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Corresponding Author	FamilyName	**Yanai**
	Particle	
	Given Name	**R. D.**
	Suffix	
	Division	Department of Sustainable Resources Management
	Organization	State University of New York College of Environmental Science and Forestry
	Address	1 Forestry Drive, Syracuse, New York, 13210, USA
	Phone	
	Fax	
	Email	rdyanai@syr.edu
	URL	
	ORCID	http://orcid.org/0000-0001-6987-2489
Author	FamilyName	**Mann**
	Particle	
	Given Name	**T. A.**
	Suffix	
	Division	Department of Sustainable Resources Management
	Organization	State University of New York College of Environmental Science and Forestry
	Address	1 Forestry Drive, Syracuse, New York, 13210, USA
	Phone	
	Fax	
	Email	
	URL	
	ORCID	
Author	FamilyName	**Fahey**
	Particle	
	Given Name	**T. J.**
	Suffix	
	Division	Department of Natural Resources
	Organization	Cornell University
	Address	Ithaca, New York, 14853, USA
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

Author	FamilyName	**Reinmann**
	Particle	
	Given Name	**A. B.**
	Suffix	
	Division	Environmental Science Initiative
	Organization	CUNY Advanced Sciences Research Center
	Address	New York, New York, 10031, USA
	Division	Department of Geography and Environmental Science
	Organization	Hunter College
	Address	New York, New York, 10065, USA
	Phone	
	Fax	
	Email	
	URL	
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Abstract

Soil respiration is the largest single efflux in the global carbon cycle and varies in complex ways with climate, vegetation, and soils. The suppressive effect of nitrogen (N) addition on soil respiration is well documented, but the extent to which it may be moderated by stand age or the availability of soil phosphorus (P) is not well understood. We quantified the response of soil respiration to manipulation of soil N and P availability in a full-factorial N x P fertilization experiment spanning 10 years in 13 northern hardwood forests in the White Mountains of New Hampshire, USA. We analyzed data for 2011 alone, to account for potential treatment effects unique to the first year of fertilization, and for three 3-year periods; data from each 3-year period was divided into spring, summer, and fall. Nitrogen addition consistently suppressed soil respiration by up to 14% relative to controls ($p \leq 0.01$ for the main effect of N in 5 of 10 analysis periods). This response was tempered when P was also added, reducing the suppressive effect of N addition from 24 to 1% in one of the ten analysis periods (summer 2012–2014, $p = 0.01$ for the interaction of N and P). This interaction effect is consistent with observations of reduced foliar N and available soil N following P addition. Mid-successional stands (26–41 years old at the time of the first nutrient addition) consistently had the lowest rates of soil respiration across stand age classes (1.4–6.6 µmol CO_2 m−2 s−1), and young stands had the highest (2.5–8.5 µmol CO_2 m−2 s−1). In addition to these important effects of treatment and stand age, we observed an unexpected increase in soil respiration, which doubled in 10 years and was not explained by soil temperature patterns, nutrient additions, or increased in fine-root biomass.

Keywords (separated by '-')

MELNHE - multiple element limitation - fine-root biomass - Hubbard brook - Bartlett - Jeffers brook

Footnote Information

Author Contributions: TJF designed the soil respiration study and oversaw data collection from 2008 to present. TAM collected the most recent 2 years of data and analyzed the full time series, with input from ABR, who also analyzed the root biomass data. The manuscript was drafted by TAM and improved by RDY and TJF, with input from ABR. RDY herded cats in the overall MELNHE study, which was the brainchild of TJF.The online version contains supplementary material available at https://doi.org/10.1007/s10021-024-00912-1.

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Nitrogen and Phosphorus Addition Affect Soil Respiration in Northern Hardwood Forests

T. A. Mann,[1] R. D. Yanai,[1]* T. J. Fahey,[2] and A. B. Reinmann[3,4]

[1]Department of Sustainable Resources Management, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, New York 13210, USA; [2]Department of Natural Resources, Cornell University, Ithaca, New York 14853, USA; [3]Environmental Science Initiative, CUNY Advanced Sciences Research Center, New York, New York 10031, USA; [4]Department of Geography and Environmental Science, Hunter College, New York, New York 10065, USA

ABSTRACT

Soil respiration is the largest single efflux in the global carbon cycle and varies in complex ways with climate, vegetation, and soils. The suppressive effect of nitrogen (N) addition on soil respiration is well documented, but the extent to which it may be moderated by stand age or the availability of soil phosphorus (P) is not well understood. We quantified the response of soil respiration to manipulation of soil N and P availability in a full-factorial N x P fertilization experiment spanning 10 years in 13 northern hardwood forests in the White Mountains of New Hampshire, USA. We analyzed data for 2011 alone, to account for potential treatment effects unique to the first year of fertilization, and for three 3-year periods; data from each 3-year period was divided into spring, summer, and fall. Nitrogen addition consistently suppressed soil respiration by up to 14% relative to controls ($p \leq 0.01$ for the main effect of N in 5 of 10 analysis periods). This response was tempered when P was also added, reducing the suppressive effect of N addition from 24 to 1% in one of the ten analysis periods (summer 2012–2014, $p = 0.01$ for the interaction of N and P). This interaction effect is consistent with observations of reduced foliar N and available soil N following P addition. Mid-successional stands (26–41 years old at the time of the first nutrient addition) consistently had the lowest rates of soil respiration across stand age classes (1.4–6.6 µmol CO$_2$ m^{-2} s^{-1}), and young stands had the highest (2.5–8.5 µmol CO$_2$ m^{-2} s^{-1}). In addition to these important effects of treatment and stand age, we observed an unexpected increase in soil respiration, which doubled in 10 years and was not explained by soil temperature patterns, nutrient additions, or increased in fine-root biomass.

Key words: MELNHE; multiple element limitation; fine-root biomass; Hubbard Brook; Bartlett; Jeffers Brook.

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*Corresponding author; e-mail: rdyanai@syr.edu

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HIGHLIGHTS

- Nitrogen addition reduced soil respiration by up to 14% in northern hardwood forests.
- Soil respiration was lowest in mid-successional stands (26-41 years since harvest).
- Soil respiration doubled in 10 years and was not explained by increasing temperature.

