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Localized basal area affects soil respiration temperature sensitivity in a coastal deciduous forest

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Abstract. Soil respiration (R_s), the flow of CO_2 from the soil surface to the atmosphere, is one of the largest carbon fluxes in the terrestrial biosphere. The spatial variability of R_s is both large and poorly understood, limiting our ability to robustly scale it in space. One factor in R_s spatial variability is the autotrophic contribution from plant roots, but it is uncertain how the presence of plants affects the magnitude and temperature sensitivity of R_s. This study used 1 year of R_s measurements to examine the effect of localized basal area on R_s in the growing and dormant seasons, as well as during moisture-limited times, in a temperate, coastal, deciduous forest in eastern Maryland, USA. In a linear mixed-effects model, tree basal area within a 5 m radius (BA_5) exerted a significant positive effect on the temperature sensitivity of soil respiration. Soil moisture was the dominant control on R_s during the dry portions of the year, while soil moisture, temperature, and BA_5 all exerted significant effects on R_s in wetter periods. Our results suggest that autotrophic respiration is more sensitive to temperature than heterotrophic respiration at these sites, although we did not measure these source fluxes directly, and that soil respiration is highly moisture sensitive, even in a record-rainfall year. The R_s flux magnitudes (0.46–15.0 μmol m^{-2} s^{-1}) and variability (coefficient of variability 10 %–23 % across plots) observed in this study were comparable to values observed in similar forests. Six R_s observations would be required in order to estimate the mean across all study sites to within 50 %, and 518 would be required in order to estimate it to within 5 %, with 95 % confidence. A better understanding of the spatial interactions between plants and microbes, as well as the strength and speed of above- and belowground coupling, is necessary to link these processes with large-scale soil-to-atmosphere C fluxes.

1 Introduction

Soil respiration (R_s), the flow of CO_2 from the soil to the atmosphere, is among the largest C fluxes in the terrestrial biosphere (Granier et al., 2000; Bond-Lamberty, 2018; Le Quéré et al., 2018) but remains poorly constrained both temporally and spatially at all scales. Unlike other large C fluxes such as net primary production, net ecosystem exchange, and gross primary production, R_s cannot be measured, even indirectly, at scales larger than a few square meters (Bond-Lamberty et al., 2016). Though global-scale R_s varies between vegetation types and biomes (Raich et al., 2002; Raich and Schlesinger, 1992), and responds to disturbances such as land use and climate changes (Hursh et al., 2017; Schlesinger and Andrews, 2000), it is uncertain how these patterns arise from local-scale variability, limiting our ability to robustly scale the process.

One obstacle to robust measurements of R_s is that the spatial and temporal variability is both large and poorly understood. This high variability has consequences for the sampling strategy required to accurately measure R_s at the stand scale (Rodeghiero and Cescatti, 2008; Saiz et al., 2006) and limits our ability to upscale R_s measurements to eddy covariance tower scales (Barba et al., 2018). Controls on the spatiotemporal variability of R_s differ among sites and ecosystems and include plant species, ecosystem productivity (Reichstein et al., 2003), soil temperature (Fang et al., 1998), moisture, spatial variability of vegetation, management, and soil compaction (Epron et al., 2004). The collective responses of plants and microbes to these factors determine the sensitivity of ecosystems to changes in temperature, precipitation, and other global change factors.

Plant root respiration constitutes ∼ 50 % of R_s in many ecosystems (Subke et al., 2006). At ecosystem scales, a number of studies have examined how the spatial distribution of R_s is affected by vegetation. R_s is typically higher closer to tree stems (Epron et al., 2004; Tang and Baldocchi, 2005) and with higher nearby stem density (Schwendenmann and Macinnis-Ng, 2016; Stegen et al., 2017). Photosynthesis is also a driver of the rhizospheric component of soil respiration (Hopkins et al., 2013) and influences seasonal trends in root contribution to total soil respiration (Brændholt et al., 2018; Högberg et al., 2001). Any spatial influences of plants on the magnitude and environmental sensitivities of R_s might thus be expected to be strong in temperate deciduous forests, as such forests tend to be highly productive (Gillman et al., 2015; Luyssaert et al., 2007).

