# Belowground Carbon Fluxes and Changing Climatic Conditions: Evaluating Responses and Improving Mechanistic Modeling

A Thesis Presented in Partial Fulfillment of the Requirements for the Degree of Master of Science with a Major in Natural Resources in the College of Natural Resources University of Idaho by Danielle M. Berardi

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## **Authorization to Submit Thesis**

This thesis of Danielle Berardi, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Belowground Carbon Fluxes and Changing Climatic Conditions: Evaluating Responses and Improving Mechanistic Modeling," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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#### Abstract

Forests have an important role in the global carbon cycle, are a known regulator of climate, and are valued globally for the ecosystem services they provide to society. It is critical to improve our understanding about the exchange of carbon dioxide between forest ecosystems and Earth's atmosphere. Specifically, there is a need for improved mechanistic understanding of the component fluxes of soil respiration (R<sub>s</sub>): autotrophic respiration (R<sub>a</sub>; roots and associated mycorrhizae) and heterotrophic respiration (R<sub>h</sub>; free-living soil microbes and soil fauna involved in decomposition). We examined the responses and relative contributions of these components to manipulated soil moisture. We found that heterotrophic respiration significantly responds to moisture additions regardless of season while autotrophic respiration did not. We also found that widely used and accepted methods for survey measurements (versus automated) were not sufficient to build relationships with abiotic factors for diurnal, monthly, and annual scaling, thus eliminating commonly used gap-filling procedures. Because survey measurements are often used to validate model results, it is critical that they be done over varying time periods (some diurnal) and be paired with automated measurements.

When comparing our experimental data to modeled results, we found that DayCent, a daily time-step process-based biogeochemical model, underestimates annual heterotrophic respiration by several magnitudes compared to our temperate mixed conifer forest site. This is likely because DayCent, like most traditional ecosystem models, simulates decomposition through first order kinetics which inadequately represents microbial processes. Recent research has found that including microbial mechanisms explains 20 percent more spatial heterogeneity. We manipulated the DayCent heterotrophic respiration model to include a more mechanistic representation of microbial dynamics and compared the new model with our continuous and survey observations. By using a more representative and fully calibrated model of soil carbon dynamics, we are better able to predict feedbacks between climate and soil carbon pools to inform decisions and provide benefits to society through improvements to ecosystem modeling.

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# Dedication

To my partner, Matt Dunkle, and my scary science lady friends, Kathryn Baker, Kelli Roemer, Rebecca Sheridan, and Eloise Zimmerman. They were always there to provide me with support, encouragements and healthy outlets for stress when I needed it.

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#### **CHAPTER 1: Literature Review**

Atmospheric carbon dioxide, CO<sub>2</sub>, has been increasing since the industrial revolution in the late 1800s. Because CO<sub>2</sub> is a greenhouse gas, the increase has led to changes in Earth's mean annual temperature, warming the planet (Lashof & Ahuja, 1990). In 2016, 196 of Earth's sovereign nations gathered in Paris, France (known as the Paris Climate Accord) to agree to and sign a treaty committing to mitigating climate change, primarily through reductions of greenhouse gas emissions. To date, every single country in the world except for the United States of America has signed the treaty. Despite the lack of US federal agreement to the treaty, many states and cities in America have decided to commit to the emissions reductions, regardless. Emission reduction strategies in the US will not only rely on reduced fossil fuel usage, but land management strategies as well (Miles & Kapos, 2008, Paustian *et al.*, 2000), especially those regarding temperate forests (Birdsey *et al.*, 2006, Canadell & Raupach, 2008, Jandl *et al.*, 2007).

As one of the largest carbon sinks (Birdsey *et al.*, 2007), forests hold a great potential for climate change mitigation through maximizing carbon sequestration and storage through conservation, reforestation, forest restoration, and improved management practices. Forest carbon balance is determined by quantifying the amount of carbon being taken up by the ecosystem through photosynthesis or gross primary production (GPP), minus the losses from the ecosystem through ecosystem respiration (Chapin *et al.*, 2006). Forests that are removing more carbon dioxide than the amount of carbon dioxide that they are releasing are carbon 'sinks'. Ecosystem respiration is made up of both autotrophic and heterotrophic respiration. Autotrophic respiration is from plant growth respiration and maintenance of existing tissues and originates from both aboveground (wood and leaves) and belowground (roots and mycorrhizae) sources. Heterotrophic respiration occurs at and below the soil surface through microbial decomposition of surface and soil organic matter. For the purposes of this study, all references to respiration will be referring to soil respiration from this point forward.

Climate change is causing changing precipitation patterns and increased temperatures which is leading to more frequent and severe drought as well as more frequent and severe rain events. These climate change induced drought events are reducing forest carbon sinks from local to continental scales and potentially altering the forest carbon balance (Anderegg et al., 2013, Schwalm et al., 2012, van der Molen et al., 2011). Depending on intensity and longevity, drought events can in turn feedback to local and regional climate by altering the net greenhouse gas balance, water use, and albedo of the landscape (O'Halloran *et al.*, 2012). The occurrence of drought induced forest mortality events has been extensively documented globally and has been increasing in the recent decades as drought becomes more frequent and severe (Allen et al., 2010). Extensive droughts in both Europe and the Western United States in 2003 resulted in large reductions of forest primary production and resulted in many forested areas to shift from carbon sinks to carbon sources (Ciais et al., 2005, Schwalm et al., 2012). However, there is less consensus regarding the effects of drought on forest soil carbon dynamics. Environmental variables such as soil moisture and soil organic matter (SOM) inputs from plants, which are limiting factors for the temperature sensitivity of decomposition, are shifting as a result of climate change (Davidson & Janssens, 2006). Given the key role of forests in climate regulation, understanding forest response to drought and the feedbacks to the atmosphere is a key research and education priority globally (Law, 2014, USGCRP, 2009).

Within forest ecosystems, soils store approximately half of the ecosystem carbon (Pan *et al.*, 2011). Globally, soil carbon efflux is responsible for contributing approximately 10% of atmospheric CO<sub>2</sub> annually (Raich & Potter, 1995), and is commonly the largest source of CO<sub>2</sub> from terrestrial ecosystems (Gaumont-Guay *et al.*, 2009, Jassal *et al.*, 2007, Ryan & Law, 2005). Carbon flux from soil to the atmosphere is lost in the form of CO<sub>2</sub> which is a byproduct of cellular respiration (R<sub>a</sub>; from roots and mycorrhizae) and from the decomposition of biotic components (R<sub>h</sub>) that make up the soil. Because of this, soil carbon efflux is commonly referred to as soil respiration. As climates shift due to anthropogenic induced warming, refining our understanding of CO<sub>2</sub> fluctuation from soils to the atmosphere forest ecosystems will remain

carbon sinks or become sources in the future and predicting the feedbacks that will occur between soils and the atmosphere. (Cox *et al.*, 2000, Reichstein *et al.*, 2003). As drought and increased temperatures alter the timing of soil dry down, the timing of fine root growth and die-off will shift as well, thus affecting the timing and rate of autotrophic respiration from roots and associated mycorrhizae. Decomposition by soil microbes is responsible for breaking down organic carbon inputs from coarse and fine woody debris, litter, root exudates, and dead roots and mycorrhizae into either recalcitrant soil carbon or labile soil carbon with the byproduct of CO<sub>2</sub> released to the atmosphere. The rate of decomposition is dependent on soil organic matter (SOM) availability, soil moisture, and soil temperature, all of which are influenced by drought conditions and/or severe rain events (Figure 1.1 and Figure 1.2). We expect that drought or altered precipitation events will likely impact forest soil respiration by altering the balance and timing between the heterotrophic (root and associated mycorrhizal fungi; R<sub>a</sub>) components (Doughty *et al.*, 2015).