INTRODUCTION

The largest fluxes in the global carbon cycle are the movements of carbon into and out of terrestrial ecosystems by photosynthesis and respiration, respectively (Le Quéré and others 2018). In temperate broadleaf forests, about 70% of ecosystem respiration comes from soils (Goulden and others 1996; Janssens and others 2001; Law and others 1999; Ryan and Law 2005), and rates of soil respiration change as forests progress through successional development. Because soil temperature is one of the primary drivers of soil respiration (Luo and others 2001; Bronson and others 2008; Bond-Lamberty and Thomson 2010), young stands exhibit high rates of soil respiration prior to canopy closure (Ewel and others 1987; Xiao and others 2014). Fine-root biomass, which reaches a maximum at canopy closure (Peichl and Arain 2006; Helmisaari and others 2002), likely contributes to the high soil respiration associated with young stands as well. Available nitrogen (N) decreased for the first 20 years following clearcutting and reached a maximum roughly 50 years later in aspen stands in Michigan (White and others 2004). Perhaps as a result of these multiple factors, studies of soil respiration across stand age have come to inconsistent conclusions: Some studies report increases in soil respiration with age (Gough and others 2005), some report a decrease (Ewel and others 2011; Tedeschi and others 2006), and another reports interannual variation in the effect of stand age on soil respiration (Irvine and Law 2002). On top of these developmental factors, seasonal changes in microbial communities (Sorensen and others 2018) and rates of root growth (Abramoff and Finzi 2016) could also be expected to affect soil respiration.

Generally, rates of carbon partitioning belowground—and therefore soil respiration—are higher in low-fertility forests because greater effort is required for soil resource acquisition (Bae and others 2015; Bloom and others 1985; Gower and others 1994; Litton and others 2007). Relationships between N availability and forest carbon cycling are particularly well studied, and much of that research has demonstrated reduced soil respiration with increased N availability (Bowden and others 2004; Burton and others 2004; Bae and others 2015; Kang and others 2016). Mechanistically, responses of the soil priming effect to N addition can explain the suppression of soil respiration: when soil nutrients are scarce, autotrophic inputs of labile carbon and N stimulate the turnover of more recalcitrant pools of carbon, releasing resources that were previously immobilized in that recalcitrant material and increasing belowground respiration from autotrophs and heterotrophs alike (Kuzyakov and others 2000). In contrast, when nutrients are readily available–as is the case when N is added in experimental conditions–nutrient acquisition does not depend upon those immobilized resources that are released through soil priming, and soil respiration decreases. Further, under conditions of N excess, added N can reduce rates of decomposition through the down-regulation of the activity of ligninolytic enzymes (Carreiro and others 2000; Knorr and others 2005).

While the preponderance of evidence indicates that N addition suppresses soil respiration, other factors help to determine the magnitude of that effect. Duration of fertilization (Bowden and others 2004; Burton and others 2004; Nohrstedt and others 1989), site fertility, and stand age (Kang and others 2016) can all affect the degree to which soil respiration is reduced by added N. Importantly, Bowden and others (2004) detected an initial increase in soil respiration in northern hardwood stands treated with added N followed by a long-term suppressive effect. Clarifying the effects that these variables have on soil respiration will improve understanding of this important source of atmospheric carbon.

Although temperate forests have long been assumed to be N limited, there is increasing evidence that both N and phosphorus (P) are important and may be co-limiting (Elser and others 2007; Vadeboncoeur 2010; Rastetter and others 2013). The study of Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE) in the White Mountains of New Hampshire is the longest-running NxP manipulation experiment in a temperate forest, and it provides an excellent setting for exploring relationships among nutrient availability, stand age, and many ecosystem characteristics. Among other findings, the MELNHE study has detected increased tree-diameter growth in response to added P (Goswami and others 2018) and fine-root growth responses to added N (Shan and others 2022) or N plus P (Li and others 2023). To date, few studies outside of those conducted within the MELNHE experiment (Kang and others 2016; Bae and others 2015) have explored the interactive effects of site fertility and stand age on soil respiration, and few studies have tested how N availability may interact with availability of P or other macronutrients, such as P (Zheng and others 2023).

In this study, we tested for effects of low-level N and P addition on soil respiration across stands of three age classes in the MELNHE experiment. Our dataset spans 10 years of treatments (2011–2020) and includes three seasons (spring, summer, and fall) of soil respiration measurements. Fine-root biomass was measured in 2015–2016 to serve as a covariate for soil respiration. We predicted that soil respiration would be highest in young stands (25–35 years old) prior to canopy closure and that the response to nutrient additions would be most pronounced in these stands. We expected a reduction in soil respiration due to N addition, as has been observed in similar experiments (Burton and others 2004), but not due to P addition, in keeping with a recent meta-analysis of forest studies (Zheng and others 2023). With regard to temporal effects, we expected transient responses to treatments as various ecosystem components adjusted to changing soil nutrient availability (Bowden and others 2004). Finally, we predicted that the effect of N and P addition on soil respiration would vary by season, reflecting seasonal changes in root growth and soil microbial communities.

METHODS

Site Description

This study was conducted in 13 stands in the White Mountain National Forest of New Hampshire, USA (Table 1). Stands were of three successional stages: two early successional stands (19–21 years old at the beginning of the study in 2009), six mid-successional stands (24–39 years old in 2009), and five mature stands (80–126 years old in 2009). Stands were located in three sites: nine at Bartlett Experimental Forest (44°2–4‘ N, 71°9–19‘ W; elevation 250–500 m), two at Hubbard Brook Experimental Forest (43°56‘ N, 71°44‘ W; elevation 500 m), and two at Jeffers Brook (44°2′ N, 71°53′ W; elevation 730 m). Soils in all stands were formed in glacial drift and are predominantly Spodosols with a range of drainage characteristics (Bailey 2020; Vadeboncoeur and others 2012). Precipitation is evenly distributed throughout the year and amounts to about 145 cm annually (Hubbard Brook Watershed Ecosystem Record 2021). Average daily temperatures at Hubbard Brook Experimental Forest range from −8 °C in January to 19 °C in July (USDA Forest Service 2020), but differences in elevation and aspect across the sites result in considerable temperature differences. Since 1965, total inorganic N deposition measured at Hubbard Brook W6 has declined from a maximum of 10 kg ha^{-1} y^{-1} in 1991 to a minimum of 2 kg ha^{-1} y^{-1} in 2020, averaging 4 kg ha^{-1} y^{-1} from 2009 to 2020, the period of our study (Hubbard Brook Watershed Ecosystem Record 2021). Phosphorus deposition is very low (0.04 kg P ha^{-1} y^{-1}), usually below detection (Yanai 1992).

Tree species composition varied with stand age, as is typical in the northern hardwood forest type (Table 1 and Figure 1). Mature stands were representative of the typical northern hardwood forest: sugar maple (*Acer saccharum* Marsh.), yellow birch (*B. alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.). Young and mid-successional stands consisted of red maple (*A. rubrum* L.), striped maple (*A. pensylvanicum* L.), pin cherry (*Prunus pensylvanica* L.f.), paper birch (*Betula papyrifera* Marsh.), yellow birch, and American beech.

Each of the 13 MELNHE stands includes four treatment plots, each of which has received one of four nutrient treatments annually early in the growing season beginning in 2011: N addition (3 g N m^{-2} y^{-1} in the form of pelletized NH_4NO_3), P addition (1 g P m^{-2} y^{-1} in the form of granular NaH_2PO_4), N plus P (at the same rates), or neither (control). In most stands, plots measure 50 m × 50 m including a 10 m buffer around a 30 × 30 measurement area. Plots in two of the mid-aged stands have smaller measurement areas (20 m × 20 m), and three stands have smaller buffers (5 m to 7.5 m), due to the small size of the stands.