This study examines the effect of tree proximity on measured R_s in a mid-Atlantic, deciduous forest in the Chesapeake Bay, USA, region. We hypothesized that

i. the amount of basal area close to R_s measurement locations would exert a significant and positive effect on measured R_s after taking into account the effects of abiotic drivers;

ii. this effect would occur in the growing (leaf on) season but not in the dormant (leaf off) season, because root respiration is much higher during the growing season; and

iii. this effect would be stronger during drier times of year, because trees might maintain access to deep soil moisture (Burgess et al., 1998) and thus continue respiring even when the surface soil is dry.

To test these hypotheses, we performed a spatially explicit analysis of 1 year of frequent R_s measurements in a temperate coastal deciduous forest in eastern Maryland, USA. Our study was conducted in the Chesapeake Bay watershed, an area subject to rapid rates of sea level rise (Ezer and Corlett, 2012; Sallenger et al., 2012) that may exert significant effects on the carbon cycling of coastal ecosystems (Rogers et al., 2019).

2 Methods

2.1 Site characteristics

This study was conducted in a mid-Atlantic, temperate, deciduous forest at the Smithsonian Environmental Research Center (SERC) in Edgewater, MD, USA. Three sites were chosen along Muddy Creek, a stream draining into an arm of the Chesapeake Bay. Each site was separated by ∼ 1 km (Fig. 1b). These sites were comprised of both lowland and upland forest with a mean annual precipitation of 1001 mm and mean annual temperature of 12.9 °C (Pitz and Megonigal, 2017). Dominant tree species include *Liriodendron tulipifera*, *Fagus grandifolia*, and *Quercus* spp.; soil types vary between Collington, Wist, and Annapolis soil (Table 1). At each site, three 20 m × 40 m plots were installed, separated by ∼ 25 m, and oriented perpendicular to the creek. The total elevation change between plots at each site was ∼ 2 m. Within each plot, we installed four 20 cm diameter PVC collars, randomly separated from each other by 2–15 m, for a total of 36 measurement collars. Collars were installed ∼ 1 week prior to the first sampling and left in place for the duration of the study.

2.2 Soil respiration and ancillary measurements

Soil respiration measurements were taken using an infrared gas analyzer (IRGA; LI-8100A, LI-COR Inc., Lincoln, NE) with a 20 cm diameter opaque soil chamber attached. Measurements were taken every 10–14 d from April 2018 to April 2019. The IRGA measures concentrations every second over a one-minute period and calculates the CO_2 flux as the exponential regression of CO_2 accumulation in the closed chamber system over unit area and time; two successive measurements were taken at each collar and averaged. Vegetation was removed from inside the collar, and new vegetation was reclipped as necessary, to remove any aboveground autotrophic flux, so that the IRGA was measuring only soil-to-atmosphere CO_2. Soil moisture and temperature (T_5) were recorded at 5 cm depth, using auxiliary sensors attached to the LI-8100A, at the same time as soil respiration measurements. Temperature at 20 cm depth (T_{20}) was also recorded using a handheld thermometer at the time of measurement.

2.3 Local basal area measurements

We recorded distance from the soil collar, diameter at breast height (1.37 m), and species of each tree within a 15 m radius of each soil respiration measurement point (Fig. 1a). Dead trees were included in the dataset but only account for < 1 % of total forest basal area. Cumulative basal area was calculated at each 1 m radial distance from the collar, summing the cross-sectional areas of all trees within each distance. Tree root extent can be highly variable, but generally roots extend at least to the edge of the tree canopy (Stone and Kalisz, 1991). Mature tree canopies at SERC are ∼ 5 m in radius (Stephanie C. Pennington, personal observation, 2018), and we adopted this distance as an a priori assumption to test for the effect of basal area at 5 m (BA_5) on R_s.

