Soil Respiration Following Canopy Disturbance

in a Northern Michigan Forest

Thesis

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Abstract

Carbon storage in eastern U.S. forests is threatened by stem-girdling invasive insects, along with natural succession as pioneer tree species age and die. In Northern lower Michigan we are investigating the impact of these disturbances on above- and below-ground carbon cycling across a mixed hardwood and pine forest. In spring 2008, early successional tree species, such as aspen (Populus grandidenta and P. tremuloides), were experimentally girdled in the Forest Accelerated Succession Experiment (FASET), while a nearby long-term research site, Ameriflux (AF), remained undisturbed. Soil respiration ($R_s$) is known to be responsive to disturbance and comprises the largest fraction of total ecosystem respiration ($R_e$). However, determining effects of management on $R_s$ is complicated by difficulties accurately measuring temporal variability in soil respiration and biophysical controlling factors such as soil temperature and soil water content (SWC). The objective of this study was to quantify $R_s$ (soil CO$_2$ efflux) and its constraints and drivers in disturbed and undisturbed forests and under early successional and late successional tree species. $R_s$, temperature, and SWC were intensively measured at four instrumented sites and extensively measured across the landscape along a number of 1km transects. A nested study design featured paired sites under early- and late-successional tree canopies (aspen and oak) in disturbed and undisturbed forest (FASET and AF). $R_s$ was measured every hourly at the soil pits using an automated closed-chamber CO$_2$ efflux system and biweekly along the 1km transects using a portable closed-chamber CO$_2$ efflux system. $R_s$ decreased under the canopy of disturbed aspen trees compared to controls aspen trees but was unchanged under the canopy of disturbed oak trees compared to control oak trees. Temperature sensitivity of $R_s$ as measured by a Q$_{10}$ analysis, decreased under both aspen and oak trees in the disturbed forest compared to the control forest, indicating a possible decoupling between biophysical drivers and $R_s$ following disturbance. A wavelet coherence analysis showed time-varying patterns of $R_s$ responses to temperature and moisture, allowing inspection of diurnal $R_s$ hysteresis as well as large effluxes associated with intermittent precipitation events. The
results of this study show that further research is needed on the underlying mechanisms that control soil respiration and ultimately the C cycle of disturbed forest ecosystems.
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Field of Study

Major Field: Environment and Natural Resources
Table of Contents

Abstract .................................................................................................................................................. ii
Acknowledgements ........................................................................................................................... iv
Vita ....................................................................................................................................................... v
List of Tables ....................................................................................................................................... vii
List of Figures ...................................................................................................................................... viii
List of Abbreviations and Nomenclature ........................................................................................... x
Introduction ......................................................................................................................................... 1
Methods ............................................................................................................................................. 11
Results ............................................................................................................................................... 24
Discussion ......................................................................................................................................... 47
Conclusion ......................................................................................................................................... 54
References .......................................................................................................................................... 57
Appendix A: Curvefit MATLAB Program......................................................................................... 64
Appendix B: Site Photographs of AAS and FAS ................................................................................. 69
Appendix C: More Wavelet Coherence Analysis ............................................................................... 72
Appendix D: More Temperature-Moisture Efflux Analyses ............................................................... 79
Appendix E: Phenoperiod Temperature-Moisture Efflux Analyses ................................................... 82
Appendix F: Nighttime NEE Comparison with Soil Respiration Measurements ................................ 85
Appendix G: Hydrology .................................................................................................................... 88
List of Tables

Table 1. Soil Carbon Content at AF and FASET ................................................................. 12
Table 2: $Q_{10}$ Summary by site and phenoperiod ............................................................ 39
List of Figures

Figure 1. UMBS vegetation map showing soil biophysical pits in relation to FASET and AF........13
Figure 2. Autochambers in relation to soil pit.................................................................15
Figure 3. Detail of automated chamber setup...............................................................17
Figure 4. Matlab analysis window showing nonlinear curve fit......................................19
Figure 5. 2011 Autochamber soil CO$_2$ efflux..............................................................25
Figure 6. 2011 Autochamber soil CO$_2$ efflux..............................................................26
Figure 7. 2011 Manual LI6400 soil CO$_2$ efflux............................................................27
Figure 8. Semivariogram depicting spatial soil CO$_2$ efflux variability...........................28
Figure 9. Nighttime AF autochamber soil CO$_2$ efflux and nighttime AF NEE..................30
Figure 10. Measured and modeled C fluxes at Ameriflux.............................................31
Figure 11. Soil 15 cm temperature in degrees C.........................................................32
Figure 12. Soil 15 cm volumetric water content.........................................................33
Figure 13. Gravimetric Leaf Moisture Percentage.........................................................34
Figure 14. Dry leaf mass measured from each chamber at each site...............................34
Figure 15. AAS soil CO$_2$ efflux versus soil temperature at 15 cm...............................35
Figure 16. Residuals when using Soil Temperature to predict Soil CO$_2$ Efflux at AAS.......36
Figure 17. Soil CO$_2$ efflux residuals from Q$_{10}$ analysis plotted against Soil Moisture at 15 cm.....37
Figure 18. 2011 LAI data showing leaf-on and full leaf-out...........................................38
Figure 19. Phenoperiod 1 AAS Soil CO$_2$ Efflux Q$_{10}$..................................................39
Figure 20. Phenoperiod 2 AAS Soil CO$_2$ Efflux Q$_{10}$..................................................39
Figure 21. Continuous wavelet transforms....................................................................42
Figure 22. Cross wavelet transforms of pairs of AAS biophysical variables.....................45
Figure 23. Cross wavelet transform of FAS soil CO$_2$ efflux and 15 cm soil temperature....46
Figure 24. Cross wavelet transform of FAS soil CO$_2$ efflux and 15 cm soil moisture........47
Figure 25. Cross wavelet transform of FOS soil CO$_2$ efflux and 15 cm soil moisture........48
Figure 26. Cross wavelet transform of AOS soil CO$_2$ efflux and 15 cm soil moisture........48
Figure 27. Soil CO$_2$ efflux differences AAS-FAS............................................................51
Figure 28. AAS looking North.................................................................71
Figure 29. FAS looking North.................................................................72
Figure 30. FOS looking Northeast, Autochamber #1.................................73
Figure 31. FOS looking South, Autochamber #2..........................................73
Figure 32. AOS – Continuous Wavelet Transforms.........................................75
Figure 33. FAS – Continuous Wavelet Transforms.........................................76
Figure 34. FOS – Continuous Wavelet Transforms.........................................77
Figure 35. AOS – Cross Wavelet Transforms..............................................78
Figure 36. FAS – Cross Wavelet Transforms..............................................79
Figure 37. FOS – Cross Wavelet Transforms..............................................80
Figure 38. FOS Temperature-efflux correlation and residual-SWC correlation..................81
Figure 39. FAS Temperature-efflux correlation and residual-SWC correlation..................82
Figure 40. AOS Temperature-efflux correlation and residual-SWC correlation..................83
Figure 41. FAS PP1 temperature-efflux correlation and PP2 temperature-efflux correlation........84
Figure 42. AOS PP1 temperature-efflux correlation and PP2 temperature-efflux correlation........85
Figure 43. FOS PP1 temperature-efflux correlation and PP2 temperature-efflux correlation........86
Figure 44. FASET nighttime NEE versus autochamber measured Rs................87
Figure 45. Gap-filled Re nighttime data versus autochamber measured Rs...............88
Figure 46. C fluxes at FASET. NEE and GPP - comparison with respiratory effluxes........89
Figure 47. AAS Volumetric SWC versus Soil Matrix Potential..........................90
Figure 48. Data from all working SWC sensors at AOS.................................91
Figure 49. Data from all working SWC sensors at FOS.................................91
Figure 50. Data from all working SWC sensors at AAS.................................92
Figure 51. All data from working SWC sensors at FAS.................................92
List of Abbreviations and Nomenclature

C=Carbon
CO₂=Carbon Dioxide
[CO₂]= Carbon Dioxide Concentration
Dₐ = CO₂ Diffusion Coefficient in the free air
Dₛ = CO₂ Diffusion Coefficient in the soil
DOY=Day of Year
GPP=Gross Primary Production
IRGA= Infrared Gas Analyzer
LAI= Leaf Area Index
LI-6400-09= LiCor 6400 with soil respiration cuvette
N= Nitrogen
NEE= Net Ecosystem Exchange
NPP= Net Primary Productivity
PAR= Photosynthetically Active Radiation
Rₐ= Autotrophic Soil Respiration
Rₑ= Ecosystem Respiration
Rₕ= Heterotrophic Soil Respiration
Rₛ= Soil Respiration
SWC= Soil Water content (% vol. water/vol. soil)
SOM= Soil Organic Matter
Tₛ = Soil Temperature (°C)
UMBS= University of Michigan Biological Station
Q₁₀ = Temperature Sensitivity of Soil Respiration
QAQC= Quality Assurance and Quality Control
ξ= Gas Tortuosity Factor
Introduction

Background

Carbon (C) sequestration is an emergent property of ecosystems, calculated as ecosystem Gross Primary Production (GPP) minus Ecosystem Respiration ($R_e$). Therefore, Net Ecosystem Production (NEP) is the balance of C fixed in photosynthesis minus C released through respiration. Belowground respiration accounts for a majority of ecosystem respiration and adds approximately 10 times more carbon to the atmosphere than anthropogenic emissions (Schimel, 1995). Whether respiration or photosynthesis is more variable, and hence more important in explaining regional and global NEP, is a matter of debate (Valentini et al., 2000; Luyssaert et al., 2007; Desai et al., 2008).

Forest Carbon Cycle

Forest ecosystems account for a majority of terrestrial carbon fixation and $R_e$ consumes 77-85% of GPP (Luyssaert et al., 2007; Hanson et al., 2000). In forests, trees are the primary producers and through photosynthesis they fix C from the atmosphere to form energy-rich carbohydrates. These labile C compounds can be respired for the leaves’ energy use or transported through the phloem to the roots. Roots use C for their own maintenance respiration and new growth. As roots and root hairs grow, they slough off root sheathes, exude sugar, and trade carbohydrates with their mycorrhizal fungal symbionts in exchange for nitrogen, phosphorous, and other nutrients (Luo & Zhou, 2006). Heterotrophic decomposing organisms break down discarded C compounds as well as stored carbohydrates in dead roots, fungi, and other microorganisms; this C from belowground litter, as well as C from aboveground leaf litter, is returned to the atmosphere as respired CO$_2$. A small fraction of the total GPP is retained year-to-year as NEP in living biomass, mainly as tree stems (Curtis et al., 2005). A smaller fraction is retained as recalcitrant additions to total soil organic matter (SOM), which increases as an ecosystem ages (Gaudinski et al., 2000). The residence time of carbon in SOM can be years to centuries, depending on the physical and chemical protection of SOM, as well as temperature and moisture constraints on decomposition (Belay-Tedla et al., 2009).
respiration is primarily dependent on the amount and quality of soil C inputs, temperature, and moisture (Ryan & Law, 2005). CO₂ respiration in soil layers diffuses through soil micropores and macropores to the soil surface, where it leaves the soil system as soil CO₂ efflux (Luo & Zhou, 2006). In this document, the terms soil respiration (Rₛ) and soil CO₂ efflux will be used interchangeably.

**Forest Carbon Storage Prospects**

Forests are increasingly stressed by an array of anthropogenic and natural disturbances. Temperate forests in the northern hemisphere have been a net sink of carbon in recent years as a result of regrowth from historical disturbance (Caspersen et al., 2000) and growth enhancement from increased atmospheric [CO₂]. This developing carbon sink is threatened by increasing tree mortality and succession (van Mantgem et al., 2009). While widespread tree mortality alone would tend to decrease stored aboveground C, roughly half of a forest’s C is stored below-ground (Curtis et al., 2005). Depending on the rate of respiration of belowground C, these forests could be either net C sinks or sources.

**Disturbances:**

*Climate Change*

Global climate change can affect forest C cycle processes in a number of ways. First, elevated levels of CO₂ could increase photosynthetic efficiency, leading to increased GPP (Boisvenue & Running 2006). This “growth enhancement” of extra C would be assimilated throughout the above- and belowground portions of the ecosystem (Curtis & Wang, 1998). Alternately, increased temperatures could enhance the rate of microbial decomposition, decreasing soil C stores. Autotrophic respiration could also be increased if trees were stressed from a combination of increased temperature and decreased moisture (Bond-Lamberty & Thomson, 2010). The net effect of anthropogenic climate change on ecosystem carbon balance is yet to be determined.