Although the mechanisms of respiration have been a topic of study for more than a century (Arrhenius, 1889, van't Hoff, 1884), the response of soil respiration to changing environmental variables is not adequately understood. Because they play different functional roles in an ecosystem (i.e. primary production or decomposition), the individual flux components respond differently to the multitude of environmental drivers. The major variables that are known to contribute to regulating the release of CO<sub>2</sub> from soils are soil temperature (Melillo *et al.*, 2011), soil moisture (Brockett *et al.*, 2012), carbon allocation by trees (Van Groenigen *et al.*, 2014), SOM and net primary productivity (NPP) as shown in Figure 1.1. Of these variables, the most rigorously studied in relation to its influence on soil respiration is soil temperature.

There have been extensive field and laboratory studies examining how soil respiration increases with temperature (Hamdi *et al.*, 2013). Controlled laboratory experiments isolating heterotrophic respiration have found that heterotrophic respiration increases exponentially with soil temperature (Kirschbaum, 1995). The temperature sensitivity of

soil respiration is referred to as the Q<sub>10</sub>. Despite how well this has been studied, there is still a lack of agreement on the quantification of temperature sensitivity of heterotrophic respiration, and in turn, total soil respiration (Kirschbaum, 2006). There have also been many incubation experiments characterizing how increasing soil moisture with controlled temperature increases heterotrophic respiration until soil conditions become anaerobic (Conant *et al.*, 2004, Cook & Orchard, 2008, Moyano *et al.*, 2012). Since autotrophic respiration is tightly coupled to photosynthesis, it has been found that it mostly decreases in response to decreasing soil moisture (Atkin & Macherel, 2008). However, because the component fluxes are difficult to isolate *in situ*, much uncertainty remains surrounding the response of component fluxes to long-term and changing soil moisture conditions (Heinemeyer *et al.*, 2007a, Hinko-Najera *et al.*, 2015).

Soil respiration is typically measured manually weekly or bimonthly during the growing season, rather than with automated respiration systems that are costly and have large power requirements. In order to estimate seasonal or annual respiration from survey measurements, models are used to fill in the gaps. However, most models that we rely on for soil respiration are empirical or inadequately mechanistic (Wieder *et al.*, 2013). Gap filling models are known to poorly estimate seasonal and annual respiration when compared to automated measurements (Gomez-Casanovas et al., 2013). Most commonly, gap filling models only rely on the relationship between total soil respiration and soil temperature. They are based on the assumption that respiration has a constant temperature sensitivity throughout the entire spectrum of temperatures an ecosystem will experience (Arrhenius, 1889, van't Hoff, 1884), which is not representative of reality (Davidson et al., 2006, Lloyd & Taylor, 1994). Soil moisture is often not included in empirical models that predict seasonal to annual soil respiration despite being a known limiting factor to temperature sensitivity. The accuracy of how well these models gap fill soil respiration varies between climate regions. As already discussed, the components of soil respiration respond differently to the environmental variables that empirical models rely on, yet usually only total respiration is measured and gap filled. This might contribute to how poorly empirical models calculate annual respiration. Additionally, empirical models are not good predictors into the future since they rely

solely on past and present conditions. Studies designed to provide mechanistic knowledge about the response to respiration and component fluxes to changing temperature and precipitation regimes are necessary to improve current and future estimates of soil carbon dynamics.

Regional to global estimates of soil respiration in response to changing precipitation patterns will require the use of remote sensing data (i.e. satellite imagery and measurements) to scale fluxes based on experimental evidence to larger regions. Use of remote sensing land cover estimates from satellite data has been successfully used to estimate global forest carbon cycling by either relying on assumptions about respiration (e.g. fixed ratios (Running *et al.*, 2013)), combined satellite data with process-based modeling (Turner *et al.*, 2007, Van Tuyl *et al.*, 2005), or developed relationships with ground-based data (Jägermeyr et al., 2014). More recently, ecological site data from a global network of flux towers with MODIS satellite data proved that total ecosystem respiration could be predicted from temperature and plant productivity (Jägermeyr *et al.*, 2014). However, there has been little to no development of satellite based estimates of soil respiration, especially the impacts of soil moisture, a known and important determinant of soil respiration (Carbone *et al.*, 2011). By identifying the relative contributions of heterotrophic (microbial) respiration and autotrophic (root and mycorrhizal) respiration with experimental manipulation of precipitation patterns and modeling, there is potential for estimates to be scaled to a larger region using a combination of NASA satellite sensor data of daily soil moisture and temperature, forest cover and ancillary forest attributes to compute total soil respiration, R<sub>h</sub> and R<sub>a</sub> in the future.

Most field observations of respiration response to drought conditions are strictly observational. There are only a few existing studies that manipulate soil moisture conditions through either irrigation inputs (Ruehr *et al.*, 2012) or throughfall reduction (Cleveland *et al.*, 2010). In this study, we investigated the impacts of changing precipitation patterns on ecosystem respiration at the University of Idaho Experimental Forest through experimental manipulation of increased precipitation events during the growing season. The forests of Northern Idaho are part of the Northern Rockies ecoregion and typically experience late-summer drought under historical climate conditions with less than 5% of the annual precipitation occurring during the summer months (Figure A.8). In recent years, this region has been experiencing drought conditions more severe than its 30-year average (Figure A.9). At our field site, this results in soil moisture dropping to less than 0.025 m<sup>3</sup>m<sup>-3</sup> in the top 30 cm over the growing season. Recently, these forests are experiencing increasing threats from fire and severe drought from the 2015 and 2016 western US heat waves, increasing the potential for tree mortality. The forest contains many commercially valuable species over 1050 m elevation gradient consisting of white pine (Pinus monticola), western red cedar (Thuja plicata), Douglas-fir (Pseudotsuga menzeseii), western larch (Larix occidentalis), grand fir (Abies grandis), and ponderosa pine (Pinus ponderosa). Most trees are between 80 – 90 years old with a few remnant old-growth western red cedars, western white pine, Dougfir, and western larch. Some old stumps remain indicating that the site was likely cut in the 1930s. There is also a deep charcoal layer in the soil suggesting a previous stand replacing fire. The site has a 30-year mean annual temperature and mean annual precipitation of 7.4  $^{\circ}$ C and 81 cm (Table 3.1), respectively.





### CHAPTER 2

*Primary goals and objectives.* The main goal of this study was to determine the impact of changing precipitation patterns on the separate components of forest soil respiration at ecosystem to landscape level scales and determine the best methodology for scaling soil respiration components temporally in the Northern Rockies Ecoregion. Through this data driven and modeling approach we evaluated the following objectives and hypotheses:

Objective 1. Determine the relative impact of varying precipitation patterns on forest soil respiration components. The specific hypothesis that was tested by this objective is that drier soil conditions will reduce total soil respiration by decreasing both R<sub>h</sub> and R<sub>a</sub>, however, R<sub>a</sub> will be reduced in larger magnitude than R<sub>h</sub>. We based this hypothesis on previous work that suggests the R<sub>a</sub> is more sensitive to soil moisture than R<sub>h</sub> (Carbone et al. 2011; Hinko-Najera et al. 2015), but that both are likely to be reduced in extended drought conditions. Exclusion collars designed to separate the component fluxes of soil respiration (R<sub>h</sub>, R<sub>a</sub>, as well as the mycorrhizal and root portions of R<sub>a</sub>) were placed in replicated control and treatment plots. The watering treatment mimicked 6.6 mm of precipitation weekly from June through September. Although it would have been ideal to mimic precipitation events larger than just 6.6 mm so that there would be a larger influence on soil moisture, we were limited by water availability at our site. The rationale for watering treatments (versus water exclusion) is that if drought conditions were to persist (as predicted for the season), we needed to examine the response of respiration in non-severe drought conditions. In other words, drought is a naturally occurring 'experiment' at our field site and we needed to add moisture to test the response of each respiration component during the growing season.