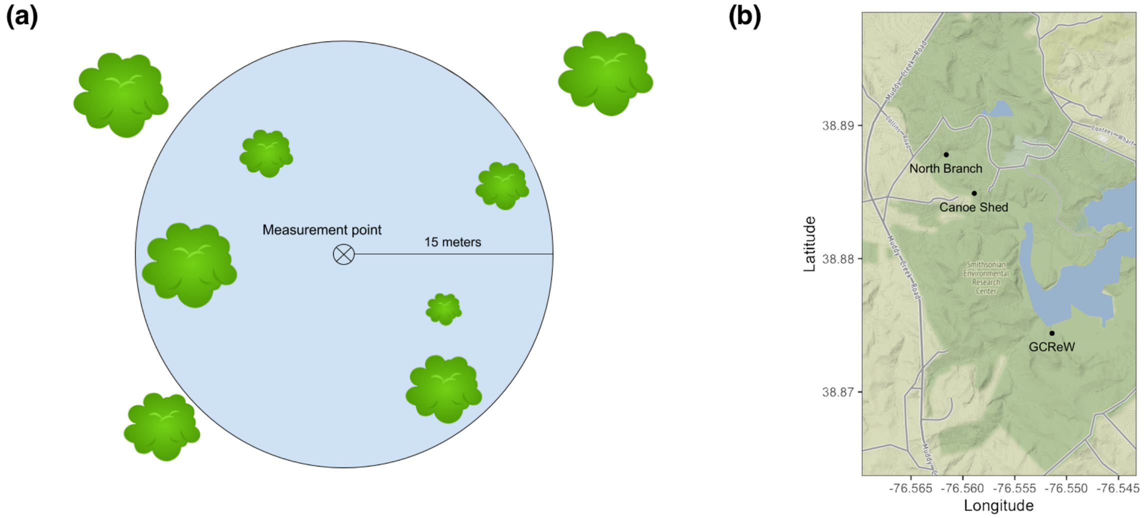

Figure 1. (a) Tree proximity measurement schematic. Distance to each tree was recorded within a 15 m radius of each soil respiration measurement point, along with diameter at breast height (DBH) and species. **(b)** Map of the Smithsonian Environmental Research Center with the three sites labeled in black. (Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL. © OpenStreetMap contributors 2019. Distributed under a Creative Commons BY-SA License.)

Table 1. Study site characteristics of each site along Muddy Creek, including trees per hectare, cumulative basal area, main soil types, and dominant tree species by percent of basal area. Values are the mean ± standard deviation of $N = 3800\,\mathrm{m}^2$ plots.

Site	Trees (ha^{-1})	BA ($\mathrm{m}^2\,\mathrm{ha}^{-1}$)	Dominant soil type	Dominant tree species (by BA %)	Altitude (m)
GCReW (38.876° N, 76.553° W)	637.5 ± 57.3	45.2 ± 7.3	Collington–Wist complex; Collington and Annapolis soils	28 % *Liriodendron tulipifera* 11 % *Quercus* spp. 11 % *Fagus grandifolia*	3–10
Canoe Shed (38.884° N, 76.557° W)	529.2 ± 93.8	40.4 ± 6	Annapolis fine sandy loam	26 % *Quercus* spp., 23 % *L. tulipifera* 20 % *F. grandifolia*	7–10
North Branch (38.887° N, 76.563° W)	806.9 ± 180.7	34.5 ± 7.8	Collington and Annapolis soils; Collington, Wist, and Westphalia soils	42 % *F. grandifolia* 26 % *Quercus* spp. 12 % *Liquidambar styraciflua*	8–20

2.4 Statistical analysis

Respiration data were checked visually for artifacts or unusual outliers, but we did not exclude any data a priori. Data were then combined with the proximity measurements described above based on collar number. We used a linear mixed-effects model to test for the influence of BA_5 on R_s, treating temperature, soil moisture (SM), and BA_5 as fixed effects and site as a random effect (Eq. 1). R_s frequently follows a nonlinear response in relation to SM, so a quadratic SM term (Sierra et al., 2015) was included in the model. The dependent variable R_s was transformed by taking its natural logarithm to minimize heteroscedasticity, and thus the full linear model was specified as

$$\log(R_\mathrm{s}) \sim T_5 \cdot \mathrm{BA}_5 + T_{20} \cdot \mathrm{BA}_5 + \mathrm{SM} + \mathrm{SM}^2. \tag{1}$$

We used restricted maximum likelihood estimation using the lme4 package (Bates et al., 2015) in R version 3.5.3 (R Development Core Team, 2019). All models were examined for influential outliers and deviations from normality. Nonsignificant terms were then eliminated using a forward-and-back stepwise algorithm (using the R package MASS version 7.3-47) based on the Akaike information criterion (AIC). Residuals from all fitted models were plotted and checked for trends or heteroscedasticity.