*Aerosol Pollution*

Humans affect ecosystems in more ways than changing atmospheric [CO₂]; for example, humans are now the largest source of fixed nitrogen to planetary ecosystems, particularly in close proximity to industrial and urban centers. GPP can decrease when aerosol pollution directly injures plants or blocks photosynthetically active radiation (PAR), a primary determinant of GPP. Some research has shown that nitrogen deposition can indirectly decrease Rₛ (Olsson et al., 2005); this is explained through the Tradeoff Hypothesis, which predicts that plants will
"trade" less carbohydrate to their mycorrhizal symbionts when N is readily available (McGuire et al., 1995).

**Succession**

Regrowing temperate forests experience natural succession when pioneer species, which grow rapidly but have short lifespans, give way to slower growing, longer lived species. Urbanski et al. (2007) detail a case where succession appears to increase C storage due to increased GPP, despite simultaneously increasing R. The impact of this change in community structure will undoubtedly affect ecosystem C storage, but the ultimate results are unknown (Gough et al., 2007; Desai et al., 2008).

**Invasive species**

Invasive species can radically alter the biogeochemistry of terrestrial ecosystems, especially when working in combination with climate change (Peltzer et al., 2010). While much work has been done on invasive species in general, not as much research has focused on species that impact the linkage of GPP with R. Wood-boring insects chew cavities through the phloem of trees in their search for carbohydrates (Morehouse et al., 2008); their activity can terminate the flow of recent photosynthate (carbohydrates) from the leaves to the roots, resulting in root starvation followed by tree senescence and concomitant decrease in GPP. Although the ultimate cause of natural forest disturbances may be tree physiological stress induced by succession, climate change, or aerosol pollution, the proximal cause is often tree girdling by insects (McDowell et al., 2008).

**Experimental Manipulations of Forest Soils**

Soil is extremely complex and variable in spatial and temporal dimensions and includes a large diversity of very small organisms (Bradford & Ryan, 2008). Soil is also opaque and can only be accessed by techniques that disturb the intertwined networks of roots, fungal hyphae, and soil pores. There are a number of different approaches employed to examine soil structure and function, and each approach has its own advantages and disadvantages (Hanson et al., 2000; Kuzyakov, 2006). It is possible to directly investigate soil through excavation, but this inevitably destroys the system under investigation. However, excavation can yield information after the completion of an experimental treatment. Measurements of root biomass, soil organic carbon, dissolved organic carbon, and microbial biomass are usually obtained destructively.

Researchers have developed a number of techniques for investigating belowground respiration without disturbing the soil environment (Luo & Zhou, 2006). For example,
techniques to investigate the subsurface environment can rely on manipulations of surface processes. Manipulations of surface processes include addition or removal of litter, trenching to exclude roots, as well as girdling. A large body of literature has examined the impact on soil processes after clearing vegetation through clipping vegetation or logging trees (Bormann & Likens, 1994). However, these approaches alter the microenvironment of the soil, disturbing litter and mineral horizons to a greater or lesser degree, increasing exposure to wind and sunlight, and concomitantly altering temperature and moisture characteristics (Kuzyakov, 2006).

Any of the above techniques can be used as an experimental manipulation solo or in combination with other techniques, but the artificial nature of many of them raises doubts about how informative they can be for understanding natural, undisturbed soil processes. Tree girdling stands out as an experimental manipulation with ecological homology; many forests naturally experience girdling from wood-boring insects. In addition, girdling has been practiced as a forest management technique for hundreds of years (Noel 1970). Girdling a tree involves cutting phloem while leaving xylem intact. Since phloem carries sugars from the leaves to the roots, it is this tissue that is often preferentially consumed and severed by wood-boring insects. Insect pests, including the invasive emerald ash borer as well as native pine bark beetles, girdle trees (van Mantgem et al., 2009). However, few studies have investigated the biogeochemical impacts of wood-boring insect outbreaks.

Studies that use experimental girdling to investigate soil respiration can help elucidate impacts from wood-boring pests as well as help disentangle the various drivers of $R_s$. For example, scientists have conducted experimental girdling to measure the ratio of autotrophic to heterotrophic respiration (Hogberg et al., 2001; Luo & Zhou, 2006). Girdling is different from wind-throw, fire, logging, and other disturbances because much of the structure of the forest remains intact, at least at first. The intact xylem tissue allows many trees to continue to produce leaves for two or more years post-girdling (Johnson & Edwards, 1979). The continued production of leaves, and their transpiration of water, minimizes alterations to soil physical properties (light, temperature, moisture) during the experiment (Luo and Zhou 2006). However, many girdling studies do eventually find large increases in the amount of light and soil moisture as tree canopies thin and die (Bhupinderpal-Singh et al., 2003).

**Methods for Measuring Soil CO$_2$ Efflux**

There are a number of methods for measuring soil respiration, and each has its advantages and disadvantages. Measurement can be accomplished using either open or closed
systems, where open systems do not obstruct the natural efflux of CO$_2$, while closed systems temporarily capture soil CO$_2$ within a chamber. Systems can also be classified as manual or automatic, depending upon whether they require human presence to operate.

*Open Systems*

Open systems include open-topped aboveground chambers with a single aboveground sensor as well as gradients of multiple CO$_2$ sensors buried in the soil. CO$_2$ sensor gradients can be sampled manually by withdrawing gas samples, but more commonly they consist of automatic solid-state CO$_2$ sensors such as the Carbocap sold by Vaisala. Each sensor is buried at a defined depth in the soil and automatically measures [CO$_2$] at short time intervals. The flux between depth layers is calculated using

$$F = -D_s \frac{dC}{dz},$$

Eqn. 1

where $D_s$ is the CO$_2$ diffusion coefficient in the soil, $C$ is the concentration of [CO$_2$], and $z$ is the vertical distance between sensors. $D_s$ is defined as

$$D_s = \xi D_a$$

Eqn. 2

where $\xi$ is the gas tortuosity factor of the soil, and $D_a$ is the CO$_2$ diffusion coefficient in the free air (Millington and Quirk, 1961). If [CO$_2$] at the surface and at depth is known, a soil CO$_2$ efflux can be calculated, but this derived efflux is extremely susceptible to the value of $\xi$ chosen, and this value can only be broadly estimated using soil texture tables (Millington and Quirk, 1961; Moldrup et al., 2011). Also, the installation and maintenance of buried soil CO$_2$ sensors necessarily entails soil disturbance which can create unnatural soil structure, production, and efflux of CO$_2$. Despite these limitations, the technique has been shown to correlate well with other $R_s$ measurement techniques and is now widely used (Tang et al., 2005; Baldocchi et al., 2006).
Open topped chambers measure the change in [CO$_2$] when air of a standardized initial CO$_2$ concentration is mixed with soil CO$_2$ efflux and resampled by an IRGA at the top of the chamber. The change in [CO$_2$] can be used to calculate the soil CO$_2$ flux using the equation

$$CO_2 = \frac{[V(C_{t1} - C_{t2})]}{A (t1 - t2)}$$

Eqn. 3

where $V$ is chamber volume, $C_i$ is the [CO$_2$] inside the chamber at time $t$, and $A$ is the area of the chamber (Widen & Lindroth, 2003). This open system does not disturb the soil environment as much as the multisensor approach described above, but it does disturb the near-soil atmospheric boundary layer. Blowing air across the soil surface can create pressure effects that tend to draw out soil air, creating unnaturally high soil CO$_2$ effluxes (Widen & Lindroth, 2003).

Closed Systems

Closed systems capture soil CO$_2$ efflux in a chamber, circulating air samples to an IRGA and then back to the chamber to measure the increasing [CO$_2$] in the chamber. Closed systems include the portable, manual LI-6400-09 IRGA (Li-Cor, Lincoln, NE, USA) as well as the custom-built automated (autochamber) system at UMBS. The return of sampled air to the closed chamber can result in uneven mixing of chamber air that disturbs the near-soil atmospheric boundary layer. Uneven mixing of chamber air can be dealt with using a small fan to mix the air within the chamber. Care must be taken to keep the speed of the fan as low as possible so it does not create pressure effects (LI-COR, 2002). However, opening and closing chamber lids, or the placement of the chamber on the soil surface, can also create pressure differentials that alter soil CO$_2$ efflux (Ryan & Law, 2005). Pressure effects can be reduced using a pressure equalization port, which consists of a piece of tubing from the inside to the outside of the chamber (Jassal et al., 2005). The tube is long and thin enough so that diffusion is minimal, but pressure changes can still be transmitted along its length.

Another problem with closed systems is the effect of increasing chamber [CO$_2$] on the rate of soil CO$_2$ efflux: as the partial pressure of CO$_2$ in the chamber approaches the soil CO$_2$ partial pressure, the rate of [CO$_2$] efflux decreases nonlinearly (Davidson et al., 2002). The LI-6400-09 avoids nonlinear efflux measurements by scrubbing the chamber [CO$_2$] to below-
ambient concentration and then measuring the increase of [CO$_2$] over a short span during which the measurements are presumably linear (LI-COR, 1998).

In the LI-6400-09, soil CO$_2$ flux is calculated from [CO$_2$] measurements with equation 4:

$$F_C = \frac{kPV}{S(T + 273)} \left( \frac{\partial C}{\partial t} + \frac{C}{1000 - W} \frac{\partial W}{\partial t} \right)$$

\text{Eqn. 4}

where $k =1.2028$, $P$ is the atmospheric pressure in kPa, $V$ is the volume of the chamber in cm$^3$, $S$ is the surface area covered by the chamber in cm$^2$, $T$ is the chamber temperature in °C, $C$ is the concentration of CO$_2$, $t$ is time, and $W$ is the water concentration of the chamber air in μmol water per mol air.

Manual closed systems have the advantage of being portable and can be used to sample extensively from a broad spatial area, but they can only sample one place at a time and are extremely time-consuming to operate. In addition, they can be very heavy and difficult to carry over uneven terrain.

Automated chambers have the advantage that they can be set up in large arrays to continuously monitor soil respiration over a local area. However, all autochambers typically share a single IRGA so the spatial distribution is limited by the length of tubing that can practically connect them. The longer the tubing, the longer it takes for air samples to move from the chamber to the IRGA and then back to the chamber. For this reason, tubing that is longer than 100 feet is generally not practical (LI-COR, 2011, personal communication). Sharing a central IRGA is accomplished by sequentially switching between the chambers in the array, so that each chamber is sampled once per cycle. However, this also creates a limitation on the number of chambers, length of sample period, and return frequency; with more chambers there must either be shorter sample periods, or each chamber must be sampled less frequently.

Automated chambers can accomplish continuous sampling during all hours of day and night and in inclement weather when manual sampling is not feasible. However, automated chambers must be maintained regularly to insure their proper functioning. The action of wind and rain can damage hinges and exposed instrumentation. Growing plants must be kept out of the way of chamber lids and intake tubing must be kept clear of insects. Additionally, the
constant opening and closing of chamber lids can itself generate soil disturbance and often
displaces either the chamber and/or the proper sealing of the lid on the chamber.

It is not practical to scrub CO$_2$ to ambient levels every time an automatic chamber closes
so other approaches are needed to deal with nonlinear effluxes. One approach involves closing
chambers for short periods of time in order to keep observed effluxes linear, but the length of
time during which linear effluxes can be assumed depends on soil texture and soil [CO$_2$]. This
linear assumption is used by a Licor autochamber system (LI-8100, Li-Cor, Lincoln, NE, USA)
which does not scrub chamber [CO$_2$] and therefore closes for a maximum of 5 minutes (LI-COR,
2008). Another approach simply takes the nonlinear efflux and fits a nonlinear function to the
data rather than a linear function. The several advantages of using this approach include a more
accurate curve fit to the chamber [CO$_2$] data, the derivation of a number of associated
parameters such as soil [CO$_2$] and soil conductance to gaseous diffusion, and the ability to
quality control data points based on the statistical features of these parameters.

*Data Processing*

Once data is collected it must be managed and processed. Automated systems
generate very large data sets with concomitant problems identifying gaps or bad data points
(Vargas et al., 2011). Dealing with very large datasets can be accomplished using data
manipulation software such as MATLAB, special data visualization programs such as Tableau,
and statistical techniques such as continuous wavelet coherence and cross wavelet
transformation (Vargas et al., 2011).

*Objectives and Hypotheses*

The objectives of this study were to quantify soil respiration (R$_s$) between different
forest canopy tree species (Aspen and Oak) and between disturbed (FASET) and undisturbed
(Ameriflux) forests. These conditions will be referred to as FASET Aspen Site (FAS), FASET Oak
Site (FOS), Ameriflux Aspen Site (AAS) and Ameriflux Oak Site (AOS).

Soil CO$_2$ efflux, based on the contributing ratio of autotrophic respiration (R$_a$) to
heterotrophic respiration (R$_h$), is expected to display a combination of altered temporal patterns
and responses to biophysical drivers. These data will document changing belowground
processes and lead to increased understanding of overall carbon cycle linkages in this forest
ecosystem.

