Tree proximity affects soil respiration dynamics in a coastal temperate 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 time and space. One factor in $R_s$ spatial variability is the autotrophic contribution from plant roots, but it is uncertain how the proximity of plants affects the magnitude and temperature sensitivity of $R_s$. This study examined the effect of tree proximity 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 5 m (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 (0.3-16.6 µmol m^{-2} s^{-1}) and variability (coefficient of variability 10%-22% across plots) observed in this study were comparable to values observed over decades in similar forests. We estimate that four R_S observations were required to be within 50% of the stand-level mean, and 311 to be within 5%, at 90% confidence. A better understanding of the spatial interactions between plants and microbes that results in measured R_S is necessary to link these processes with large scale soil-to-atmosphere C fluxes.

Introduction

Soil respiration (R_S), the flow of CO_2 from the soil to the atmosphere, is an important carbon (C) flux at ecosystem (Granier et al., 2000) to global scales. R_S is among the largest C fluxes in the terrestrial biosphere (Bond-Lamberty, 2018; Le Quéré et al., 2018), but poorly constrained at large scales, and thus it is important to understand its variability and sensitivity to processes such as land use and climate changes (Hursh et al., 2017; Schlesinger and Andrews, 2000). 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 ~1 m^2 (Bond-Lamberty et al., 2016), limiting our ability to robustly scale it in time and space. One obstacle to robust measurements is that the spatial variability of R_S is both large and poorly understood. Controls on the spatial variability of R_S differ among sites and ecosystems and include plant species, leaf habit, ecosystem productivity (Reichstein et al.,
2003), soil temperature, moisture, spatial variability of vegetation, management, and soil compaction (Epron et al., 2004). 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).

At large scales, $R_s$ differs between vegetation types and biomes (Raich et al., 2002; Raich and Schlesinger, 1992), implying that the spatial distribution of vegetation might strongly affect $R_s$ via plant root respiration, which 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 (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 $R_s$ might be expected to be particularly strong in temperate, deciduous forests, as such forests tend to be especially 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 stronger 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 one year of frequent $R_s$ measurements in a temperate coastal deciduous forest in eastern Maryland, USA. To our knowledge, no study has examined the influences of trees on spatial variation of $R_s$ 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).

Methods

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 Chesapeake Bay. Each site was separated by ~1 km (Figure 1a). 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 x 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 4, 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.
Soil respiration measurements were taken using an infrared gas analyzer (LI-8100A, LI-COR Inc., Lincoln, NE) with a 20 cm diameter soil chamber attached. Measurements were taken every 10-14 days from April 2018 to April 2019. The IRGA measures concentrations every second over a one minute period and calculates the CO\textsubscript{2} flux as the linear or exponential regression of CO\textsubscript{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 re-clipped as necessary, to remove any aboveground autotrophic flux, so that the IRGA was measuring only soil-to-atmosphere CO\textsubscript{2}.

Soil moisture and temperature (T\textsubscript{5}) were also 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\textsubscript{20}) was also recorded using a hand-held thermometer at the time of measurement.

Tree proximity measurements

We recorded distance from the soil collar, diameter at breast height (1.37 m), and species of each tree within a 15 meter radius of each soil respiration measurement point (Figure 1b). 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 (S. Pennington, personal observation), and we adopted this distance as an a priori assumption to test for the effect of basal area at 5 meters (BA\textsubscript{5}) on R\textsubscript{s}. 

Tree proximity measurements
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 BA5 on Rs, treating temperature, soil moisture, BA5 as fixed effects, and site as a random effect. To ensure homoscedasticity of model residuals, the dependent variable Rs was transformed by taking its natural logarithm. 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. Non-significant 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. Residuals from all fitted models were plotted and checked for trends or heteroscedasticity.

Our secondary hypotheses, that effect of BA5 varies with growing season and soil moisture, were tested by subsetting the Rs data. We treated April 15-October 14 as the growing season, based on 2018 leaf-out and senescence, and October 15-April 14 as the dormant season. Soil moisture data were split up into equal thirds (low, <0.188 m³ m⁻³; medium, 0.188-0.368 m³ m⁻³; and high, >0.368 m³ m⁻³; all values volumetric). We then applied the statistical model described above to each subset of the data.

We used the spatial variability between collars within individual plots to estimate the number of samples required for a robust estimate of the Rs 'population mean', i.e., a spatially-representative mean. Specifically, we used a Student’s t-test to calculate this based on the standard deviation of hourly Rs, the desired power of the test, and the allowable delta (difference from the true mean value), following Davidson et al. (2002).