Our secondary hypotheses, that the effect of BA_5 varies with growing season and soil moisture, were tested by subsetting the R_s data. We treated 15 April–14 October as the growing season, based on 2018 leaf-out and senescence, and 15 October–14 April as the dormant season. Soil moisture data were split up into equal thirds (low, $< 0.188\,\mathrm{m}^3\,\mathrm{m}^{-3}$; medium, 0.188–$0.368\,\mathrm{m}^3\,\mathrm{m}^{-3}$; and high, $> 0.368\,\mathrm{m}^3\,\mathrm{m}^{-3}$;

Table 2. Sample size required to estimate soil respiration with a particular error (delta, left column, fraction of mean flux) for different statistical power values. Values are the mean (standard deviation) between plots. Power is the probability that the test rejects the null hypothesis when a specific alternative hypothesis is true and informally connotes the degree of confidence that the measurement is within some delta value of the true mean.

	Power ($1-\beta$)					
Delta	0.5	0.6	0.7	0.8	0.9	0.95
0.05	61 (24)	95 (37)	144 (55)	220 (84)	364 (138)	518 (196)
0.10	16 (6)	24 (10)	36 (14)	55 (21)	91 (35)	130 (49)
0.25	3 (1)	4 (2)	6 (3)	9 (4)	15 (6)	21 (8)
0.50	1 (1)	1 (1)	2 (1)	3 (1)	4 (2)	6 (2)

all values volumetric). We then applied the statistical model described above to each subset of the data to test for BA_5 significance in the model. The relaimpo package version 2.2-3 was used to calculate relative importance metrics for all terms in each model, in particular its lmg metric that averages sequential sums of squares over all orders of regressors (Lindeman et al., 1980), providing a robust decomposition of model R^2.

We used the spatial variability between collars within individual plots to estimate the number of samples required for a robust estimate of the R_s population mean, i.e., a spatially representative mean. Specifically, we used a Student *t* test to calculate this based on the standard deviation of hourly R_s, the desired power of the test, and the allowable delta (difference from the true mean value), following Davidson et al. (2002).

3 Results

We measured R_s, soil temperature, and soil moisture on 31 different days across the 1-year period (Fig. 2). Soil temperatures ranged from 0.1 to 27.5 °C (at 5 cm) and 1.7 to 24.4 °C (at 20 cm); volumetric soil moisture values were 0.01–0.56. R_s fluxes ranged from 0.35 $\mu mol\,m^{-2}\,s^{-1}$ (in January 2019) to 15.3 $\mu mol\,m^{-2}\,s^{-1}$ (in July 2018). The coefficient of variability (CV) between collars within plots, a measure of spatial variability, was 16.7 % ± 4.0. This implied that a large number of samples was required to estimate soil respiration accurately (Table 2).

There was large variability in the basal area and number of trees close to the measurement collars (Fig. 3). The mean number of trees within 1, 5, and 10 m distance were 1, 6, and 21 trees (with respective nearby basal areas of 0.0002, 0.24, and 0.88 m^2). Within our maximum radius of measurement, 15 m, there were on average 43 trees and 1.64 m^2 of cumulative basal area, ranging from a minimum of 0.43 m^2 to a maximum of 3.55 m^2. The forest was thus highly spatially variable in its distribution of trees relative to the R_s measurement collars.

3.1 Effect of BA on R_s

The linear mixed-effects model using temperature, soil moisture, and basal area within 5 m (BA_5) predicted 37 % of the R_s variability (conditional $R^2 = 0.37$). BA_5 was not significant by itself in a Type III ANOVA using this model ($\chi^2 = 0.081$, $P = 0.776$) but exhibited strong and significant interactions with T_5 and T_{20} in the linear model (Table 3). In addition, the residuals of a model fit without BA_5 had a significant trend with BA_5 (Fig. 4). Separating the data into growing- and dormant-season subsets provided contrasting results. In the growing season, model outputs were similar to those of the full-year model, with BA_5 having significant interactions with T_5 and T_{20} (data not shown). The dormant season model, however, was quite different: only T_{20} ($P \leq 0.000$) and soil moisture ($P = 0.0377$) were significant terms. In addition, the dormant season model explained more of the R_s variability (AIC = 119.80, marginal $R^2 = 0.48$). In summary, collars with higher basal area within 5 m had a significantly higher temperature sensitivity of soil respiration, while basal area within 5 m of sampling points was not correlated with R_s during the dormant season.