$H1.a$ FAS $R_s$ < AAS $R_s$
FAS will have less $R_s$ than AAS because girdling blocks photosynthate transfer to roots: without recent photosynthate, aspen roots would be forced to rely on stored carbohydrates, potentially limiting new investments in fine roots, mycorrhizal symbionts, and root exudates. Roots will continue to contribute to $R_A$ until they use up their stored carbohydrates, at which point they will die. Dead roots can contribute to $R_H$, but recalcitrant structural compounds decay slowly and would contribute decreasing amounts to $R_s$.

\[ H1.b \ FOS \ R_s > AOS \ R_s \]

FOS would have greater $R_s$ than AOS because of increased photosynthesis: oak trees at FASET may be released from competitive inhibition when the surrounding aspen trees are girdled. Increased light would lead to increased photosynthesis which could supply more recent photosynthates to the soil environment, potentially increasing both $R_A$ and $R_H$.

\[ H2.a \ FAS \ SWC > AAS \ SWC \]

Decreased FAS Leaf Area Index (LAI) would allow greater throughfall precipitation to wet the soil surface while at the same time decreasing transpiration of soil moisture, compared to AAS.

\[ H2.b \ FOS \ SWC < AOS \ SWC \]

Increased FOS LAI would allow less throughfall precipitation to wet the soil surface, while at the same time increasing transpiration of soil moisture, compared to AOS.

\[ H3.a \ FAS \ soil \ temp > AAS \ soil \ temp \]

Decreased FAS LAI would allow more light to reach the forest floor, increasing soil temperatures.

\[ H3.b \ FOS \ soil \ temp < AOS \ soil \ temp \]

Increased FOS LAI would allow less light to reach the forest floor, decreasing soil temperatures.

\[ H4.a \ Growing \ Season \ FAS \ Q_{10} <AAS \ Q_{10} \]

FAS may have less autotrophic respiration (H1.a); $R_H$ is less responsive to temperature than $R_A$ (Boone et al. 1998). Therefore, FAS would show less temperature sensitivity, compared to AAS.

\[ H4.b \ Growing \ Season \ FOS \ Q_{10} >AOS \ Q_{10} \]

FOS has more autotrophic respiration (H1.b); $R_A$ is more responsive to temperature than $R_H$ (Boone et al. 1998). Therefore, FOS would show greater temperature sensitivity, compared to AOS.
H5 FAS $R_i$, lags SWC < AAS $R_i$, lags SWC

$R_{ii}$ lags SM at hours to days according to microbial activity whereas $R_A$ lags SM at days to weeks (Glinski & Stepniewski, 1985; Liu et al 2002). If FAS shows overall less $R_A$ and more $R_{ii}$, soil respiration would show decreased lags, compared to AAS.
Methods

Study Environment

This study was conducted at the University of Michigan Biological Station (UMBS) in northern lower Michigan at two sites (Ameriflux and FASET) approximately 1.5 km apart. Both sites are in a mixed hardwood and pine forest ecosystem that resulted from historical disturbance during the past 200 years (Gough et al., 2007a). Forests were logged and burned repeatedly up to 1923 (Kilburn, 1960). Over the last 85 years forests have developed naturally from an initial mix of early successional species to a mixture of early- and later-successional species. Early successional species such as *Populus grandidentata* Michx. (Bigtooth Aspen), *Populus tremuloides* Michx. (Trembling Aspen), and *Betula papyrifera* Marsh. (Paper Birch) dominate some patches in the forest, while in other patches later successional species attain canopy height such as *Fagus grandifolia* Ehrh. (American Beech), *Acer saccharum* Marsh. (Sugar Maple), *Acer rubrum* L. (Red Maple), *Pinus strobus* L. (White Pine) and *Quercus rubra* (Red Oak) (Bovard et al., 2005). With secondary succession, early successional species are expected to begin senescing while canopy gaps are filled by later successional species. The understory is comprised of tree seedlings from the later successional species as well as a large amount of *Pteridium aquilinum* L. (Bracken Fern). Soils are acidic (pH =4.8) excessively drained sandy Entic Haplorthods (92% sand, 7% silt and 1% clay) (Curtis et al., 2005). Thick litter layers develop overlying a 5cm A horizon with very high organic matter content and very high fine root content. The E horizon is variably thick with no well-defined lower boundary, possibly as a result of the disturbance history (Hall, 1986). The mean annual rainfall is 817 mm and the average annual temperature is 5.5 °C (Curtis et al., 2005).

In 2008, total C and soil bulk density was measured from oven-dried, 2mm-sieved soils on the UMBS Costech Analytical CHN at UMBS, using the technique of combustion gas chromatography and thermal conductivity detection (TCD) (Unpublished data from Luke Nave). Those data are shown in Table 1.
Control and Treatment Site: Ameriflux and FASET

UMBS is the location of a long-term carbon-cycle research project known as Ameriflux (AF). The AF project consists of a national network of ecological sites that use meteorological towers and the eddy covariance technique to measure NEE and other biophysical parameters. The AF tower at UMBS has been active since 1998 (Schmid et al., 2000; Gough et al., 2007b; Gough et al., 2008). In 2007 UMBS added a second tower to measure NEE over a nearby forest stand known as the Forest Accelerated Succession Ecosystem Experiment (FASET) (Nave et al., 2011). Accelerated succession is accomplished through girdling all early successional tree species, which in this forest comprised 39% of the pre-girdling basal area. In the spring of 2008 professional sawyers, graduate students, and staff of UMBS girdled more than 7000 early successional tree species on 33 hectares surrounding the FASET tower. Girdling involves cutting and removing a band of bark and phloem, but not xylem, from the base of trees. Anthropogenic girdling is physiologically equivalent to the way bark beetles and other phloem-feeding insects naturally kill trees. Girdling effectively stops all transport of photosynthate from the tree canopy through the phloem to the roots, while leaving intact the hydraulic connections that carry water and dissolved nutrients from the tree roots through the xylem to the canopy (Noel, 1970).

During the leaf-on period of the 2011 growing season, a 75% girdling mortality rate was measured at FASET (Peter Curtis, unpublished data). There is 100% aspen mortality at the location of the automated soil respiration chambers in FASET. These trees were felled on August 17, 2009 to prevent damage to scientific instruments such as the flux tower and the automated soil respiration chambers.

Table 1. Soil Carbon Content at AF and FASET. Note incomplete replication of data.

<table>
<thead>
<tr>
<th>Horizon/ Depth</th>
<th># of samples</th>
<th>%C</th>
<th>Bulk density AF 60m</th>
<th>Bulk density FAS 60m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oi</td>
<td>0</td>
<td>43.1</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0</td>
<td>12.3</td>
<td>0.59</td>
<td></td>
</tr>
<tr>
<td>5-15cm</td>
<td>21</td>
<td>1.3</td>
<td>1.16</td>
<td>1.19</td>
</tr>
<tr>
<td>15-25cm</td>
<td>20</td>
<td>0.6</td>
<td>0.7</td>
<td>1.41</td>
</tr>
<tr>
<td>25-45cm</td>
<td>2</td>
<td>0.5</td>
<td>0.7</td>
<td>1.14</td>
</tr>
</tbody>
</table>
Soil temperature and moisture were measured at a total of four soil pits, two at FASET and two at AF (Figure 1). At each site the pits are about 20 meters apart, one under an oak-dominated canopy and the other under an aspen-dominated canopy. The pits are named corresponding to the site and canopy tree species: AF Oak Site (AOS), AF Aspen Site (AAS), FASET Oak Site (FOS), and FASET Aspen Site (FAS). The pits were installed in the spring of 2009. Each soil pit is 3 meters deep, with continuously operating soil moisture and temperature sensors.
(SDI-12 Stevens Hydra probes, Stevens Water Monitoring Systems, Inc) installed into the undisturbed side of the pit at 5, 15, 30, 60, 100, 200, and 300 cm. There are replicate sensors at 5, 15, 30, and 60 cm. Temperature and moisture data have been collected continuously since the installation of the soil pits in 2009. However, at any given time many of the installed sensors may be malfunctioning, so only a subset of the total data is available for analysis. Upon visual inspection of the data from the 2011 growing season, the auxiliary 15 cm soil temperature and moisture sensors appear to have the most consistent recordings, and these data sets were utilized for all further analyses. Systematic errors in the sensors are corrected by calibration with manually collected soil temperature and moisture data (Stangl et al., 2009). Manual soil data is collected monthly using a MiniTrace Kit (Soil Moisture Equipment Corp.) at the 0-40cm depth. Calibration indicates a small systematic error of approximately 3% in the original sensor data (He et al., 2012). Soil moisture data were smoothed with a moving averaging window (± 5 hours) to eliminate random errors.

**Litter Moisture**

Automated soil temperature and moisture sensors in the soil pits collected data from 5 to 300 cm, but did not measure biophysical variables at or above the soil surface, especially in the highly variable leaf litter layer. The amount of leaf litter in a soil respiration chamber may influence measured soil respiration by serving as a source of respiration, by providing nutrient inputs to the soil environment, by retaining rainfall and dew moisture, and by insulating the soil beneath it. To investigate the contribution of leaves to these processes, leaf litter total dry mass and percent moisture (gravimetric) were sampled at the end of the season. In each soil respiration chamber, all of the loose litter material at the soil surface was removed, bagged, and analyzed. Interestingly, removal of the entire leaf litter layer on DOY 235 had no observable effect on soil respiration, even though this sampling significantly disturbed the upper soil horizons (data not shown). This observation may indicate that the loose litter layer was no longer the source of active respiration at such a late point in the season.
Automated Chambers

Two automatic closing chambers were installed in the spring of 2011 for measuring soil CO$_2$ effluxes at each soil pit. The chambers are positioned on either side of the pit to take advantage of the deep profile soil temperature and moisture sensors, without impacting or being impacted by the soil disturbance associated with the soil pits (Figure 2).

**Figure 2.** Autochambers in relation to soil pit. Yellow line denotes boundary of soil pit instrumentation. The first autochamber located at upper right corner, second located at lower right corner. The second autochamber is closed and sampling soil CO$_2$ efflux. This is AOS, for images of the other sites, see Appendix B.
Each chamber consists of an aluminum frame with attached lid, a plexiglass chamber, and pneumatic tubing. The aluminum frame is rectangular, with four short legs that extend into the ground for stability. The frame is further stabilized with two rebar rods pounded approximately one meter into the ground and tied to the frame with steel hose clamps. A pneumatic actuator on the frame opens and closes the lid. The lid is composed of two separate pieces; one is mounted to the actuator while the other is lined with padding to form a seal on the top of chamber. The two lid pieces are connected by springs so the padded chamber lid seals flexibly with the chamber. The chamber lid contains a port for the chamber air sample tubing; the port is protected from the weather by a 3 cm plastic cone. Each chamber is a clear plexiglass cylinder with radius 14.75 cm and height 30 cm. The chambers were pounded with a sledge hammer and block 10cm into the soil so that 20 cm remains exposed above the surface to form the chamber headspace. Therefore, because the surface area of the chamber is 0.068 m², the headspace volume is 0.0144 m³. The chamber is also outfitted with a side port, through which return air tubing and electrical wire were run. The wire provides power for a small 2.5 x 2.5 cm circulating fan that gently mixes the sample airspace while sampling occurs. The fan is mounted in a protective steel shroud near the port, about 6 cm from top of chamber (14 cm from soil surface). The fan wire runs loosely through a larger 20 cm piece of tubing which extends from the inside to the outside of the chamber. This tubing allows pressure equalization, without mass movement, of air between the inside and outside of the chamber (Figure 3).
Figure 3. Detail of automated chamber setup. (Left) Lid closes and seals on chamber when pressure is applied to the pneumatic actuator. The aluminum frame was stabilized with rebar to prevent movement which could reduce the chamber seal. (Right) The closed system utilized a fan to lightly mix the air within the chamber headspace while the sample was being taken. Samples were collected from the black tube near the top center of the chamber, and analyzed air was returned via the perforated manifold at the base of the chamber. (images from Nietz, 2010)

Control Box

At each site (AF and FASET), a single control box operated each of the four chambers in turn: activating the pneumatic actuators, pulling air from the sample port, and returning air to each chamber. To operate the pneumatic actuators a manifold in the control box opened and closed a valve connected to a tank of compressed air. The compressed air was automatically maintained at 80-100 PSI by an air compressor. The manifold was controlled by a data logger (CR23X, Cambell Scientific, Inc, Logan, UT, USA). Solenoid valves, also activated by the data logger, opened and closed to pull and return sample air. A second pump pulled chamber air through the solenoid valves. This air was directed to an IRGA (LI-6252 Li-Cor, Lincoln, NE, USA) for sampling [CO₂] every two seconds. The air compressor, data logger, manifold, and solenoid valves were stored in plastic tubs for protection from rain. At the AF site, an IRGA was also housed in the control box, while at the FASET site the IRGA was housed in a permanent shed with other equipment.