All code and data necessary to reproduce our results are available in our online GitHub repository (https://github.com/PNNL-PREMIS/PREMIS-ghg) and permanently archived at Figshare (DOI if accepted).
Results

We measured $R_s$, soil temperature, and soil moisture on 31 different days across the one-year period (Figure 2). Soil temperatures ranged from 0.1 to 27.7 °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 0.17 µmol m$^{-2}$ s$^{-1}$ (in March 2019) to 16.55 µmol m$^{-2}$ s$^{-1}$ (in July 2018). The coefficient of variability (CV) between collars within plots, a measure of spatial variability, ranged from 10% to 22%. 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 (Figure 3). The mean number of trees within 1 m, 5 m, and 10 m distance were one, six, and 20 trees (with respective nearby basal areas of 0.0002 m$^2$, 0.24 m$^2$, and 0.91 m$^2$). Within our maximum radius of measurement, 15 m, there were on average 42 trees and 1.7 m$^2$ of cumulative basal area, ranging from a minimum of 0.55 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.

Effect of BA on $R_s$

The linear mixed-effects model using temperature, soil moisture, and basal area within five meters (BA$_5$) predicted almost half of the $R_s$ variability (conditional $R^2 = 0.40$). BA$_5$ was not significant by itself in a Type III ANOVA using this model ($\chi^2 = 0.495$, $P = 0.482$), but exhibited strong and significant interactions with $T_5$ and $T_{20}$ (Table 3). In addition, the residuals of a model fit without BA$_5$ had a significant trend with BA$_5$ (Figure 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
The dormant season model, however, was quite different: only T20 (P ≤ 0.001) and soil moisture (P = 0.0009) were significant terms. In addition, the dormant season model explained more of the Rs variability (AIC = 258.75, marginal R² = 0.52). In summary, collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil respiration after controlling for temperature and moisture effects, while basal area within 5 m of sampling points was not correlated with Rs during the dormant season.

Our third hypothesis was that any basal area effect on Rs would be strongest in the driest times of the year, when microbial respiration at the surface soil declines as the soil dries, but (we speculated) trees would maintain access to deeper soil moisture. There were in fact strong differences between the driest and wettest thirds of the data, but our hypothesis was not supported. In the driest third of the data, neither BA5 nor its interaction with T5 was significant (P = 0.1775 and 0.1078 respectively); T20 was never significant; and the dominant control was instead soil moisture (χ² = 20.93, P < 0.001). In contrast, the wettest-third model resembled the full-year model, with BA5 interacting with temperature, and soil moisture also significant.

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. Re-running the main statistical test across a wide range of distances, however, showed that basal area by itself was almost never significant, while its interactions with T5 and T20 were almost always significant (Figure 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 analytical choice of a 5 m radius did not appear to bias our results.
Discussion

Results and implications of Rs values

The Rs fluxes observed in this study, 0.3-16.6 µmol m\(^{-2}\) s\(^{-1}\), were comparable to values in similar forests (Giasson et al., 2013) and from the Soil Respiration Database (Bond-Lamberty and Thomson, 2010), a synthesis of annual Rs studies (0 to 14.7 µmol m\(^{-2}\) s\(^{-1}\), n = 1281 temperate deciduous studies). We observed a collar-to-collar Rs CV of 10.5-21.5%, a value also comparable to previous studies. In a study of Rs in conifer forests and grasslands, Rodeghiero (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 temperature, deciduous forests from the SRDB.

Sample size requirements to estimate annual Rs were high at SERC compared to previous studies. For example, to be within 10% of the mean Rs flux at 95% confidence required from 41 (Davidson et al., 2002) in Harvard Forest, to 72 (Adachi et al., 2005) in a secondary forest, to 133 sample points in this study. This high variability between studies likely arises because controls on the spatial variability of Rs differ among sites and ecosystems. Within forest biomes, topography and stand structure (Søe and Buchmann, 2005) can also be dominant controls that likely contribute to the high variability seen in this study.

