CYCLES AND DRIVERS OF SPATIOTEMPORAL VARIATION OF FOREST SOIL RESPIRATION AT THE INTRA-LANDFORM SCALE

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and hereby certify that, in their opinion, it is worthy of acceptance.

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Nomenclature

ANOVA	Analysis of variance
C	Carbon
C:N	Carbon:nitrogen ratio
CO_2	Carbon dioxide
CV	Cross-chamber coefficient of variation
GPP	Gross primary productivity
MOFLUX	Missouri Ozark AmeriFlux
r	Pearsons correlation coefficient
R_s	Soil respiration
$\overline{\boldsymbol{R_t}}$	Cross-chamber mean
RMSE	Root mean square error
R^2	R-Squared
$\boldsymbol{s_t}$	Cross-chamber standard deviation
SD	Standard deviation
SWC	Soil water content
T_{soil}	Soil temperature
θ	Volumetric water content

Abstract

Spatiotemporal variability of soil respiration (*R_S*) is a primary driver of large uncertainties associated with forest carbon budgets. However, most studies focus on either spatial or temporal variations, not both. As the frequency and severity of extreme weather events, such as heavy rain and drought, increase it is crucial to understand how these stressors affect the spatial variation of *R_S* to reduce uncertainties in carbon budgets. We analyzed a decades-long data set of continuous chamber measurements from a temperate deciduous forest in the central USA to examine spatiotemporal variations of *R_S* and the influence of water status on these patterns. Our findings reveal that spatial variation of *R_S* changes seasonally and is significantly affected by water status. During drought conditions, the mean daily spatial variation of summer *R_S* increased from a CV of *R_S* of 16.6% to a CV of *R_S* of 28.1%, and the daily amplitude also rose. A power analysis indicated that spatial variation observed at the MOFLUX forest prevented detection of changes in *R_S* between MOFLUX and a hypothetical forest. Spatial variability peaked at soil water content levels of 0.2 m^3 m^{-3} and 0.5 m^3 m^{-3}, indicating that in the extremes, soil water content drives spatial variation. Additionally, our analysis showed that soil water content (SWC) and soil temperature (T_{soil}) are key drivers of spatial variation of *R_S*, with the influence of these drivers shifting seasonally. During the non-growing season, soil climatic variables explained more of the spatial variation among chambers compared to the growing season. These results highlight the seasonality in the drivers of spatial variation of *R_S*, where soil climatic variables have greater explanatory power during the non-growing season. Our results demonstrate that both seasonality and extreme water

conditions significantly influence the spatiotemporal variability of R_S, providing valuable insights for improving understanding of forest R_S spatial variation.

Chapter 1: Introduction

Globally, the upper meter of soil holds about 1500 Pg of carbon (C), making it the largest terrestrial C pool (Scharlemann et al., 2014). Soil respiration (R_S) is the major pathway by which soil C is lost to the atmosphere (Bond-Lamberty & Thomson, 2010), with an estimated global flux of 85.5 ± 40.4 (SD) Pg-C y^{-1} (Lu et al., 2021). The large uncertainties associated with global R_S measurements occur due to the spatiotemporal variations of the flux. Understanding the temporal cycles and drivers of spatial variation of R_S is crucial, as this is key to decreasing uncertainties and improving projections of the carbon cycle and the climate (Knohl et al., 2008).

Forests play a key role in the global carbon cycle because they represent 31% of Earth's land area and hold 92% of all terrestrial plant biomass (FAO, 2020; Pan et al., 2011). Soil respiration is the dominant driver of ecosystem-level respiration (Davidson & Janssens, 2006; Griffis et al., 2004; Jassal et al., 2007; X. Liu et al., 2022), and the uncertainties in forest R_S estimates are primarily driven by spatial variability (Cai et al., 2023). Understanding the cycles and drivers of spatial variation of R_S within forest ecosystems is therefore critical to reduce the global C budget uncertainties (Warner et al., 2019).

Soil respiration is sensitive to environmental conditions which cause substantial variation over space and time (Gougoulias et al., 2014; Lei et al., 2021; Lu et al., 2021). The drivers of the spatial variation of R_S at all scales can be broadly grouped into biotic and abiotic factors. Biotic variables include root biomass, photosynthesis, as well as plant and microbial community composition (Tufekcioglu et al. 1999; Liu et al. 2020; Stoyan et al. 2000; Y. R. Liu et al. 2018). Abiotic factors include climatic variables such as soil temperature (T_{soil}) and soil water content, SWC (Davidson and Janssens 2006; Davidson et al. 2000), both of which are frequently used to interpret the spatial and temporal dynamics of R_S (Sotta et al. 2004; Cai et al. 2023). Drivers of spatiotemporal variation in R_S change across spatial scales and fluctuate temporally due to the seasonality and spatial variability of environmental variables that control rates of R_S (Hereș et al., 2021; Ruehr et al., 2010; Soranno et al., 2019). Understanding the dynamics of spatial variation of R_S, as well as its drivers, are thus key to reducing uncertainties of ecosystems R_S budgets (Soranno et al., 2019).

Seasonal variation of R_S has been frequently studied, with SWC and T_{soil} being strong drivers of inter-annual changes (Griffis et al., 2004; Hereş et al., 2021; Rubio & Detto, 2017; Saiz et al., 2006). To understand how seasonality influences spatial variation of R_S and its drivers, studies implementing long term observed data of R_S and its abiotic and biotic drivers must be conducted across many ecosystems (Hashimoto et al., 2015; Saiz et al., 2006). The relationships revealed with this information will enhance understanding of the spatial variation of R_S and its drivers.

Because substantial temporal and spatial variation of R_S is attributed to changes in SWC (Cai et al., 2021; Zhang et al., 2015), it is important to further understand the effects of the extremes of SWC on the spatial variation of R_S. (Shi et al., 2020). Droughts have increased in severity, frequency, and duration due to climate change (Zhao and Dai 2022), and there has been an increase in the prevalence of flash droughts, which develop quickly in a matter of weeks (Yuan et al. 2023). Droughts can cause a significant decrease in R_S (Zheng et al. 2021), yet few studies have investigated the effects of drought on the spatial variation of R_S (Ohashi et al. 2015). Heavy rainfall events have also increased due to climate change (Shukla et al., 2022). Increases in soil water content can decrease R_S (X. Liu et al., 2020), partially imposed by slower gas diffusion due to increased resistance of diffusive pathways within the soil matrix (Greenway et al., 2006). With increasing frequency of these events and the extremes of water status, understanding the effects of these events on the spatial variation of R_S and its drivers is important in understanding the changes in spatial variation of R_S under the changing climates.

The overarching goal of this research was to understand spatiotemporal cycles of R_S and determine how environmental variables shape these cycles. We also sought to understand how spatial variation of R_S changes through time at daily and annual time scales and the effects that the extremes of water stress had on those spatiotemporal cycles of R_S. Finally, we aimed to determine whether subsurface climate variables alone are adequate in describing the spatial variability of R_S, or if other variables are needed to fully describe the spatial variability of R_S.

1.2 Thesis Structure, Objectives, and Science Questions

This research is presented in two chapters, each structured as a stand-alone paper. Chapter 2 is focused on characterizing temporal patterns of the spatial variability of R_S and answering: 1) How does the spatial variation of R_S change through time at daily to annual time scales, 2) how does spatial variation of R_S change when the ecosystem is under water excess and deficit stress, and 3) how many chambers are needed to adequately detect differences in R_S between MOFLUX and another hypothetical forest during different periods of observed spatial variation? Chapter 3 presents a more detailed investigation of drivers of spatial variation to answer the question: Is spatial variability of R_S controlled by T_{soil} and SWC, or are other variables exerting influences, and do these drivers influence change with season?

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Chapter 2: Drought Impacts on the Spatial Variability of Forest Soil Respiration from Daily to Annual Time Scales

2.1 Abstract

Spatiotemporal variability of R_S is a primary driver of large uncertainties associated with forest carbon budgets. The effect of water deficit and excess on spatiotemporal variations of R_S is not well understood. Typically, studies focus on spatial variation or the temporal variation of R_S, while not having a comprehensive understanding of both over long time periods. As heavy rain and drought events increase in frequency and severity, understanding the response of spatiotemporal variability of R_S under these stressors will aid in reducing uncertainties in carbon budgets. We examined a decades-long data set of continuous chamber measurements from a temperate deciduous forest in the central United States to examine spatiotemporal variations of R_S, and how soil water excess and deficit stress influenced these patterns. We found that spatial variability peaked at the low and high ends of observed soil water content of (0.2 m^3 m^{-3} and 0.5 m^3 m^{-3}, respectively), and that spatial variation of R_S changed seasonally. Water status had a significant effect on spatial variation. Under water deficit stress, the amplitude of the daily cycle of the spatial variation of R_S was greater. Finally, we found that even periods of low spatial variation posed issues in detecting changes in R_S between two forests of similar variation. These results indicate that under the extremes, soil water content drives spatial variation. Our results demonstrate that seasonality and extreme water status interact to drive spatial variation at daily, seasonal, and interannual time scales.

2.2 Introduction

The upper meter of soil holds about 1,500 Pg of carbon (C) globally (Scharlemann et al., 2014). Soil respiration (R_S) is a major pathway by which soil C is lost to the atmosphere (Bond-Lamberty & Thomson, 2010), for which the global flux is 85.5 ± 40.4 (SD) Pg-C y^{-1} (Lu et al., 2021). For perspective, both the global R_S flux estimate and its uncertainty dwarf anthropogenic carbon dioxide emissions, which were 10.2 ± 0.8 Pg-C yr^{-1} in 2020 (Friedlingstein et al., 2022). The large uncertainties of global R_S estimates arise in part because of the substantial spatiotemporal variation of fluxes is not well-characterized. Enhancing scientific understanding of the dynamics and controls of spatiotemporal variation of R_S is crucial towards decreasing uncertainties of the respiration flux at the global scale and improving projections of the carbon cycle and climate (Knohl et al. 2008).

We focused on forests because of the key role they play in the global C cycle. Forests cover 31% of the Earth’s land area and hold 92% of terrestrial biomass (FAO, 2020; Pan et al., 2013). Forest ecosystem respiration is dominated by R_S (Davidson et al., 2006; Griffis et al., 2004; Jassal et al., 2007; X. Liu et al., 2022). Within forest ecosystems, spatial variation drives uncertainties of R_S estimates. Therefore, this is a critical area of study to reductions in the C budget uncertainties (Warner et al., 2019).

The rate of R_S is highly sensitive to environmental conditions and varies strongly over space and time (Lei et al. 2021; Lu et al. 2021; Gougoulias, Clark, and Shaw 2014). Spatial variation of R_S occurs at a range of scales spanning from the level of biomes down to microsites (Cai et al., 2023; Martin & Bolstad, 2009). While global variation of R_S is strongly defined by temperature, and topographic variability of R_S is driven by changes in soil properties and soil moisture (Hashimoto et al., 2015; Martin & Bolstad, 2009), less is known regarding how R_S varies over space and time within an ecosystem or landform due to microsite variation. Spatial scale-dependent studies are necessary to improve understanding of variation, as all scales are important in reducing errors associated with the upscaling of respiration measurements (Martin & Bolstad, 2009). Spatial variability introduces large uncertainties into comparisons of R_S rates, and sampling regimes do not adequately control for variation by increasing sample size, thereby reducing statistical power during comparisons of R_S (Kravchenko & Robertson, 2015). Even in relatively homogeneous stands, spatial variation can produce a large potential of error when estimating forest-level R_S (Hereș et al., 2021).