Data Collection

The [CO₂] data were recorded beginning 1 minute before the lid closed to flush any remaining air and establish a baseline of ambient [CO₂] in the chamber. After the lid closed, data were collected for 14 minutes at each chamber to measure increasing [CO₂]. Because the
chamber is closed, and in order to maintain pressure, sampled air is returned to the chamber (through the port in the side of the chamber) as it is being withdrawn. Because there are four chambers at each site, each chamber was sampled exactly once per hour.

**Data Processing**

Initial data processing occurred using MATLAB (Mathworks, version R2011a; see Appendix A). Because the chamber lid closing causes pressure fluctuations and turbulence, most of the data from the first two minutes are too erratic to use for the curve fit and is thrown out by the MATLAB program. Initial \([\text{CO}_2] (C_c)\) is estimated from the lowest 20 second running average \([\text{CO}_2]\) found during the second two minutes of sampling after the chamber lid closes. The MATLAB program fits a non-linear curve to the \([\text{CO}_2]\) data (Figure 4):

\[
C_c(t) = C_s - (C_s - C_0) \cdot e^{-(k \cdot t)}
\]

**Eqn. 5**

Where \(C_c\) is the concentration of \(\text{CO}_2\) in ppm at time \(t\), \(C_s\) is the soil \([\text{CO}_2]\) (ppm), \(C_0\) is the \([\text{CO}_2]\) (ppm) at time \(t=0\), and \(k\) is given by

\[
k = \frac{S + g_s}{\rho V}
\]

**Eqn. 6**

Where \(S\) is the chamber surface area (0.068 m\(^2\)), \(g_s\) is the soil conductance to \(\text{CO}_2\) (mol/mol), \(\rho\) is the molar density of air (41.6 mol/m\(^3\)), and \(V\) is the chamber volume (0.0144 m\(^3\)). The program fits Eqn 5 to the \(C_0\), \(t\), and \(C_c\) data and outputs values of \(C_0\), \(C_s\), \(k\), for each chamber closing. The program also outputs records of the curvefit \(r^2\), sum of squares for error (SSE) and Durban-Watson (DW) statistic. Durban-Watson statistics are used to measure bias when data do not fit the expected nonlinear function (Eqn 5). Output files are transferred to Excel (Microsoft Office 2010) and the \(C_0\), \(C_s\), and \(k\) values are then used to calculate the diffusional flux of soil \(\text{CO}_2 (D_c)\) at the soil surface using

\[
D_c = (C_s - C_0) \cdot g_s
\]

**Eqn. 7**
Substituting equation 6 for \( g \), Eqn.7 can be re-written as:

\[
D_c = (C_s - C_o) \cdot \left[ \left( \frac{\rho V}{5} \right) \cdot k \right]
\]

Eqn. 8

Figure 4. Matlab analysis window showing nonlinear curve fit (Eqn. 5) to raw [CO\(_2\)] data for a single autochamber closing interval.

**Quality Control**

Data are sorted in Excel by \( r^2 \), SSE, DW, \( C_o \), and \( C_s \). By adjusting parameter values in the MATLAB curvefitting program, it was possible to achieve extremely good fits to the observed data so that even small discrepancies in the above statistical tests indicated errors in data collection. For example, automated chambers may fail to close completely, in which case the observed [CO\(_2\)] does not conform to the expected nonlinear function (Eqn 5). Values of \( r^2 \) lower than 0.98 and values of SSE greater than 10,000 were marked as suspect. Upon inspection of many MATLAB analysis windows, these quality control cutoffs reliably flagged erroneous data. However, some chamber closings with good \( r^2 \) and SSE values had obviously erroneous observed
[CO₂], necessitating the use of a Durban-Watson (DW) statistic for further quality control. DW statistics are used to measure error when the residuals of a curve fit are autocorrelated. Through trial-and-error, DW values lower than 0.2 were found to indicate erroneous data collection. As a further test for the validity of the curve fits, values of Cₒ less than 350 and greater than 900 were flagged because these values do not naturally occur in this forest. Also, Cₛ values less than 530 and greater than 10,000 were flagged as outliers. Values of Cₛ less than 530 do not occur in this system; values greater than 10,000 are possible, but in the case of the data collected here indicate unconstrained curve fits which would yield biased estimates of Rₛ because the corresponding values of k are less than 0.0001. These very high Cₛ and very low k values cannot be measured accurately with the existing autochamber setup. Less than 5% of curve fits were flagged for exceeding a Cₛ of 10,000 or falling below a k of 0.0001. Most k values are close to 0.001, which fits published estimates of gas diffusivity in soil (Millington & Quirk, 1960).

Each site has two autochambers, and each chamber closes for 15 minutes every hour; therefore there are two independent site measurement of Rₛ each hour. If both measurements were unflagged by quality control, they were averaged to yield hourly site Rₛ data. These hourly site-averaged data were graphed in Excel or Tableau and used in all further analyses. The finished dataset of automated soil efflux measurements spans a little over one hundred days from the start of the growing season in early May (DOY 129) to the end of August (DOY 235).

**LI-6400-09 Measurements**

The LI-6400-09 portable soil respiration chamber was used to manually quantify Rₛ. Measurements were taken biweekly along a number of long-term transects radiating from the center of FASET and AF at spatially dispersed 10 cm radius PVC collars. The collars are installed 2.5-5 cm into soil so that approximately 1-3 cm of collar is visible above the soil surface. Most collars are reinstalled each growing season, but at time of measurement, care is taken not to disturb the collars. Any leaves that overlap the collars are cut to allow the LI-6400-09 chamber to form a good seal with the collar.

Protocols are according to the LI-6400-09 manual (LI-COR, 2004). Ambient [CO₂] is determined by placing the unit near the soil surface to sample the atmospheric boundary layer approximately 5 cm above the soil. Then the LI-6400-09 chamber is gently placed on the PVC collar and the sampling program started. The sampling program scrubs the [CO₂] in the chamber to 10 PPM below ambient and then measures the increase of [CO₂] in the chamber
until it is 10 PPM above ambient. The program repeats this process a total of three times. Each
time it outputs a linear fit to the observed CO₂ efflux, and after three cycles it outputs an
averaged $R_s$. Manual LI-6400-09 data are reported as biweekly averages of all collars at AF or
FASET.

**NEE**

Two flux towers, one at Ameriflux and one at FASET, measure carbon Net Ecosystem
Exchange (NEE). The sensors located at 34m and 32m on the Ameriflux and FASET towers,
respectively, exhibited a 1:1 NEE relationship prior to girdling. When windspeed is above 0.35 m
s⁻¹, as measured by a 3-dimensional sonic anemometer, CO₂ concentrations, as measured by a
closed-path IRGA, are inferred to NEE using the eddy covariance technique (Schmid et al., 2003).
Measurements are collected at 10 Hz and then compiled into half-hour averages (Nave et al.,
2011). NEE is equal to $R_s$ during the dormant season and at night, when GPP is assumed to be 0.
When dormant-season or nighttime windspeed is too low to yield reliable estimates of NEE, or
when sensors malfunction, site-specific empirical relationships of $R_s$ to soil temperature and
moisture are used to gap fill $R_s$ (Curtis, et al., 2005). During the growing season, the same
formulas are used to extrapolate $R_s$ during the day. GPP is then inferred as the difference
between daytime NEE and $R_s$. When daytime windspeed is too low to yield reliable estimates of
NEE, or when sensors malfunction, GPP is gap filled with the mean of 100 neural network
simulations (Nave et al., 2011). The flux towers integrate NEE over a large area, usually tens to
hundreds of hectares, so it is possible for the FASET tower measured fluxes to originate outside
of the FASET girdling treatment. However, for the purposes of my analysis, I did not correct the
FASET flux data for probability that fluxes originated within the FASET footprint (Nave et al.,
2011).

**$Q_{10}$ Analysis**

Soil respiration is expected to respond exponentially to increased soil temperature as
long as soil moisture is not limiting (Davidson et al., 2006; Ruehr & Buchman, 2010). To
understand the relationship between soil biophysical factors and soil CO₂ efflux, $R_s$ and soil
temperature data were plotted in Excel and fit using the van ‘t Hoff exponential function:

$$R_s = Ae^{BT} \qquad \text{(where } Q_{10} = e^{Bx_{10}})$$

Eqn. 9
where T is temperature and A and B are fitted parameters. The van ‘t Hoff function is the most commonly used empirical temperature dependency function in soil respiration research, although other functions such as the Arrhenius and the Lloyd and Taylor are also used in special circumstances, such as to extend $Q_{10}$ relationships to very high or low temperatures (Davidson et al., 2006).

**Wavelet Analysis**

Large datasets from automated measurements require specialized statistical techniques (Savage et al., 2008) to tease out correlations. Time series data are traditionally analyzed using cross correlation, which measures the similarity of two time series at various time lags. However, when datasets are nonstationary (i.e. changing means) cross correlation is not warranted without subtracting trends from the data. Furthermore, cross correlation can only measure correlations between time series for one time lag at a time, but biophysical factors such as soil temperature, soil moisture, and GPP may regulate soil respiration at a range of time scales, with effects delayed from hours to weeks to seasons (Vargas et al., 2010). Identifying periodicities in these data sets may allow identification of changing drivers of soil respiration. A technique to identify periodic patterns must be able to distinguish inconsistent correlations; different factors may alternate in driving soil respiration so that no single factor has explanatory power over the entire growing season. One technique which allows the computation of time-varying correlation is the short time Fourier transform (STFT). STFT views a given dataset through a small moving window and computes the power spectrum separately within each window, thereby producing a visualization of any periodicities in a time-frequency plane. But, to achieve a higher temporal resolution the segment length must be reduced, engendering a corresponding decrease in frequency resolution (Torrence & Compo, 1998).

An alternate approach is to convolve the signal with a series of wavelet functions. This continuous wavelet transform is defined as

$$\tilde{\psi}(\eta) = \sqrt{\frac{\delta t}{s \sqrt{\pi}}} \exp(i \omega s \eta) \exp\left(-\frac{\eta^2}{2}\right)$$

**Eqn. 10**
where $\psi(\eta)$ is the mother wavelet function. A commonly used choice of mother wavelet is a sine wave bounded by a Gaussian envelope; the “Morlet” wavelet:

$$\tilde{W}_i(s) = \sum_{t=-\infty}^{\infty} x_i \psi^* \left[ \frac{(t'-t)\delta t}{s} \right]$$

Eqn. 11

The power of the signal is then given as a function of time and scaled by the amplitude of the wavelet transform (Grinstead et al., 2004). The advantage of this approach is that the segment/window width is chosen optimally at each frequency, rather than using a fixed window as in STFT. Wavelet analysis, as this technique is known, has been widely used in the last 15 years to study a variety of meteorological and biophysical systems (Torrence and Comp 1998; Vargas et al., 2010). Wavelet analysis can be interpreted as a spectral map illustrating the changing nature of periodicities in a single dataset through time. Cross wavelet analysis results when wavelet analysis is used to visualize the temporal correlation between two different datasets. Wavelet analyses were conducted using Matlab Wavelet Coherence Analysis package WTC-R16 (Grinsted, Moore, Jevrejeva, 2008).
Results

Soil CO$_2$ Efflux

Autochamber-measured efflux

Each of the four sites showed different daily and seasonal trends in soil CO$_2$ efflux over the 106 day period of observation, from DOY 129-235 (Figure 5). At all chambers, respiration gradually increased from initial lower values between 1 and 4 μmol CO$_2$ m$^{-2}$ s$^{-1}$ to consistent values above 4 μmol CO$_2$ m$^{-2}$ s$^{-1}$ by mid-summer (~DOY 185). Efflux increased to peaks between 7 and 9 μmol CO$_2$ m$^{-2}$ s$^{-1}$ at the height of summer before beginning a slow decline toward the end of the measurement period. Superimposed on these seasonal trends were weekly oscillations (5-10 days) that became more pronounced toward the end of the season.