Soil Respiration

Soil respiration collars were constructed using 20 cm I.D. PVC pipe, sharpened and inserted about 3 cm into the forest floor. In 2009, five collars were installed in each plot, avoiding tree boles, boulders, large roots, and areas with severe drainage restriction. In 2010, these collars were moved to more systematic locations, and in 2014, two collars were added to each plot, for a total of seven collars per plot (Fahey and others 2021). Collars were reinstalled and replaced as needed. Soil respiration was measured in all 13 stands from 2009 to 2020 (that is, including two pretreatment years) using the Li-COR 8100 Soil Respiration System (Licor Bio-

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Table 1. Stand Characteristics.

Stand	Site	Age class	Year cut	Elevation (m)	Aspect	Slope (%)	Basal area (m^2 ha^{-1})	Fine-root biomass (g m^{-2})
CI	BEF	Early successional	1990	570	Flat to SE	5–20	9.5	211
C2	BEF	Early successional	1988	340	NE	15–30	10.8	225
C3	BEF	Mid-successional	1985		NNE	8–20	20.9	137
C4	BEF	Mid-successional	1978	410	NE	20–25	26.3	206
C5	BEF	Mid-successional	1976	5?0	NW	20–30	19.7	156
C6	BEF	Mid-successional	1975	460	NNW	13–20	29.6	185
C7	BEF	Mature	-1890	440	ENE	5–10	32.8	279
C8	BEF	Mature	1883	350	NE	5–35	40.5	296
C9	BEF	Mature	1890	440	NE	10–35	31.7	308
HBM	H3EF	Mid-successional	1970	500	S	10–25	27.6	157
HBO	H3EF	Mature	-19[illegible]	500	S	25–35	27.1	254
JBM	JB	Mid-successional	-1[illegible]74	730	WNW	25–35	24.0	133
JBO	JB	Mature	1915-1929	730	WNT.V	30–40	35.6	238

Fine-root biomass was measured in 2015–2016.

sciences, Lincoln, NE) following all manufacturer recommendations. The LiCOR 8100 was re-calibrated by the manufacturer every 2 years through the duration of the study. Measurements were made between 9 AM and 4 PM with most occurring between the hours of 10 AM and 2 PM (Fahey and others 2021). The stands in which measurements were made and the number of times those stands were visited varied across years because of limitations of funding, personnel, or site access. In all years, soil respiration was calculated from 90 s of CO_2 concentration measurements. Soil temperature was measured simultaneously with soil respiration using a handheld resistance thermometer at a depth of 10 cm adjacent to each collar. In total, 16,667 individual soil respiration readings were conducted over the course of the study.

Root Biomass

Soil cores for root biomass were collected in all stands in the late summer of 2015 (stands C1, C2, C4, C6, C7, C9) or 2016 (C3, C5, C8, HBM, HBO, JBM, JBO). Two locations ~ 1 m downslope from each of the original five soil respiration collars were sampled for a total of 10 cores from each plot. When rocks or large roots obstructed the selected sampling location, a nearby alternate location was sampled. Cores were collected to a depth of 30 cm using PVC pipe with an inside diameter of 5 cm and divided by depth into two subsamples: 0 to 10 cm soil depth and 10 cm to 30 cm soil depth.

Fine roots (< 1 mm in diameter) were picked from the soil cores by hand. Roots 1–5 mm in diameter were also picked but are not reported here. Dead roots, which were identified by their lack of structural integrity, were excluded, as were herbaceous roots. Fine roots were oven-dried at 60 °C and weighed.

Data Analysis

Nutrient Addition and Stand Age

We tested for effects of nutrient addition and stand age on soil respiration with repeated-measures, mixed effect analyses of variance (ANOVA) using the ‘lmer’ function in the ‘lme4’ package (Bates and others 2015) in RStudio version 2022.07.2 + 576. Grouping years provided enough data to distinguish responses within seasons and over time, as the number of measurements in any

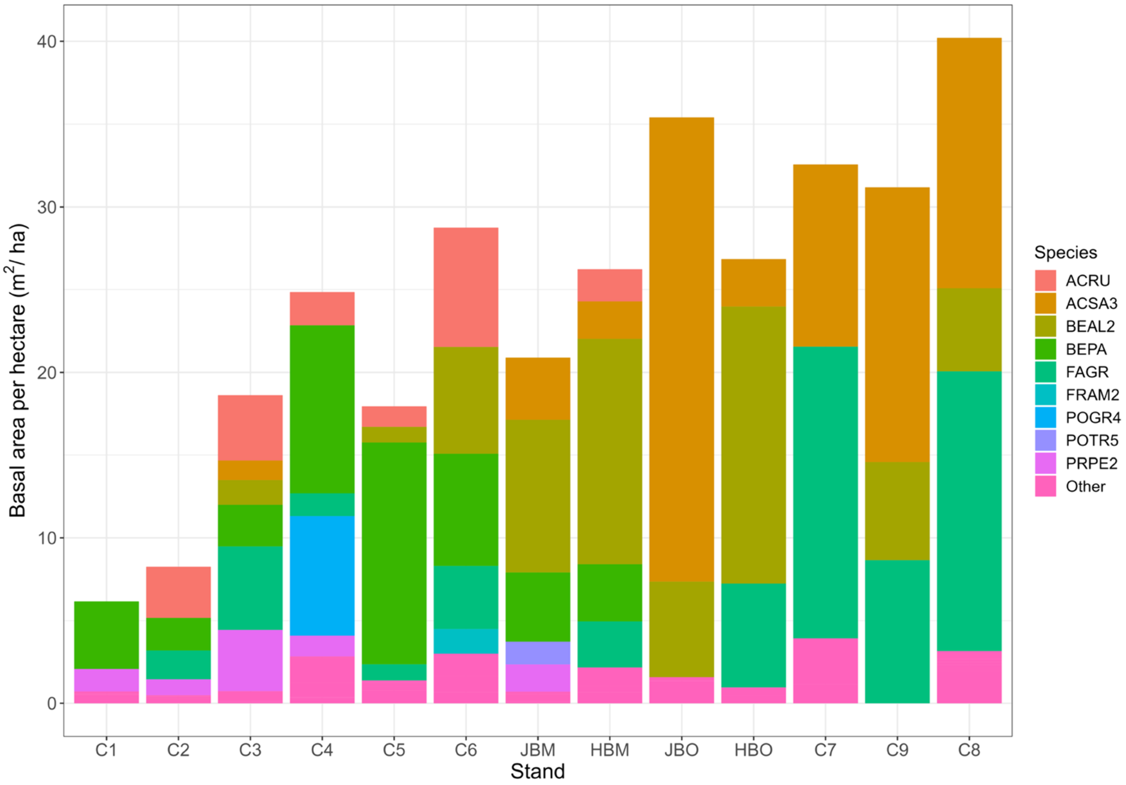


Figure 1. Basal area by species and stand. Stands are arranged from left to right in order of increasing stand age. Tree species are represented using USFS species codes: ACRU = *Acer rubrum*, ACSA3 = *A. saccharum*, BEAL2 = *B. alleghaniensis*, BEPA = *Betula papyrifera*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, POGR4 = *Populus grandidentata*, POTR5 = *P. tremuloides*, PRPE2 = *Prunus pensylvanica*.