Accounting for this variation is especially important when there are hotspots and/or hot moments of biological activity (Hagedorn, 2006; Martin & Bolstad, 2009). For example, Epron et al. (2006) quantified the spatial variation of R_S across a topographic gradient in a tropical rainforest on 5 m^2 plots (N=30) distributed along transects. Within each plot, they made gridded measurements at 30 locations, and found plot-level R_S means and coefficients of variation (CVs) that ranged from 2.20 to 6.46 μmol m^{-2} s^{-1}, and 23% to 73%, respectively (Epron et al. 2006). Capturing fine scale spatial variations of R_S relationships with different environmental variables within ecosystems is necessary to bring into large scale models to reduce the uncertainties in global R_S estimates (Huang et al., 2020).

The spatiotemporal variation of R_S at fine, inter-landform levels, is driven by edaphic factors including soil chemistry, soil texture, soil structure, and topography (Tain 2019; Jiang et al. 2020; Martin and Bolstad 2009). Root biomass, microbial community structure, the carbon:nitrogen ratio (C:N), leaf litter production, the total organic substrate and its accessibility can all contribute to spatial variation in R_S from microsite to ecosystem scales (Fang et al., 1998; Irvine & Law, 2002; Stoyan et al., 2000; Xu & Qi, 2001). These soil edaphic factors change across landscapes, and through these differences, shape variations in soil microclimate (Turner 1981). Soil structure and its pore space has a direct effect on the water retention of a soil, which play a key role in defining soil water content (SWC) and the thermal environment (Vereecken et al., 1989).

Soil temperature (T_{soil}) and SWC are key drivers of spatial variability of R_S (Davidson et al., 2000: Davidson & Janssens, 2006). Indeed, these two variables accounted for 40-80% of the variation of R_S within two field studies (Balogh et al., 2011; Mäkiranta et al., 2008). In an experimental study, R_S increased by 28% in response to warming of soil and air temperatures by 1.29 °C and 1.56 °C, respectively (Nyberg & Hovenden, 2020). The dependency of R_S on T_{soil} can, however, break down under water-limited or water-excess ecosystem states, when SWC dominates control of R_S (Zhang et al., 2015).

The strong role the extremes of water status play in constraining R_S make them key areas of study. Droughts have increased in severity, frequency, and duration because of climate change (Zhao and Dai 2022), and there has been an increase in the prevalence of flash droughts, which develop quickly in a matter of weeks (Yuan et al., 2023). Droughts can cause a significant decrease in R_S (Zheng et al., 2021), yet few studies have investigated the effects of drought on the spatial variation of R_S (Ohashi et al., 2015). Heavy rainfall events have also increased due to climate change (Shukla et al., 2022). Increases in soil water content can decrease R_S (X. Liu et al., 2020), partially imposed by slower gas diffusion due to increased resistance of diffusive pathways within the soil matrix (Greenway et al., 2006).

The goal of this research was to characterize the spatial variability of R_S at sub-daily to seasonal timescales in an upland *Quercus-Carya* (oak-hickory) forest, and to determine how these patterns shift during water excess and deficit. This research aimed to answer three questions: i) How does the spatial variation of R_S change through time at daily to annual time scales, ii) how does the variation change when the ecosystem is under excess and deficit water stress, and iii) how many chambers are needed to detect differences in R_S between two forests during different periods of observed spatial variation? We hypothesized that spatial variation is highest during the growing season, and that spatial variation depends on ecosystem water status, decreasing as water deficit and excess stress intensifies. We further hypothesized that we need more chambers than currently available to detect small differences in R_S between two forests. We analyzed decades of automated chamber measurements to quantify spatial variation of R_S across chamber measurements to evaluate our hypotheses.

2.3 Methods

2.3.1 Site Description

Data have been collected over two decades at the Missouri Ozark AmeriFlux (MOFLUX) site (38° 45' 19.3" N, 92° 12' 17.1" W). The MOFLUX site was established in 2004, and continuous, automated R_S measurements have been made since that time. The site is located at the University of Missouri's Baskett Forest within the Ozark Border Region of central Missouri. The broader region is made up of forested areas in the south and agricultural croplands to the north. The climate is warm, humid, and continental. During the growing season, rainfall is highly variable, and therefore the area is prone to seasonal drought, with plant physiological water deficit stress exacerbated during periods with low rainfall because of the thin soils (Gu et al., 2016). The major vegetation type is second-growth, upland oak-hickory forest (Pallardy et al., 1988). Important tree species include *Quercus alba* L. (white oak), *Q. velutina* Lam. (black oak), *Carya ovata* (Mill.) K. Koch *(*shagbark hickory), *Acer saccharum* Marsh. (sugar maple), and *Juniperus virginiana* L. (eastern red cedar) (Gu et al., 2015).

The dominant soils at MOFLUX are Weller silt loam and Clinkenbeard very flaggy clay loam (Gu et al., 2015; Soil Survey, et. al. 2022). Weller soils are taxonomically classified as fine, smectitic, mesic, Aquaretic Chromic Hapluadalfs, and Clinkenbeard soils are clayey-skeletal, mixed, superactive, mesic Typic Argiudolls (Soil Survey, et. al. 2022).

2.3.2 Soil Respiration

The rate of R_S, or the total soil CO_2 efflux, was measured using automated chambers positioned around the MOFLUX eddy covariance tower. Data from 2004-2013 were collected using a custom, 8-chamber system (Edwards & Riggs, 2003). After March of 2013, measurements have been made using a commercially available, automated 16-chamber system with co-located near surface soil temperature and moisture measurements at each chamber (model 8100A Li-Cor Inc., Lincoln NE). The chambers were placed with the intention of representing the forest demographic by placing them under important tree species (Liu et al., 2020). Both chambers were flow-through non-steady state chamber designs (Edwards & Riggs, 2003). A single measurement lasted 7 minutes for the 8- chamber system, and 3.5 minutes for the 16- chamber system, therefore for both the 8- and 16-chamber systems, a full measurement cycle took approximately one hour (Liu et al., 2020).

From 2004–2013, near surface volumetric soil water content (SWC) was measured using water content reflectometers co-located near each chamber (model CS616, Campbell Scientific Inc., Logan, UT, USA), while soil temperature was measured with thermocouples at 5 cm depth at three locations near the chambers. Soil temperature and SWC measurements were made every 30 seconds and recorded as 30-minute averages. Since 2013 when the LI-8100A system was installed, SWC and soil temperature have been measured at each chamber using time domain reflectometers and thermistors, with samples recorded each time a chamber closes to measure R_S. For this research, we used data collected from 2005 through 2016, before trenching experiments were initiated.

2.3.3 Calculations and Analyses:

The statistic used to quantify spatial variation was the cross-chamber coefficient of variation (CV) of R_S. Calculations were implemented to isolate the spatial variation signal. This was accomplished by first aggregating data over a period of interest to compute chamber-level mean values, which were then used to compute the cross-chamber means ($\overline{R_t}$), standard deviations (s_t) and CVs, where the *t* subscripts represent time. The $\overline{R_t}$ was computed according to:

$$\overline{R_t} = N^{-1}\sum_{i=1}^{N}\overline{R_{t,\iota}} \qquad [2.1]$$

where $\overline{R_{t,\iota}}$ is the mean R_S of the i^{th} chamber, computed by aggregating observations over the designated time period, and *N* is the number of chambers. The s_t and CV were computed according to:

$$s_t = \sqrt{(N-1)^{-1}\sum_{i=1}^{N}(\overline{R_{t,\iota}} - \overline{R_t})^2} \qquad [2.2]$$

and

$$CV_t = s_t/\overline{R_t} \qquad [2.3]$$

We examined the temporal dynamics of spatial variation at seasonal and sub-daily time scales by applying equations 2.1–2.3 to data subjected biweekly temporal aggregation, and seasonally averaged mean daily cycles of 30-minute R_S estimates, respectively.

A potential source of bias in these calculations is the influence of missing data on the chamber-level mean estimates ($\overline{R_{t,\imath}}$). We therefore tested the influence of missing data on biweekly and daily cycle statistics by analyzing time periods where we had no missing data. Here, we analyzed time periods without missing observations and generated sets of data with synthetic gaps. The synthetic data sets were characterized by different fractions of missing observations that were randomly injected. There were five permutations generated for each gap fraction. The mean of each synthetic dataset was then compared to the ‘true’ mean computed from data without any missing observations. The threshold for data screening was identified as the smallest gap fraction for which the mean deviated by more than one standard error from the true mean computed without any missing data. The data retention thresholds for computing biweekly statistics, and the daily cycles were 75% and 50%, respectively.

2.3.4 Soil water content effects on spatial variation

We conducted an analysis to investigate the influence of SWC on the spatial variation of R_S. We calculated the half-hourly cross chamber mean R_S and CV of R_S for all years during the growing season (DOY 120-300). We binned SWC to the nearest thousandth and then computed the mean of the calculated cross chamber R_S and the CV of R_S at each SWC. Next, overall water status groups were evaluated by determining what effect increasing water content had on R_S. These groups were identified visually and were as follows: Low, where increasing SWC resulted in an increase in R_S (SWC < 0.275 m^3 m^{-3}). Medium, where increasing SWC resulted in no change in R_S (0.275 m^3 m^{-3} < SWC < 0.375 m^3 m^{-3}). High, where increasing SWC resulted in a decrease in R_S (SWC > 0.375 m^3 m^{-3}).

2.3.5 Annual Cycles

Biweekly CVs of R_S were computed to examine how the spatial variation of R_S changes temporally across seasons, and how drought influences the annual cycle. The MOFLUX site experiences strong interannual variability in precipitation and drought stress (Gu et al., 2016). We knew a priori that our data record included the major drought year of 2012 (Hoerling et al., 2014). The intense drought conditions induced significant ecosystem water stress that decreased net ecosystem C uptake and suppressed R_S (Wood et al., 2023).

To test the effect of temporal and drought effects on the spatial variation of R_S, we conducted a multifactorial ANOVA on bi-weekly CVs of R_S.

$$\sqrt{CV} = \mu + Year + Season + WaterStatus + (Year{:}Season{:}WaterStatus) + \epsilon$$

where √CV is the normalized square root of the biweekly CV which was done to meet the assumptions of an ANOVA, μ is the overall mean, *Year* defines the year of the observation, *Season* defines the meteorological season of the observation, *WaterStatus* indicates the ecosystem water status of Low, Medium, or High, and *Year:Season:WaterStatus* is the three-way interaction. Post-hoc multiple means comparison was conducted using a Tukey’s honest significant difference test.

2.3.6 Daily Cycles

Spatiotemporal variation of R_S was examined at sub daily time scales by analyzing the mean daily cycles of the half-hourly cross-chamber CV of R_S. We examined how the daily cycles of the CV of R_S changed seasonally across the mean daily cycle and a known drought year. Seasons were examined to demonstrate differences in the daily cycles. To do so, we computed anomalies by subtracting the mean CV of a seasonal daily cycle from each time step, thus centering the cycle on the 0 of the y-axes. The mean daily cycle was calculated by averaging the seasonal sub-daily CV of R_S cycles for all years except 2012. The daily cycle for the drought year was calculated using data from 2012, which experienced a drought during the growing season. Both years cycles were examined for the daily amplitude of CV of R_S that was exhibited by each season.