The FOS and AOS measurements were indistinguishable throughout the measurement time period, indicating that $R_s$ does not differ markedly between oak stands in AF and oak stands in FASET. In contrast, the FAS and AAS diverged widely, and in differing directions, in the beginning and at the end of the season. In the beginning of the growing season, FAS consistently showed higher peaks in soil respiration activity compared to AAS, but then around DOY 165 AAS began showing extremely high peak soil CO$_2$ efflux (up to 9.5 μmol CO$_2$ m$^{-2}$ s$^{-1}$). These high effluxes seemed anomalous at first, but AAS continued to show high effluxes through the end of the season. In contrast, effluxes at FAS began to taper off around DOY 205, consistently showing lower respiration than the other 3 sites (Figure 6).
Figure 5. 2011 hourly autochamber soil CO$_2$ efflux ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) from DOY 129-235. Points are the hourly quality-controlled mean (n=2) at the four soil pits.
Figure 6. 2011 Autochamber soil CO$_2$ efflux, smoothed 24-hour mean from DOY 130-236. Gaps in data indicate malfunctions in the autochamber array and/or suspicious measurements flagged by quality control. DOY=Day of Year.

$R_s$, measured by LI-6400-09

Soil CO$_2$ measurements taken by arrays of automated chambers suffer from a number of limitations, the most important of which is their limited spatial extent. Because autochambers must be tethered to a central control box and IRGA, the spatial extent of their measurements is limited to less than one hectare. Furthermore, because it is impractical to relocate, recalibrate, and re-equilibrate the autochambers, they remain fixed throughout the growing season so their true spatial coverage is only a small sample of the array’s entire spatial extent. Because soil respiration is spatially variable, it is important to check the data from autochambers with other sources of data, such as the portable LI-6400-09.

Portable measurements of soil respiration across the extent of the AF and FASET forests showed an overall similar trend compared to the autochambers, from low (~3 μmol CO$_2$ m$^{-2}$ s$^{-1}$)
effluxes at the beginning of the season to higher effluxes (5-8 μmol CO$_2$ m$^{-2}$ s$^{-1}$) later in the season (Figure 7). However, these biweekly measurements did not show an initial peak at FASET, but rather a consistently lower efflux, compared to AF. In fact, the LI-6400-09 measurements show FASET soil CO$_2$ efflux increasing to a peak later than (but lower than) AF.

![Figure 7](image.png)

**Figure 7.** 2011 Manual LI6400 soil CO$_2$ efflux measured at points along 1km transects in AF and FASET. Error bars indicate one standard deviation. DOY=Day of Year.

**Spatial Variability of Soil CO$_2$ Efflux**

Spatial variability of soil CO$_2$ efflux is high. Observations with the 6400-09 indicated that effluxes could vary more between collars a few meters apart than between plots several hundred meters apart. To understand the spatial autocorrelation between soil effluxes I constructed a preliminary semivariogram in late August, 2010. Instantaneous CO$_2$ effluxes were measured with the 6400-09 along a 1 m transect at points spaced 10 cm apart. The entire process took about 15 minutes and half of the points were rechecked to insure inter-measurement consistency (data not shown). A semivariogram was computed according to the
methods described in Stoyan et al. (2000) by averaging the variance between all pairs of points 10 cm apart, all pairs of points 20 cm apart, etc (Figure 8).

Figure 8 indicates that variability between pairs of soil CO$_2$ efflux measurements increases to about 80 cm, after which the variability appears constant in this limited data set. If this one-time experiment is accurate, paired measurements of soil CO$_2$ effluxes 80 cm or more apart can be considered independent. Measurements closer than 80 cm are probably more correlated to one another than chance alone would suggest, and any statistical use of such closely paired points should take into account spatial autocorrelation.

![Figure 8](image)

**Figure 8.** Semivariogram depicting average variance between pairs of soil CO$_2$ efflux measurements at various distances. Soil CO$_2$ efflux variance is measured in μmol m$^{-2}$ s$^{-1}$. Trendline is shown to emphasize expected logistic form of semivariance.

**NEE and Soil Respiration**

Spatial representativeness of autochamber $R_s$ measurements can be partially checked through comparison to tower-derived NEE data, which integrates ecosystem gas exchanges over many acres. There appears to be a positive correlation between nighttime ecosystem
respiration ($R_s$) and $R_v$ (Figure 9a). However, there is also a large scatter, indicating that either aboveground respiration is highly variable or that autochamber measurements of $R_v$ do not accurately integrate total belowground respiration at the ecosystem level. Given the differences observed between autochamber-measured soil respiration and manually-measured soil respiration, the latter seems quite possible. However, when nighttime NEE is gap-filled using modeled $R_s$, the relationship is much better, indicating that the empirical formulas derived by Curtis et al. (2005) are good predictors of autochamber-measured $R_v$ (Figure 9b). See Appendix F for relationships between FASET measured and modeled $R_s$ and $R_v$. 
Figure 9. a) TOP: Ameriflux nighttime autochamber soil CO$_2$ efflux plotted against measured $R_e$. b) BOTTOM: Ameriflux nighttime autochamber soil CO$_2$ efflux plotted against gap-filled (modeled) nighttime $R_e$.

To further compare autochamber-measured $R_s$ to $R_e$, time series data of Ameriflux $R_e$ and $R_s$ (AAS and AOS) were plotted along with GPP and NEE. Figure X shows that daily mean $R_s$ and $R_e$ are remarkably similar, except for a week early in the growing season (DOY 141-152) when $R_e$ anomalously increased, and a period around DOY 172 when AAS effuxes diverged from both AOS and $R_e$. According to these data, $R_s$ accounts for virtually 100% of $R_e$ throughout much
of the rest of the growing season, although $R_s$ is more variable than $R_e$. Interestingly, the enhanced variability of $R_s$ in comparison with $R_e$ appears to occur out of phase with NEE, implying a lower variability in GPP than shown here; GPP is calculated as $\text{NEE} + R_e = \text{GPP}$, so if AAS and AOS effluxes $R_s$ were substituted for $R_e$ the greater (antiphase) variability in autochamber-measured $R_s$ would help explain variability in NEE and hence dampen the calculated variability in GPP.

![Graph showing carbon fluxes at Ameriflux](image)

**Figure 10.** 2011 Measured and modeled C fluxes at Ameriflux, smoothed 24-hour means. GPP and NEE inverted to facilitate comparison with respiratory effluxes. REgf = gap-filled $R_e$. DOY = Day of Year.

**Biophysical data**

*Soil Temperature*

Soil temperature at 15 cm increased during the first half of the growing season, from a low of 8 degrees C to a high of about 17 C (Figure 11). During the second half of the growing season the temperature reached as high as 22 C before beginning a gradual decline to less than 31
18 C. Throughout the period of record, temperature appears to oscillate on both a diurnal and a weekly time scale, corresponding to the day-night cycle and to synoptic-scale weather fronts.

Soils temperatures did not differ by large margins between the four soil pits; at most, inter-pit differences amounted to slightly more than two degrees C early in the growing season. Interestingly, these largest differences were observed between the AF Oak Site (AOS) and the FASET Oak Site (FOS), while lesser differences were observed between the AF Aspen Site (AAS) and the FASET Aspen Site (FAS). These differences may be due to differential canopy cover and litter thickness which would impact the fraction of rain and solar radiation reaching the soil surface.

![Figure 11. Soil 15 cm temperature, degrees C. DOY= Day of Year.](image)

*Soil Moisture*

Volumetric soil water content (SWC) appears to show larger relative inter-site differences than temperature (Figure 12). At the beginning of the growing season, FOS was the wettest site, with about 4% more (total) SWC than AOS, the driest site. Early in the growing
season, SWC at all sites remained relatively high in these excessively drained sandy soils, between about 8% and 15% SWC. During the summer, SWC responds significantly to a small number of large rain events (for this dataset, approximately 9 rain events). In the middle of the season large rain events briefly spiked SWC to above 20%, but overall the trend is one of drying soils with average SWC falling below 5%. Such low moisture levels probably correspond to the permanent wilting point of plants; most understory vegetation, especially ferns, browned and died by the end of the observational period (see Appendix G for SWC and matric potential comparison as well as SWC data from all layers and all sites).

![Graph showing soil moisture content over DOY](image)

**Figure 12.** Soil 15 cm volumetric water content. DOY=Day of Year.

**Litter**

Large differences were observed in litter moisture and litter dry mass between and within sampling sites (Figure 13 and 14). It appears that the litter under oak canopy was wetter
than that under aspen canopy, although the variability between chambers was greater under oak than under aspen canopy. At AF, increased moisture corresponded with the increased total amount of litter mass under oak canopy, but at FASET the aspen canopy had produced as much, if not more, litter than the oak canopy.

**Figure 13.** Gravimetric leaf moisture content for each chamber and site. Note that there are two chambers at each site.

**Figure 14.** Dry leaf mass measured from each chamber at each site.
Soil Respiration Response to Temperature

To investigate constraints and drivers of \( R_s \), the relationship between \( R_s \) and 15 cm soil temperature was plotted and fit by exponential van ’t Hoff functions. An example plot for AAS is shown below (Figure 15). Site data were fit by functions with a \( Q_{10} \) between 1.81 (FAS) and 2.93 (AAS) and had \( r^2 \) values ranging from 0.6 to 0.75. Residuals were plotted by DOY to visualize possible autocorrelation (Figure 16). Autocorrelation is apparent when residuals cluster non-uniformly above or below the x-axis. Temporal autocorrelation of residuals was observed for all chambers, indicating either that \( R_s \) responds slowly or with some time-delay to temperature (hysteresis) or that other time-varying factors also control soil respiration. To check for the influence of SWC on soil CO\(_2\) efflux, residuals from the temperature-efflux analysis were plotted against 15cm soil moisture data (Figure 17). Surprising, there was not an overall relationship for any site, indicating that in this system soil moisture does not have a consistent effect on soil respiration. It remains possible, however, that different biophysical drivers could have different effects at different times of the year.

![Graph showing Soil CO\(_2\) efflux versus soil temperature at 15 cm.](image)

**Figure 15.** AAS soil CO\(_2\) efflux versus soil temperature at 15 cm. \( Q_{10} = 2.93 \) See Appendix D for AOS, FOS, and FAS Analyses. See Table 1 for summary \( Q_{10} \) statistics.
Figure 16. AAS soil CO$_2$ efflux residuals from Q$_{10}$ analysis plotted against DOY (Day of Year).
Phenoperiod Responses

To test whether different biophysical drivers have different effects at different times of year, the growing season was split into two phenoperiods based on Leaf Area Index (LAI) data (Chris Vogel, unpublished data). Schmid et al. (2003) propose growing season start at UMBS occurs when soil temperature at 5 cm rises above 13 C. In 2011, this occurred on DOY 132, three days after the beginning of the apparent growing season. Leaf phenological data (pers. observation) indicated leaf-out beginning on DOY 129, and this was also the beginning of LAI data collected at UMBS in 2011. Therefore, DOY 129 was used as the beginning of the growing season. Leaf phenology was further used to divide the growing season into the leaf-on period (phenoperiod 1: DOY 129-169) during which canopy LAI rapidly increased and the full leaf-out period (phenoperiod 2: DOY 170-235) during which canopy LAI remained approximately constant (Figure 18). The experiment concluded on DOY 235 before leaf senescence significantly decreased canopy LAI.

Figure 17. AAS soil CO₂ efflux residuals from Q₁₀ analysis plotted against volumetric soil moisture at 15 cm.

\[ y = -71.117x^2 + 14.229x - 0.3628 \]
\[ R^2 = 0.0381 \]
Figure 18. 2011 LAI data showing leaf-on and full leaf-out for AF and FASET 60 m sites. Note that soil CO$_2$ efflux data collection ended on DOY 235. DOY=Day of Year.
Figure 19. Phenoperiod 1 (DOY 129-169) AAS Soil CO$_2$ efflux plotted against Soil Temperature at 15 cm ($Q_{10} = 2.31$).

Figure 20. Phenoperiod 2 (DOY 170-235) AAS soil CO$_2$ efflux plotted against soil temperature at 15 cm ($Q_{10} = 2.37$).
Comparison of AAS 15 cm soil temperature and soil CO$_2$ efflux for the two phenoperiods (Figure 19 and 20, above) revealed a much weaker correlation ($r^2$ of 0.35 and 0.37) than when the entire growing season was used. Applying the same phenoperiod analysis to all four sites yields the data in Table 2. Overall, phenoperiod 1, which spans the springtime leaf-out period, showed much higher sensitivities to temperature ($Q_{10}$ values) than the mid-summer phenoperiod 2. See Appendix E for phenoperiod $Q_{10}$ analyses of each site.

