Soil respiration, leaf litter production, and belowground carbon allocation in the context of a long-term NxP fertilization experiment

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Introduction
Resource partitioning in plants

Over the last 150 years, the global carbon cycle has been disrupted by the anthropogenic enhancement of atmospheric carbon dioxide (CO_2) concentrations (Quéré et al., 2018). Because of the role of carbon as the foundational element of all life on Earth, its effects upon global climate patterns, and its influence upon a number of biogeochemical processes, understanding how carbon moves through natural systems and how those systems will be affected by the disruption of the carbon cycle is of critical importance. Vegetation constitutes a major pool in the global carbon cycle, storing as much as 650 gigatons of carbon, or the equivalent of 75% of the atmospheric carbon dioxide (CO_2) reservoir (Quéré et al., 2018). Through photosynthesis, plants transform CO_2 into chemically stable carbohydrates, an energy source that can be transported to support vital functions such as growth, defense, reproduction, and nutrient acquisition. All of a plant's chemical resources—and these energy-rich carbohydrates in particular—are distributed such that growth-limiting nutrients can be acquired at higher rates (Chapin et al., 1987); that is, when demand for a particular nutrient is high, available resources are invested heavily in tissues, cells, or proteins specialized in the acquisition of that nutrient. As such, nutrient supply and demand act as powerful drivers of resource partitioning, pushing all plants toward an optimized equilibrium state in which resources are allocated so that all nutrients are equally limiting to plant growth (Bloom et al., 1985; Litton et al., 2007; Rastetter & Shaver, 1992).

The primary goal of this study is to test for an effect of soil nitrogen (N) and phosphorus (P) availability on litterfall and soil respiration, two of the largest fluxes in the carbon cycle of temperate forests. These data will also allow for an estimation of belowground carbon allocation (BGCA) using the following approximation proposed by Raich and Nadelhoffer (1989): BGCA = soil respiration - litterfall. In sum, the following questions will be explored:
1. Is soil respiration affected by N and P addition?
2. Is leaf litter production affected by N and P addition?
3. How are patterns of BGCA affected by nutrient additions?

Methods
Site Description

This study was conducted in thirteen stands in the White Mountains of New Hampshire, USA. Stands are of three successional stages: young (30-35 years old), mid-successional (42-50 years old), and mature (91-137 years old). Stands are spread across three sites in the White Mountain National Forest: nine at Bartlett Experimental Forest (BEF), two at Hubbard Brook Experimental Forest (HBEF), and two at Jeffers Brook (JB). Tree species composition varies across stands, but mature stands are representative of the typical northern hardwood forest: sugar maple (*Acer saccharum*), paper birch

(*Betula papyrifera*), yellow birch (*B. alleghaniensis*), and American beech (*Fagus grandifolia*). Young and mid-successional consist of red maple (*A. rubrum*), striped maple (*A. pensylvanicum*), pin cherry (*Prunus pensylvanica*), yellow birch, and American beech. Soils in all stands were formed in glacial till and are predominantly Spodosols with a wide range of drainage characteristics (Bailey, 2020).

The study stands are part of the Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE) study, established in 2011 as the first long-term full-factorial NxP fertilization experiment in a temperate forest. MELNHE is currently funded by the United States Department of Agriculture and the National Science Foundation. Within each of the 13 stands in the MELNHE project are four treatment plots, each of which receives one of four nutrient treatments annually: N addition (30 kg N ha^{-1} yr^{-1} in the form of NH_4NO_3), P addition (10 kg P ha^{-1} yr^{-1} in the form of NaH_2PO_4), N plus P (at the same rates), or neither. Within each plot is an "inner" area in which nutrient additions were made. Soil respiration and litterfall measurements will be made in this area as well.

Field methods

Leaf litter has been collected annually in the MELNHE stands since 2008. Collections are made from five litter traps systematically arranged in each 30m x 30m treatment area: four baskets are about 22 meters from the corners of the treatment area and one is in the center. Twigs and other woody materials are removed from collected samples, and the samples are oven-dried at 60°C before their oven-dried mass is recorded. For this study, the litterfall record spanning 2008 to 2020 will be analyzed.

Soil respiration has been measured in these stands since 2008 using LiCOR devices. The number of measurements recorded each year and the stands in which those measurements were made has varied from one year to the next (Table 1). Respiration collars are systematically distributed throughout each inner treatment area, and 90-second measurements of soil CO_2 efflux are made at each collar. Thanks to the funding provided by the Sussman foundation, the 2020-2021 sampling year will be the most complete sampling year in the dataset, with measurements taking place at every stand beginning from spring 2020 and lasting until the first snowfall of autumn 2020.

Finally, BGCA will be approximated and tested for responses to N and P addition. This approximation will be made using the method proposed by Raich and Nadelhoffer: BGCA $\approx R_s - P_a$, where R_s represents soil respiration and P_a represents aboveground detrital inputs (Raich & Nadelhoffer, 1989).