2.3.7 Power Analysis

To determine the ability of our chamber systems to test for differences in R_S between two forests at different levels of spatial variation we conducted a power analysis. Using the mean R_S and SD of R_S from three events, the highest and lowest observed spatial variation of the mean annual cycle and the highest spatial variation of the drought year, we performed a power analysis for a two-sample t test. Increasing percentages of R_S from 10%-75% were calculated for the mean R_S at the chosen time. Then an effect size, Cohens d (Cohen, 1988), was calculated according to:

$$d = (\overline{R_2} - \overline{R_1})/\sigma_1 \tag{2.4}$$

where $\overline{R_1}$ is the mean R_S observed at the time of interest, $\overline{R_2}$ is a simulated percentage of increase from 10%-75%, and σ_1 is the SD of sampled R_S. Finally, the percentage increases in R_S that had a lower calculated effect size than the one achieved by the current chamber system were then inspected further to determine how many chambers would be needed to detect such a difference at a power of 0.8.

All analysis were conducted in RStudio ver. 2023.12.0.369

2.4 Results

2.4.1 Spatial Variation Shifts with Soil Water Content

The SWC binned mean R_S has a quadratic relationship with mean SWC (Fig. 2.1A). SWC binned mean R_S increases to 0.275 m^3 m^{-3}, where it levels out at 0.375 m^3 m^{-3}, and then begins to decrease at 0.375 m^3 m^{-3} (Fig. 2.1A). There were local peaks in the CV of R_S at a SWC of 0.2 m^3 m^{-3}, and 0.5 m^3 m^{-3} (Fig 2.1B).

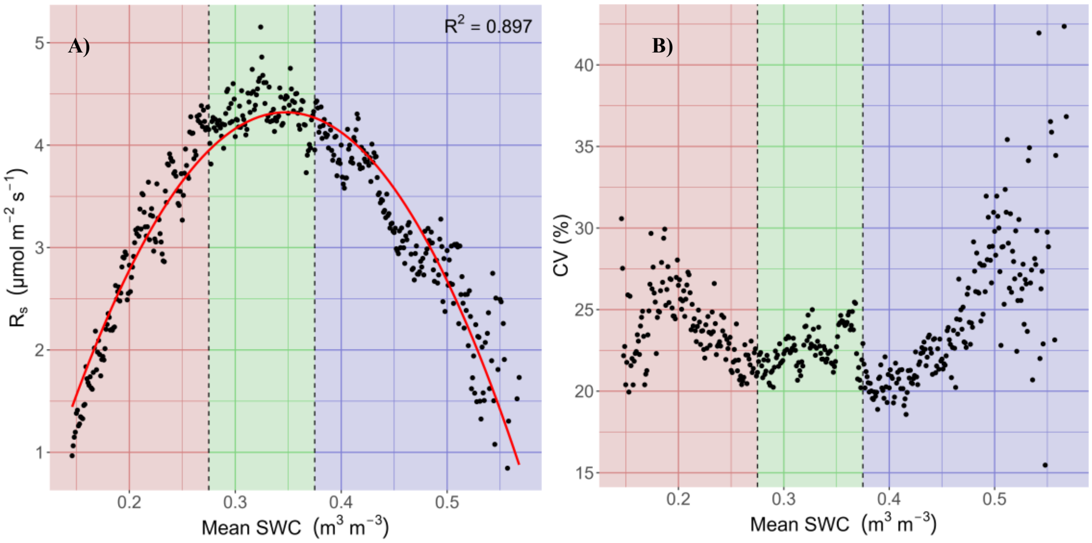

Figure 2.1: The relationships between the mean cross-chamber soil respiration (R_S) (A) and the cross-chamber coefficient of variation (CV) of R_S (B) with mean soil volumetric water content (SWC) in the growing seasons from 2005 to 2012. The 30-minute means and CVs of R_S were binned by SWC, and then averaged. R_S and CV were binned to the nearest thousandth SWC. Background colors signify the water status groups.

2.4.2 Annual Cycles of Spatial Variation of R_S

For the biweekly aggregation periods, the average CV of R_S in the mean annual cycle was 18 ± 3.5%, with a minimum of 12.9% during the fall and maximum of 25.1% during the winter (Fig. 2.2B). For all the annual cycles, the minimum CV of 3.7% was achieved in the fall of 2009, and maximum CV of 38.9% was achieved during the summer drought of 2012 (Table 2.1).

Table 2.1: Descriptive statistics summarizing biweekly coefficients of variation (CV) of R_S for each year. With year the cycle is from, mean CV ± SD, minimum and maximum biweekly CVs of R_S from the cycle, and observations (N) for within the cycle.

Year	**Average CV ± SD (%)**	**Minimum CV (%)**	**Maximum CV (%)**	**N**
2005	21 ± 5.5	9.4	27.2	22
2006	23 ± 7.8	10.4	36.8	25
2007	13 ± 5.8	5.2	24.3	22
2008	14 ± 4.7	8.1	26.2	23
2009	12 ± 5.2	3.7	23.4	20
2010	17 ± 6.5	6.9	27.5	20
2011	19 ± 6.4	10.4	33.4	19
2012	23 ± 8.8	5.4	38.9	23
2014	20 ± 2.7	15.7	23.7	11
2015	17 ± 5.2	9.8	24.7	15
2016	16 ± 2.2	10.6	18.3	12

The spatial variation of bi-weekly mean R_S showed distinct seasonal patterns (Fig. 2.2). The absolute spatial variation, as indicated by the SD, peaked in the summer when biological activity and fluxes were greatest (Fig. 2.2A). In contrast, the mean annual cycle of the bi-weekly CV of R_S peaked in the winter, gradually decreasing through the year (Fig. 2.2B). The annual cycle of the cross-chamber SD differed in 2012 relative to the mean annual cycle (Fig. 2.2A). The SD decreased during the summer drought, until a rewetting event at day of year 250, when the SD soon returned to values similar to the mean annual cycle (Fig. 2.2A). In contrast, the CV of R_S increased during the summer drought of 2012, until a rewetting event at around day of year 250, where the CV of R_S

soon returned to values close to that of the mean annual cycle (Fig. 2.2B). These results indicated that the spatial variation of R_S was modulated by drought (Fig. 2.2B).

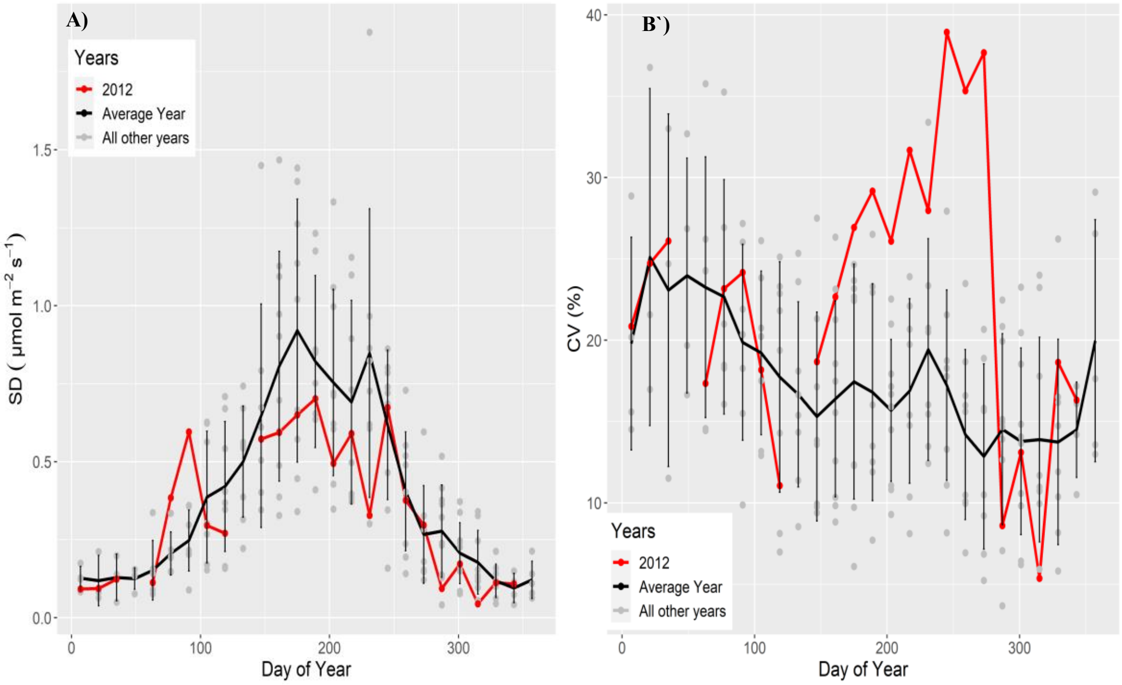

Figure 2.2: There were distinct annual cycles of bi-weekly A) absolute and B) relative spatial variation, as represented by the cross-chamber standard deviation (SD) and the coefficient of variation (CV) of soil respiration (R_S), respectively. Both cycles were modulated by drought conditions. The black lines represent the mean annual cycles of all years except 2012 (a major drought year) and error bars represent ± 1 SD. The gray circles represent individual values in all years except 2012, which are shown as the red lines.

We found that Season, Water Status, and Year all had significant effects on √CV of R_S. Additionally, the interaction effects between these independent variables also had a significant effect on the √CV of R_S (Table 2.2).

Table 2.2: Statistics of test for spatial variation from a multi-factorial ANOVA, with the √CV of R_S as the dependent variable, and Season, Water Status, Year, and all the interactions as the independent variables.

Independent Variables	***df***	**Mean Square**	**F**	**p**
Season	3	7.064	30.828	**<0.001**
Water Status	2	3.065	13.378	**<0.001**
Year	9	3.551	15.498	**<0.001**
Season × Water Status	6	0.520	2.267	**0.041**
Season × Year	23	0.978	4.270	**<0.001**
Water Status × Year	12	0.757	3.305	**<0.001**
Season × Water Status × Year	6	0.613	2.676	**0.018**
Total	121	.0229		

Ecosystem water status had a significant effect on √CV of R_S (Table 2.2. Figure 2.3). The √CV for medium and low water status was significantly higher than under high water status (Figure 2.3).

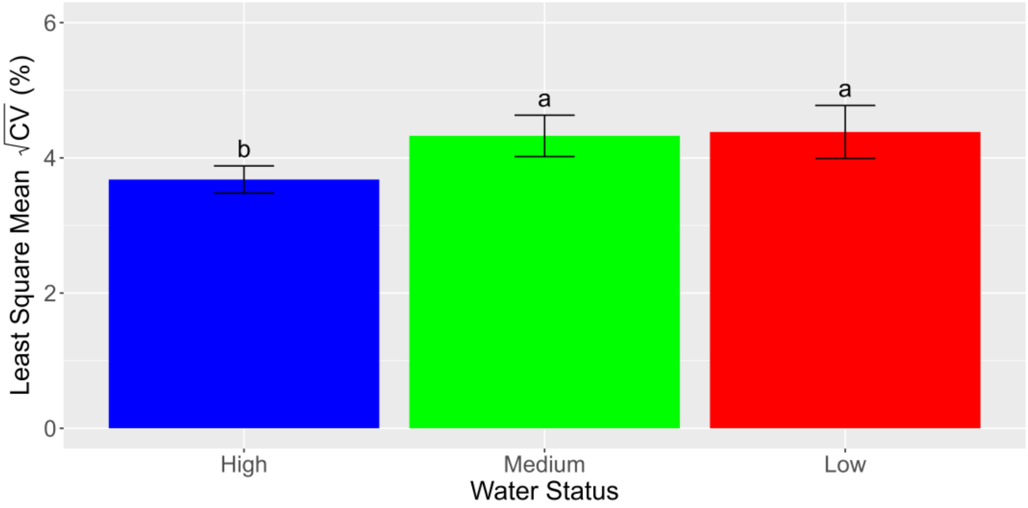

Figure 2.3: The spatial variation of soil respiration (R_S) was influenced by water status. Shown is the least square mean of √CV of R_S for high soil water content (SWC > 0.375 m^3 m^{-3}), medium (0.275 m^3 m^{-3} < SWC < 0.375 m^3 m^{-3}), and low (SWC < 0.275 m^3 m^{-3}) status represented by blue, green, and red, respectively. Error bars represent the standard error. Bars with different letters are significantly different at α = 0.05.