<u>Objective 2. Incorporate a more process based model of total soil respiration ( $R_s$ ),  $R_h$ , and  $R_a$  in the DayCent biogeochemical model. The specific hypothesis we tested was that the uncertainty in model estimates of soil respiration will be reduced by at least 20% by including site specific soil temperature and soil moisture sensitivity and improving the</u>

representation of microbial processes in the heterotrophic respiration proportion of the model (Allison *et al.*, 2010, Wieder *et al.*, 2013). We expect that overall uncertainty in forest ecosystem carbon uptake (net ecosystem exchange) will also be reduced. Remote sensing of these abiotic components and other forest attributes could be used to scale respiration to larger areas (regional to continental). Modeled estimates of soil respiration (and soil temperature and soil moisture) can then be compared with remote sensing estimates when they become available at finer resolutions. We were unable to complete the remote sensing objectives of the study design as the sensor (radar portion) of the NASA SMAP satellite broke shortly after launch.

### CHAPTER 3: Methodologies and Evaluation of Gap Filling Techniques

### 3.1 Methods

*Study Site.* The study was carried out in a mixed conifer forest stand in the University of Idaho Experimental Forest (46.801°N, -116.810°W) April – November 2016. This region typically experiences a period of late-summer drought that is becoming more prolonged with climate change. The mean annual temperature and precipitation (1986 – 2016) for the site are 7.4°C and 810 mm, respectively (DAYMET,Thornton, 2017a). For the year that the study was conducted, the mean annual temperature was 8.9°C and the annual precipitation was 973 mm (Figure 3.2 and 3.3; SNOTEL).

The site consists of six one-acre plots that were established as part of a larger project to test the impacts of natural late-summer drought on forest carbon and water cycling. The plots each contain four 3-meter radius subplots arranged in the center, north, southeast, and southwest orientations of the plot where ongoing measurements are being made of soil carbon, root biomass and production, soil respiration, dendrometer bands, and sap flow to capture the spatial variability of the plot. For this study, three subplots (1 control, 2 treatment) were used within three of the larger one-acre plots in order to leverage existing plot instrumentation and measurements. Climate data from a University of Idaho Experimental Forest meteorological station located 1.28 km from the study site was used for temperature, precipitation, relative humidity, radiation and wind speed data. The soil at our site is a silt loam with volcanic ash over loess as the parent material. The soil depth ranges from 74 cm to 117 cm (SSURGO). See table 3.1 for a complete list of site level characteristics.

*Climate.* Our study region has been experiencing monthly accumulated drought indices (e.g. Palmer Drought Severity Index (PDSI)) below (i.e. more severe) the 30-year average over the last few years, with 2015 being the most severe (Figure A.9). Drought conditions for 2016 were moderately below the 30-year average, falling just barely into the 2<sup>nd</sup> quartile. The monthly Standardized Precipitation Index (SPI) showed a mix of above and below average months over the growing season for 2016 (Figure A.1, A2, A.3, A.4, A.5, A.6, A.7, and A.8). April, May and June was unusually dry with only a few, mostly minor, precipitation events (Figure 3.2) resulting in the beginning of soil dry down occurring in early May (Figure 3.4). Soil moisture averaged over the top 30 cm of soil declined to less than 0.1 m<sup>3</sup>m<sup>-3</sup> around mid-July and reached an extreme low of 0.025 m<sup>3</sup>m<sup>-3</sup> in September. Soil abruptly rewetted in early October due to an unusually high amount of precipitation (Figure A.7).

Soil respiration, temperature and moisture measurements. Soil moisture sensors (CS616, Campbell Scientific, Utah, USA) were placed horizontally at 5 cm, 20 cm and 80 cm depths in a central location within each plot. Additionally, soil moisture and soil temperature probes (CS650, Campbell Scientific, Utah, USA) were installed vertically within each subplot that soil respiration data was being collected to attain average soil moisture for the top 30 cm of soil and the soil surface temperature. These probes were not installed until June 2016. Soil moisture data prior to their installation was attained from the average soil moisture of the corresponding plot's 5 cm and 20 cm soil moisture probes, and soil temperature data from the nearby weather station's soil temperature sensor at a depth of 2 cm. There was not a significant difference in response of soil respiration between using the two sources of data for either soil moisture or soil temperature.

Separation of soil respiration components. For our experiment, we used an exclusion design. Within each subplot, we monitored the components of soil respiration using an innovative paired collar design adapted from Heinemeyer and colleagues (2007b) which we installed in November 2015, five months prior to beginning respiration measurements. We installed exclusion collars adjacent to the traditional shallow collars, as depicted in Figure 3.1, so we could determine autotrophic and heterotrophic respiration. The shallow total root, mycorrhizal, and soil microbial (RMS) collars (Figure 3.5) were inserted to the depth of the litter layer to attain an airtight seal without damaging any roots (Wang et al. 2005); a mycorrhizal and microbial (MS) collar and a microbial (S) collar are installed to a depth of 30 cm and have four windows covered in 41 μm nylon mesh screens (allows ingrowth of ectomycorrhizal (EM) hyphae and recruitment of soil microbes, but excludes roots) and with 1 μm mesh (allows recruitment of soil microbes but exclude roots and EM hyphae) respectively. Exclusion collars were inserted to a depth of 30 cm because measurements of soil and root column biomass at the site have found that over 90% of the fine root biomass is in the top 30 cm. All PVC collars were 10 cm in diameter and were surveyed weekly between 10:00 AM and 2:00 PM from April through November using an infrared gas analyzer (EGM-5, PP Systems, Amesbury, MA, USA). Collars were inserted approximately six months prior to collecting soil respiration measurements to limit the effects of increased respiration from the increase of dead root biomass.

In addition to survey measurements, nine automated forced diffusion chambers (eosFD, Eosense Inc., Nova Scotia, Canada) were placed on all the collars at one plot (two treatment subplots, one control subplot) from mid-July to mid-November. These automated chambers provided respiration measurements at 10-minute intervals which were then converted to hourly averages for the duration of their deployment. Automated measurements provide a more in-depth picture of the mechanisms that drive daily soil respiration through accurate representation of the diurnal pattern of soil respiration. Automated measurements allow for a more precise estimation of growing season total respiration and validation of gap filling methodology from survey measurements. In combination with survey measurements which were taken over a broader spatial extent, the automated measurements of respiration allow us to improve our temporal scale.

*Treatment.* Treatment subplots were watered weekly on the day prior to survey measurements ensuring that CO<sub>2</sub> pulse released from water pushing CO<sub>2</sub> from soil pore space to the surface was not captured in respiration measurements. The watering treatment mimicked 6.6 mm of rainfall over a square meter with a pair of collars in the center, as depicted by the blue squares in Figure 3.1. Due to the remoteness of the site, watering was achieved by filling a watering can to a known volume (from a rain barrel) and watering as evenly as possible over each square meter. Treatment took place June

through September, adding a total of 105.6 mm of precipitation to the site annual total for each plot. Although precipitation at our site was far above the 30-year average, the summer of 2016 experienced extreme drought with less than 5% of the annual precipitation occurring between June through October. Therefore, the timing of precipitation is more accurately what our watering treatment altered. During late summer when soil moisture content was extremely low, sensors were unable to detect any moisture impacts to the soil of the treatment, although respiration did noticeably respond.

*Problems and issues.* Although collars were installed the standard six months prior to taking respiration measurements (Heinemeyer *et al.*, 2007a), severed fine and coarse roots in the exclusion collars did not decompose over that period of time. This resulted in elevated heterotrophic respiration due to the increase in available organic matter. This effect was compounded in the treatment collars. Because of this, we were unable to accurately subtract heterotrophic respiration from total respiration to estimate autotrophic respiration (e.g. RMS-S =  $R_a$ ). Therefore, only heterotrophic respiration and total respiration were evaluated in most analyses.

Since the pulse of CO<sub>2</sub> released during a rain event includes the artifact of water flushing CO<sub>2</sub> from pore space in the soil rather than respiration alone, automated chamber measurements for the 24-hours immediately follow watering treatments were excluded from the evaluation of respiration response to soil temperature and respiration response to soil moisture. Due to instrumentation failure, R<sub>s</sub> was not evaluated for the automated measurements of the control plots. Additionally, due to site-wide power failure, hourly averages of soil respiration were not evaluated for October.

Occasionally, collars were disturbed by rodents or ant colonies between or during, in the case of ants, survey measurements. When disturbances occurred, collars were repaired if necessary and measurements for that week were excluded from data analysis.

