:N ratio (6.2). Differences in C:N ratios are based on averages of empirical measurements for these functional groups (Kirchman, 2012). The traits characterizing both groups are listed in Table A1. When the biomass of an individual microbial cell falls below 1/10 of its maximal possible cell size (i.e. due to starving), the cell enters into a low-metabolic dormant state, in which it still occupies a microsite, but utilizes no resources. Cells revive from this state when resources become available. We use these two groups to examine the effects of functional diversity on DRW respiration.

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