There were strong differences between the driest and wettest thirds of the data, but our hypothesis that any basal area effect would be strongest in the driest time of year was not supported. In the driest third of the data, neither BA_5 nor its interaction with T_5 was significant ($P = 0.096$ and 0.054 respectively); T_{20} was never significant; and the dominant control was instead soil moisture ($\chi^2 = 15.23$, $P < 0.001$). In contrast, the wettest-third model resembled the full-year model, with BA_5 interacting with temperature and soil moisture also significant.

3.2 Sensitivity test

Our a priori choice of 5 m for the basal area test was one of many possible choices and could potentially bias the results, as the actual extent of tree roots at these sites is unknown. Refitting the main statistical model and calculating variable importance metrics across a wide range of distances, however, showed that basal area and its interactions with T_5 and T_{20} were almost always statistically significant (Fig. 5). Generally, the BA effects were not significant at short (< 3 m) distances; this is expected, given that few collars were that close to trees. Interestingly, the BA effects remained significant all the way to our maximum measured distance of 15 m. In summary, our a priori analytical choice of a 5 m radius did not appear to bias our results.

4 Discussion

The R_s fluxes observed in this study, 0.35–15.3 $\mu mol\,m^{-2}\,s^{-1}$, were comparable to values in similar forests (Giasson et al., 2013) as well as those from the Soil Respiration Database (SRDB; Bond-Lamberty

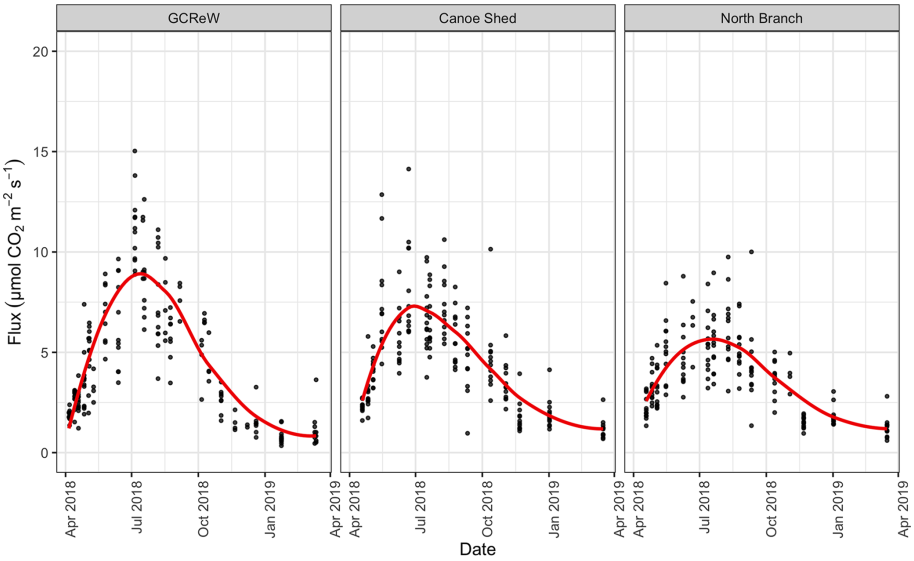

Figure 2. CO$_2$ flux over time from April 2018 to April 2019 for 36 measurement points across three sites; red line shows the seasonal trend using a loess smoother.