Season had a significant effect on the √CV of R_S (Table 2.2, Figure 2.4). Fall exhibited the lowest spatial variability, followed by spring and summer which each were significantly higher than fall, and finally winter, which exhibited the highest spatial variability of any season (Figure 2.4). The interaction effect between water status and seasonality reveals differences within season and water status combinations (Figure 2.4), indicating that water status and seasonality together play a role in regulating the spatial variability in R_S.

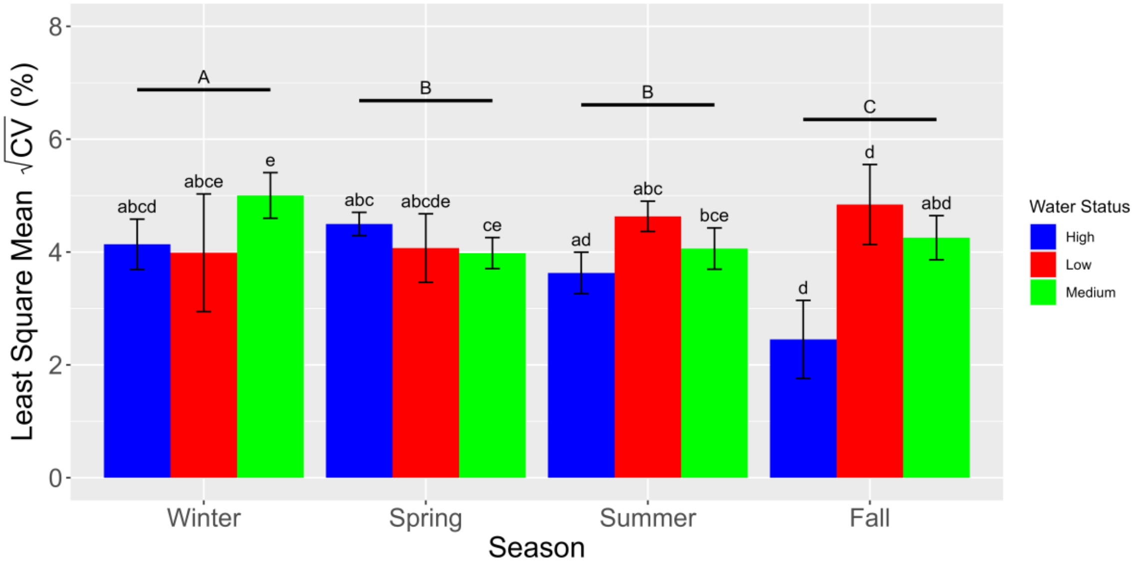

Figure 2.4: Season had a significant effect on √CV of soil respiration (R_S), and the interaction of season and water status had a significant √CV of R_S. Shown is least square mean of √CV of R_S across seasons and water status with high soil water content ($SWC > 0.375\ m^3\ m^{-3}$), medium ($0.275\ m^3\ m^{-3} < SWC < 0.375\ m^3\ m^{-3}$), and low ($SWC < 0.275\ m^3\ m^{-3}$) water status is represented by blue, green, and red respectively. Error bars represent standard errors. Bars not sharing lowercase lettering denote significant differences of water status season interaction at $\alpha = 0.05$, while uppercase letters above season groupings denote differences in the means of the main effect for season.

2.4.3 Daily Cycles of Spatial Variation of R_S

Daily cycles of the spatial variation of R_S showed differences in amplitude depending on season (Fig. 2.5A). The mean daily cycles of the CVs of R_S peaked at midday during the spring and winter seasons, and at night during the summer and fall seasons (Fig. 2.5A). In the drought year of 2012, the amplitude of the daily cycle of summer was large, with the lowest values of the CV of R_S during the drought year occurred during the summer season at mid-day and peak values overnight (Fig. 2.5B).

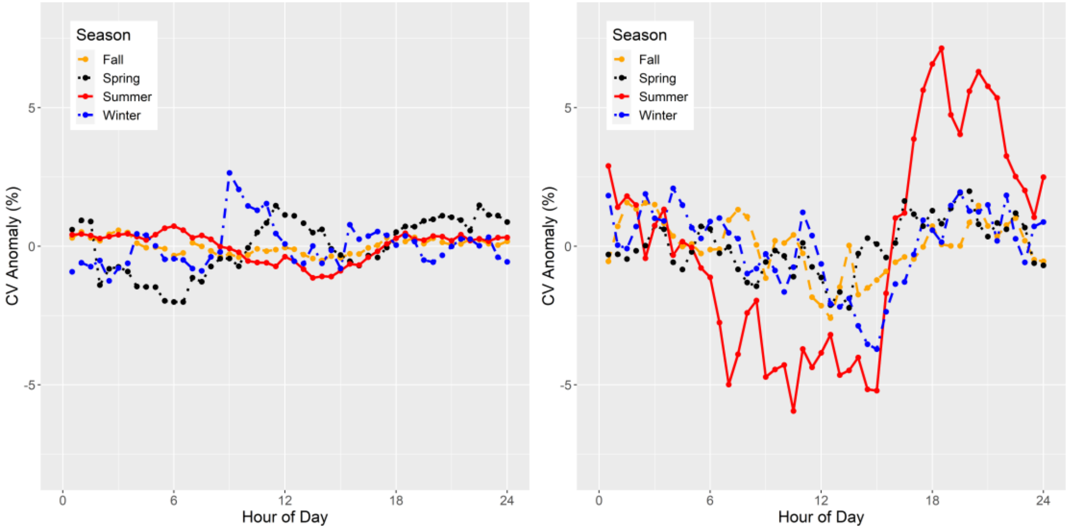

Figure 2.5: The anomalies of mean daily cycles of the spatial variation (as represented by the cross-chamber coefficient of variation, (CV) of soil respiration (R_S) during different seasons for A) mean daily cycles of all years except 2012, and B) the major drought year of 2012. The CV anomalies are the difference of the half hour CV of R_S value and the mean CV of R_S of the daily cycle of interest. The anomalies were shown here to ease comparison of the phasing and amplitudes of the daily cycles. For context, the mean value of the mean daily cycles in fall, spring, summer, and winter were 14.6%, 20.4%, 16.6%, 20.2%, respectively; while the drought year daily cycles were 19.0%, 18.4%, 28.1%, and 18.9% respectively.

2.4.4 Spatial variation of R_S effect on detectable differences in R_S

This analysis examined the impact of observed spatial variation of R_S on the ability to detect differences between mean R_S rates at MOFLUX and a hypothetical respiration rate at another forest. We then determined the number of chambers required to detect differences in R_S. The power analysis was performed on three time periods, the lowest CV of the mean annual cycle, the highest CV of the mean annual cycle, and the highest CV in the drought year 2012.

The maximum CV of R_S of the annual cycle was 25.1% (Fig. 2.2B, Table 2.1), with the mean R_S ± SD being 0.45 ± 0.12 µmol C m^2 s^{-1}. We calculated the achievable effect size for 16 chambers to be 1.02 at 0.8 power (Fig. 2.6A). Given the observed spatial variation of this period, we calculated the effect sizes for a multitude of hypothetical R_S rates in another forest. The effect size captured by our chambers, paired with the effect sizes needed to capture the increases in R_S showed that during this period of observed spatial variation we could capture a 27% increase in R_S (Fig. 2.6B), with more chambers needed to achieve 0.8 power on increases less than 27% (Fig. 2.6C).

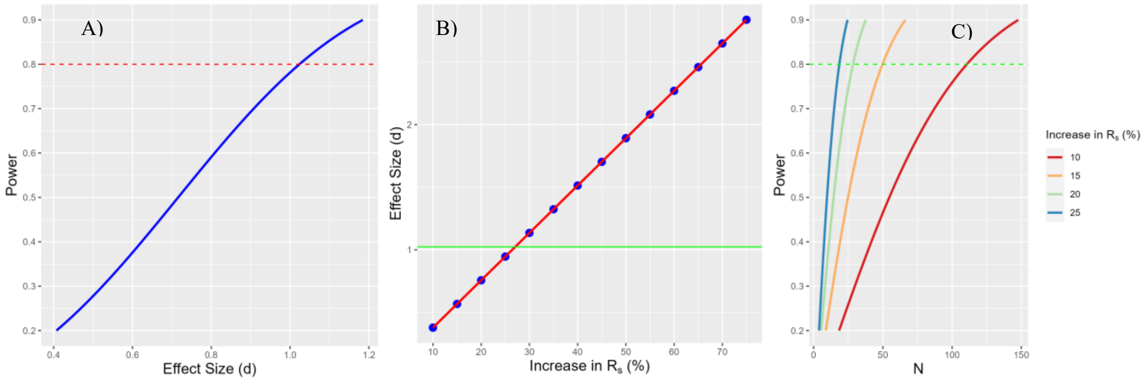

Figure 2.6: Power analysis for a two-sample t-test to determine sample size needed to detect increased soil respiration (R_S), using the period of highest spatial variation observed in the mean annual cycle. A) The blue line shows the power achieved at different effect sizes for a 16-chamber system, the red line depicts the lowest achievable effect size at 0.8 power. B) The blue points show the effect size needed to detect the increase in R_S, and the green line illustrates the lowest achievable effect size to achieve a power of 0.8. Effect sizes below the green line are lower than what is achievable with 16 chambers. C) Green line indicates the number of chambers needed to achieve 0.8 power; each curve represents a percent increase in R_S that had a lower effect size than achievable with current number of chambers.

The lowest CV of R_S of the mean annual cycle was 12.9% during the fall (Fig. 2.2B, Table 2.1), with the mean ± SD being 2.11 ± 0.27 µmol C m^2 s^{-1}. We calculated the achievable effect size for 16 chambers to be 1.02 at 0.8 power (Fig. 2.7A). Given the information of this period, we calculated the effect sizes for a multitude of hypothetical R_S rates in another forest. The effect size captured by our chambers, paired with the effect sizes needed to capture the increases in R_S showed that during this period of observed spatial variation we could capture a 13% increase in R_S (Fig. 2.7B). With more chambers needed to achieve 0.8 power on increases less than 13% (Fig. 2.7C).