*Estimating annual Rs, Rh, and Ra.* Prior to calculations of seasonal and annual estimates of respiration, components of R<sub>s</sub> were separated at the scale of individual measurements following Heinemeyer et al. (2007a):

- 1.  $R_s = RMS$
- 2.  $R_a = RMS S$
- 3.  $R_{root} = RMS MS$
- 4.  $R_{myc} = MS S$
- 5.  $R_h = S$

Several methodologies are commonly used to estimate annual respiration from survey measurements. We selected three empirical models with varying degrees of complexity and compared their accuracy to our automated respiration measurements. Linear interpolation is the most basic method of gap filling. Gaps in R<sub>soil</sub> between survey measurements were extrapolated at half-hour intervals using the following equation:

$$R_{soil} = R_{soil}(t_0) + (t - t_0) \frac{R_{soil}(t_1) - R_{soil}(t_0)}{t_1 - t_0}$$

Where  $R_{soil}(t_0)$  and  $R_{soil}(t_1)$  represented the  $R_{soil}$  values adjacent to the missing value. This model assumes that  $R_{soil}$  changes at a constant rate between measurements and that the time in which measurements are taken are representative of the daily average. The latter is not necessarily true or could consistently be true, but can be accounted for by ensuring that measurements are consistently taken at a reasonably representative time of day. Due the first assumption, this model does not take diurnal fluctuation of soil respiration into account.

The most commonly used method for gap filling (Gomez-Casanovas *et al.*, 2013) incorporates the Arrhenius temperature sensitivity ( $E_0$ ) relationship to create a reference respiration ( $R_{ref}$ ) at a reference temperature ( $T_{ref}$ ) between gaps (Lloyd & Taylor, 1994):

$$R_{soil}(T) = R_{ref} \cdot e^{E_0 \cdot \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)}$$

Where  $T_{ref}$  is the mean annual soil temperature for the site (although often set to 10°C as a default).  $T_{ref}$  for our site was 7°C for 2016.  $E_0$  was assumed to be the constant for the entire year (308.56 K<sup>-1</sup>).  $T_0$  represents the lower temperature limit for  $R_{soil}$ , which is - 46°C.

The third gap filling function that we used is a modified version of the previous equation that incorporates the interactive effects of soil temperature and moisture proposed by Reichstein and colleagues (2003):

$$R_{soil}(T) = R_{ref} \cdot e^{E_0(RSWC) \cdot \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)} \cdot \frac{RSWC}{RSWC_{1/2} + RSWC}$$

Where RSWC is relative soil water content (RSWC = SWC/SWC<sub>FC</sub>), where SWC (or VWC) is soil water content in  $m^3 m^{-3}$ , SWC<sub>FC</sub> is soil water content at field capacity and RSWC<sub>1/2</sub> is the RSWC where  $R_{soil}$  is half its maximal value at a given temperature. SWC<sub>FC</sub> was approximated as the SWC 24-hours following the maximum reached SWC (0.467 m<sup>3</sup>m<sup>-3</sup>). In this model,  $E_0$  is assumed to be 400 K<sup>-1</sup> at first approximation and then is multiplied by RSWC.

All statistical analysis and gap filling procedures were performed in R Studio version 3.2.1 (R Team).

*Model description.* Model simulations of forest productivity and soil carbon dynamics were performed using DayCent (version 4.5), the daily timestep version of the biogeochemical model CENTURY which has been broadly used to simulate the effects of past, current and shifting climates, as well as disturbance, on ecosystem processes in forest and agricultural systems (Hartman *et al.*, 2007, Hudiburg *et al.*, 2017, Savage *et al.*, 2013). Our 6-acre study site was represented by a single point in the model.

Inputs for site calibration of the model include vegetation cover, daily precipitation, daily minimum and maximum temperature, soil texture, soil bulk density and disturbance events. For our study, DayCent was parameterized to model soil organic carbon dynamics to a depth of 30 cm. Model outputs that we evaluated included soil C and N stocks, live and dead biomass, and aboveground and belowground net primary production and heterotrophic and autotrophic respiration.

In DayCent, disturbances are scheduled and can be parameterized to imitate severity through coupled impacts to the ecosystem (e.g., biomass killed, nitrogen loss, soil eroded). To simulate fire in DayCent, the fire model is parameterized to include the combusted and/or mortality fraction of each carbon pool including live and dead wood, foliage and coarse and fine roots that occurs with each fire event. Similarly, erosion is also prescribed as an event that occurs in the same year of the observed fire event in order to simulate the resulting erosion as a product of a fire.

*Model parameterization.* Site characteristics, soil parameters and disturbance related events were parameterized for our site using available site–specific observations and publicly available climate and soil databases. Daily minimum and maximum temperature and precipitation data required for the model were acquired from DAYMET (Thornton, 2017b) for a 30 year period. Soil texture and classification were obtained from the United States National Resource Conservation Service (NRCS) SSURGO database (NRCS, 2010).

The model was calibrated to the site using a 2000 year spin up. In the model spin up, a stand replacing canopy fire (kills 99% of photosynthetic material and removed 80% of woody plant material) was scheduled at a 200-year interval and followed by an erosion event that resulted in a loss of soil organic matter and overall soil carbon storage. Site level characteristics were adjusted until spin up model outputs of soil carbon fell within a 95% confidence interval of the conditions that we found at our site. All DayCent model schedule files for the spin up and subsequent simulations are included in Appendix B.

After model calibration, the model was run for the 20<sup>th</sup> century spanning from 1930 – 2014. The 20<sup>th</sup> century model run was initiated with a clear-cut that removed 95% of the trees, mimicking the legacy of our site, which was followed by a regrowth of the mixed conifer forest composition that is characteristic of what exists in our site now. Following the 20<sup>th</sup> century model run, two versions of the subsequent years, 2015-2017, were modeled. One simulated the control conditions, using Prism weather data for the site without any modifications. The other simulated the watering treatment by adding weekly irrigation effects during the treatment period of 2016.

*Heterotrophic respiration incubation experiment.* In addition to evaluating the effects of soil moisture on heterotrophic respiration *in situ*, an incubation experiment was performed using soil from the Moscow Mountain field site. Soil was collected from six locations around the field study site. Soil was then dried for 48 hours at 100° C and then sieved at 2 mm to remove roots and any large organic material. Soil was then mixed together into one large tub (36" x 18" x 8").

The tub of soil was then place in a climate controlled growth chambers that maintained a constant temperature of 16.5°C. Two Decagon MPS-6 soil water potential sensors and two EC-5 soil moisture sensors, were placed different locations within the bin to attain average soil moisture and soil water potential throughout the soil. Additionally, because of the low sensitivity of the MPS-6 sensors in extremely dry conditions, water potential measurements were taken using a WP4C (Decagon, Pullman, WA, USA) until soil moisture was increased to within the high-resolution range of the automated sensors. Soil respiration measurements (6 repetitions per sample period) were taken using an EGM-5 CO2<sub>2</sub> infrared gas analyzer for 6 days.

Initial measurements were taken after soils had acclimated in the growth chambers for 24 hours. Each day, after respiration, VWC and water potential measurements were taken, water was added to the samples and they were mixed thoroughly to attain as homogenous soil moisture and water potential as possible throughout each sample. For the first 3 days, 10% of the original dried mass of each sample was added in water. On

the fourth and fifth days, this was increased to 20% to attain water contents closer to field capacity by the end of the study period.

Table 3.1

Site level Characteristics	
Latitude, Longitude	46.801°N, -116.810°W (Moscow Mtn, Idaho)
Soil carbon	86 Mg C ha <sup>-1</sup>
Soil texture	Sand: 20%; Silt: 65%; Clay: 15%
Bulk density	0.80
Mean annual precipitation	810 mm (30 year average)
Mean annual temperature	7.4°C (30 year average)









#### 3.2 Results

Separating the components of soil respiration. We found that both MS and S exclusion collars often had a much higher respiration flux than the RMS collars. This was partly an artifact of the severed roots that remained in the collar after installation. They did not adequately decompose within the six-month timeframe as they were expected to. After the 2016 field season, we found that 9.89 g ( $\pm$  0.10 g) of root material remained in exclusion collars. This is approximately 67% of the root biomass that we would expect in the volume of the collars when compared with average plot live root biomass. Because of this, we were unable to separate autotrophic respiration from heterotrophic respiration as we expected. However, the seasonal pattern of autotrophic respiration can still be useful to evaluate even though the magnitude is not correct. It is evident that autotrophic respiration becomes water limited much earlier in the season (e.g. June or sooner) than heterotrophic respiration (e.g. August; Figure 3.6).