given year and season was low. We consistently collected data in the summer, but due to the availability of personnel and access to study sites, spring and fall measurements were collected less frequently (Appendix A). The post-treatment dataset was broken into four time periods to capture transient effects: 2011 (the 1st year of nutrient additions), 2012–2014, 2015–2017, and 2018–2020. Within each of those time periods, the data were analyzed separately by season: spring (March 15–May 31), summer (June 1–August 30), and fall (August 31–November 26). With the exception of spring 2015–2017, measurements were collected in each season in each time period for a total of 11 analysis periods.

The response variable was generated at the plot scale by first taking the median soil respiration rate for each measurement date because the mean was sensitive to the presence of outliers. Those values were then averaged within each analysis period to produce a single value for each plot in each analysis period, because we had only one estimate of root biomass measured in the summer of 2015 or 2016, not one for each visit. Fixed effects were N addition, P addition, stand age, and all their interactions. Stand age was a categorical factor, with stands C1 and C2 classified as early successional; C3, C4, C5, C6, HBM, and JBM classified as mid-successional; and C7, C8, C9, HBO, and JBO classified as mature (Table 1). In addition to those fixed effects, average fine-root biomass (defined here as roots < 1 mm in diameter from 0 to 30 cm soil depth) and soil temperature were included as covariates. Random effects included stand nested within site.

Fine-Root Biomass

When the mixed effect ANOVA described above indicated a significant relationship ($p < 0.05$) between soil respiration and fine-root biomass, those relationships were described with linear equations and coefficients of determination. In these analyses, the response variable was the average of the plot median soil respiration values in the analysis period of interest, and the fixed effect was the average plot root biomass per soil core. These analyses were conducted using the ‘lm’ function in R.

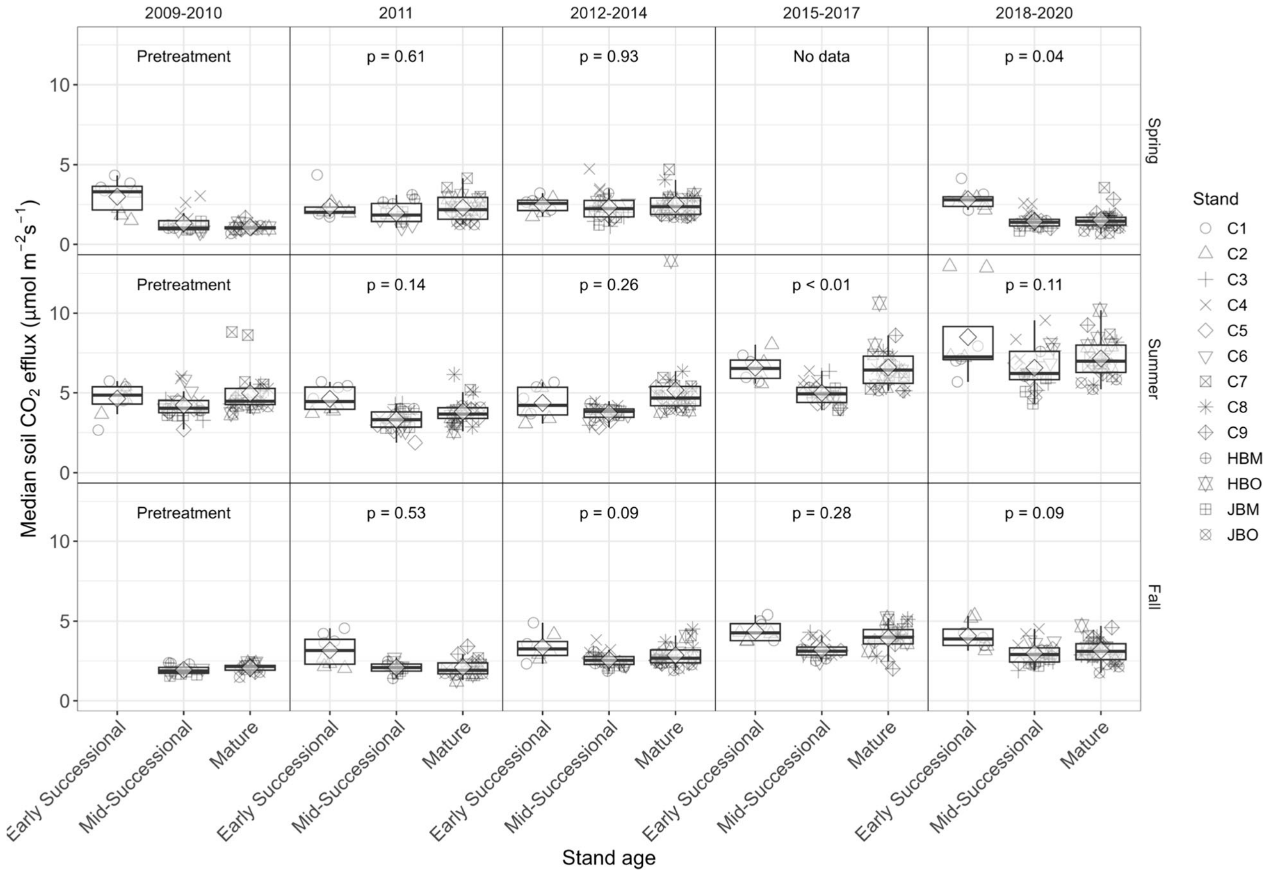


Figure 2. Boxplots of soil respiration by stand age and analysis period. Gray diamonds indicate the average for a given age class. P values indicate significance of the stand age effect in the larger ANOVA model.

Treatment effects on fine-root biomass were analyzed as the response variable in ANOVA of a mixed linear effect model generated using the ‘lmer’ function in the ‘lme4’ R package (Bates and others 2015). This model included stand age, N addition, P addition, and the interaction of N addition and P addition as fixed effects. Random effects included stand nested within site.

Changes in Soil Respiration Over Time

We used a mixed effects linear model to quantify changes in soil respiration from 2009 to 2020 for each season. The response variable for this analysis was the plot median respiration value for the season for each year, log transformed to achieve normality of residuals. Fixed effects were year as a continuous variable, N addition, P addition, and their three-way interaction. A soil temperature covariate, calculated using the median soil temperature in each plot during each season in each year, was also included in the models. Stand nested within site was used as the random effect.

