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Soil life in reconstructed ecosystems: Initial soil food web responses after rebuilding a forest soil profile for a climate change experiment

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ABSTRACT

Disrupting ecosystem components, while transferring and reconstructing them for experiments can produce myriad responses. Establishing the extent of these biological responses as the system approaches a new equilibrium allows us more reliably to emulate comparable native systems. That is, the sensitivity of analyzing ecosystem processes in a reconstructed system is improved by excluding the period when observed phenomena are primarily responses caused by establishing the experiment rather than effects of imposed treatments; achieved by determining the extent of any pulse of activity caused by preparatory procedures. A native forest soil was physically disrupted when it was collected, sieved, and then rebuilt in lysimeters in a controlled-environment study evaluating the influence of elevated atmospheric CO₂ concentration and elevated atmospheric temperature on the reconstructed soil that was planted with Douglas-fir (Pseudotsuga menziesii Mirb. Franco) seedlings. Generally, soil food web populations responded in two phases during the exposure as indicated by preliminary evaluation of the 4.5-year dataset. Also, previous work indicated that relatively elevated soil CO₂ effluxes occurred during the first phase, suggesting that food web populations may have responded to carbon sources made available when the soil was harvested and its profile reconstructed in the lysimeters. Results are presented for bacterial and fungal biomass, numbers of protozoa and nematodes to gain insight on whether the first phase responses are attributable to the acute stress of physically disrupting the soil. We found clear relationships between changes in predator and prey populations. A prominent spike for many of the food web populations occurred the year after the climate exposures began. Except for total bacterial biomass and total fungal-hyphae biomass, overall food web responses generally were unrelated to treatments. It appears that initial food web population responses were related to increased availability of soil carbon caused by establishing the experiment. Our results provide insights into determining the length of time to maintain reconstructed forest ecosystems before responses are observed related to experimental treatments. It appears that as long as 3 years elapsed before the soil food web appeared to recover from the acute physical disturbance; 1 year of recovery prior to commencing the climate exposures to allow the soil to rest after it was reconstructed, plus approximately the first 2 years of maintaining the climate treatments. Accounting for consequences of such periods of adjustment is critical for forecasting whether comparable natural ecosystems will be net sources or sinks of elevated concentrations of atmospheric CO₂.

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1. Introduction

Disrupting ecosystems can produce a variety of transient and longer term responses. These may include system energetics,

nutrient cycling, the structure of a community, and a number of general system-level characteristics, e.g., the reversal of autogenic successional trends, increased tendencies for parasitism and other negative interactions, and decreased tendencies for mutualism and other positive interactions (Odum, 1985). For studies examining the fate of C in response to climate change drivers, the amount of soil organic matter (SOM) in a physically disturbed soil initially can rapidly decrease (Davidson and Ackerman, 1993), and nitrogen (N) mineralization and nitrification can be stimulated (Johnson et al., 1995 and references therein).

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Whether the reconstructed system emulates the comparable native system is one issue to address in all studies involving reconstructed ecosystems. Johnson et al. (1995) examined this question while studying effects of CO_2 and N on growth of Ponderosa pine (*Pinus ponderosa* Laws.) seedlings. They found that their results for the controlled-environment chamber study, which utilized $0.027~\text{m}^3$ pots, contradicted those obtained in the comparable field study. Increased rates of N mineralization became evident soon after the experiment was initiated resulting in a redesign of the sampling protocol to address whether the pot systems would recover during the 32-week experiment.

Odum (1985) suggested that disturbance will lead to enriched food webs as resources become available or the environment becomes more favorable for the enriched food web. This does not imply that an enriched food web is preferable, but rather that more microbial food resources become available. These food sources may be derived from plant material killed by the disturbance or from organic matter previously unavailable to microbes. As Odum (1985) postulated, such a condition can be indicated by increased community respiration as the system "pumps out" the short-term disorder (Westerman and Kurtz, 1973; Hoosbeek et al., 2004; Hirotsugu et al., 2007; Ohm et al., 2007), i.e., the system comes to equilibrium again. Lin et al. (2001), working in our chambers, found evidence generally consistent with this response. Using stable isotope signatures of soil CO2 efflux and of its component sources they proportioned total efflux into its sources. The greatest relative changes in proportional contributions occurred in the second year, specifically from oxidation of native SOM that was present when the native soil was initially collected. The authors speculated that increased total CO₂ efflux resulted from enriched food web conditions caused by physically disrupting soil aggregates as the soil was prepared and placed into the lysimeters. They cautioned that such responses, unless understood and noted, can alter inferences drawn from experiments if they are not allowed to recover from disturbances caused by initiating the experiment.