Interactions between basal area and temperature sensitivity on Rs

Many studies have examined whether autotrophic respiration (Rs) or heterotrophic respiration (Rh) is more temperature-sensitive, and reached varying conclusions (Aguilos et al., 2011; Boone et al., 1998; Wang et al., 2010). In this study, however, collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil respiration after controlling for temperature and moisture effects. This suggests that Rs is more sensitive to temperature than Rh at these sites, even though we did not directly measure the autotrophic and heterotrophic source fluxes contributing to the overall Rs flux.
Mechanistically, these findings could be explained by a number of processes. For example, when substrate supply from root exudates is ample, $R_s$ tends to be more sensitive to temperature (Luo and Zhou, 2006), presumably because $R_s$ can be tightly coupled with photosynthesis and thus roots, which access the photosynthate before microbes, respond more strongly to temperature changes. There is also abundant evidence that soil moisture influences temperature sensitivity: Susseela 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.

**Soil moisture controls on BA significance**

We hypothesized that BA$_5$ effect would be particularly strong during the driest third of the year, but 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 hypothesis 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 $R_s$. Spatial variation in soil moisture (CV 2.5%-18.7% between plots) was probably due to the topographic variability of our study site, which allowed some measurement points to drain more quickly than others, producing a wide range of soil moisture conditions.

**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 $R_s$ and potentially making $T_{20}$ a dominant control during these times.

**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, nor 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 $R_n$ and $R_a$. This study design still provides useful spatial information, however: the 15 m max distance in Figure 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).

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.

Conclusion

Autotrophic respiration was found to be more sensitive to temperature than heterotrophic respiration, and collars with higher basal area within 5 m had significantly higher temperature sensitivity. $R_s$ is also highly moisture-sensitive at these sites, with large differences among $R_s$ controls in low- versus high-moisture times. These findings, in conjunction with large sample size requirements, suggest soil respiration at this site to be highly dynamic and variable. This could have implications for measurement requirements in sites with particular stand structures. A better understanding of the spatial interactions between plants and microbes that results in measured $R_s$ is necessary to link these processes with collar- and ecosystem-scale soil-to-atmosphere $C$ fluxes.

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Author contributions
This study was designed by B.B.-L. and S.C.P. All fieldwork and data analysis was performed by S.C.P., except for the statistical analysis, which was written by B.B.-L. N.M., J.P.M., and J.C.S. provided feedback on the study design, analysis, and interpretation of results. S.C.P. wrote the manuscript in close collaboration with all authors.

References


Bond-Lamberty, B.: New techniques and data for understanding the global soil respiration flux,


Epron, D., Nouvellon, Y., Roupsard, O., Mouvondy, W., Mabiala, A., Saint-André, L., Joffre, R.,


376 Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J. and Watts, J.: The sensitivity of
377 soil respiration to soil temperature, moisture, and carbon supply at the global scale, Glob.
379 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C.,
381 Andrews, O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L.,
382 Chevallier, F., Chini, L. P., Ciais, P., Cosca, C. E., Cross, J., Currie, K., Gasser, T., Harris, I.,
384 Kautz, M., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N.,
385 Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P. M. S.,
386 Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., Nojiri, Y., Padin, X. A., Peregon, A., Pfeil, B.,
387 Pierrot, D., Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R.,
388 Skjelvan, I., Stocker, B. D., Tian, H., Tilbrook, B., Tubiello, F. N., Laan-Luijkx, I. T. van der,
391 Data, 10(1), 405–448, 2018.
392 Luo, Y. and Zhou, X.: Soil Respiration and the Environment, Elsevier/Academic Press,
393 Amsterdam., 2006.
394 Luyssaert, S., Inglis, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S.,
395 Schulze, E.-D., Wingate, L., Matteucci, G., Aragão, L. E. O. C., Aubinett, M., Beer, C., Bernhofer,
396 C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J. L., Ciais, P., Cook, B. D., Davis, K.
397 J., Dolman, A. J., Gielen, B., Goulden, M. L., Grace, J., Granier, A., Grele, A., Griffis, T. J.,
398 Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R. B., Hollinger, D. Y., Hutyra, L. R., Kolari,
P., Kruijt, B., Kutsch, W. L., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A.,
Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J. B.,
Moors, E. J., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O.,
Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C. A., Smith, M.-L., Tang, J., Valentini, R., Vesala,
T. and Janssens, I. A.: CO2 balance of boreal, temperate, and tropical forests derived from a

Misson, L., Gershenson, A., Tang, J., McKay, M., Cheng, W. and Goldstein, A. H.: Influences of
canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a

National Weather Service: Record Rain and Flooding of 2018, [online] Available from:

Pitz, S. and Megonigal, J. P.: Temperate forest methane sink diminished by tree emissions,

Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its

Raich, J. W., Potter, C. S. and Bhagawati, D.: Interannual variability in global soil respiration,

R Development Core Team: R: A language and environment for statistical computing. Version

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J. D., Valentini, R., Banza, J., Casals, P.,
Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel,
W. C., Ourcival, J.-M., Pereira, J., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M. B.,
Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D.: Modeling temporal and
large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biochemical Cycles, 17(4), art. no. 1104 (15 p.), 2003.


respiration across a permafrost transition zone: spatial structure and environmental correlates,


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 mean ± standard deviation of N=3, 800 m² plots.