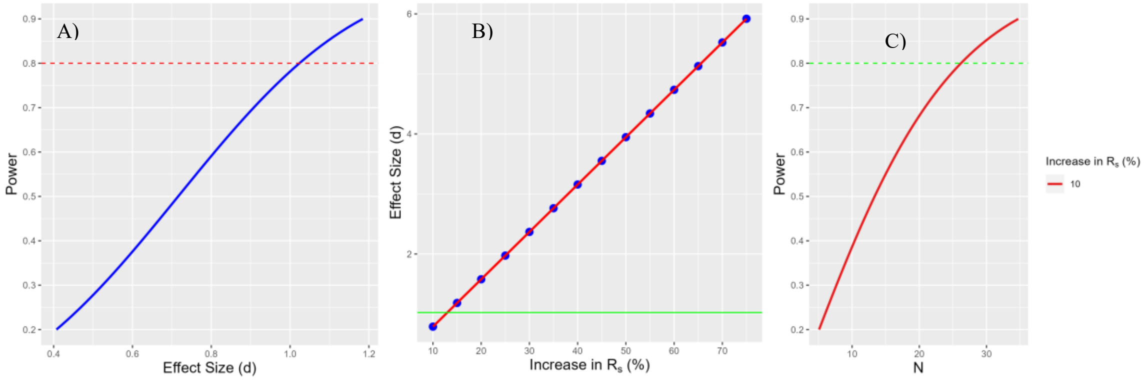

Figure 2.7: Power analysis for a two-sample t-test to determine sample size needed to detect increased soil respiration (R_S), using the period of lowest spatial variation observed in the mean annual cycle. A) The blue line shows the power achieved at different effect sizes for a 16-chamber system, the red line depicts the lowest achievable effect size at 0.8 power. B) The blue points show the effect size needed to detect the increase in R_S, and the green line illustrates the lowest achievable effect size to achieve 0.8 power. Effect sizes below the green line are lower than what is achievable with 16 chambers. C) Green line indicates the number of chambers needed to achieve 0.8 power; each curve represents a percent increase in R_S that had a lower effect size than achievable with current number of chambers.

The highest CV of R_S of the 2012 annual cycle was 38.9% during the peak of the summer drought (Fig. 2.1B, Table 2.1), with the mean R_S ± SD being 1.7 ± 0.67 µmol C m^2 s^{-1}. We calculated the effect size for 8 chambers to be 1.51 at 0.8 power (Fig. 2.8A). Given the information of this period, we calculated the effect sizes for a multitude of hypothetical R_S rates in another forest. The effect size captured by our chambers, paired with the effect sizes needed to capture the increases in R_S showed that during this period of observed spatial variation we could capture a 59% increase in R_S (Fig 2.8B). With more chambers needed to achieve 0.8 power on increases less than 59% (Fig 2.8C).

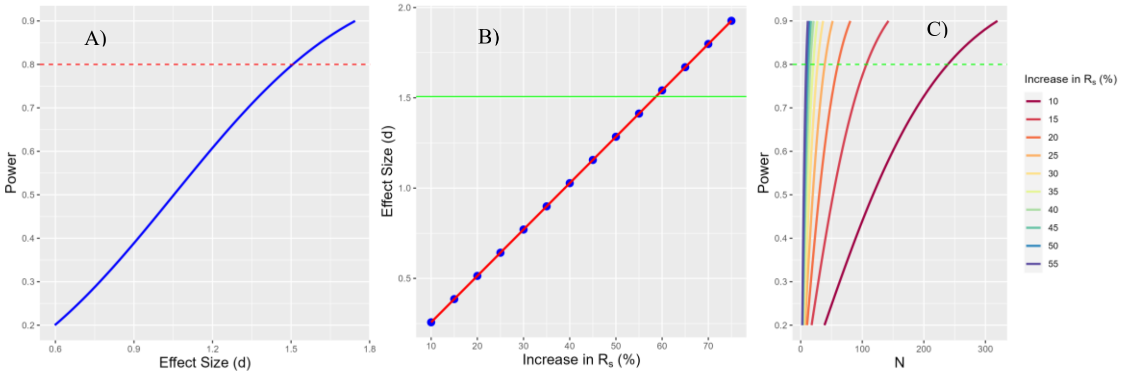

Figure 2.8: Power analysis for a two-sample t-test to determine sample size needed to detect increased soil respiration (R_S), using the period of highest spatial variation observed in the drought year 2012. A) The blue line shows the power achieved at different effect sizes for an 8-chamber system, the red line depicts the lowest achievable effect size at 0.8 power. B) The blue points show the effect size needed to detect the increase in R_S, and the green line illustrates the lowest achievable effect size to achieve a power of 0.8. Effect sizes below the green line are lower than what is achievable with 8 chambers. C) Green line indicates the number of chambers needed to achieve 0.8 power; each curve represents a percent increase in R_S that had a lower effect size than achievable with current number of chambers.

The power analysis displayed a necessity of more chambers to detect differences in R_S rates of MOFLUX and a hypothetical increase in R_S (Table 2.3). During the drought year of 2012, the highest observed spatial variability disrupted detecting differences in R_S of up to 59% with an 8-chamber system (Table 2.3). We found that during this period of observed spatial variation at the site, 239 chambers were needed to detect a 10% increase in R_S (Table 2.3).

Table 2.3: Results of each power analysis detailing the ability of the current chamber to detect differences in a theoretical increase in soil respiration (*R_S*) and how many chambers needed to detect a 10% increase in *R_S*. Chambers is the current number of chambers during sampling. Effect size is the effect size detectable by the current chamber system. Capturable difference is the percentage increase that is capturable by the current chamber system. Chambers 10% is how many chambers are needed to detect a 10% increase in *R_S* at the period of observed spatial variation.

Time period sampled	**Chambers (n)**	**Effect Size (d)**	**Capturable difference**	**Chambers 10% (n)**
Mean annual cycle low	16*	1.02	13%	27
Mean annual cycle high	16*	1.02	27%	111
2012	8	1.51	59%	239

*The chambers numbers were 8 or 16 in the years used to calculate the mean annual cycle, with 16 being chosen as it is the highest number of chambers used.

2.5 Discussion

Describing both magnitude and patterns of spatial variation in *R_S* at different scales and factors driving variation is an issue ecologists currently face (Soranno et al., 2019). While studies have shown how SWC can drive spatial and temporal variability in *R_S* (Cai et al., 2021; Zhang et al., 2015), few studies have examined the effects of water stress of excess and deficit on the spatiotemporal cycles exhibited by forest *R_S* (Cai et al. 2023). In this study, we aimed to understand how the spatial variation of *R_S* changes through time at daily to annual time scales, and how the variation changes when the ecosystem is under excess and deficit water stress.

The relationship between the mean *R_S* and SWC follows a clear quadratic relationship ($R^2 = 0.897$), when we analyzed the CV of *R_S* relative to SWC, distinct patterns emerge (Fig 2.1). Previous studies identified a similar quadratic relationship (X.

Liu et al., 2020); however, our analysis focused on a new relationship between the CV of *R_S* and SWC, which revealed peaks of spatial variation at both low and high ecosystem water status, at ~0.2 and ~0.5 m^3 m^{-3} SWC respectively (Fig. 2.1). Notably, the highest CV of *R_S* was found for conditions of extreme wetness (Fig. 2.1). Similar patterns have been observed in other ecosystems, where the extremes of water status led to increased spatial variability of *R_S* (Shi et al., 2020; Zhang et al., 2015). The increase in spatial variation at higher SWC, and sharp decline after could be due to increased resistance to soil CO_2 diffusion exhibited by waterlogged soil (Author & Kursar, 1989; Sotta et al., 2004). Although this was not reflected in the annual cycles water status Tukey HSD, we hypothesize that the high temporal resolution for this analysis allowed us to capture high water content that typically would drain from soil pores due to gravity (Gardner, 1962) and not be reflected in the bi-weekly mean values used in the ANOVA analysis.

Seasonality had a significant influence on CV of *R_S* (Table 2.2, Fig. 2.4), which is consistent with previous work, noting the changes in CV of *R_S* through time due to the changes to environmental conditions and vegetation (Shi et al., 2020). Our results also concurred with previous research on the effects of SWC on spatial variation of *R_S*. In a tropical forest, it was found that during dry periods, despite lower *R_S*, there was higher relative variability in measurements (Rubio & Detto, 2017). It has also been reported that when under drought conditions, an increase in spatial heterogeneity of measured *R_S* occurred (Shi et al., 2020). When we examined the interaction between water status and season, we observed changes compared to the previous analysis of these factors in isolation. Specifically, seasons and the extremes of water status, which were previously shown as significantly different, are not consistent in the interaction (Fig. 2.3 & 2.4), with the interannual changes in biotic and abiotic factors driving R_S shaping different relationships across the season water status combinations (Hereș et al., 2021; Jiang et al., 2020; Zhang et al., 2015).

Overall, under the drought conditions, we saw an increase in the spatial variation of R_S at the daily time scale (Fig. 2.5). The spatiotemporal variability in the daily cycles concurs with previous research. The SWC has been found shape differences in daily cycles, and T_{soil} along with forest structure could create spatial heterogeneity (Rubio & Detto, 2017). Other studies found that the relationship between SWC and canopy openness can create spatial variation in daily R_S (Cai et al., 2021). We note the lowest point in the observed CV of R_S during the midday of the drought year (Fig. 2.5). While the daily mean cycle of summer experienced some decrease in its CV of R_S during the midday, this effect was much more exacerbated in the drought year. We hypothesized that the decreased spatial variation at mid-day during the drought year was due to the combination of heat and water deficit stress decreasing R_S overall, this has been seen in some studies, where drought caused decreased R_S at midday, but R_S rebounded overnight. Soil moisture availability under drought conditions has been found to be the main factor influencing R_S in drought conditions (Wood et al. 2013; Correia et al. 2012; Almagro et al. 2009). It has also been observed that while under drought conditions the heterotrophic respiration (R_h) and autotrophic respiration (R_a) components of R_S behave differently, with R_h being more sensitive to drought than R_a, with shifts in the ratio of contribution of R_h to R_s being positively correlated to SWC (Zheng et al., 2021). These responses, in combination with observed correlations of R_h with litter depth and R_a with aboveground biomass could lead to differences in spatial variability within a daily cycle (Mäkiranta et al., 2008).

The power analyses for a two-sample t-test revealed that the uncertainties associated with R_S due to spatial variation created problems in successfully testing for differences amongst two forests R_S (Fig. 2.6, Fig. 2.7, Fig 2.8). This presents large issues for determining differences across forests, even when determining relatively high (59%) increases in R_S during periods of substantial spatial variability. Previous studies show that large sampling efforts are required to reduce the uncertainties associated with spatial variation of R_S (Hereș et al., 2021), something our results confirmed. Our results support previous studies that show when determining differences in R_S, even periods of low spatial variation can issue create issues (Cai et al., 2023a). We found even under the lowest spatial variation of the mean annual cycle, 16 chambers were insufficient for detecting a 10% increase in mean forest R_S (Fig. 2.6). This presents an issue to studies interested in differences in R_S measurements at the landform or global scale, meaning that small variations in R_S could be unaccounted for due to the uncertainties associated with spatial variation.

This work described the effect of different levels of water status on spatiotemporal cycles not previously explored, as well as the relationship water status has on the spatial variation of R_S. This research has filled a knowledge gap of how water deficit and excess stress affect spatial variation of R_S. There is a growing need to understand the drivers of spatial variation of R_S (Cai et al. 2023). While previous studies have reported on the effects of SWC on the spatial variation of R_S (Rubio & Detto, 2017), an analysis like this one including both spatiotemporal and the relationship between SWC and the CV of R_S has not been done. Previous studies observed the increase in the CV of R_S but did not examine the effects drought caused between two annual cycles and focused more on interannual variability (Shi et al., 2020).

Our research was based on daily and annual cycles; therefore, we cannot entirely explain what factors controlled the spatial variation of R_S. Studies have shown both SWC and T_{soil} being controlling factors in the spatiotemporal cycles of R_S (Cai et al., 2021; Giasson et al., 2013), we aimed to define whether soil climate drove the spatial variation of R_S at our site in Chapter 3. We also did not partition our R_S measurements into heterotrophic (R_h) and autotrophic (R_a) components, meaning we cannot determine how abiotic factors effected the spatial variation of these respiration components differently, it has been shown that these components do respond differently (Savage et al. 2013; Wang et al. 2014). Regardless of these components and effects, we did find that water status had a significant effect on spatiotemporal cycles of R_S and its relationship with the spatial variation of R_S.