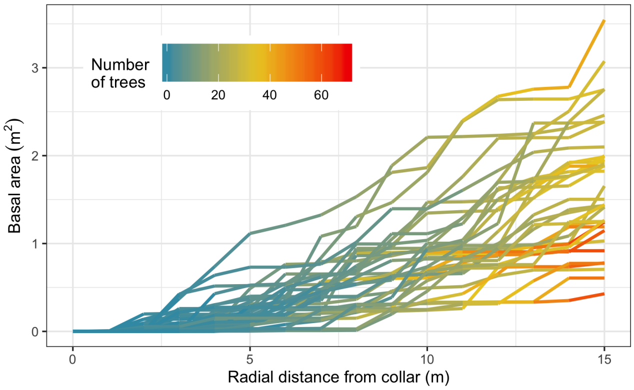

Figure 3. Cumulative basal area for each soil collar ($N = 36$) up to 15 m. Color indicates the number of trees at each distance, and each line is an individual collar.

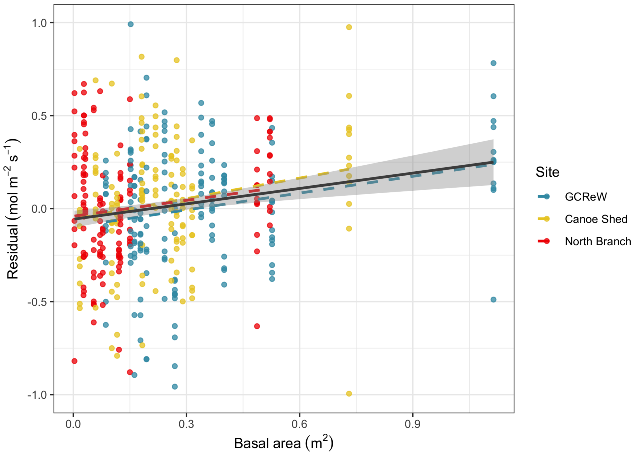

Figure 4. Residuals of a soil respiration model, incorporating temperature and soil moisture as independent variables, versus cumulative tree basal area within 5 m, by site. Each point is an individual observation (see Fig. 2). Regression lines are shown for each site; the black line is the overall trend. Note that five extreme points are out of the plot but are accounted for in the regression lines.

and Thomson, 2010), a synthesis of annual R_s studies (0 to 14.7 µmol m^{-2} s^{-1}, $n = 1281$ temperate deciduous studies). We observed a R_s CV of 10 %–22 % between plots, a value also comparable to previous studies. In a study of R_s in conifer forests and grasslands, Rodeghiero and Cescatti (2008) reported 28.9 %–41.5 % variability, Davidson et al. (2000) about 30 % in forest ecosystems, and a much broader range (0.11 %–84.5 %) for temperate, deciduous forests from the SRDB.

Sample size requirements to estimate annual R_s were high at SERC compared to previous studies. For example, to be within 10 % of the mean R_s flux at 95 % confidence required from 41 sample points (Davidson et al., 2002) in Harvard Forest, to 72 (Adachi et al., 2005) in a secondary forest, to 130 in this study. Within forest biomes, topography and stand structure (Søe and Buchmann, 2005) can be dominant controls. Significant spatial variation in stand structure and topography across the study domain may have resulted in the high variability seen in this study. In particular, the measurement points at our study sites ranged from 3 to 15 m in elevation (Table 1), as at all sites the land rises quickly away from Muddy Creek. These elevation gradients mean that some measurement points drain more quickly than others, creating strong differences in soil water content (CV 16.7 % ± 4.0 within plots) and thus R_s. This is consistent with the idea