RESULTS

Soil Respiration as a Function of Stand Age and Fine-Root Biomass

Although we predicted that soil respiration would decrease with stand age, mid-successional stands had the lowest rates of soil respiration (averaging 1.4–6.6 μmol CO_2 m^{-2} s^{-1} across stands, depending on the analysis period) and early successional stands had the highest rates (2.5 to 8.5 μmol CO_2 m^{-2} s^{-1}); mature stands were intermediate (1.5 to 7.2 μmol CO_2 m^{-2} s^{-1}). Differences with stand age were significant in both spring 2018–2020 ($p = 0.04$ for the main effect of age) and summer 2015–2017 ($p < 0.01$; Figure 2). Stands of different ages differed significantly in the response of soil respiration to N addition in four analysis periods. With only one exception among those four analysis periods, the suppressive effect of N was strongest in early successional stands, followed by mature stands, then mid-successional stands ($p \leq 0.06$ for the interaction of N x stand age, Figure 3).

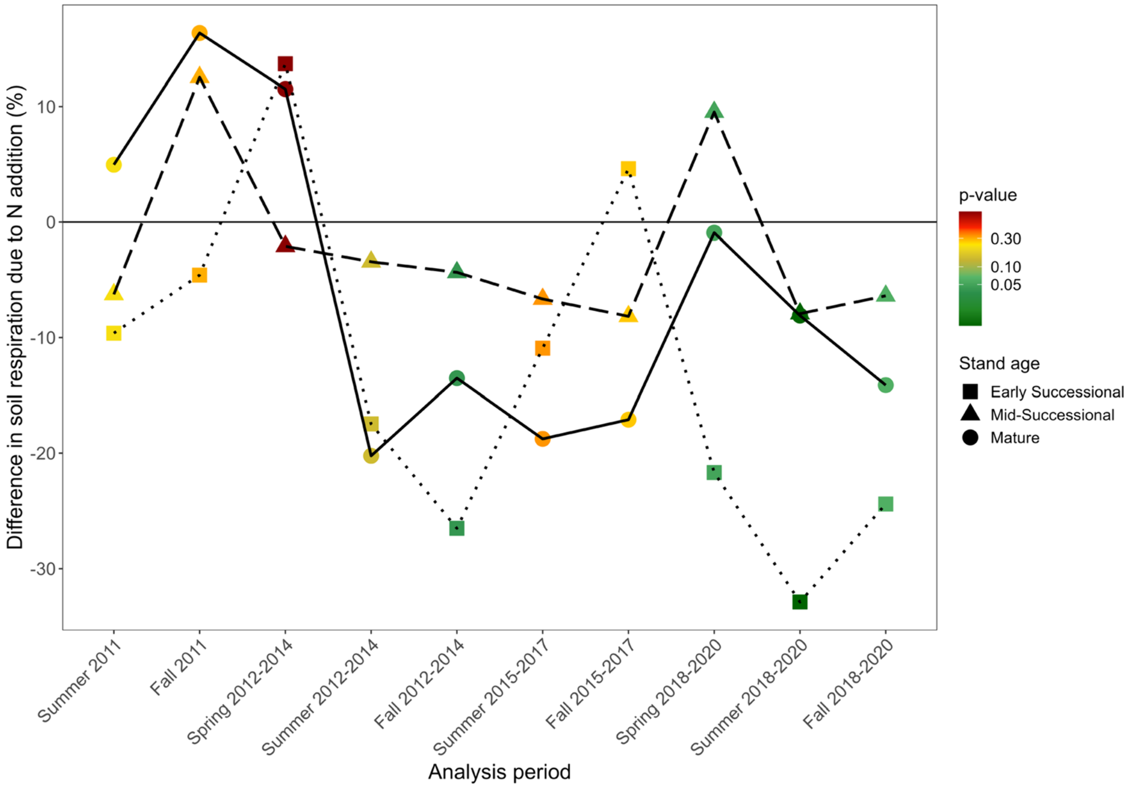


Figure 3. Magnitude of N effect on soil respiration by analysis period and stand age. Colors indicate p-values for analysis of the interaction effect of N and stand age upon soil respiration. No data were collected during spring 2015–2017.

Fine-root biomass, which was measured in 2015–201[illegible]aried with stand age ($p = 0.01$ for the main effect of stand age), with the mid-successional stands having 30% lower root biomass than the young sands and 32% lower root biomass than the mature stands. As expected, soil respiration was positively correlated with fine-root biomass. This relationship was statistically significant in the summer 2012–2014 analysis period, when soil respiration increased by 1.33 μmol CO_2 m^{-2} s^{-1} per gram of fine-root biomass ($p = 0.10$ for the coefficient of fine-root biomass in linear regression, Figure 4). Fine-root biomass was not consistently affected by N addition ($p = 0.31$), P addition ($p = 0.70$), or their interaction ($p = 0.23$).

Soil N Effects on Soil Respiration

Nitrogen addition affected soil respiration either as a main effect or in interaction with another factor in five of 11 analysis periods (Table 2 and Figure 5). N addition resulted in significant declines in soil respiration during summer 2012–2014 (14% decline; $p = 0.01$ for the main effect of N), summer 2015–2017 (13% decline; $p = 0.01$), and summer 2018–2020 (13% decline; $p < 0.01$) analysis periods (Figure 3). We also observed a significant effect of N addition on soil respiration that was consistently strongest in early successional stands (Figure 5, 22–33% suppression during summer analysis periods). This resulted in a significant interaction of N addition and stand age ($p = 0.05$ in spring and $p = 0.01$ in summer).

Soil P Effects on Soil Respiration

Soil respiration was consistently lower in P-treated plots than in their controls (Figure 6), but those differences were not sufficiently consistent to be statistically significant (Table 2), except during fall 2012–2014, when respiration was 6% lower in plots treated with P ($p = 0.04$ for the main effect of P). Unlike the effect of N addition, differences across stand age classes in the effect of P addition on soil respiration were never statistically significant and were not consistent in direction (Figure 6).