2.6 Conclusions

Our study enhanced scientific understanding of the factors influencing the spatial variation of R_S. We found that spatial variability peaked at a soil water content of 0.2 m^3 m^{-3} briefly and began to continually increase above 0.5 m^3 m^{-3}. We found that spatial variation of R_S changed temporally, and this temporal cycle changed under different levels of water status. Daily cycles of spatial variation of R_S increased in amplitude while under drought conditions, with the lowest spatial variation observed in the midday, peaking overnight. Finally, we found that spatial variation of R_S presents an issue in determining increases in R_S across forests, even under periods of low variation. These results indicate that under extreme highs and lows, soil water content drives spatial variation. Our results demonstrate that seasonality and water status interact to drive spatial variation at daily, seasonal, and interannual time scales. This work can help direct studies of spatial variation of R_S to the extremes of water status and increase the ability to constrain the carbon budgets of terrestrial ecosystems.

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Chapter 3: The Seasonality of the Drivers of Spatiotemporal Variation of Forest Soil Respiration

3.1 Abstract

Spatial variability of soil respiration (R_S) is a primary driver of the large uncertainties associated with forest R_S. The drivers of spatial variation of R_S are not well understood. We sought to determine how SWC and T_{soil} drive spatial variation of R_S, and how these drivers shift through different seasons. We examined a decades-long data set of continuous chamber measurements from a drought-prone temperate deciduous forest in the central USA to examine drivers of spatiotemporal variations of R_S, and how seasonality influenced these patterns. We fit models at the chamber level and analyzed residuals to determine whether soil climate is the primary driver of spatial variability. We found that for both the full year and growing season, non-modeled predictor variables exhibited spatial variation amongst chamber residuals. We found that during the non-growing season, soil climate variables explained more of the spatial variation of R_S amongst chambers. Our results indicate that there is seasonality in the drivers of spatial variation of R_S, and that soil climatic variables can explain more variation within the non-growing season than the growing season. This could in part be due to the changes in biological activity throughout the year.

3.2 Introduction

Soil respiration (R_S) is the second largest terrestrial flux of CO_2, globally releasing 85.5 ± 40.4 Pg-C y^{-1} (Lu et al., 2021; Xu & Shang, 2016), of which nearly 40-90% originates from forest ecosystem R_S (Xu and Shang 2016; Rodtassana et al. 2021). The large uncertainties of global R_S arise, in part, due to the substantial spatiotemporal variations of these fluxes. In forest ecosystems, the primary cause of uncertainty is the considerable spatial variation of R_S (Cai et al. 2023). The significant contribution of forest ecosystem R_S to the global C cycle underlines the importance of improving the understanding of forest ecosystems C fluxes and its dynamics.

The drivers of spatial variation in R_S can be broadly grouped into biotic and abiotic factors. Biotic variables include root biomass, photosynthesis, and plant and microbial community composition (Tufekcioglu et al. 1999; Liu et al. 2020; Stoyan et al. 2000; Y. R. Liu et al. 2018). Abiotic factors include variables such as soil texture, soil structure, and chemical properties (Jiang et al., 2020; Martin & Bolstad, 2009; Tain, 2019). Additionally, subsurface climatic variables, soil temperature (T_{soil}) and soil water content (SWC) are crucial in the spatial variation of R_S (Davidson et al., 2000; & Janssens, 2006). T_{soil} and SWC are frequently used to interpret the spatial and temporal dynamics of R_S (Sotta et al. 2004; Cai et al. 2023). T_{soil} and SWC have also been shown to affect the autotrophic (R_a) and heterotrophic (R_h) respiration components differently, with R_h found to be more sensitive to SWC changes than R_a (Zheng et al., 2021).

The key drivers of spatial variation change across spatial scales. At small scales of 1-10 m, variation was driven by forest floor litter mass, root mass, carbon and nitrogen pools, or root nitrogen concentration (Martin & Bolstad, 2009). While at ecosystem levels, topography can lead to changes in spatial patterns due to the influence of terrain on soil climatic variables (Jiang et al., 2020; Martin & Bolstad, 2009). T_{soil} is a primary driver of R_S, where R_S responds positively to increasing T_{soil} (Raich & Schlesinger, 1992). T_{soil} is also a primary determinant of the seasonal shifts observed of R_S (Hereș et al., 2021;

Wood et al., 2013). Where SWC is not a limiting factor, T_{soil} will continually increase R_S (Han et al., 2014). The importance of SWC in the regulation of R_S has been reported in a multitude of studies (Cai et al. 2021; Martin and Bolstad 2009; Cai et al. 2023). For instance, in a meadow steppe, the largest spatial variation of R_S observed was during drought conditions, where SWC became a major explanatory variable (Shi et al., 2020). Dependence of R_S on T_{soil} can begin to breakdown at low SWC (Almagro et al., 2009).

Both SWC and T_{soil} are responsible for variation observed across time and space (Cai et al., 2021, 2023a; X. Liu et al., 2020). The influence of these drivers varies by the season, making the variables' overall contributions to spatial variation of R_S change, even in relatively uniform stands (Hereș et al., 2021). Understanding the drivers of spatial variability and how they change throughout time across multiple ecosystems is important to better improve our understanding of global C cycles (Soranno et al., 2019).

Here, we aimed to test whether soil climate alone drives spatial variation of R_S in an upland *Quercus-Carya* (oak-hickory) forest. We looked to answer the question: Is spatial variability of R_S controlled by T_{soil} and SWC alone, or are other variables exerting influences, and do these drivers change with seasonality? We hypothesized that the spatial variation of R_S is controlled by T_{soil} and SWC differences when the forest is in the non-growing season, but during the growing season, other factors associated with belowground biological activity play a role in shaping the spatial variation. To test our hypothesis, we examined data from automated chamber measurements with co-located soil climate measurements to account for soil climate's influence on spatial variability of R_S.

3.3 Methods

3.3.1 Site Description:

We analyzed rich historical data sets collected at the Missouri Ozark AmeriFlux (MOFLUX) site (38°45'19.3"N, 92°12'17.1"W). The MOFLUX site was established in 2004, and continuous, automated R_S measurements have been made since that time. The site is located at the University of Missouri's Baskett Forest, which sits within the Ozark Border Region of central Missouri. The broader region is made up of forested regions in the south and agricultural croplands to the north. The climate is warm, humid, and continental. During the growing season, rainfall is highly variable, and therefore the area is prone to seasonal drought, with plant physiological water stress exacerbated during periods with low rainfall because of the comparatively thin soils (Gu et al., 2016). The major vegetation type is second-growth, upland *Quercus-Carya* (oak-hickory) forest (Pallardy et al., 1988). Important tree species include *Quercus alba* L. (white oak), *Carya ovata* (Mill.) K. Koch (shagbark hickory), *Q. velutina* Lam. (black oak), *Acer saccharum* Marsh. (sugar maple), and *Juniperus virginiana* L. (eastern red cedar) (Gu et al., 2015). The dominant soils at MOFLUX are Weller silt loam and Clinkenbeard very flaggy clay loam (Gu et al., 2015; Soil Survey, et. al. 2022). Wellers are taxonomically classed as: fine, smectitic, mesic, Aquaretic Chromic Hapluadalfs, and Clinkenbeard's are clayey-skeletal, mixed, superactive, mesic Typic Argiudolls (Soil Survey, et. al. 2022). These soils vary in their capacity to supply water. Specifically, Wellers can hold 24.19 cm of total plant-available water, whereas Clinkenbeard's can hold only 5.12 cm (Soil Survey, et. al. 2022).

3.3.2 Soil respiration measurements:

The rate of R_S is measured using automated chambers, positioned around the MOFLUX eddy-covariance tower. Since 2013, measurements have been made using a commercially available, automated 16-chamber system with co-located near surface soil temperature and moisture measurements at each chamber (Li-Cor Inc., Lincoln NE). The chambers were placed with the intention of representing the forest demographic by placing them under important species (Liu et al., 2020). For the system, a full measurement cycle took an hour.

Since 2013 the LI-8100A system was used to measure R_S, water content and soil temperature have been measured at each chamber using time domain reflectometers and thermistors, with samples recorded each time a chamber closes to measure R_S.

3.3.3 Data Analysis:

The objective of our research was to determine whether subsurface climate was enough to describe spatial variation or are other factors necessary in accounting for the spatial variation, and whether this changes throughout the year. Analyses will isolate temperature and moisture effects from other bio-geophysical factors with the objective of determining whether subsurface climate or other drivers control spatial variation. We used half hourly chamber data (R_S, SWC, T_{soil}) from 2014 to 2016 to examine the shifting dynamics of the drivers of R_S in different portions of the year. The model was fit at each chamber for all the available data. This was to determine whether soil climate influenced spatial variation of R_S during the full year, we analyzed relationships among chamber residuals. We examined residuals separately for the growing season (day of year 120-300) and the non-growing season (day of year < 120 and day of year > 300) for further determination of how soil climate variables shape spatial variation R_S.

We fit the same regression model that Liu et al., (2020) used for previous analyses of MOFLUX R_S data:

$$R_{s_t} = \beta_0\, e^{(\beta_1 \times T_t)} e^{(\beta_2 \times \theta_t)+(\beta_3 \times \theta_t^{\,2})} + \beta_4 \qquad [3.1]$$

where T is soil temperature (°C), θ is volumetric water content ($m^3\ m^{-3}$), R_S is soil respiration ($\mu mol\ m^{-2}\ s^{-1}$), the t subscript indicate time, and β_0, β_1, β_2, β_3, β_4 model coefficients. The nonlinear model was fitted to the chamber-level data of R_S, soil moisture, and soil temperature data (2014–2016).

Following the fitting of the chamber level models (Eq. 3.1) we examined the correlation of model residuals across all 16 chamber collars following the methods of Giasson et al (2013). Chamber-level residuals represent unexplained variance in the model, and correlation amongst chamber residuals indicates missing variables within the model. To do this, we used the Pearson correlation coefficient (r) to measure linear correlation amongst chamber residual pairs. The distribution of r for different times of the year was then examined to determine whether spatial variation of non-modeled variables was present. Wider distributions of residual correlations indicate spatial variation of missing variables, shown by the variation in the correlation of residuals across the chamber collars.

All analysis were conducted in RStudio ver. 2023.12.0.369

3.4 Results

Chamber model R^2 and root mean square error (RMSE) both show varying goodness of fits, indicating spatial variability in the validity of soil climate variables as predictor for R_S (Table 3.1). Variability of the model parameters implies that the R_S model's ability to accurately predict R_S changes across space. For instance, certain chambers have higher R^2 values and lower RMSE, indicating a stronger relationship with T_{soil} and SWC used in the model. Conversely, some areas exhibit lower R^2 values and higher RMSE, showing missing model variables (Table 3.1).

Table 3.1: Chamber-level model fittings, showing the chamber # model coefficients (b1, b2, b3, b4) ± Standard Error (SE), R^2, and RMSE.