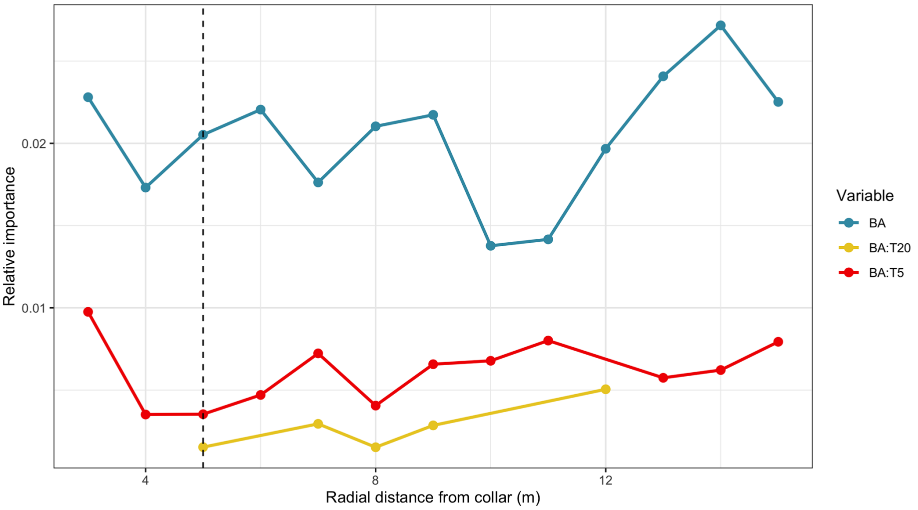

Figure 5. Test of robustness of results, run at various distances from soil respiration measurement collars (x axis). Lines show the variable importance (calculated as R^2 partitioned by averaging over orders; see Methods) of basal area (BA), as well as the interaction of BA and temperatures at 5 and 20 cm (T_5 and T_{20} respectively). Vertical dashed line shows the 5 m radius used in Table 3 and Fig. 4 results. Note that the missing BA : T_{20} (in yellow) dots at distances < 5 and > 12 m mean that the terms were dropped from the model and are thus not significant.

Table 3. Summary of the linear mixed-effects model testing the main hypothesis of the effect of nearby tree basal area on soil respiration (the dependent variable). Terms tested include soil temperature at 5 and 20 cm (T_5 and T_{20} respectively), basal area (BA), and soil moisture (SM). Model AIC = 381.6, marginal $R^2 = 0.36$.

	Value	Degrees of freedom	t value	p value
(Intercept)	-0.767 ± 0.148	440	-5.199	0.000
T_5	0.010 ± 0.009	440	1.055	0.292
BA_5	0.022 ± 0.219	440	0.098	0.922
T_{20}	0.095 ± 0.011	440	8.397	0.000
SM	2.505 ± 0.699	440	3.581	0.004
$\mathrm{I(SM^2)}$	-3.542 ± 1.144	440	-3.095	0.002
$T_5 : \mathrm{BA}_5$	0.079 ± 0.036	440	2.181	0.030
$\mathrm{BA}_5 : T_{20}$	-0.069 ± 0.041	440	-1.689	0.092

that topographic complexity can be an important and complex factor in R_s variation across sites (Riveros-Iregui et al., 2011).

4.1 Interactions between basal area and temperature sensitivity on R_s

Many studies have examined whether autotrophic respiration (R_a) or heterotrophic respiration (R_h) is more temperature sensitive and reached varying conclusions (Aguilos et al., 2011; Boone et al., 1998; Wei et al., 2010). In this study, the Type III SS interaction between BA_5 and temperature was highly significant, meaning that collars with higher basal area within 5 m exhibited significantly higher temperature sensitivity of soil respiration. This suggests that R_a might be more sensitive to temperature than R_h at these sites. However, it is important to note that we did not directly measure the autotrophic and heterotrophic source fluxes contributing to the overall R_s flux. Instead, we assume that collars closer to trees have a larger fraction of R_s contributed by R_a, an assumption also made in previous studies such as Tang and Baldocchi (2005).

Mechanistically, these findings could be explained by a number of processes. When substrate supply from root exudates is higher during the growing season, R_s tends to be more sensitive to temperature (Luo and Zhou, 2006), presumably because under these conditions R_s is tightly coupled with photosynthesis (Ekblad and Högberg, 2001), as roots access photosynthate before microbes, and thus can respond more strongly to temperature changes. Leaf phenology likely also plays a role in a deciduous forest such as the one studied here, where the growth of photosynthetically active foliage in the spring can promote carbon allocation belowground and hence R_a. Input of leaf material in the fall may also stimulate R_h (Curiel Yuste et al., 2004; Epron et al., 2001; Ruehr et al., 2010) and is dependent on tree size and distribution (Bréchet et al., 2011).

There is also abundant evidence that soil moisture influences temperature sensitivity: Suseela et al. (2012), for example, found that R_s is less sensitive to temperature during water-limited times. If trees' roots have access to water consistently, their respiratory flux R_a measured at the soil surface as part of R_s will be more temperature sensitive on average, because R_a will be limited by soil moisture less frequently

(Misson et al., 2006). It is important to note that these various mechanisms are not mutually exclusive.