Autotrophic respiration appears to be higher in the control in Figure 3.6, however, this is likely not accurate. This is probably because heterotrophic respiration was much more elevated in the treatment than in the control as a result of increased moisture availability (Figure 3.13 also shows this) so when heterotrophic respiration was subtracted from the total respiration collar that did not have excessive dead root and mycorrhizae material, it resulted in causing autotrophic respiration to appear lower than it likely was (as explained in the methods about problems and issues). This could suggest that autotrophic respiration did not respond as strongly to the watering treatment as heterotrophic respiration.

*Characterization of the relationship between respiration and soil temperature and moisture.* In Northern Idaho forests, as temperatures increase in the summer with very few precipitation events, the soils become extremely dry in the top 30 cm of soil with the annual minimum soil moisture occurring on Oct. 3<sup>rd</sup> at a value of 0.025 m<sup>3</sup> m<sup>-3</sup>. Due to limited accessibility of water, we were unable to add enough water during watering treatments to increase the soil moisture between treatment and control subplots to the intended 30% above ambient, however we still saw a response from both total soil respiration and heterotrophic soil respiration to the watering treatment.

Both total respiration and heterotrophic respiration did not respond completely as expected to soil temperature and soil moisture. We found that the relationship between respiration and these environmental drivers varied between both the control and treatment subplots and survey and automated measurements of respiration, as shown by Figure 3.7 and Figure 3.8. There was not a significant relationship between soil respiration and temperature under control conditions for survey measurements (Figure 3.11; R<sub>s</sub>: p-value = 0.2031; R<sub>h</sub>: p-value = 0.07369), however there was a significant relationship between soil respiration and temperature under treatment conditions (R<sub>s</sub>: p-value = 4.19E-5; R<sub>h</sub>: p-value = 0.0159).

The correlation between heterotrophic respiration and soil temperature was also stronger with continuous measurements ( $R^2 = 0.2362$ ; p-value = 2.20E-16) compared to survey ( $R^2 = 0.1382$ ; Figure 3.11). Under treatment conditions, the differences in the relationship between survey and automated measurements under both control and treatment conditions were significantly different with p-values <.05, respectively. Under both control and treatment conditions, the relationship between the components of soil respiration and soil temperature and relative soil water content was much stronger than that just between soil respiration and soil temperature. Moreover, under control conditions, both automated and the survey measurements of respiration showed strong positive relationships with soil moisture but had varying slopes. The automated measurements showed that respiration increased at a much higher rate with soil moisture than the survey measurements detected, especially heterotrophic.

Although the relationships between the components of soil respiration and soil temperature were weakened by the watering treatment, there was a negative (significant) relationship between R<sub>myc</sub> and soil temperature with the automated measurements. For the control, the automated measurements showed a strong negative

correlation between the components of respiration and soil temperature, whereas the survey measurements showed weaker and mildly positive correlation. Mycorrhizal respiration appears to be more dependent on soil moisture and less dependent on soil temperature than other components of  $R_s$ .

Heterotrophic respiration incubation experiment. In our laboratory incubation experiment, heterotrophic respiration responded exactly as expected to increases in soil moisture.  $R_h$  increased exponentially to increases in soil moisture over the 6-day experiment (Figure 3.9, 3.10). The correlation was very strong with an  $R^2$  of 0.97487 with a significant p-value (0.00873). Additionally, the relationship between soil respiration and volumetric water content was slightly stronger and more significant than that with water potential ( $R^{2-}$  = 0.95753 & p-value = 0.0326). This confirms that our field measurements of VWC, rather than soil water potential are an adequate representation of soil water content in relation to the soil type.

*Evaluating the diurnal pattern of soil respiration.* The magnitude and timing of the daily maximum and minimum of soil respiration vary throughout the year. Here, we used automated respiration data to determine the average hourly respiration for heterotrophic respiration and total soil respiration. For the treatment, measurements taken during the 24 hours following the weekly watering treatment were removed from this analysis to exclude the pulse release of CO<sub>2</sub> caused by water infiltration. For heterotrophic respiration, we evaluated the season shift of the diurnal pattern for both the control and the treatment (Figure 3.12), whereas we only evaluated the pattern of total soil respiration for the treatment due to equipment failure of the automated forced diffusion chamber on the total respiration collar in the control plot (Figure 3.13). Due to power failure in October, there was not enough automated data to evaluate the hourly average. For comparison of how the daily minimum and maximum correspond to the diurnal pattern of soil temperature, Figure 3.11 depicts the hourly average soil temperature for control and treatment plots during the same timeframe. The dashed vertical lines are placed at 10:00 AM and 2:00 PM on all of these figures to show the time period during which survey respiration measurements took place during this study

which is in accordance with the typical protocol for *in situ* field studies of soil respiration.

There is a seasonal shift in the timing of the average daily minimum of heterotrophic respiration that differs between control and treatment in August (Figure 3.12). For the control, the minimum heterotrophic respiration efflux occurs around 10:00 am in August, September and November. In July and August, the daily minimum flux of heterotrophic respiration and total soil respiration occurs well before 10:00 AM for the treatment. In September and November (and likely in October), the daily minimum flux of heterotrophic respiration and total soil respiration for the treatment occurred approximately at 10:00 AM. For all four months evaluated, the minimum soil temperature occurred between 5:00 AM and 10:00 AM which is approximately the time that minimum respiration for both control and treatment of heterotrophic respiration and total soil respiration and treatment of heterotrophic respiration for both control and treatment of heterotrophic respiration and treatment of network in July and September for the treatment. The maximum rate of respiration for both control and treatment of heterotrophic respiration and treatment of heterotrophic respiration and treatment of network in July and September for the treatment.

Heterotrophic respiration flux was lower in the control than in the treatment for August and September. However, in November, when soil rewetting was occurring, the rate of soil respiration was higher in the control than in the treatment. This was likely a result of more SOM available for microbial decomposition in the control than in the treatment at this time. There wasn't as much SOM in the treatment in November because microbial organisms were less water limited and had higher rates of decomposition throughout the growing season.

*Comparison of Modeled and Observed Annual Soil Carbon Flux.* DayCent estimates of annual soil carbon flux from our site didn't fall within the 95% confidence interval for either control or treatment of total soil respiration and heterotrophic respiration. For heterotrophic respiration, there was a smaller confidence interval for the control than the treatment. The opposite was true for total respiration.








diffusion chambers in the top row of the figure and survey measurements in the bottom row of the figure. Soil moisture content (v/v) is an average of soil moisture over the top 30 cm of soil.



measured as volumetric water content at 16.5°C.





(blue) or soil temperature and relative soil water content for continuous and survey measurements under (a) control and (b) treatment conditions.









## 2.3 Discussion

Separating the components of soil respiration. Many methods have been tested to isolate the belowground CO<sub>2</sub> efflux measurements of roots, mycorrhizae, and microbes, however, they each come with drawbacks. Using isotopes to identify the source of respiration is one of the most accurate methods but it is extremely expensive and therefore not cost effective for research that is beyond a small spatial scale. Trenching around plots to disconnect roots from an area can be disruptive to the flow of ground water and not necessary spatially representative of an ecosystem. Exclusion methods can attain coverage over larger spatial scales but disturbs the soil column when removing roots. The hope in using the deep collar with mesh windows design developed by Heinemeyer and colleagues (2007a) was that it would have a minimal influence on the flow of ground water, keep the soil column intact and be cost effective. It did achieve all of these goals, however, the roots that were severed within the collars during installation did not completely decompose before measurements began 6 months later, or even by the end of our measurement campaign an entire year later. The study that the 6-month root decomposition time was based, originated in the UK, where the winter temperatures are much warmer and soil moisture never drops below 0.20 m<sup>3</sup>m<sup>-3</sup> during the year. Because of the climatic differences, the roots in our collars did not decompose within the same time frame as they did at the UK study site. It is possible that this was compounded by the effects of years of drought, especially the extreme drought of 2015, on the microbial community at our site, thus yielding slower decomposition rates.