<table>
<thead>
<tr>
<th>Phenoperiod</th>
<th>$Q_{10}$</th>
<th>AAS</th>
<th>AOS</th>
<th>FAS</th>
<th>FOS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenoperiod 1</td>
<td>($r^2$)</td>
<td>2.93$^a$ (0.68)</td>
<td>2.84$^b$ (0.59)</td>
<td>1.81$^c$ (0.47)</td>
<td>2.39$^d$ (0.75)</td>
</tr>
<tr>
<td>Phenoperiod 2</td>
<td>($r^2$)</td>
<td>2.31$^a$ (0.37)</td>
<td>3.86$^b$ (0.74)</td>
<td>3.12$^c$ (0.68)</td>
<td>2.97$^c$ (0.74)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Phenoperiod</th>
<th>$Q_{10}$</th>
<th>AAS</th>
<th>AOS</th>
<th>FAS</th>
<th>FOS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenoperiod 1</td>
<td>($r^2$)</td>
<td>2.37$^a$ (0.35)</td>
<td>2.28$^a$ (0.25)</td>
<td>1.27$^b$ (0.04)</td>
<td>1.86$^a$ (0.32)</td>
</tr>
</tbody>
</table>

Table 2. $Q_{10}$ Summary by site and phenoperiod. Different superscript letters indicate significant differences within each row ($p<0.01$). Data analysis from JMP (SAS, Inc) Nonlinear Curvefit Toolbox.
Wavelet Analysis

Wavelet analysis was used to visualize time varying changes in the pattern of AAS soil CO₂ efflux, moisture, and temperature (Figure 21). Figure 21 is laid out with half-hourly time intervals on the x-axis and “period” on the y-axis. Period can be interpreted as the wavelength of oscillations in the signal. Every point in time-period space (t,p) is assigned a color to indicate the amplitude of wavelengths of length p at time t, where brighter reds indicate more power in the indicated wavelength. Black lines outline areas of significance when measured against AR1 “red” noise.

Soil CO₂ efflux shows strong periodicity in the middle of the season above wavelengths of 200, corresponding to wavelengths on the order of weeks and months (Figure 21a). It also shows a region of significant power at hourly frequency on DOY 172-174 and again on DOY 179 (timestep 2200 and 2400 on the x-axis). These cycles may be due to artifacts or unexplained phenomena that occurred at AAS during rainstorms that occurred during these time periods. It is also interesting to note that a diurnal cycle (which would have period 48 on the y-axis) in soil CO₂ efflux is not significant in this analysis.

15 cm soil moisture at AAS shows a strikingly different pattern from soil CO₂ efflux. The continuous wavelet transform (Figure 21b) shows only a few regions of very high power, probably corresponding to rain events that left the ground wet for days and weeks afterward. One time period between DOY 150-191 (timestep 1000-3000 on the x axis) had high around p=512, or about 10 days. These oscillations are probably a result of intermittent rain events that occurred at regular 7-10 day intervals in June.

15 cm soil temperature at AAS also shows a unique pattern, with a significant diurnal cycle (period = 48) with little activity at shorter time scales (Figure 21c). Instead, most of the power in the temperature data are in frequencies with wavelength on the order of 6-10 days (period 300-500), with a clear trend toward increasing length later in the season. This fits the observed weather patterns (see temperature data above, Figure 11).
Figure 21. Continuous wavelet transforms of a) AAS efflux, b) 15cm soil moisture, and c) 15cm soil temperature data. Time steps (half-hours) are on the x-axis and period (frequency, also in half-hour time steps) is represented on the y-axis. Color denotes relative power in the signal.
To understand how the biophysical drivers of soil temperature and moisture are related to soil CO$_2$ efflux at AAS through time, the Cross Wavelet Transforms (CXT) of the above data were plotted (Figure 22). This figure can be interpreted similarly to the Continuous Wavelet Transforms, with the addition of small arrows to indicate phase correlation. For example, in the first CXT (Figure 22a) soil temperature and CO$_2$ efflux are compared to show areas where both signals have high power. Arrows pointing to the right indicate that the two signals are in phase at a particular time and at a particular wavelength. Arrows rotate clockwise to indicate progressively increasing delays between the soil temperature and soil CO$_2$ efflux data, so that arrows pointing downward indicate oscillations that are delayed by ¼ wavelength, arrows pointing to the left indicate oscillations that are delayed by ½ wavelength (i.e. antiphase) and arrows pointing up indicate oscillations that are delayed by ¾ wavelength. Arrows cannot be used to definitively ascertain causality, although in this system in makes more sense for increases in temperature to drive increased soil respiration than it does for increased soil respiration to causes increases in soil temperature. Nonetheless, an arrow pointing up could indicate either that soil respiration lags soil temperature by ¾ period, or that soil respiration leads soil temperature by ¼ period.

Figure 22a, below, shows that the region of strong diurnal rhythms in the soil temperature data (at period = 48) also has strong explanatory power for the soil CO$_2$ efflux data, as multiple regions throughout the time series show significant power and correlation between the two datasets. Indeed, most of the arrows in this region point downward, indicating that soil CO$_2$ efflux lags soil temperature changes by ¼ wavelength, which in this case is 24/4=6 hours. This may indicate diurnal hysteresis, which has been observed in many other soil respiration studies (Phillips et al., 2011; Vargas et al., 2008; Li et al., 2011). There are also strong regions of shared power in both signals for longer wavelengths in the middle of the season, with oscillations on the order of period = 500, or about 10 days. The arrows in these regions predominantly point right or slightly down from right, indicating that oscillations tend to occur in-phase or only slightly lagged at the multi-day scale.

In contrast, Figure 22b shows a different pattern for the CXT of AAS 15 cm soil moisture and soil CO$_2$ efflux. Here, a strong rain event near time point 2100 (approximately DOY 172) dominates the power spectral density, showing significance from the sub-hour level to nearly the 1024 period (about 21 days), and continuing from around DOY 173 through much of the rest of the season. This indicates that SWC has strong explanatory power for soil respiration after
DOY 172. Interesting, arrows corresponding to one week (period=500) initially (near DOY 172) point right-down, indicating a delay in soil CO$_2$ efflux relative to soil moisture, but as the season goes on the arrows straighten out and point right, indicating that the soil moisture and soil respiration signals are phase-locked at weekly timescales throughout the second half of the growing season.
Figure 22. Cross wavelet transforms of pairs of AAS biophysical variables: a) Efflux X 15cm Soil Temperature and b) Efflux X 15cm Soil Moisture. Time in half-hours is on the x-axis and period (frequency) in half-hours is on the y-axis. Color denotes relative power in the signal. Arrows show phase direction: arrows pointing forward occur when changes in temperature or moisture co-occur with changes in efflux. Arrows rotate clockwise to indicate increasing lags between temperature and moisture changes. Lags are calculated as a function of period, so an arrow pointing down at period 64 indicates a lag of 64/4 = 16 half hours, or 8 hours. See Appendix C for all of the site CXT analyses.
CXT analyses at all sites showed that lags between soil temperature and $R_s$ varied throughout the growing season; for example, at FAS, diel lags rotate from in-phase to $\frac{1}{4}$ period out-of-phase and back (Figure 23). This observation of hysteresis may help explain low $r^2$ values in $Q_{10}$ plots.

![Cross Wavelet Transforms of FAS soil CO$_2$ efflux and 15 cm Soil Temperature](image)

**Figure 23.** Cross Wavelet Transforms of FAS soil CO$_2$ efflux and 15 cm Soil Temperature.

Wavelet analysis also shows broadly similar $R_s$ responses to SWC between sites, with some interesting differences. A large rainstorm on DOY 172 increased SWC to the highest levels observed during the measurement period (Figure 12) and caused the autochamber sensors at FASET to malfunction; because manual LI-6400-09 data were not collected, our knowledge of the magnitude of effluxes during this time is incomplete. Nonetheless, CXT analysis at all sites shows strong local correlations at a wide range of periods originating from DOY ~170, indicating that this rainstorm impacted soil respiration for weeks at every site. At Ameriflux, both sites measured extremely high short-term effluxes, resulting in in-phase (right arrows) responses to SWC (Figure 22b and 26). At FASET, the lack of response (due to missing data), combined with long-term $R_s$ responses to soil temperature, resulted in out-of-phase (left arrow) responses to
SWC (Figure 24 and 25). During the second half of the growing season, SWC continued to show significant explanatory power for $R_s$ oscillations at both Aspen sites (AAS and FAS, Figure 22b and 24), while it did not show as much power for the Oak sites (FOS and AOS, Figure 25 and 26).

**Figure 24.** FAS - Cross Wavelet Transforms of FAS soil CO$_2$ efflux and 15 cm soil moisture. Phase arrows generally point left around time period 2000 (=DOY 172), indicating soil CO$_2$ efflux and 15 cm soil moisture vary out-of-phase. Compare to Figure 22b.
Figure 25. FOS - Cross Wavelet Transforms of FOS soil CO\textsubscript{2} efflux and 15 cm soil moisture. There are fewer regions of significant power late in the season as compared to FAS (Figure 24).

Figure 26. AOS - Cross Wavelet Transforms of AOS soil CO\textsubscript{2} efflux and 15 cm soil moisture. There are fewer regions of significant power late in the season as compared to AAS (Figure 22b).
Discussion

Belowground carbon cycle response to disturbance

H1.a FAS \( R_s < AAS \) and H1.b FOS \( R_s > AOS \),

A sudden termination in the flow of energy and carbon from leaves to roots is expected to have an impact on root metabolism. Without recent photosynthate, tree roots must rely on stored carbohydrate reserves for their immediate respiratory needs; when they consume all of their carbohydrates, they begin to die. At FASET, elevated rates of fine root death were measured as early as 2009 (Nave et al., 2011). With the cessation of autotrophic respiration, heterotrophic respiration will become dominant as microbes decompose newly available substrate. At each of these steps \( R_s \) could increase or decrease based on changes to controlling and contributing factors that also vary in space and time. However, based on work from previous studies, we hypothesized (H1.a) that soil respiration, which integrates a wide number of these belowground processes, should decrease following girdling. Alternately, the girdling disturbance may be transitory and respiration might be expected to return to baseline by the time of this research in the fourth year following girdling. Recovery of forest structure and composition is relatively rapid following disturbances that primarily impact forest canopies, such as hurricanes (Chazdon, 2003). Growth by ungirdled trees, such as oak, in the FASET plot has been observed to increase to compensate for decreased LAI by aspen (Gough, 2011 FEST meeting). Therefore, we hypothesized (H1.b) that under oak canopy, respiration would increase to parallel aboveground carbon investment and gain.

To test the first hypothesis, a comparison between AAS and FAS is necessary (below, Figure 27). The autochamber data show that FAS \( R_s \) starts out slightly (but significantly) greater than AAS early in the season and then declines to levels significantly much lower than the untreated forest by the middle to end of the growing season. The 1km transect data confirm that FASET generally has lower \( R_s \) compared to AF. The effect size, calculated as the greatest observed difference (ratio of treatment efflux to control efflux) was 0.5 around DOY 226.
according to the autochambers, and 0.54 on DOY 194 according to the manual soil respiration measurements.

These data indicate that soil respiration can be reduced by up to 50% following girdling. Hogberg et al., (2001) found a significant decrease in soil respiration within days of girding a Scotts pine forest, and eventually found a 50% decrease in respiration (effect size=0.5) during that growing season. Many other researchers have confirmed a similar effect size in temperate forests: Scott-Denton et al. (2006), Subke et al. (2004), and Johnsen et al. (2007) all found identical (0.5) effect sizes. Binkley et al. (2006) found a smaller effect in a Eucalyptus plantation (0.76) which was confirmed by Chen et al. (2010) in Acacia and Eucalyptus plantation (0.64 and 0.78, respectively). Morehouse et al. (2008) and Ekberg & Gleixner (2007) did not find any effect on soil respiration in Ponderosa pine and Norway spruce forest, respectively, although their studies were conducted several years after girdling. Given that the current research was performed in the fourth year post-girdling, in a forest where only a subset of trees were girdled, the magnitude of the effect size (0.5) is noteworthy.

There was no consistent significant difference in $R$, between the treatment and control oak sites (H1.b). This indicates that the FASET oak trees may not be responding with enhanced belowground C allocation to the aboveground changes taking place around them.
**Figure 27.** Soil CO$_2$ daily mean efflux difference AAS-FAS. Significant differences (blue) based on t test (where n=4 chambers and 2-tail alpha=0.01)

**Biophysical Drivers: Soil Moisture**

*H2.a FAS SWC > AAS SWC and H2.b FOS SWC < AOS SWC*

Although one of the stated points of girdling trees, as opposed to logging them, is an attempt to maintain normal temperature and moisture regimes in the soil environment, a majority of published studies find large increases in SWC under girdled trees (Kuzyakov, 2006). SWC could increase if trees are girdled incorrectly, accidentally cutting xylem tissue as well as phloem. SWC might also increase as a result of decreased transpiration due to decreased LAI and root death or increased precipitation throughfall to the soil because of decreased LAI. Although Chen et al. (2010) found no effect in an Acacia plantation, they did find an increase in soil moisture (effect size=1.21) in a Eucalyptus plantation. Morehouse et al. (2008) found a similar effect (1.14) in a Ponderosa pine forest following natural insect girdling. Kaiser et al.
(2010) found a larger increase (1.4) and Ekberg & Gleixner (2007) found an extremely large increase (2.8). Alternately, SWC could decrease if evaporation increases due to increased solar radiation and advective airflow near the soil surface; Li et al. (2009) and Scott-Denton et al. (2006) found a decrease in soil moisture following girdling (effect size = 0.79 and 0.71, respectively).