Interactive Effects of N and P on Soil Respiration

We found important interactive effects of N and P addition, whereby P tended to ameliorate the suppressive effects of N on soil respiration. In summer 2012–2014, soil respiration was 14%

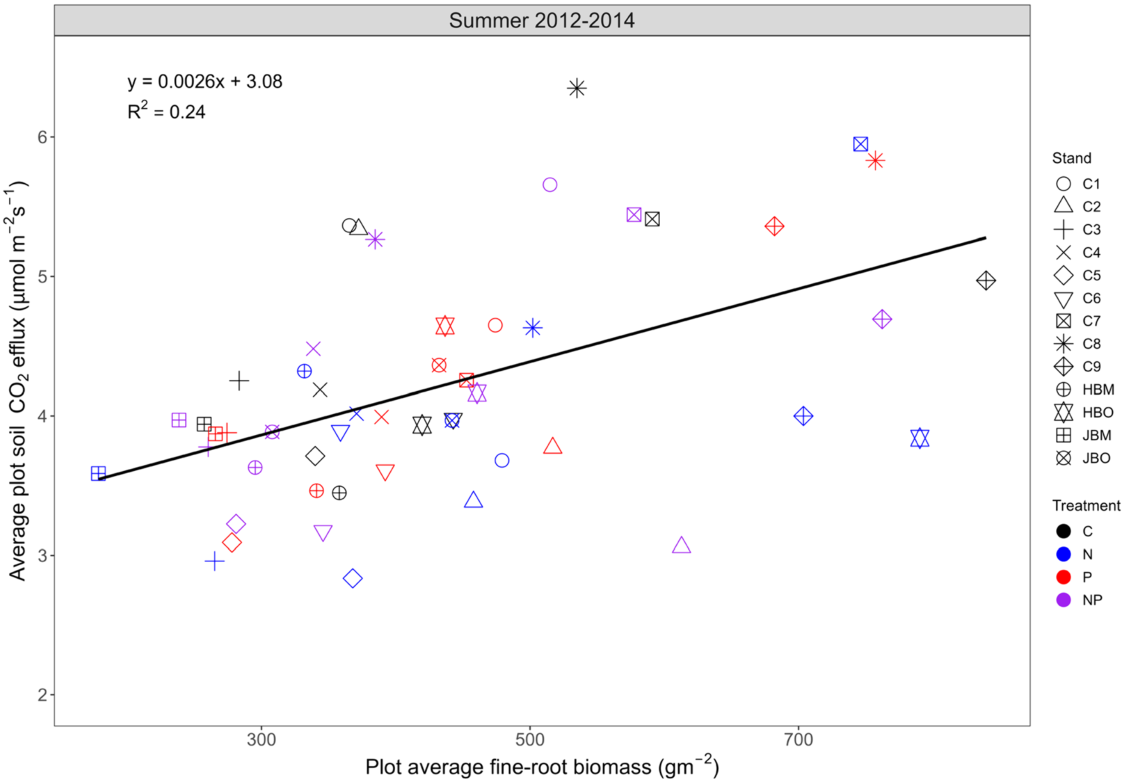


Figure 4. Average soil respiration during summers 2012–2014 as a function of root biomass for all 52 plots reported in this study.

lower in plots receiving N (p = 0.01 for the main effect of N, Figure 3). In that same analysis period, however, while N reduced soil respiration 24% in the absence of P, it reduced soil respiration by only 1% when P was also added (p = 0.01 for the interaction of N x P). In fall 2012–2014, the addition of N alone reduced soil respiration 20%while the addition of N in the presence of added P soil respiration was reduced by only 3%(p < 0.01 for the interaction of N x P). A significant N x P interaction was not detected in any other analysis period.

Increases in Soil Respiration Over Time

Separate from the effects of N and P, we observed an unexpected increase in soil respiration over the course of this study (Figure 7). Between 2009 and 2021, summer soil respiration increased by 7% per year for an 118% increase over that 13-year period (p < 0.01 for the coefficient of year in linear regression). Spring soil respiration increased 11% annually for a 232% increase over the course of the study (p < 0.01), and fall soil respiration increased 5% per year for an increase of 89% over the course of the study (p < 0.01). These time trends were independent of any treatment effects ($p \geq 0.37$ for all interactions of time, N, and P in linear regression), but temperature was positively correlated with soil respiration within each season (p < 0.01 for the coefficient of temperature in spring and fall; p = 0.08 for summer).

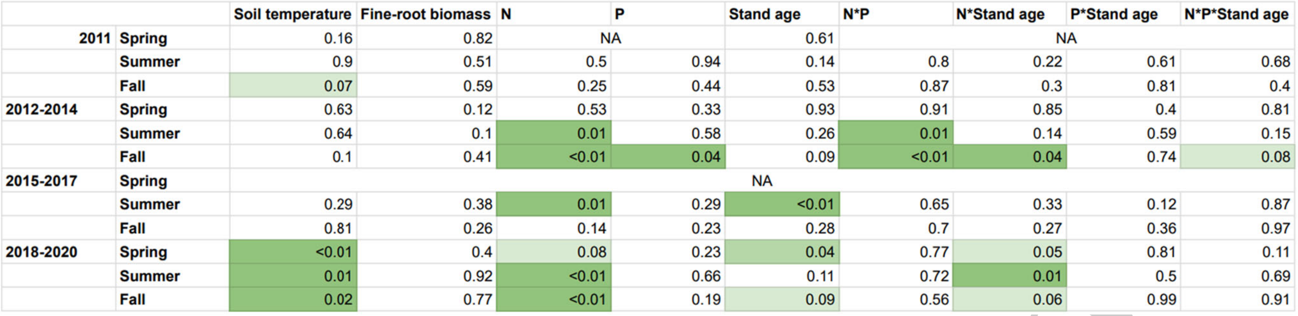
Discussion

Nitrogen Effects

Our finding that N additions reduced soil respiration was consistent with two analyses from our study sites early in the experiment. Pretreatment soil respiration was lowest in plots with high N mineralization and high nitrification (Bae and others 2015). After fertilization began in 2011 until 2013, soil respiration was most reduced in N-fertilized plots in stands with low pretreatment rates of N cycling, specifically N mineralization and litterfall N flux (Kang and others 2016).

Other studies have similarly shown that increased soil N availability suppresses forest soil respiration. For example, 13 years of moderate N

Table 2. *P* Values for Main Effects and Interaction Effects on Soil Respiration by Analysis Period.



		Soil temperature	Fine-root biomass	N	P	Stand age	N*P	N*Stand age	P*Stand age	N*P*Stand age
2011	Spring	0.16	0.82	NA		0.61	NA			
	Summer	0.9	0.51	0.5	0.94	0.14	0.8	0.22	0.61	0.68
	Fall	0.07	0.59	0.25	0.44	0.53	0.87	0.3	0.81	0.4
2012-2014	Spring	0.63	0.12	0.53	0.33	0.93	0.91	0.85	0.4	0.81
	Summer	0.64	0.1	0.01	0.58	0.26	0.01	0.14	0.59	0.15
	Fall	0.1	0.41	<0.01	0.04	0.09	<0.01	0.04	0.74	0.08
2015-2017	Spring	NA								
	Summer	0.29	0.38	0.01	0.29	<0.01	0.65	0.33	0.12	0.87
	Fall	0.81	0.26	0.14	0.23	0.28	0.7	0.27	0.36	0.97
2018-2020	Spring	<0.01	0.4	0.08	0.23	0.04	0.77	0.05	0.81	0.11
	Summer	0.01	0.92	<0.01	0.66	0.11	0.72	0.01	0.5	0.69
	Fall	0.02	0.77	<0.01	0.19	0.09	0.56	0.06	0.99	0.91