In order to disentangle the components of soil respiration, it will require compromising some aspect of natural conditions if severed roots will not decompose within a reasonable timeframe. Since this study was completed, we have reinstalled exclusion collars at sites on Moscow Mountain. When installing, we removed the soil from within the collars in layers and removed all roots greater than 2 mm in diameter (e.g. coarse roots). We then replaced the soil in the collar, maintaining the soil layers in the appropriate layers and maintained soil structure as much as possible. Litter and duff layers were maintained, and placed on top of the soil. Separating microbial respiration

by placing collars in large gaps between trees (Brumme, 1995, Ruehr *et al.*, 2012, Tang *et al.*, 2005) would not be possible without removing trees at our site because of the high density of the stand (> 80 trees per 10-meter radius plot). Removing trees would cause the same root decomposition dilemma as severing root by the deep collars. The only existing method that would not be disruptive to natural conditions would be using isotopes to determine if the respiration path was though tree roots or the soil, but as stated previously, isotopes are cost prohibitive at the spatial scale of our study. Although removing the roots disturbs the soil column, it might be the most effective method for separating the components at our site. It is likely that the side effects of this will be minimal after 6 months to a year.

Characterization of the relationship between respiration and soil temperature and *moisture.* The clear discrepancies between automated and survey measurement soil respiration and moisture and temperature indicates that survey measurements may not be frequent enough to capture the true relationship between respiration and the abiotic variables that influence it. Our automated data shows that soil respiration responds as expected, with a typical exponential increase in respiration with temperature, with the exception of when the soil rewets in the fall. When soil rewets in the fall, temperature no longer seems to matter as much and respiration rates dramatically increase. This is likely because soil microbes have been deprived of water throughout much of the summer and are taking advantage of the resource as soon as it's available. The high rates of respiration corresponding with low temperatures during fall rewet is less pronounced in the treatment, likely because there was less readily accessible SOM for microbial activity since there were higher rates of decomposition throughout the summer due to the watering treatment. These relationships observed by the half-hourly automated measurements in the control suggest that the extreme drought occurring at our site causes soil moisture to become a limiting factor for respiration regardless of the increase in temperature. Other studies evaluating the relationship between soil temperature and respiration and soil moisture and respiration have been located in regions that do not experience soil moisture conditions below 0.1 m<sup>3</sup> m<sup>-3</sup> at any point throughout the year (Borken *et al.*, 2006, Heinemeyer *et al.*, 2012). This result heeds

caution in the use of annual respiration models that are based solely on survey measurements and soil temperature in ecosystems that experience extreme prolonged drought during the growing season.

*Evaluating the diurnal pattern of soil respiration.* Our results indicate that the diurnal pattern of soil respiration varies throughout the season. Because there is not a perfect relationship between soil respiration and temperature, strategies for estimating annual soil respiration from survey measurements also rely on the timing of survey measurements to be representative of the daily peak soil respiration which is commonly considered to be between 10:00 AM and 2:00 PM. During September and November, figures 3.6 and 3.7 demonstrate that the lowest rates of respiration spanned this timeframe. This likely is a contributing factor as to why survey measurements underestimated the seasonal respiration when compared to the seasonal total calculated from continuous measurements. Additionally, the diurnal fluctuation of respiration varies in magnitude seasonally and between control and treatment plots, further indicating that the magnitude in which respiration responds to temperature is driven by soil moisture (Figure 3.6, 3.7, & 3.9).

Although adapting the times of survey measurements with seasonal shifts in soil moisture availability would help to improve that representation of daily average respiration, it would not solve the discrepancies in the relationship of respiration and soil temperature and moisture captured by survey measurements and automated measurements. It is apparent that our ability to accurately estimate annual soil respiration dramatically increases with the annual number of respiration records for any method of gap filling (Gomez-Casanovas *et al.*, 2013). Given that we found that our survey measurements did not have a significant relationship with soil temperature in the un-watered plots but did in the watered, we need to re-evaluate the use of soil temperature for annual estimates of soil respiration in environments that experience extreme drought. This will be an increasing concern for predicting how soil respiration will respond to increasing severity and frequency of drought as climates warm and shift globally.

It is evident that there is a seasonality to the diurnal fluctuation of both heterotrophic respiration and total soil respiration at our site as shown by figures 3.12 and 3.13. The magnitude of the fluctuation also varies over the season. The difference in the timing of the average daily minimum of heterotrophic respiration between the control and the treatment in August suggests that these seasonal shifts are dependent on soil moisture. For heterotrophic respiration, the largest average magnitude of respiration flux occurred in July for the watered plots and in November for the control.

We found that the simple linear interpolation method of estimating annual soil respiration was the most accurate for both R<sub>s</sub> and R<sub>h</sub>. This is likely because method is largely dependent on catching the daily average of soil respiration during survey measurements rather than explicitly attempting to determine the diurnal patterns of respiration using half hourly soil temperature or soil moisture. Determining the timeframe that daily average respiration occurs is imperative for improving the accuracy of the simple linear interpolation method. Because we found that the diurnal pattern of soil respiration shifts throughout the season, likely due to the interaction effect of soil temperature and soil moisture on respiration, it may be necessary to adjust the time of survey measurements throughout the year.

These variables will be impacted by climate change, making it increasingly important that we improve our ability to predict and quantify how they will in turn affect soil carbon fluxes and determine how we may be able to manipulate them (i.e. conservation) to maximize soil carbon storage. Due to the nature of belowground processes, it is difficult to disentangle the varying mechanistic responses of autotrophic and heterotrophic respiration to environmental variables (Hanson *et al.*, 2000).

## 2.4. Conclusion.

Belowground fluxes are complex and difficult to disentangle. Further research is necessary to explore whether survey measurements are sufficient in areas that

experience extreme drought during the growing season to estimate annual respiration. It is possible that due to increasing severity and length of drought in this region, that the timing of heterotrophic respiration might shift to periods with accessible soil moisture. Additional research is necessary to determine how autotrophic respiration will respond. Expand on how my results compare with the literature and what questions this brings up.

- Allen Cd, Macalady Ak, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest ecology and management, **259**, 660-684.
- Allison Sd, Wallenstein Md, Bradford Ma (2010) Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience, **3**, 336-340.
- Anderegg Wrl, Kane Jm, Anderegg Ldl (2013) Consequences of widespread tree Mortality triggered by drought and temperature stress. Nature Climate Change, **3**, 30-36.
- Arrhenius S (1889) Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Säuren. Zeitschrift für physikalische Chemie, **4**, 226-248.
- Atkin Ok, Macherel D (2008) The crucial role of plant mitochondria in orchestrating drought tolerance. Annals of botany, **103**, 581-597.
- Birdsey R, Pregitzer K, Lucier A (2006) Forest carbon management in the United States. Journal of environmental quality, **35**, 1461-1469.
- Birdsey Ra, Jenkins Jc, Johnston M *et al.* (2007) North American forests. In: *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle.* (ed King Awd, L.; Zimmerman, G.P.; Fairman, D.M.; Houghton, R.A.; Marland, G.; Rose, A.Z.; Wilbanks, T.J.) pp Page, Asheville, NC, National Oceanic and Atmospheric Administration, National Climatic Data Center.
- Borken W, Savage K, Davidson Ea, Trumbore Se (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Global Change Biology, **12**, 177-193.
- Brockett Bf, Prescott Ce, Grayston Sj (2012) Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada. Soil Biology and Biochemistry, **44**, 9-20.
- Brumme R (1995) Mechanisms of carbon and nutrient release and retention in beech forest gaps. Plant and Soil, **168**, 593-600.
- Canadell Jg, Raupach Mr (2008) Managing forests for climate change mitigation. science, **320**, 1456-1457.
- Carbone M, Still C, Ambrose A *et al.* (2011) Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration. Oecologia, **167**, 265-278.