Monitoring food web organisms can reflect responses to various environmental drivers, from daily or weekly (e.g., activity of bacteria and fungi for fluctuations in temperature, moisture, nutrient availability) to seasonally (total bacterial and fungal biomass for carbon availability, temperature and moisture) (Ingham and Thies, 1996). One of the overarching goals of the 4.5-year climate exposure project, of which the research reported herein is a component, was to determine whether the reconstructed soil-seedling systems would be net sources or sinks of C. Examining soil food web dynamics would contribute to meeting this goal by understanding temporal patterns of the detrial food web to create and stabilize SOM. Odum (1985) further suggested that systems may respond differently to chronic stress that continues for an extended period compared with responses to acute stress that are followed by a period of recovery. Our experimental system experienced both an acute stress, i.e., the harvesting of the soil and its placement in the lysimeters, and a chronic stress, i.e., the climate treatments. It would be helpful to any project where the soil system has been perturbed, to be able to assess responses related to such an acute stress as well as assess responses related to the chronic stress. Preliminary observations of the entire food web dataset from the 4.5-year climate exposure period yielded two distinct phases for responses of the soil food web populations; the first phase lasting approximately 2 years (data not shown). Responses of soil food web populations during this initial 2-year period of the climate exposure regimen, plus the procedures used in the year prior to commencing the climate treatments to establish the experimental ecosystems, are the focus of the work reported herein. Results are presented for bacterial and fungal biomass, numbers of protozoa and nematodes. This information will aid in identifying the magnitude of, and length of time for, early system responses that may reflect effects of the acute stress of disturbing the soil. This information also will contribute to estimating the length of time needed to maintain experiments using reconstructed ecosystems to understand the variety of responses observed.

2. Materials and methods

2.1. Experimental facility, soil, seedlings and litter

Twelve SPAR (Soil Plant Atmosphere Research) chambers were used to contain the soil and vegetation, and to provide the altered climate conditions [see Tingey et al. (1996) for details about chamber performance]. Briefly, each chamber has a 1 m \times 2 m footprint (2 m²) and collectively, the 12 independently monitored and controlled chambers form a portion of an environment-tracking, sun-lit, controlled-environment facility that links atmospheric, plant and soil processes. Each chamber consists of a 1 m deep lysimeter (2 m³ vol.), and an aboveground aluminum-framed canopy (1.5 m tall at the back, sloping to 1.2 m tall at the front, 3.18 m³ vol.) that is covered with a 3 mil clear Teflon® film. An important characteristic of the facility is that it can, in real time, simulate natural seasonal and diurnal changes in atmospheric CO2, air and soil temperatures, vapor pressure deficit (VPD), and soil moisture.

The soil was derived from a glacially worked, volcanic parent material and is classified as a coarse-loamy, mixed, frigid, Typic Hapludand. This soil represents about 30% of the soils supporting growth of Douglas-fir in the Oregon Cascade Mountains (personal communication, Douglas Shank, USDA Forest Service, Willamette National Forest). The soil has three master mineral horizons [A horizon (\sim 10 cm thick), a B horizon (\sim 60 cm thick), and a C horizon (\sim 20 cm thick)] and a 6 cm thick forest floor litter surface layer (O horizon). Since the B horizon is large, it was treated as two horizons (B1 and B2, 30 cm each) as it was placed into the lysimeters and instrumentation was installed.

The soil was excavated by horizon adjacent to an old-growth Douglas-fir stand situated at 1220 m in the Cascade Mountains directly east of Corvallis (see Johnson et al., 2006 for more details). Soil collection and placement in the lysimeters was accomplished in two phases. This was done so that the majority of the soil could rest for a period before planting the seedlings, and recover from disturbance caused by its excavation, sieving (>2.5 cm material removed) and placement in the chambers. In phase one, within a few days of arriving in Corvallis in summer 1992, the sieved soil horizons and associated instrumentation and samplers were installed by layers and then each layer tamped to adjust the soil to the native bulk density. The lysimeters were not covered with the chamber canopies until the seedlings were planted (1993). In the interim the soil received only ambient precipitation (i.e., summer drought conditions with increased precipitation occurring from fall through spring).

In phase one, cover crops were planted in the reconstructed partial soil profile to aid in regaining macrostructure, and to reduce the amount of any mineralized nitrogen that may have been produced by relocating the soil. Buckwheat (*Fagopyrum esculentum* Moench) was planted shortly after reconstructing the soil profile and was allowed to grow until shoots were harvested and removed in late Fall 1992. Next, a mixture of faba bean (*Vicia faba* L.) and hairy vetch (*Vicia villosa* Roth) was planted and was allowed to grow until Spring 1993 when shoots were harvested.

Phase two of reconstructing the soil profile occurred in summer 1993, and began 48 h prior to planting the Douglas-fir seedlings when fresh A horizon was collected adjacent to the soil collection site used previously. The A horizon provided fresh native soil flora

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