Cells shaded dark green contain p-values < 0.05, and cells shaded light green contain p-values > 0.05 and < 0.10.

additions (50 kgN/ha-y) at Harvard Forest in Massachusetts caused a 15% reduction in soil respiration (Bowden and others 2004) similar to that observed after 8 years of low-level N additions (30 kgN/ha-y) in northern hardwood forests in Michigan (Burton and others 2004). Together with these studies, our experiment indicates that a 13–15% reduction may be typical for the effect of long-term N additions on soil respiration in cool temperate broadleaf forests. Although we did not explore the mechanisms driving these responses of soil respiration to N addition, several possible causes have been suggested in the literature. Most studies suggest that suppression of heterotrophic respiration by added N is the primary explanation. For example, Burton and others (2004) indicated that N suppression of soil respiration in sugar maple forests was not caused by reduced root respiration, as root biomass, turnover and specific root respiration rate were unaffected by the treatments. Kuzyakov and others (2000) suggested that because N addition reduces plants' dependence upon N resources generated by microbes, plants contribute less carbon to the belowground community for the purpose of 'priming' decomposition. Because of this reduced carbon influx, effluxes of CO_2 are ultimately reduced. It is also possible that a reduction in microbial biomass or diversity in N-fertilized plots (Compton and others 2004; Allison and others 2007; Frey and others 2004) could be responsible for declines in soil respiration. In a global meta-analysis, Treseder (2008) noted a roughly 15% reduction in microbial biomass under N addition, and this biomass response was correlated with soil respiration responses. Increased N availability may impede lignolytic enzyme activity (Carreiro and others 2000; Janssens and others 2010), especially in high lignin detritus (Knorr and others 2005).

Phosphorus Effects

The absence of a main effect of P was consistent with two previous studies conducted in our study site early in the experiment, which both failed to detect an effect of P on soil respiration. The first study, conducted prior to the annual nutrient additions that began in 2011, found no effect of available soil P on soil respiration (Bae and others 2015). The second study reported that between spring 2010 and September 2013, annual P additions did not affect soil respiration (Kang and others 2016). The absence of a detectable P effect over the duration of the present experiment is consistent with those findings. Similarly, two recent meta-analyses (Feng and Zhu 2019; Zheng and others 2023) concluded that soil respiration is not significantly affected by P addition in temperate forests. Notably, although forest production components typically increase with addition of N and P together, no significant response of soil respiration to combined NP addition was observed for a global meta-analysis (Zheng and others 2023). In contrast, P addition stimulated soil respiration in tropical forests, possibly reflecting very low soil P availability (Feng and Zhu 2019).

The addition of P in the MELNHE study, however, had the effect of reducing resin-available soil N (Fisk and others 2014), and this is reflected in reductions in foliar N under P addition (Gonzales and Yanai 2019; Hong and others 2022). This effect of P on soil N may explain the NP interactions we observed, in which P addition significantly reduced the suppressive effect of N on soil respiration.

Stand Age Effects

Previous studies of the relationship between stand age and soil respiration have found conflicting re-

Figure 5. Plot median soil respiration by treatment and analysis period. Gray diamonds indicate treatment means.

sults, with some reporting increases in soil respiration with age (Gough and others 2005), some reporting a decrease (Ewel and others 2011; Tedeschi and others 2006), and another reporting interannual variation in the effect of stand age on soil respiration (Irvine and Law 2002). Negative relationships between stand age and soil respiration have been attributed to higher soil temperatures in aggrading stands and the large quantities of post-harvest detrital residue (Ewel and others 2011). Positive relationships, on the other hand, are typically attributed to increases in fine-root biomass (Gough and others 2005). In our stands, fine-root biomass was significantly lower in mid-successional stands than in early and late-successional stands (Table 1). As detailed in the Results, in most periods there was a trend toward lowest soil respiration in mid-successional stands (Figure 2) corresponding to the fine-root biomass pattern.

One notable interaction of stand age with treatment was observed. In analysis of summer data from 2018 to 2020, N effects varied by stand age ($p = 0.01$), with the suppression of soil respiration by added N being greatest in early successional stands (32% in early successional stands versus 8% in mid-successional stands and 9% in mature stands). We speculate that this effect could be related to intense competition for environmental resources, including soil nutrients, in the early successional stands (Fahey and others 1994). If the intensity of that competition was relieved by the addition of N, then belowground allocation by those trees might decrease.

Fine-Root Effects

Respiration by tree roots comprises a significant proportion of soil respiration in forest ecosystems. For example, in mature northern hardwood forests at Hubbard Brook, root respiration contributed an estimated 39% of soil respiration (Fahey and others 2005). Thus, a response of root growth or root biomass to nutrient additions would be expected to influence soil respiration. However, as noted earlier, Burton and others (2004) demonstrated that N suppression of soil respiration in four sugar maple stands was not caused by reduced root respiration. Similarly, although we found that fine-root biomass