Preliminary results

Preliminary analysis of data collected in 2020 indicates that soil respiration is reduced 17% by N addition ($p=0.03$). This is a well documented phenomenon consistent with previous findings conducted on these sites (Kang et al., 2016) and in other long-term N-addition studies (Bowden et al., 2004). Soil respiration typically increases shortly after N additions begin but is reduced following years of continual fertilization. This suppressive effect has been attributed to changes in the soil microbial community and reductions in root activity caused by excess N.
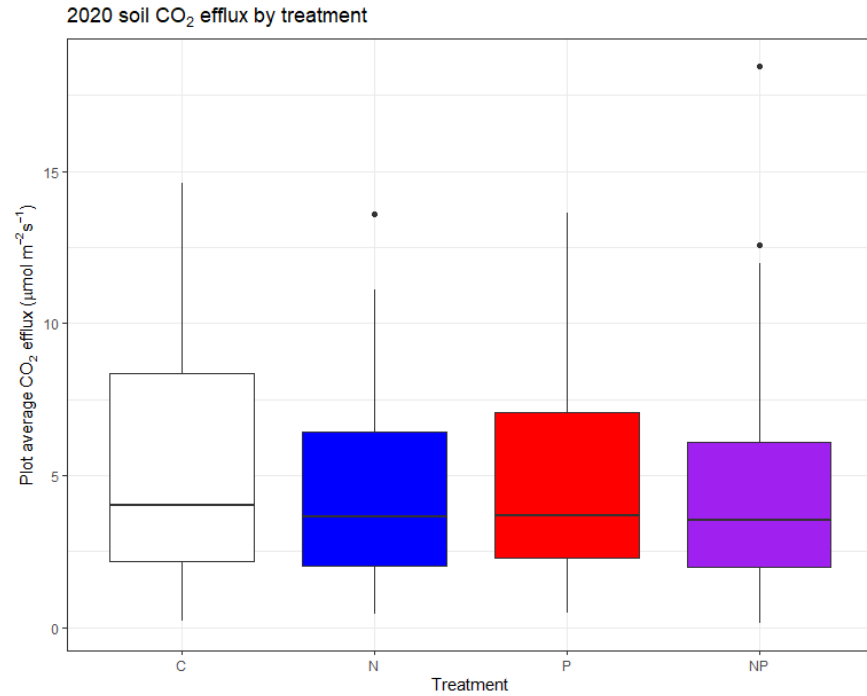
Figure 1. 2020 soil CO_2 efflux by treatment

Because of the essential role that N plays in the structure of chlorophyll and RuBisCO—and the traditional thinking that vegetative productivity in northern hardwood forests is N-limited—I expected the litter data to show evidence of N limitation. However, preliminary analysis shows that in 2020, litter production was reduced 6% by P addition (p=0.04, Figure 2).
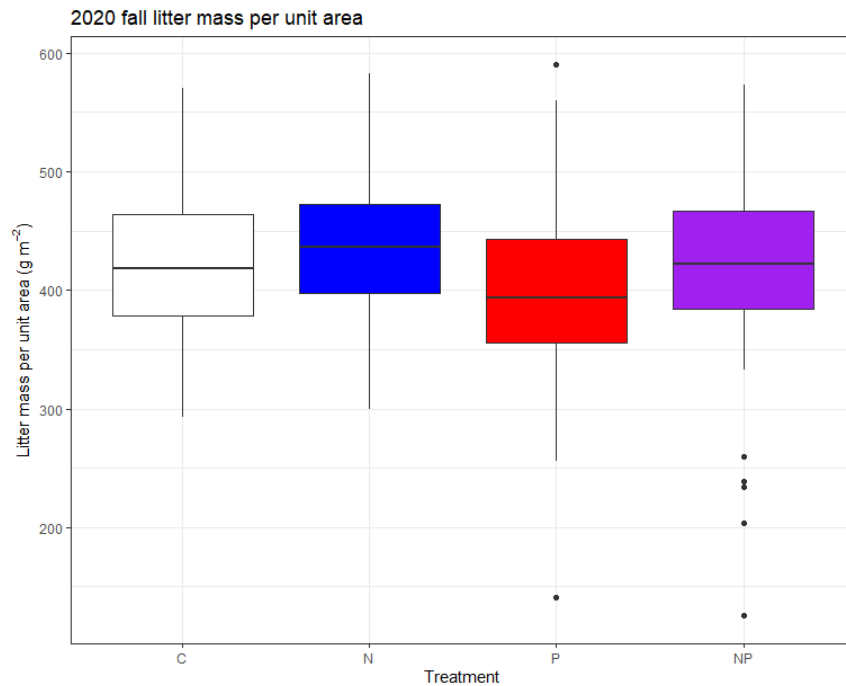
Figure 2. Litter mass per unit area by treatment

This finding is even more surprising when considering the outcomes of other studies conducted in the MELNHE experiment. Specifically, Goswami et al. (2018) reported that P addition significantly increased the annual relative basal area increment of trees in the MELNHE study. Since foliage is the engine that drives vegetative productivity, one might expect that litter mass would mirror growth outcomes, but these preliminary results show the opposite effect. It may be the case, however, that with added P, trees in the northern hardwood ecosystem are simply able to grow more efficiently, achieving greater growth with less investment in foliar production. While N is indisputably essential to photosynthesis, P availability has been found to affect several steps of the Calvin cycle (Campbell & Sage, 2006) and is a key element of important metabolic compounds such as ATP and $NADP^+$. Perhaps greater P availability increases photosynthetic efficiency by facilitating the production of these compounds, thereby limiting the need for a carbon investment in foliage. This would seem to be supported by other research (Reich et al., 2009) and help to explain the growth effect of added P.

Current and future work

Next steps in this project will include integrating the 2020 soil respiration and litter data into the long-term MELNHE record and reproducing analyses like those done here using the complete datasets. Then, I plan to generate annual soil respiration and litterfall budgets in order to estimate BGCA. As discussed previously, doing so will offer a more complete understanding of how N and P control two of the largest components of the terrestrial carbon cycle. Specifically, it will shed light on the processes that result in fluxes into and out of the soil carbon pool, which is among the largest reservoirs of global carbon. When this research is complete, I hope to publish the product in a peer-reviewed journal. Without the support of the Edna Bailey Sussman Fund, this research—and the products that will be generated because of it—would not have been possible, and I am grateful for their generosity.

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