Chamber #	**R^2**	**RMSE**	**b0**	**b1**	**b2**	**b3**	**b4**
1	0.73	0.98	1.15 ± 0.009	0.04 ± 0.0005	8.05 ± 0.288	-9.29 ± 0.435	-1.78 ± 0.031
2	0.75	1.39	1.66 ± 0.024	0.03 ± 0.0005	5.21 ± 0.113	-8.18 ± 0.198	-3.46 ± 0.074
3	0.79	0.84	1.02 ± 0.002	0.04 ± 0.0005	19.86 ± 0.426	-28.62 ± 0.652	-1.24 ± 0.033
4	0.70	0.92	1.91 ± 0.048	0.03 ± 0.0005	1.69 ± 0.185	-0.48 ± 0.314	-2.68 ± 0.059
5	0.77	1.07	1.06 ± 0.003	0.04 ± 0.0005	16.65 ± 0.292	-26.18 ± 0.487	-1.80 ± 0.036
6	0.77	0.60	1.09 ± 0.006	0.04 ± 0.0007	13.52 ± 0.321	-21.90 ± 0.541	-1.26 ± 0.040
7	0.78	0.72	1.01 ± 0.001	0.03 ± 0.0004	28.69 ± 0.751	-44.33 ± 1.177	-2.03 ± 0.029
8	0.75	0.99	1.28 ± 0.013	0.04 ± 0.0005	6.74 ± 0.213	-8.95 ± 0.365	-1.98 ± 0.039
9	0.68	1.04	1.79 ± 0.037	0.02 ± 0.0005	3.98 ± 0.137	-5.58 ± 0.218	-3.09 ± 0.079
10	0.69	0.97	1.07 ± 0.006	0.03 ± 0.0005	15.66 ± 0.416	-23.09 ± 0.624	-2.05 ± 0.045
11	0.69	1.25	3.08 ± 0.103	0.02 ± 0.0004	-0.14 ± 0.132	3.50 ± 0.228	-4.12 ± 0.106
12	0.73	1.09	2.64 ± 0.063	0.02 ± 0.0005	1.91 ± 0.071	-2.43 ± 0.116	-3.71 ± 0.094
13	0.65	1.30	1.79 ± 0.037	0.03 ± 0.0007	3.88 ± 0.111	-5.59 ± 0.175	-2.91 ± 0.090
14	0.59	1.58	1.67 ± 0.042	0.03 ± 0.0008	4.67 ± 0.167	-6.62 ± 0.249	-3.27 ± 0.124
15	0.60	1.21	1.66 ± 0.036	0.03 ± 0.0008	4.12 ± 0.141	-6.26 ± 0.229	-2.42 ± 0.079
16	0.69	1.27	2.31 ± 0.057	0.03 ± 0.0006	2.93 ± 0.080	-4.90 ± 0.141	-3.45 ± 0.114

3.4.1 Model Residual Analysis Results

Residuals from the full year chamber level models displayed a wide range of correlations, indicating spatial variation of non-modeled variables (Fig 3.1 & 3.4A). The r values had a mean of 0.42 ± 0.14 (SD), with a minimum value of 0.12 and maximum of 0.76. This indicates that there are more variables needed in explaining spatial variation in R_S during the full year. We further broke down the data into growing season and non-growing season to analyze the validity of soil climate as predictors in different periods of the year.

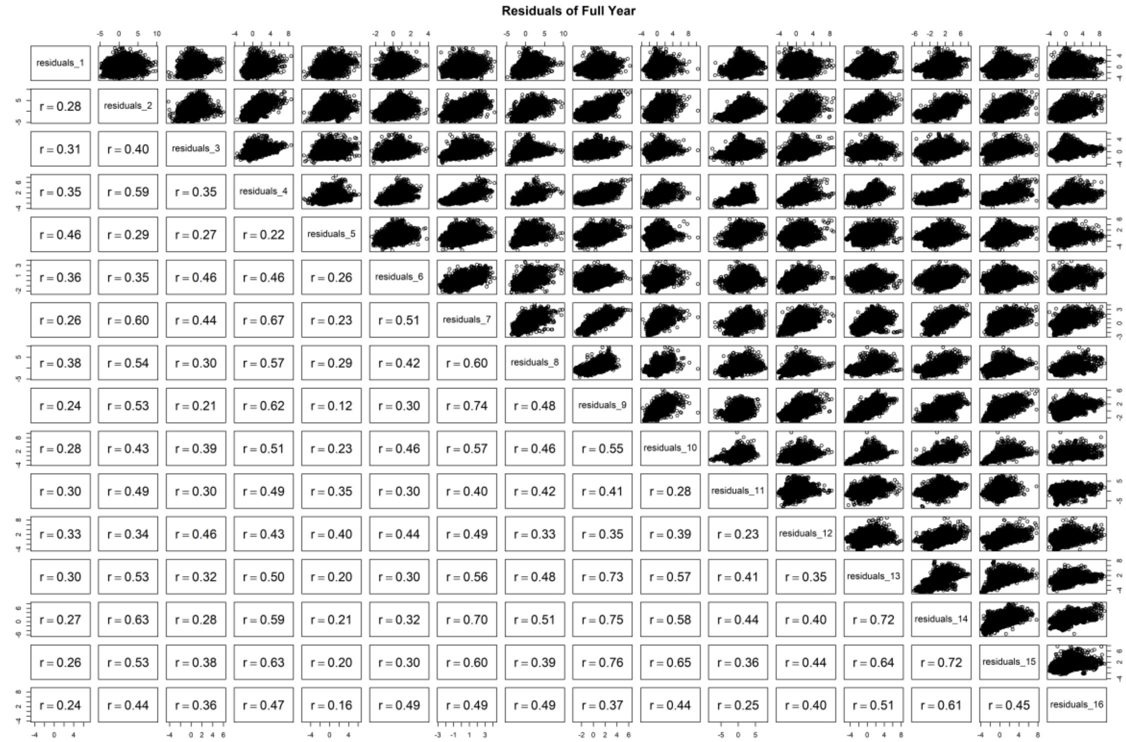

Figure 3.1: There was a range of correlations amongst chamber-level model residuals, indicating spatial variation of non-modeled variables for all the data. The scatterplot matrix of chamber level model residuals from all the data. The upper right of the diagonal is scatterplots of model residuals across chambers. The lower left of the diagonal lists the Pearson's correlation coefficient (r) of the corresponding chamber residual pairs. All r values were significant ($p < 0.01$).

Residuals of the growing season had a wide range of correlations, indicating spatial variation of non-modeled variables (Fig 3.2 & 3.4B). The r values had a mean of 0.41 ± 0.16 (SD), with a minimum value of 0.09 and maximum of 0.76. When examined in the histogram, we see a wide display of correlations amongst chamber residuals (Fig. 3.4B). This indicates that more variables are needed to explain the spatial variation of R_S during the growing season.

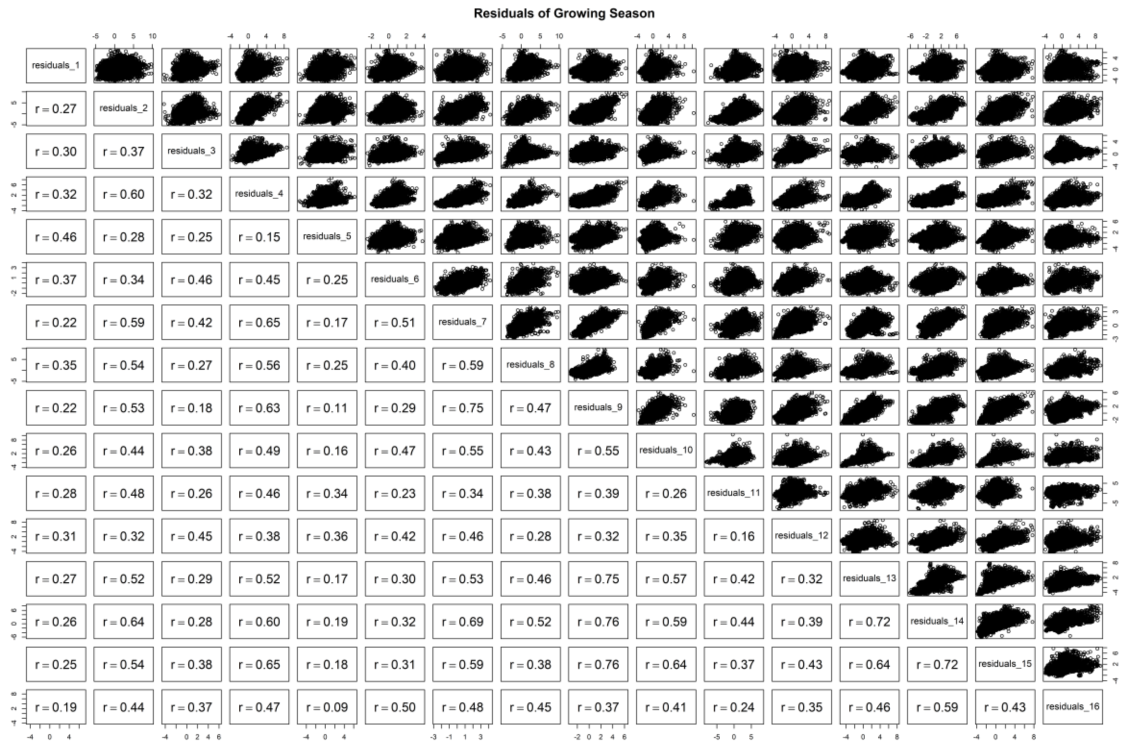

Figure 3.2: There was a range of correlations amongst chamber level model residuals, indicating spatial variation of non-modeled variables for the growing season. The scatterplot matrix of chamber-level model residuals from growing season days. The upper right of the diagonal is scatterplots of model residuals across chambers. The lower left of the diagonal lists the Pearson's correlation coefficient (r) of the corresponding chamber residual pairs. All r values were significant ($p< 0.01$).

Residuals of the non-growing season displayed a tighter range of correlations than the previous analyses, indicating lower spatial variation of non-modeled variables (Fig 3.3 & 3.4C). The r values had a mean of 0.51 ± 0.13 (SD), with a minimum value of 0.09 and maximum of 0.74. When examined in the histogram, we see a wide display of correlations amongst chamber residuals (Fig. 3.4C). This indicates that there is less spatial variation in non-modeled variables in the non-growing season as compared to the growing season.

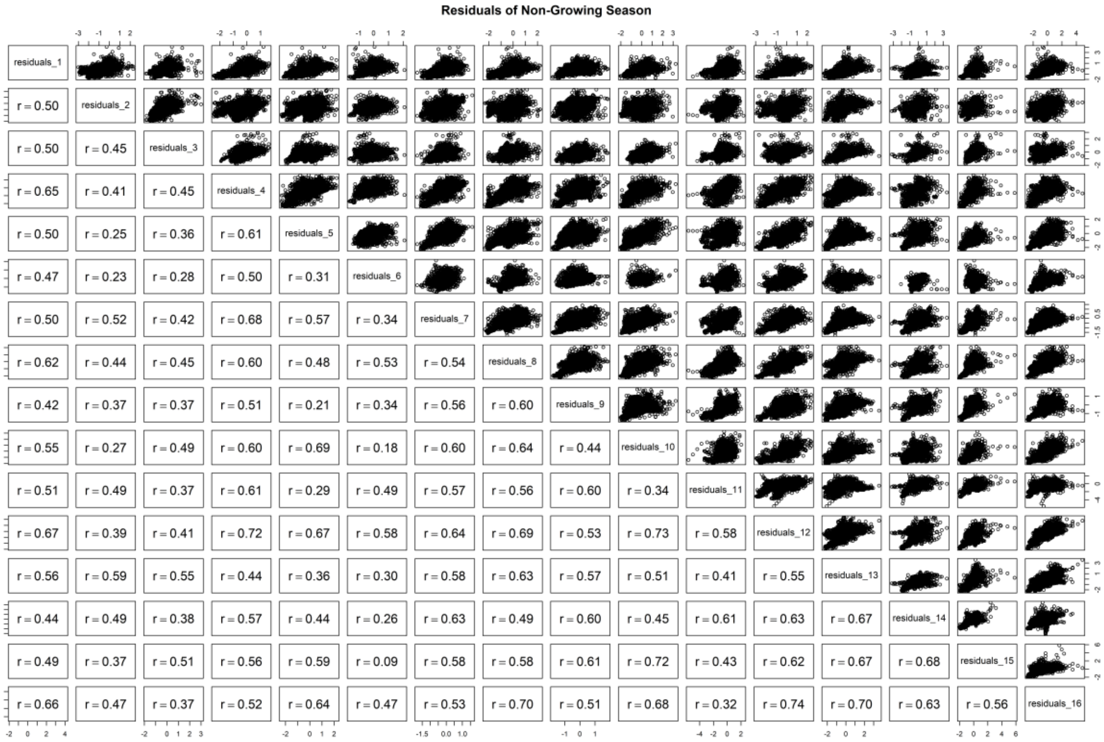

Figure 3.3: There was a range of correlations amongst chamber level model residuals, indicating spatial variation of non-modeled variables during the non-growing season. The scatterplot matrix of chamber level model residuals from non-growing season days. The upper right of the diagonal is scatterplots of model residuals across chambers. The lower left of the diagonal lists the Pearson's correlation coefficient (r) of the corresponding chamber residual pairs. All r values were significant ($p < 0.01$).