In this study, girdling appears to increase SWC by as much as two-fold (effect size = 2) late in the season (H2a), but there were also hydrological changes between the ungirdled oak sites (FOS and AOS)(Figure 10). While FOS had the highest soil moisture levels early in the season, it had the lowest soil moisture by the end of the season(H2b). If LAI increased at FOS, the observed pattern could be explained by increased transpiration and decreased precipitation throughfall. The muted response of FAS soil moisture to the overall late-season drying trend is also noteworthy because it could imply decreased transpiration in response to the girdling treatment. The decreased moisture of FAS litter compared to FOS litter could also be caused by increased solar irradiance through the more open canopy at FAS.

**Biophysical Drivers: Soil temperature**

- **H3.a FAS soil temp > AAS soil temp** and **H3.b FOS soil temp < AOS soil temp**

Soil temperature was hypothesized to increase following girdling due to decreased canopy leaf area (LAI). LAI is expected to decline as trees respond to the girdling treatment with morbidity and eventually mortality. Trees are often able to compensate for lower water and nutrient levels in their xylem by producing less leaves, and this has been observed for several girdling treatments (Noel, 1970; Edwards & Ross-Todd, 1979). Morehouse et al. (2008) found an increase in soil temperature several years after girdling took place in response to decreased LAI. Based on the known temperature dependency of $R_s$, especially $R_{ns}$, increased soil temperature could confound decreases in $R_s$ at girdled sites with increased $R_{ns}$ (Davidson et al., 2006; Davidson et al., 2010). However, the present study did not observe major differences in soil temperature between girdled and ungirdled sites (H3a; Figure 9). Indeed, the largest discrepancies were between AOS and FOS, with AOS showing slightly higher temperatures, especially early in the growing season (H3b). This may be due to the lower soil moisture at AOS compared to FOS; water has a high thermal mass and may insulate soil from temperature changes. Interactions between SWC and soil temperature are a confounding effect when temperature and moisture are used to model soil respiration.
Soil CO$_2$ Efflux versus Soil Temperature and Soil Moisture: $Q_{10}$ Analysis

$H4.a$ Growing Season FAS $Q_{10}$ $<$AAS $Q_{10}$ and $H4.b$ Growing Season FOS $Q_{10}$ $>$AOS $Q_{10}$

Results of a $Q_{10}$ temperature sensitivity analysis for the entire growing season dataset and for two subsets (phenoperiod 1 and 2) show clear differences between the treated aspen site (FAS) and the three other soil pits (Table 2). In particular, FAS has lower $R_s$ sensitivity to temperature during the height of the growing season (phenoperiod 2) when autotrophic organisms may contribute most to $R_s$. The low $Q_{10}$ reported from FAS appears to indicate a significant departure from normal patterns of $R_s$ regulation by temperature, and support my hypothesis ($H4.a$). While there were significant differences between AOS and FOS, the results are confusing and did not support my hypothesis ($H4.b$).

If the decrease in $R_s$ (~50%) at FAS is due entirely to decreased $R_A$, then the $Q_{10}$ analysis implies $R_H$ has a lower temperature sensitivity than $R_A$ during phenoperiod 2 at our site. This interpretation is supported by Boone et al. (1998) who found that roots and associated rhizosphere have a much higher $Q_{10}$ than bulk soil. However, their review has been questioned by a number of other studies that have measured much larger $Q_{10}$ values in root-free soil compared to soil with autotrophic inputs (Li et al., 2011; Hogberg, 2010). Li et al. (2011) ascribed the difference to the fact that heterotrophic $R_s$ occurs in-phase (or with small lag) to soil temperature oscillations, whereas root respiration displays substantial delays. Diurnal hysteresis has been hypothesized to be the result of autotrophic contributions, perhaps from diurnal patterns in photosynthate production or transport, although it may also be explained by the physics of heat flow (Baldocchi et al., 2006; Phillips et al., 2011). Hogberg (2010) used a large 20-day temperature decrease in the middle of the growing season to show that $R_A$ does not respond to temperature fluctuations at all. Hogberg ascribes apparently large $Q_{10}$ values for $R_A$ to the strong seasonality of tree belowground C allocation, which occurs in-phase with the strong seasonality of soil temperature cycles.

A large increase in soil temperature at our study sites corresponded with a large increase in $R_s$ during phenoperiod 1, which led to large $Q_{10}$ values. But whether this relationship indicates the temperature sensitivity of $R_A$, $R_H$, or even $R_s$ remains uncertain. Janssens et al., (2003) point out that the time period used to estimate $Q_{10}$ can determine covarying (and hence confounding) factors such as root biomass and activity. Davidson et al. (2005) argue that a variety of mechanisms, from enzyme kinetics to substrate supply, can covary with and confound $R_s$ $Q_{10}$ estimates. Production and transport of recent photosynthate from tree canopies to roots
probably increased at the same time soil temperature was rapidly warming. Although the forest canopy is a net sink of stored carbohydrates during leaf-out, fine roots begin growth in tandem with leaves (Gough et al., 2010; Fahey & Hughes, 1994). In 2011, NEP became negative (i.e. net ecosystem carbon gain) around DOY 145 and, based on work by Gough et al. (2009) in the same forest, net export of recent photosynthate from canopy to roots usually begins around DOY 170-190. Certainly by the middle of the growing season, $R_A$ contribution to $R_s$ should be greater than at the beginning of the season.

At shorter timescales and in the second half of the growing season, the relationship between $R_s$ and soil temperature becomes increasingly decoupled at all sites. Based on an assumed increase in $R_A$ at all sites except FAS, decoupling would be expected if $R_A$ is less sensitive to temperature, exhibits greater lags to temperature, or is driven by independent factors such as PAR. But then why does FAS exhibit the largest decoupling (weakest $Q_{10}$ relationship)? Perhaps RH becomes increasingly substrate or moisture-limited by the second half of the growing season. However, it remains possible that the observed decoupling was confounded by other factors such as the presence of mixed autotrophic and heterotrophic respiration at all sites (even FAS), respiration integration from an entire soil column versus temperature measured in one layer, variable errors associated with soil macrofauna such as earthworms, and further unknown sources of variability. In conclusion, $Q_{10}$ analysis is incapable of distinguishing between changes in $R_s$ mediated by changing soil temperature as opposed to changes mediated by other drivers that happen to covary with temperature.

**Wavelet analysis**

$H3$ FAS $R_s$, *lags* SWC $<$ AAS $R_s$, *lags* SWC

2011 was cold and wet, especially around DOY 172 when a week-long rain storm significantly impacted SWC and $R_s$, as evidenced by CWT analyses of SWC and $R_s$ at all four sites. We had hypothesized that FAS $R_s$ would show less delay to changing SWC based on the widespread observation that soil microbial activity responds more rapidly than tree roots physiology (Glinski & Stepniewski, 1985; Liu et al 2002; Carbone et al., 2011). Depending on the time scale analyzed, lags may be due to root growth, CO$_2$ storage and transport in xylem (Aubrey & Tesky, 2004), changing soil CO$_2$ diffusivity, or substrate supply to microbes (Kuzyakov & Gavrichkova, 2010). The observed lags early in the growing season (Figure 22b and 24) appear to be longer at FAS than AAS but may be due to patchy data collection during storm events, as well as the dynamics of synoptic meteorology. Generally speaking, SWC and soil temperature
varied out of phase during the early growing season because frontal passage was driven by cool arctic air masses; as soil dried out after each storm (decreasing SWC), temperatures gradually increased until the next front brought increased SWC and decreased temperatures. As long as SWC is not limiting, soil temperature is the predominant driver of $Rs$, so the general early growing season relationship between SWC and $Rs$ is out-of-phase (antiphase). Interestingly, a strong in-phase response was observed for the operational autochambers at Ameriflux (Figure 22b and 26), indicating that storm events, at least at Ameriflux, are correlated with idiosyncratic soil CO$_2$ efflux and/or soil respiration responses. Other studies have also observed large $Rs$ responses to rain events (Fierer & Schimel, 2003), and have argued that they can significantly impact total seasonal $Rs$ (Xu & Baldocchi 2004). Malfunction of the autochambers at FASET during the crucial DOY 172 rainstorm makes direct comparison impossible, but depending on the cause of the anomalous effluxes (CO$_2$ storage and transport, $R_h$ or $R_s$ stimulation) FAS might also show similar or different responses.

Soil moisture did not appear to be limiting for $Rs$ until after DOY 190 when SWC decreased to around 3% volumetric SWC (Figure 12). Importantly, above 3% SWC, changes in SWC do not confer a consistent change in $Rs$, but around 3% SWC even small moisture additions can lead to large increases in $Rs$. Therefore, the effects of SWC on $Rs$ may be mediated through transport of substrate during episodic rain events. Alternately, because the wilting point in these sandy soils is around 3% SWC, rapid changes in soil water matric potential might change the physiological state or osmotic environment of microbes and fine roots (Romberger et al., 1986).

Late-season changes in the importance of SWC to $Rs$ under different tree canopies may be driven by differences in tree physiology. Based on CXT analyses, it appears that SWC continues to drive $Rs$ below aspen trees throughout the growing season, while dampened changes in SWC under oak trees exert less effect on $Rs$ in the second half of the season (Figures 22b, 24, 25, and 26). Overall, this pattern confirms other observations of differential responses of oak and aspen trees to water stress (Julia Thomsen, UMBS undergraduate REU, unpublished data). Thomsen found that oak trees are able to continue transpiration in the face of late-season SWC decreases by efficiently accessing deeper groundwater and allowing leaf water potentials to drop very low. If continued photosynthetic carbon gain is deposited in root reservoirs, oak root respiration may be less sensitive to seasonal drought than either aspen root respiration (AAS) or microbial respiration (FAS).
Conclusions

Limitations and Future Directions

The soil environment is characterized by both small and large-scale temporal and spatial heterogeneity and there are multiple sampling techniques to deal with the resulting variability of soil property data. In this experiment, two approaches were taken to sample soil respiration: extensive sampling across a wide spatial distribution using the manual closed chamber LI-6400-09 IRGA, and intensive sampling with an array of specially-built autochambers. Without constructing a full semivariogram of the distribution of soil CO$_2$ effluxes across the forest and throughout the growing season it is impossible to state conclusively whether the limited sampling undertaken in this study is sufficient to characterize the true extent of soil respiration at UMBS, let alone over a larger swath of Northern mixed hardwood forest. However, a preliminary variogram (Figure 8) showed that chambers 80 cm or more apart can be considered independent measures of soil CO$_2$ efflux, and based on this statistical assumption significant differences were observed between $R_s$ under girdled and ungirdled trees. However, no consistent statistically significant differences in total $R_s$ were observed under oak trees in the disturbed forest compared to oak trees in the undisturbed forest.

Autochambers were sited to take advantage of paired soil pits instrumented with a gradient of moisture and temperature sensors. These sensors allow comparison of the biophysical properties and any treatment effects that might affect soil respiration. The siting of the autochambers is necessarily a once-per season task: they are not easily moveable and, once moved, take several days to equilibrate. The problem of whether the autochambers are representative is not minor; an autochamber sited over an actively growing root or a burrowing animal would yield widely different measurements from one sited over a patch of soil containing no major roots or soil fauna, although the continuing development of ground-penetrating radar may yield improved detection of roots in the near future (Butnor et al., 2003). Through comparisons of autochamber-measured $R_s$ with $R_s$ measured along extensive transects and $R_e$ measured by the eddy covariance method, it appears that autochamber measurements can
accurately describe changes in $R_s$. It is also important to note that some of the sources of respiratory variability, such as the presence and type of nearby trees, is the subject of the study and so is not considered confounding. Differences between aspen and oak patches may also contribute to the many complex drivers of differences in observed soil $CO_2$ efflux. For example, litter quality (N content) between oak and aspen patches may also vary, but was not controlled for in this study.

However, my research does point toward the need for more data collection. Variability between paired soil temperature/moisture sensors in a single pit was often greater than temperature and moisture differences between pits and between sites. Similarly, variability between paired autochambers at each soil pit was at times greater than soil $CO_2$ efflux between pits and between sites. This indicates that the biophysical and respiration differences between the pits are not always large enough to overwhelm within-site variability: current sampling density at each pit does not always yield enough measurement precision to provide statistical power in distinguishing between pits.