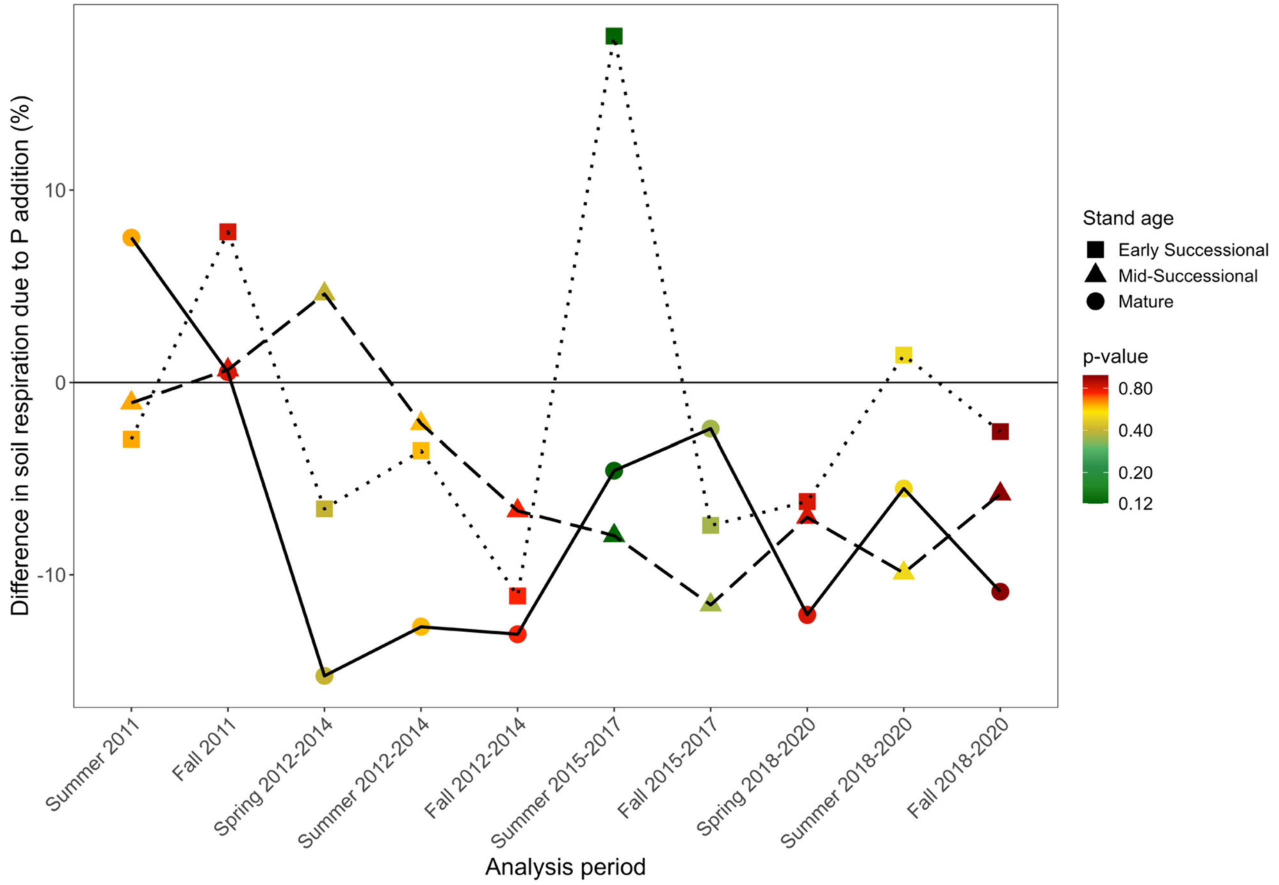


Figure 6. Magnitude of P effect on soil respiration by analysis period and stand age. Colors indicate p-values for analysis of the interaction effect of N and stand age upon soil respiration. No data were collected during spring 2015–2017.

was a significant predictor of soil respiration across our plots ($p = 0.10$), the reduction in soil respiration under N addition was not likely due to changes in root biomass, which actually increased in response to N addition (our unpublished data) and which was included as a covariate in the model.

Fine-root growth has been measured using in-growth cores in several of our stands. Surprisingly, given our observation that N suppresses soil respiration, in the three mature stands at Bartlett, fine-root growth was highest in plots receiving N alone (in 2013–2015; Shan and others 2022), while in two young stands (C1, C2 in 2017–2018) and three mid-age stands (C5, C6, HBM in 2021–2022), root growth was significantly greater in plots treated with both N and P than in control or single-nutrient addition plots (Li and others 2023; Jenn Butt, unpublished). Increases in growth with N or N + P addition would be expected to result in increased soil respiration, but we detected a suppressive effect of N on respiration. Thus, neither fine-root biomass nor fine-root growth explains the suppressive effect of N on soil respiration.

Temporal Effects

We expected transient changes and seasonal differences in the response of soil respiration to nutrient addition as various components of the process adjust to changes in nutrient availability (Bowden and others 2004; Zheng and others 2022). The N suppression of soil respiration by N was detected primarily in the summer season when soil temperature is highest and fluxes are greatest. This N suppression was consistent throughout most of the study period.

We did not anticipate any long-term trend in soil respiration, and the causes of the clear and significant 118% increase in summer soil respiration over the 10-year study are unknown. This temporal pattern was not explained by increases in soil temperature (Figure 7), treatment, or changes in instrumentation. A similar pattern has been observed at other locations in the Hubbard Brook Experimental Forest (our unpublished data and Angela Possinger, personal communication). One possible contributor is increasing

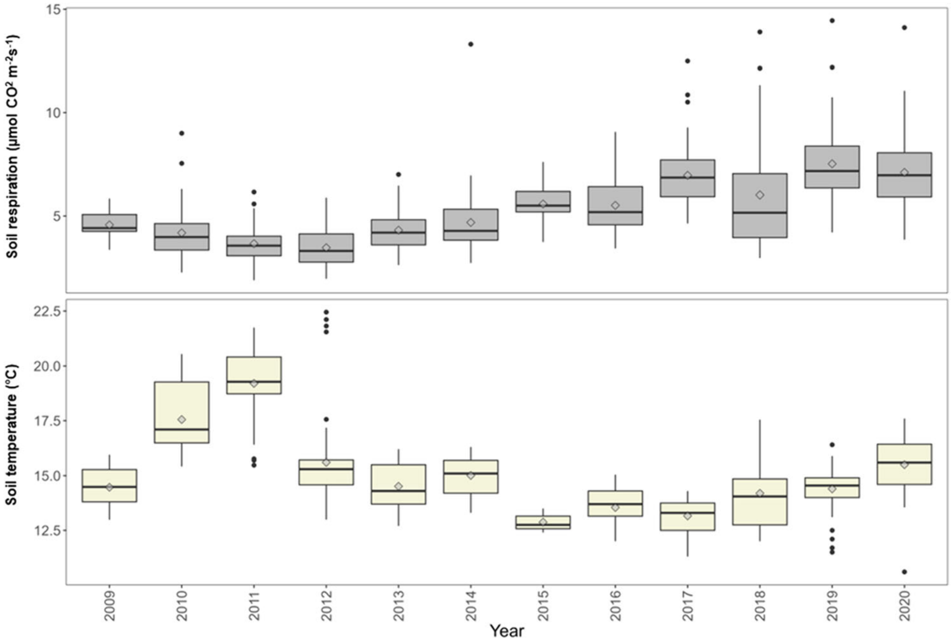


Figure 7. Distribution of plot median (**a**) soil respiration (µmol CO_2 m^{-2} s^{-1}) and (**b**) soil temperature (°C) for summer measurement periods. Gray diamonds represent annual means of these medians. Two high respiration values from 2018 (28.6 µmol m^{-2} s^{-1} and 38.5 µmol m^{-2} s^{-1}) are off the chart.

belowground carbon allocation due to a stimulation of photosynthesis by increasing atmospheric CO_2 (Ainsworth and Rogers 2007). Another possible contributor is increasing fine-root biomass. The biomass of $<$ 5 mm diameter roots increased by 14% from 2008 to 2010 (pretreatment) to 2015–2016, but not at all from 2015–2016 to 2021–2022 (our unpublished data). Thus, it is unlikely that increasing fine-root biomass was an important driver of the doubling of soil respiration from 2011 to 2020 (Figure 7).

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DATA AVAILABILITY

Fahey, T.J., R.D. Yanai, S. Li, and T. Mann. 2021. Multiple Element Limitation in Northern Hardwood Experiment (MELNHE): Soil respiration at Hubbard Brook Experimental Forest, Bartlett Experimental Forest and Jeffers Brook, central NH USA, 2008—present ver 2. Environmental Data Initiative. https://doi.org/https://doi.org/10.6073/pasta/eb37cd72ccaa3e9197c461f0c1c734eb (Accessed 2023–05-26).

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