- Chapin Fs, Woodwell Gm, Randerson Jt *et al.* (2006) Reconciling Carbon-cycle Concepts, Terminology, and Methods. Ecosystems, **9**, 1041-1050.
- Ciais P, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature, **437**, 529-533.
- Cleveland Cc, Wieder Wr, Reed Sc, Townsend Ar (2010) Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. Ecology, **91**, 2313-2323.
- Conant Rt, Dalla-Betta P, Klopatek Cc, Klopatek Jm (2004) Controls on soil respiration in semiarid soils. Soil Biology and Biochemistry, **36**, 945-951.
- Cook Fj, Orchard Va (2008) Relationships between soil respiration and soil moisture. Soil Biology and Biochemistry, **40**, 1013-1018.
- Cox Pm, Betts Ra, Jones Cd, Spall Sa, Totterdell Ij (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature, **408**, 184-187.
- Davidson Ea, Janssens Ia (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature, **440**, 165.
- Davidson Ea, Janssens Ia, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q10. Global Change Biology, **12**, 154-164.
- Doughty Ce, Metcalfe Db, Girardin Caj *et al.* (2015) Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature, **519**, 78-82.
- Gaumont-Guay D, Black Ta, Mccaughey H, Barr Ag, Krishnan P, Jassal Rs, Nesic Z (2009) Soil CO2 efflux in contrasting boreal deciduous and coniferous stands and its contribution to the ecosystem carbon balance. Global Change Biology, **15**, 1302-1319.
- Gomez-Casanovas N, Anderson-Teixeira K, Zeri M, Bernacchi Cj, Delucia Eh (2013) Gap filling strategies and error in estimating annual soil respiration. Global change biology, **19**, 1941-1952.
- Hamdi S, Moyano F, Sall S, Bernoux M, Chevallier T (2013) Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions. Soil Biology and Biochemistry, **58**, 115-126.
- Hanson P, Edwards N, Garten Ct, Andrews J (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry, **48**, 115-146.

- Hartman Md, Baron Js, Ojima Ds (2007) Application of a coupled ecosystem-chemical equilibrium model, DayCent-Chem, to stream and soil chemistry in a Rocky Mountain watershed. ecological modelling, **200**, 493-510.
- Heinemeyer A, Hartley Ip, Evans Sp, Carreira De La Fuente Ja, Ineson P (2007a) Forest soil CO2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. Global Change Biology, **13**, 1786-1797.
- Heinemeyer A, Hartley Ip, Evans Sp, Carreira De La Fuente Ja, Ineson P (2007b) Forest soil CO2flux: uncovering the contribution and environmental responses of ectomycorrhizas. Global Change Biology, **13**, 1786-1797.
- Heinemeyer A, Wilkinson M, Vargas R, Subke J-A, Casella E, Morison Ji, Ineson P (2012) Exploring the" overflow tap" theory: linking forest soil CO2 fluxes and individual mycorrhizosphere components to photosynthesis. Biogeosciences, **9**, 79.
- Hinko-Najera N, Fest B, Livesley Sj, Arndt Sk (2015) Reduced throughfall decreases autotrophic respiration, but not heterotrophic respiration in a dry temperate broadleaved evergreen forest. Agricultural and Forest Meteorology, **200**, 66-77.
- Hudiburg Tw, Higuera Pe, Hicke Ja (2017) Fire-regime variability impacts forest carbon dynamics for centuries to millennia. Biogeosciences, **14**, 3873.
- Jandl R, Lindner M, Vesterdal L *et al.* (2007) How strongly can forest management influence soil carbon sequestration? Geoderma, **137**, 253-268.
- Jassal Rs, Black Ta, Cai T, Morgenstern K, Li Z, Gaumont-Guay D, Nesic Z (2007) Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand. Agricultural and Forest Meteorology, **144**, 44-57.
- Jägermeyr J, Gerten D, Lucht W, Hostert P, Migliavacca M, Nemani R (2014) A highresolution approach to estimating ecosystem respiration at continental scales using operational satellite data. Global Change Biology, **20**, 1191-1210.
- Kirschbaum Mu (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and biochemistry, **27**, 753-760.
- Kirschbaum Muf (2006) The temperature dependence of organic-matter decomposition—still a topic of debate. Soil Biology and Biochemistry, **38**, 2510-2518.
- Lashof Da, Ahuja Dr (1990) Relative contributions of greenhouse gas emissions to global warming. Nature, **344**, 529-531.

- Law Be (2014) Regional analysis of drought and heat impacts on forests: current and future science directions. Global Change Biology, **20**, 3595-3599.
- Lloyd J, Taylor J (1994) On the temperature dependence of soil respiration. Functional ecology, 315-323.
- Melillo Jm, Butler S, Johnson J *et al.* (2011) Soil warming, carbon–nitrogen interactions, and forest carbon budgets. Proceedings of the National Academy of Sciences, **108**, 9508-9512.
- Miles L, Kapos V (2008) Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implications. science, **320**, 1454-1455.
- Moyano Fe, Vasilyeva N, Bouckaert L *et al.* (2012) The moisture response of soil heterotrophic respiration: interaction with soil properties. Biogeosciences, **9**, 1173-1182.
- O'halloran Tl, Law Be, Goulden Ml *et al.* (2012) Radiative forcing of natural forest disturbances. Global Change Biology, **18**, 555-565.
- Pan Y, Birdsey Ra, Fang J *et al.* (2011) A large and persistent carbon sink in the world's forests. Science, **333**, 988-993.
- Paustian K, Six J, Elliott E, Hunt H (2000) Management options for reducing CO2 emissions from agricultural soils. Biogeochemistry, **48**, 147-163.
- Raich Jw, Potter Cs (1995) Global patterns of carbon dioxide emissions from soils. Global Biogeochemical Cycles, **9**, 23-36.
- Reichstein M, Rey A, Freibauer A *et al.* (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Global biogeochemical cycles, **17**.
- Ruehr Nk, Martin Jg, Law Be (2012) Effects of water availability on carbon and water exchange in a young ponderosa pine forest: Above- and belowground responses. Agricultural and Forest Meteorology, **164**, 136-148.
- Running Sw, Thornton Pe, Nemani R, Glassy Jm (2013) Primary Productivity from the Earth Observing System. Methods in Ecosystem Science, 44.
- Ryan Mg, Law Be (2005) Interpreting, measuring, and modeling soil respiration. Biogeochemistry, **73**, 3-27.
- Savage Ke, Parton Wj, Davidson Ea, Trumbore Se, Frey Sd (2013) Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest. Global change biology, **19**, 2389-2400.

- Schwalm Cr, Williams Ca, Schaefer K *et al.* (2012) Reduction in carbon uptake during turn of the century drought in western North America. Nature Geosci, **5**, 551-556.
- Tang J, Baldocchi Dd, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. Global Change Biology, **11**, 1298-1304.
- Thornton Pe (2017a) Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2 doi:10.3334/ORNLDAAC/1219. pp Page.
- Thornton Pe (2017b) Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2 doi:10.3334/ORNLDAAC/1219. pp Page.
- Turner Dp, Ritts Wd, Law Be *et al.* (2007) Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. Biogeosciences, **4**, 597-612.
- Usgcrp (2009) Climate Literacy: The Essential Principles of Climate Science, A Guide for Individuals and Communities. pp Page, US Global Change Research Program. Retrieved from: <u>http://www.globalchange.gov/resources/educators/climate-literacy</u>.
- Van Der Molen Mk, Dolman Aj, Ciais P *et al.* (2011) Drought and ecosystem carbon cycling. Agricultural and Forest Meteorology, **151**, 765-773.
- Van Groenigen Kj, Qi X, Osenberg Cw, Luo Y, Hungate Ba (2014) Faster decomposition under increased atmospheric CO2 limits soil carbon storage. Science, 1249534.
- Van Tuyl S, Law Be, Turner Dp, Gitelman Ai (2005) Variability in net primary production and carbon storage in biomass across Oregon forests--an assessment integrating data from forest inventories, intensive sites, and remote sensing. Forest Ecology and Management, **209**, 273-291.
- Van't Hoff Jh (1884) *Etudes de dynamique chimique*, Muller.
- Wieder Wr, Bonan Gb, Allison Sd (2013) Global soil carbon projections are improved by modelling microbial processes. Nature Climate Change, **3**, 909-912.





