<table>
<thead>
<tr>
<th>Site</th>
<th>Trees (ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>Dominant Soil Type</th>
<th>Dominant Tree Species (by BA %)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GCReW (38.876 °N, 76.553 °W)</td>
<td>637.5 ± 57.3</td>
<td>44.6 ± 4</td>
<td>Collington-Wist complex; Collington and Annapolis soils</td>
<td>28% <em>Liriodendron tulipifera</em>&lt;br&gt;11% <em>Quercus spp.</em>&lt;br&gt;11% <em>Fagus grandifolia</em></td>
</tr>
<tr>
<td>Canoe Shed (38.884 °N, 76.557 °W)</td>
<td>529.2 ± 93.8</td>
<td>40.4 ± 6</td>
<td>Annapolis fine sandy loam</td>
<td>26% <em>Quercus spp.</em>,&lt;br&gt;23% <em>L. tulipifera</em>,&lt;br&gt;20% <em>F. grandifolia</em></td>
</tr>
<tr>
<td>North Branch (38.887 °N, 76.563 °W)</td>
<td>806.9 ± 180.7</td>
<td>34.5 ± 7.8</td>
<td>Collington and Annapolis soils; Collington, Wist, and Westphalia soils</td>
<td>42% <em>F. grandifolia</em>,&lt;br&gt;26% <em>Quercus spp.</em>,&lt;br&gt;12% <em>Liquidambar styraciflua</em></td>
</tr>
</tbody>
</table>
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 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 within some delta value of the true mean.

<table>
<thead>
<tr>
<th>Delta</th>
<th>0.05</th>
<th>0.6</th>
<th>0.7</th>
<th>0.8</th>
<th>0.9</th>
<th>0.95</th>
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<tr>
<td>0.05</td>
<td>63 ± 21</td>
<td>97 ± 33</td>
<td>147 ± 50</td>
<td>226 ± 76</td>
<td>373 ± 124</td>
<td>532 ± 175</td>
</tr>
<tr>
<td>0.10</td>
<td>16 ± 6</td>
<td>25 ± 9</td>
<td>37 ± 13</td>
<td>57 ± 19</td>
<td>94 ± 31</td>
<td>133 ± 44</td>
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<td>0.25</td>
<td>3 ± 1</td>
<td>4 ± 2</td>
<td>6 ± 2</td>
<td>10 ± 4</td>
<td>15 ± 5</td>
<td>22 ± 7</td>
</tr>
<tr>
<td>0.50</td>
<td>1 ± 1</td>
<td>1 ± 1</td>
<td>2 ± 1</td>
<td>3 ± 1</td>
<td>4 ± 2</td>
<td>6 ± 2</td>
</tr>
</tbody>
</table>
Table 3. Summary of linear mixed-effects model testing 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 = 662.7, marginal $R^2 = 0.72$.

<table>
<thead>
<tr>
<th>Term</th>
<th>Value</th>
<th>Std.Error</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
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Figure 1 | a) Tree proximity measurement schematic. Distance to each tree was recorded within a 15 meter radius of each soil respiration measurement point, along with DBH and species. b) Map of the Smithsonian Environmental Research Center with the three sites labeled in black.
Figure 2 | Mean flux over time from April 2018 to April 2019 for 36 measurement points across three sites; blue line shows the seasonal trend using a loess smoother.
Figure 3 | Cumulative basal area for each collar (N = 36) up to 15 meters; color indicates number of trees at each distance.
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 (cf. Figure 2). Regression lines are shown for each site; black line is the overall trend.
Figure 5. Test of robustness of results, run at various distances from measurement collars (x axis). Figures shows the significance (chi square p-value from Type III ANOVA of the linear mixed effects model, y axis; note logarithmic scale) of basal area (BA), as well as the interaction of BA and temperatures at 5 and 20 cm (T_5 and T_{20} respectively). Horizontal dashed line shows the standard 0.05 significance cutoff; vertical dashed line the 5 m radius used in Table 3 and Figure 4 results. Note that ‘missing’ green and blue dots at distances < 5 m mean that the terms were dropped from the model and are thus not significant.