We examined the distributions of the histograms of all time periods of analysis and found that the power of soil climatic variables as predictors for spatial variation of R_S varies throughout the year (Fig. 3.4). The wideness of the distribution of correlations describes the spatial variation of non-modeled variables. Wider distributions indicate more spatial variation of non-modeled variables.

There was still unrepresented spatial variation of non-modeled variables at all time scales (Fig. 3.4). We found that both full year and growing season data displayed greater spatial variation of non-modeled variables, indicated by the large spread of r in the model residual comparisons (Fig 3.4 A & B). Non-growing season data displayed less, but still present, spatial variation of non-modeled variables, indicated by tighter spread of r in the model residual comparisons (Fig. 3.4 C). It is important to note that all figures indicate uncaptured spatial variation associated with non-modeled effects.

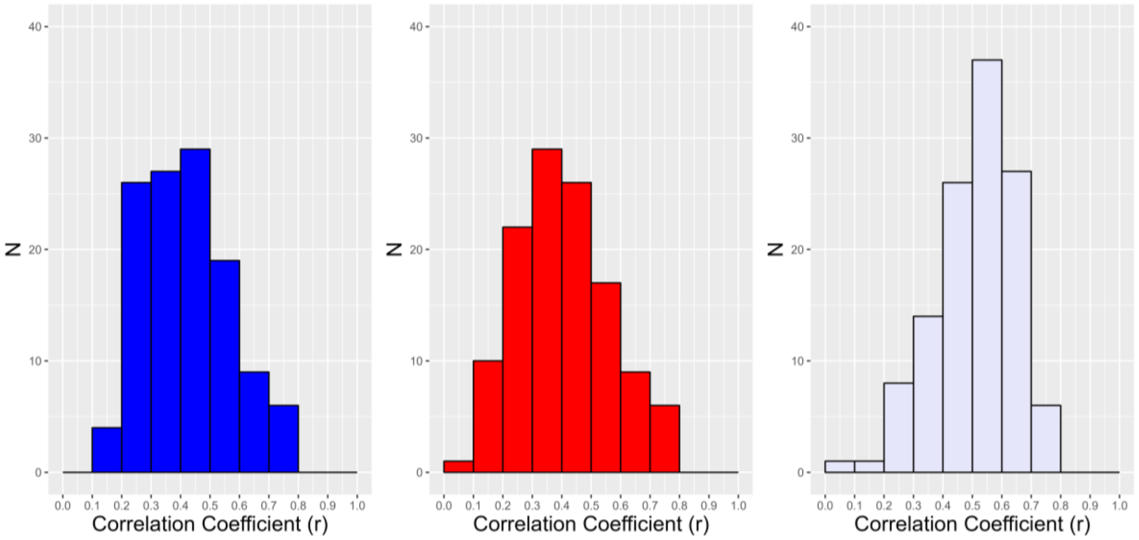

Figure 3.4: Histograms of correlation coefficients of model residuals for each time frame. Panels: A) histogram of full year data, B) histogram of growing season data, C) histogram of non-growing season data. Distribution of correlation coefficients indicates spatial variation of non-modeled variables, with wider distributions indicating higher spatial variation of non-modeled variables.

3.5 Discussion

When considering all data, analyses confirmed the importance of non-modeled variables as being important drivers of spatial variation (Fig 3.1 & 3.4). This could be driven by the large shifts in what drives spatial variation of R_S throughout a year (Hereș et al., 2021). During the growing season, canopy photosynthesis can stimulate belowground activity that contributes to spatial variation of R_S (Savage et al. 2013). Similar results have been seen in other ecosystems, where cross variograms indicated that biotic (plant & microbial biomass) drivers played an important role in ecosystem spatial variation of R_S (Shi et al., 2020). To further examine the possibility of belowground biological activity being a driver of spatial variability, separate analyses were conducted on growing season and nongrowing season data.

Our analyses of both growing and non-growing season data revealed differences in the validity of soil climate variables as drivers of spatial variation of R_S, with non-growing season spatial variation of R_S being better explained by soil climatic variables (Fig 3.2, 3.3, & 3.4 B, C). Growing season data indicated that there were non-modeled variables contributing to spatial variation of R_S (Fig. 3.2 & 3.4). This portion of unexplained spatial variation could be driven by biotic variables which previous studies have shown can drive R_S (Shi et al. 2020; X. Liu et al. 2020). Several studies indicate how photosynthesis influences R_S (Ekblad & Högberg, 2001; Vargas et al., 2011), which we hypothesize could play a role in the spatial variation observed in our measurements. This is supported by a previous work showing that models of R_S that included gross primary productivity (GPP) resulted in better model power in predicting R_S than conventional models containing only SWC and T_{soil} as predictors (X. Liu et al. 2020). The results we reported add to the evidence that biotic variables are important in explaining the spatial variation exhibited in R_S measurements (Baldocchi et al., 2006; Ekblad & Högberg, 2001; Hereș et al., 2021; Ruehr et al., 2010). Heres et al. (2021) investigated the seasonality in controls of R_S and found that variables outside of soil climate, including plant biomass, are needed in fully describing spatial variability during the growing season.

Finally, we found that during the non-growing season, soil microclimate had more influence on spatial variability of R_S (Fig. 3.3 & 3.4). This agrees with previous studies, where it was found that during winter, spatial variations in R_S are primarily driven by temperature (Hereș et al., 2021). Furthermore, non-growing season R_S is driven by the R_h component (J. Tang et al., 2005). R_h is primarily driven by soil climatic variables such as SWC and T_{soil} (X. Tang et al., 2020). Our study agreed with these findings in the broader context of R_S, where we found the spatial variation of R_S during the non-growing season was better explained by soil climate (Fig. 3.3 & 3.4). We found evidence that agrees with the findings of previous work regarding the drivers of the spatial variation in a temperate forest, where snow pack drove variations in T_{soil} and SWC which held dominant controls over spatial patterns of R_S (Contosta et al., 2016).

Our approach gave new insights to the seasonality of drivers of spatial variation, showing that soil climate varies in its strength explaining spatial variation throughout the year. However, this approach was limited by not including biotic variables, such as GPP which has previously been shown to be a strong predictor of temporal variations of R_S (X. Liu et al. 2020). Another drawback is that we did not separate R_S into its R_a and R_h respiration components. These components are known to respond differently to environmental variables (Savage et al. 2013; Wang et al. 2014; Zheng et al. 2021). These R_S components also differ across seasons, where non-growing season respiration is dominated by R_h respiration (J. Tang et al., 2005), and the growing season contains photosynthetically active canopy, driving R_S via fixated sugars (X. Liu et al. 2020; Vargas et al. 2011).

These relationships can be used to better inform what variables are important in describing spatial variation, and therefore further constraining predicted C from R_S. This work shows that other variables are important in describing spatial variation of R_S, and evidence supports that there is relation to plant activity. Moving forward, a more in-depth analysis of what other variables drive spatial variability during the growing season is needed to distinguish variables contributing to spatial variation. Furthermore, an analysis of the drivers of spatial variability of the R_a and R_h components of R_S is necessary. This could provide valuable insight on the important predictors between components, allowing better constraints on R_S budgets.

3.6 Conclusions

We sought to understand whether SWC and T_{soil} drive spatial variation of R_S, and whether these drivers shift through different seasons. This research displayed new information on the seasonality of drivers of spatial variability. We found that for both the full year and growing season data, non-modeled predictor variables exhibited spatial variation amongst chamber residuals. While we found that during the non-growing season, soil climate variables explained more of the spatial variation of R_S amongst chambers Our results show that there is seasonality in the drivers of spatial variation of R_S, and that soil climatic variables can explain more variation within the non-growing season than the growing season itself. This work also indicates the need to incluide additional variables, such as biotic variables, to fully account for spatial variation of chamber R_S. Introducing the use of GPP and time lagged GPP models to further explore the drivers of spatial variation of R_S at different times of the year could lead to capturing more of the factors responsible for the spatial variability of R_S.

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Chapter 4: Conclusions and Recommendations

4.1 Conclusions

For this thesis, we aimed to understand the drivers and cycles of spatiotemporal variation of R_S. This work can lead to improving constraints on R_S budgets through reducing uncertainties due to the spatial variation of R_S by further study and quantification of the relationships found. This work advanced our understanding of the spatiotemporal cycles of forest R_S, how these cycles can be modulated by excess water and drought stress, and the seasonality exhibited by the variables controlling the spatial variation of R_S.

Results from our study showed the spatiotemporal cycles of the forest ecosystem, and how these cycles are deviated by water stress. When examining the effects of SWC on spatial variation of R_S, we found that within both high and low water status there were peaks of measured CV of R_S. With low water status peaking at 0.2 m^3 m^{-3} and decreased with changes in SWC, while high water status peaked at 0.5 m^3 m^{-3} and decreased with changes in SWC. We found that spatial variation shifts seasonally, being at its highest in the winter, followed by spring and summer, with fall exhibiting the lowest spatial variation of R_S. We also found that low ecosystem water status resulted in a significant increase in the spatial variation of R_S as compared to high ecosystem water status. Next, we found that daily cycles of spatial variation of R_S exhibited negligible amplitude in the fall and summer, whereas winter and spring have peaks in spatial variation at around the mid-day point. We observed that a drought year caused the amplitude of the daily CV of R_S cycle in summer to become larger, with minimum values at mid-day, and maximum values during nighttime. We found that even at the lowest spatial variation of our mean annual cycle, 16 chambers were not adequate in detecting 10% changes in R_S at a different forest with similar variation.

When examining the seasonality of the drivers of spatial variation of R_S, we found that when using soil climatic data as explanatory variables, spatial variation amongst non-modeled variables were found. This indicates the necessity of including additional variables, such as biotic variables, to fully account for spatial variation of chamber R_S. However, non-growing season spatial variation was better explained using soil climatic variables as explanatory variables. These results illustrate the seasonality of the drivers of spatial variation of R_S indicating that variables explanatory power shifts throughout the year.

4.2 Recommendations for future work:

1. Examine how legacy effects of drought (i.e., decreased litter production, decreased reproduction, etc.) impact spatiotemporal variability of R_S.
2. Introduce the use of GPP and time lagged GPP models to further explore the drivers of spatial variation of R_S at different times of the year.
3. Examine how ecosystem stress can change the drivers of spatial variation of R_S at different times of the year.