Figure A.10. Projected change in mean annual soil moisture for 2081-2100 under four different climate scenarios. IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

## APPENDIX B: DAYCENT INPUT FILES

Spinup Schedule file:

1	Starting year
2000	Last year
mmtn.1	00 Site file name
0	Labeling type
-1	Labeling year
-1.00	Microcosm
-1	CO2 Systems
-1	pH Effect
-1	Soil Warming
0	N input scalar option
0	OMAD scalar option
0	Climate scalar option
2	Initial system
]	Initial crop
TMCF	Initial tree
Voar Ma	onth Ontion
1	Block # Temperate Mixed
199	Last year
1	Repeats # years
1	$\begin{array}{c} \text{Autput starting vear} \\ \end{array}$
12	Output starting year
1 000	Output interval
F.000	Weather choice
n mmtn w	weather enoice
1 10	TREE
TMCF	TREE
1 10	TFST
1 350	) LAST
1 350	) TLST
-999 -99	99 X
2	Block # Canopy Burn
200	Last vear
1	Repeats # years
200	Output starting year
12	Output month
1.000	Output interval
С	Weather choice
1 10	TREE
TMCF	
1 10	TFST

Block # Temperate Mixed Repeats # years Output starting year Output month Output interval Weather choice Block # Canopy Burn Repeats # years Output starting year Output month Output interval Weather choice

HT 1 350 TLST -999 -999 X 5 Block # Temperate Mixed 599 Last year Repeats # years 1 Output starting year 401 12 Output month 1.000 Output interval С Weather choice 1 10 TREE

1 228 TREM

1 228 FIRE

1 350 TLST -999 -999 X

1 10 TREE

1 10 TFST 1 350 TLST -999 -999 X

1 10 TREE

1 10 TFST 1 228 TREM

1 228 FIRE

Last year

Last year

BRN2

ΗT

3

1

399

201

1.000

TMCF

12

С

4

1

400

400

12 1.000

С

TMCF

BRN2

TMCF

1 10 TFST

1 350 TLST

-999 -999 X

6 Block # Canopy Burn 600 Last year 1 Repeats # years 600 Output starting year 12 Output month 1.000 Output interval Weather choice С 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE HT 1 350 TLST -999 -999 X 7 Block # Temperate Mixed 799 Last year 1 Repeats # years Output starting year 601 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X 8 Block # Canopy Burn 800 Last year 1 Repeats # years 800 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE HT 1 350 TLST -999 -999 X 9 Block # Temperate Mixed 999 Last year

1 Repeats # years 801 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X 10 Block # Replacement Burn 1000 Last year 1 Repeats # years 1000 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE HT 1 350 TLST -999 -999 X 11 Block # Temperate Mixed 1199 Last year 1 Repeats # years 1001 Output starting year 12 Output month Output interval 1.000 F Weather choice mmtn.wth 1 10 TREE TMCF 1 10 TFST 1 350 LAST 1 350 TLST -999 -999 X 12 Block # Canopy Burn 1200 Last year 1 Repeats # years 1200 Output starting year 12 Output month 1.000 Output interval

С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE HT 1 350 TLST -999 -999 X 13 Block # Temperate Mixed 1399 Last year 1 Repeats # years 1201 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X 14 Block # Canopy Burn 1400 Last year 1 Repeats # years 1400 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE HT 1 350 TLST -999 -999 X Block # Temperate Mixed 15 1599 Last year Repeats # years 1 1401 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE

TMCF 1 10 TFST 1 350 TLST -999 -999 X 16 Block # Canopy Burn 1600 Last year 1 Repeats # years 1600 Output starting year 12 Output month Output interval 1.000 С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE ΗT 1 350 TLST -999 -999 X 17 Block # Temperate Mixed 1799 Last year 1 Repeats # years 1601 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X 18 Block # Canopy Burn 1800 Last year 1 Repeats # years 1800 Output starting year 12 Output month 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE

HT

1 350 TLST -999 -999 X Block # Temperate Mixed 19 1999 Last year Repeats # years 1 Output starting year 1801 Output month 12 1.000 Output interval С Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X Block # Replacement Burn 20 2000 Last year Repeats # years 1 Output starting year 2000 Output month 12 1.000 Output interval Weather choice С 1 10 TREE TMCF 1 10 TFST 1 228 TREM BRN2 1 228 FIRE ΗT 1 350 TLST -999 -999 X
20<sup>th</sup> Century Schedule File:

1930	Starting year		
2014	Last year		
mmtn.1	.00 Site file name		
0	Labeling type		
-1	Labeling year		
-1.00	Microcosm		
-1	CO2 Systems		
-1	pH Effect		
-1	Soil Warming		
0	N input scalar option		
0	OMAD scalar option		
0	Climate scalar option		
2	Initial system		
	Initial crop		
TMCF	Initial tree		
Year Mo	onth Option		
1	Block # Burn		
1930	Last year		
1	Repeats # years		
1930	Output starting year		
12	Output month		
1.000	Output interval		
F	Weather choice		
mmtn.v	vth		
1 10	TREE		
TMCF			
1 10	TFST		
1 228	3 TREM		
CE			
1 350	) TLST		
-999 -9	99 X		
2	Block # TempConifer		
2014	Last year		
1	Repeats # years		
1931	Output starting year		
12	Output month		
1.000	Output interval		
С	Weather choice		
1 10	TREE		
TMCF			
1 10 TFST			
1 350 TLST			
-999 -999 X			

Control Schedule File:

2015	Starting	year		
2017	Last year	ſ		
mmtn.1	100 S	Site file name		
0	Labeling ty	ре		
-1	Labeling ye	ear		
-1.00	Microcos	m		
-1	CO2 Syster	ns		
-1	pH Effect			
-1	Soil	Warming		
0	N input sca	lar option		
0	OMAD scal	ar option		
0	Climate sca	lar option		
2	Initial syste	em		
	Initial crop			
TMCF	Initial tr	ee		
	_			
Year Month Option				
1	Block #			
2017	Last yea	r		
1	Repeats # y	years		
2015	Output	starting year		
12	Output mo	onth		
1.000	Output ii	nterval		
F	Weather ch	noice		
mmtn_current.wth				
1 10	) TREE			
TMCF				
1 10 TFST				
1 350 TLST				
-999 -999 X				

Treatment Schedule File:

2015	Starting year		
2017	Last year		
mmtn.10	0 Site file name		
0 L	abeling type		
-1 I	Labeling year		
-1.00	Microcosm		
-1 (	CO2 Systems		
-1 p	oH Effect		
-1	Soil Warming		
0 N	l input scalar option		
0 0	) MAD scalar option		
0 0	limate scalar option		
2 I	nitial system		
In	itial crop		
TMCF	Initial tree		
Year Mor	nth Option		
1 E	Block # Water		
2015	Last year		
1 F	Repeats # years		
2015	Output starting year		
12	Output month		
1.000	Output interval		
F V	Veather choice		
mmtn cu	rrent.wth		
1 107	`REE		
TMCF			
1 107	`FST		
1 152 IRRI			
F0.6			
1 182	IRRI		
F0.6			
1 213	IRRI		
F0.6			
1 244	IRRI		
F0.6			
1 274	IRRI		
F0.6			
1 350	TLST		
-999 -990	9 X		
2 F	Rlock #_ ambient again		
2017	Last vear		
1 F	Repeats # years		
2016	Output starting vear		
-			

12 Output month 1.000 Output interval C Weather choice 1 10 TREE TMCF 1 10 TFST 1 350 TLST -999 -999 X