4.2 Soil moisture controls on BA significance

We hypothesized that any BA_5 effect would be particularly strong during the driest third of the year but instead found that only soil moisture controlled R_s during these periods, while neither temperature nor tree proximity (BA_5) was significant. This demonstrates that R_s is highly moisture sensitive at these sites but does not support our idea that trees might have access to deeper or different water sources than surface soil microbes. Soil moisture is considered to be a primary R_s control in Mediterranean and desert ecosystems (Cable et al., 2010), but interestingly even this deciduous forest, in a year with record rainfall (National Weather Service, 2019), experienced significant moisture restrictions on R_s.

4.3 Dormant season R_s controls

Tree basal area within 5 m of our R_s sampling points was not significant in the dormant season model, supporting our hypothesis that total R_a contribution is often lower during the dormant reason than the growing season (Hanson et al., 2000), which suggests that R_a contributes less to R_s during the dormant season. This is expected, given the physiological link between photosynthesis and root respiration (Sprugel et al., 1995). Interestingly, T_5 was not significant in the dormant season model, but rather T_{20} was the dominant control. The study site is in a mid-Atlantic, temperate location with cold air temperatures during the winter. Deeper soils are more insulated from cold air temperatures, allowing more favorable conditions for respiration and thus making T_{20} a dominant control on R_s during these times.

4.4 Limitations of this study

A number of limitations should be noted in our study design and execution. First, this was not a fully spatially explicit analysis; we did not map the collars relative to each other or construct a full spatial map of the forest stands (Atkins et al., 2018). Such mapping can be useful to examine the R_s spatial structure in more detail, as for example in Stegen et al. (2017), but our approach to mapping relative distances to trees provides an alternative spatial study construct. In a similar vein, Tang and Baldocchi (2005) measured R_s within a transect of two oak trees to draw inferences on the spatially variable contribution of R_h and R_a. Our study design still provides useful spatial information, however: the 15 m max distance in Fig. 5 implies that the range of a semivariogram, i.e., the distance of maximum autocorrelation, would be at least this far. This means that BA remained significant all the way to our maximum measured distance of 15 m, implying that the spatial influence of large trees persisted at least this far (Högberg et al., 2001).

Second, this study tested the effect of basal area on R_s, based on the assumption that BA is proportional to fine root biomass, the respiration of which is driven (with some time lag) by photosynthesis, and this in turn drives root respiration dynamics (Vose and Ryan, 2002). Stems with a diameter below 2 cm and understory were not inventoried or, as a result, included in the hypothesis-testing statistical models. If root respiration is instead correlated with number of stems, which are disproportionately small due to forest demographics, this would bias our results. There are not many understory/saplings at these sites (Table 1), however.

5 Conclusion

We found that measurement collars with higher tree basal area within 5 m had a significantly higher temperature sensitivity of R_s. R_s was also highly moisture sensitive at all of our study sites, with large differences among R_s in low- versus high-moisture times. These findings, in conjunction with large sample size requirements, suggests that the highly dynamic and variable nature of soil respiration at this site lends itself to localized basal area effects on R_s. This could have implications for measurement requirements in sites with particular stand structures. A better understanding of the spatial interactions between plants and microbes through R_h and R_a partitioning, as well as the speed and coupling between above- and belowground processes, is necessary to link these processes with collar- and ecosystem-scale soil-to-atmosphere C fluxes.

Code and data availability. All code and data necessary to reproduce our results are available in our online GitHub repository (https://github.com/PNNL-PREMIS/PREMIS-ghg/releases/tag/v0.3-bgs-final) and permanently archived at Zenodo (https://doi.org/10.5281/zenodo.3613839, Pennington and Bond-Lamberty, 2020).

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Author contributions. This study was designed by BBL and SCP. All fieldwork and data analysis was performed by SCP, except for the statistical analysis, which was written by BBL. NGM, JPM, and JCS provided feedback on the study design, analysis, and interpretation of results. SCP wrote the paper in close collaboration with all authors.

Competing interests. The authors declare that they have no conflict of interest.

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