**Conceptual Model**

A simple input to a complex system, in this case girdling early-successional species in a mixed hardwood forest, can have a plethora of divergent, complexly interacting outcomes. In the current research, only one of those outcomes, soil $CO_2$ efflux, was quantified. Yet soil $CO_2$ efflux integrates a large number of different interactive processes. The advantage of choosing an integrative variable is that it allows this research to simultaneously investigate a large suite of complex ecosystem variables. The disadvantage is that this analysis does not facilitate reductive investigation of mechanistic links between each system variable and soil $CO_2$ efflux. At best, general correlations can be drawn ($Q_{10}$ analysis) and patterns can be visualized (Wavelet analysis).

Therefore, my research has focused on the dominant biophysical drivers of soil respiration, temperature and moisture. Soil respiration is still a new topic of research and much remains to be investigated with new tools such as autochambers. This research could be extended using more sensors, either intensively or extensively, to better represent complex spatial patterns in the environment. A large number of correlational analyses could be attempted between soil $CO_2$ efflux and other potential biophysical drivers. And these analyses could be made more explicit in a formal quantitative model that incorporate both physical and biological drivers (CF. Phillips et al., 2011).
Further work is needed to explain the differences described in this study, as well as correlate observed changes to total ecosystem carbon storage. However, this study does reveal that the consistent response to disturbance is a reduction in R, corresponding to the terminated flow of recent photosynthate. As the girdled trees senesce, a pulse of leaf litter is followed by increased light levels and precipitation reaching the soil surface. Root death and cessation of tree transpiration lead to further increases in SWC. Increased water, light, and nutrients should sustain and enhance the root growth (and hence respiration) of trees that survive the disturbance, but that was not observed in these data. Furthermore, the observed decrease in temperature sensitivity under both oak and aspen in the disturbed forest indicates a decoupling between changing biophysical drivers and R. While the death of the dominant autotrophic organisms in this forest may decrease GPP, decreased soil respiration may partially compensate for overall ecosystem carbon balance, leading to ecosystem resistance and resilience to disturbance. The results so far show promise in unraveling the myriad interactions beneath the forest floor.
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Appendix A:
Matlab Code Used To Process 2 Second Carbon Dioxide Concentration Data

Matlab Files Used to Process Automated CO₂ Data in Order of Use
Note: All files must be opened in Matlab for the program to run

SEACFILE.m

clear all
close all
tic
% % % % tower = Faset
% data_path = 'C:\Users\conor\Documents\OSU\CURTIS LAB\Data\2011\SEAC\';
   infile= [csvread([data_path '11237.sec'],0,0);... 
   csvread([data_path '11238.sec'],0,0);...
   csvread([data_path '11239.sec'],0,0);...
      csvread([data_path '11240.sec'],0,0);...
   csvread([data_path '11241.sec'],0,0);...
   csvread([data_path '11242.sec'],0,0);...
   csvread([data_path '11243.sec'],0,0);...
   csvread([data_path '11244.sec'],0,0);...
   csvread([data_path '11145.sec'],0,0);...
   csvread([data_path '11146.sec'],0,0);...
   csvread([data_path '11147.sec'],0,0);...
   csvread([data_path '11148.sec'],0,0);...
   csvread([data_path '11149.sec'],0,0);...
   csvread([data_path '11150.sec'],0,0)];

   Year = infile(:,2);
   DOY = infile(:,3);
   hour_min= infile(:,4);  %This is the set up for the 2011 data
   Chamber= infile(:,6);
   Lid= infile(:,7);
   CO2 = infile(:,10);
clear infile

% % % % tower = Faset NOTE: need to activate text below and deactivate corresponding text above to read FASET files
% data_path = 'C:\Users\conor\Documents\OSU\CURTIS LAB\Data\2011\FSEAC\';
% infile= [csvread([data_path '11237.fac'],0,0);...
%% This is the set up for the FASET 2011 data
Year = infile(:,2);
DOY = infile(:,3);
hour_min= infile(:,4);
Chamber= infile(:,6);
Lid= infile(:,7);
CO2 = infile(:,9);
clear infile

maxlength=length(DOY);  %maxlength tell how long the files are
b=1;
a=1;
while a<=maxlength;  %maxlength needs to be equal to the number of
values in the files that are being concatinated.
b=find(hour_min==hour_min(a) & DOY==DOY(a));
hour_min(b)=(hour_min(b)+[0:length(b)-1]'/length(b));  %this
adds the extra piece to the hour_min values so there's not 30
11:56's...etc
a=a+length(b);
end

UTS = [(Chamber.*10^10) + (DOY.*10^7) + (hour_min*10^2)];

dayrange=unique(DOY);  % this shows which days are included in the files
that I'm concatinating.

[ccl cc2l nw] = findOBSwindows(4, Chamber);

results = zeros(nw,10);
for c=1:4
    for w=1:length(cc2l(c))
        %c, w, ccl, cc2l, hour_min, CO2, skip, plotYN, dofit, nmovavg
        [choppedCurve startwin endwin co20 nodata] = grabwindow(c, w, ccl, cc21, hour_min, CO2, skip, 0, 0, nmovavg);
        if nodata==0
            [fcs,gof2,output] = ConorFitRobust(choppedCurve,co20);
            [P,DW] = dwtest(output.residuals,choppedCurve(:,2));
The code snippet provided includes functions for handling data from chambers. Here is a breakdown of the functions and their purpose:

### findOBSwindows.m

This function, `findOBSwindows`, takes inputs `nchambers` and `ChamberVector` and outputs `ccl` and `cc2l`. It calculates the number of windows (`nw`) and identifies the chamber codes (`ccl{c}`) and the points between windows (`cc2l{c}`). The function iterates over each chamber, finds the windows using the ChamberVector, and counts the number of windows.

```matlab
function [ccl cc2l nw] = findOBSwindows(nchambers, ChamberVector)
    nw=0; % nw is the number of windows
    for c=1:nchambers %looping over chambers (between 1 and 8)
        ccl{c}=find(ChamberVector==c);
        cc2l{c}=[find((ccl{c}(2:end)-ccl{c}(1:end-1))>1); length(ccl{c})];
        % where the difference is greater than 1, we know that we're between windows
        nw=nw+length(cc2l{c});
    end
end
```

### grabwindow.m

This function, `grabwindow`, takes chamber number `c` and window number `w`, along with additional arguments, to calculate CO2 data for a specific window. It includes options for skipping data and fitting, which can be inputted as arguments. The function calculates the start and end of the window, gets CO2 data, and applies moving averages as needed.

```matlab
function [windowdata startwin endwin co20 nodata] = grabwindow(c, w, ccl, cc2l, hour_min, CO2, skip, plotYN, dofit, nmovavg)
    %c is chamber number
    % w is window number
    nodata=0;
    cc=ccl{c};
    cc2=cc2l{c};
    if nargin <10 %nargin is the number of arguments that have been input,
        if it's less than nine, then I don't make it do the fitting.
            nmovavg=10;
    end
    if w==1 %for the first window
        startwin = cc(1)+skip; %skip equals 20, to remove the first 40 seconds of each window...
        endwin = cc(cc2(1));
        if endwin-startwin<skip
            nodata=1;
            co20=0;
            windowdata=0;
            return
        end
        [co20 skip2]=getco20(CO2(startwin:endwin),nmovavg);
        startwin1= startwin+skip2-1;
```
sec =
floor(hour_min(startwin1:endwin)/100)*3600+60*mod(hour_min(startwin1:endwin),100);
windowdata=[hour_min(startwin1:endwin) sec CO2(startwin1:endwin)];
%this puts the hour_min and CO2 for the first start to end window into windowdata
else
    startwin = cc(cc2(w-1)+1)+skip;
    endwin = cc(cc2(w));
    if endwin-startwin<skip
        nodata=1;
        co20=0;
        windowdata=0;
    return
    end
    [co20 skip2]=getco20(CO2(startwin:endwin),nmovavg);
    startwin= startwin+skip2-1;
    sec =
floor(hour_min(startwin1:endwin)/100)*3600+60*mod(hour_min(startwin1:endwin),100); %yields seconds
    windowdata=[hour_min(startwin1:endwin) sec CO2(startwin1:endwin)];
end

timefix = find(windowdata(2:end,2)<windowdata(1:end-1,2),1); %this allows graphing with seconds on the x axis
while not(isempty(timefix))
    windowdata(timefix+1:end,2)=windowdata(timefix+1:end,2)+24*3600;
    timefix = find(windowdata(2:end,2)<windowdata(1:end-1,2),1);
end
windowdata(:,2)=windowdata(:,2)-windowdata(1,2);

if nargin <9 %nargin is the number of arguments that have been input,
if it's less than nine, then I don't make it do the fitting.
    dofit=0;
end

if dofit ==1 % if dofit is equal to 1, then it does the equation to
determine cs and k and it does the goodness of fit.
    [fcs,gof2] = JenFitRobust(windowdata,co20);
    if plotYN==1
        figure (2)
        plot(windowdata(:,2),fcs(windowdata(:,2)),'-b',windowdata(:,2),windowdata(:,3),'-r')
        xlabel('Time [sec]')%line above: plots the seacfit for the
        ylabel('CO_2 [ppm]')
        legend('Curve fit','Data')
        title([num2str(floor(windowdata(1,1)/100)) ':'
        num2str(floor(mod(windowdata(1,1),100))) ', C=' num2str(c)])
    end
else
    if plotYN==1
        figure (1)
plot(windowdata(:,2), windowdata(:,3))
xlabel('Time [sec]')
ylabel('CO_2 [ppm]')
title([num2str(floor(windowdata(1,1)/100)) ':'
m2str(floor(mod(windowdata(1,1),100))) ', C=' num2str(c)])
end

genco20.m

function [co20, Ico20] = getco20(co2,nmovavg)

%b=ones(1,nmovavg)/nmovavg;
davg=min(70,length(co2)); %finds the minimum value within the first
70 observations of CO2 data

cavg=smooth(co2(1:endavg),nmovavg); %smooth is a function for a moving
average that is within the first 70 observations, based on 10 (with 2
sec data) observation means
co20=min(cavg); %want to find the minimum CO2 within the moving
average. This will serve as Co in the equation
Ico20=find(cavg==co20,1); %create an index of where Co2 is at the
minimum within the moving average CO2

end

ConorFitRobust.m

function [fcs,gof2,output] = ConorFitRobust(choppedCurve,co20) %Input
the curve that has the first 100 sec removed, and it's windowdata and
CO2 from grabwindow.m

s=fitoptions('Method','NonlinearLeastSquares', 'Robust','Bisquare','Lower',[360 -1],'Upper',[26000 1],'StartPoint',[1100 0],'MaxFunEvals', 1000, 'MaxIter', 1000, 'Display', 'Off');
f=fitype('cs-(cs-co)*exp(-k*x)', 'problem', 'co','options',s);
[fcs,gof2,output]=fit(choppedCurve(:,2), choppedCurve(:,3), f,
'problem', co20);
end

secfit.m

function [seac]=secfit(x,co,cs,k) %this is the equation used to
calculate the variables needed to calculate the flux.

seac = cs-(cs-co)*exp(-k*x);
end
Appendix B:
Images of AAS and FAS and FOS

Figure 28. AAS looking North.
Figure 29. FAS looking North.
Figure 30. FOS looking Northeast, Autochamber #1.

Figure 31. FOS looking South, Autochamber #2.
Appendix C:
More Wavelet Coherence Analysis
Figure 32. AOS - Continuous Wavelet Transforms of AOS Soil CO$_2$ Efflux, 15 cm Soil Moisture, and 15 cm Soil Temperature.
Figure 33. FAS - Continuous Wavelet Transforms of FAS Soil CO$_2$ Efflux, 15 cm Soil Moisture, and 15 cm Soil Temperature.
Figure 34. FOS - Continuous Wavelet Transforms of FOS Soil CO₂ Efflux, 15 cm Soil Moisture, and 15 cm Soil Temperature.
Figure 35. AOS - Cross Wavelet Transforms of AOS Soil CO$_2$ Efflux and 15 cm Soil Moisture (top) and Soil CO$_2$ Efflux and 15 cm Soil Temperature (bottom).
Figure 36. FAS - Cross Wavelet Transforms of FAS Soil CO$_2$ Efflux and 15 cm Soil Moisture (top) and Soil CO$_2$ Efflux and 15 cm Soil Temperature (bottom).
Figure 37. FOS - Cross Wavelet Transforms of FOS Soil CO$_2$ Efflux and 15 cm Soil Moisture (top) and Soil CO$_2$ Efflux and 15 cm Soil Temperature (bottom).
Appendix D:
Temperature-Moisture Efflux Analyses

Figure 38. FOS Temperature-efflux correlation (top) and residual-SWC correlation (bottom).
Figure 39. FAS Temperature-efflux correlation (top) and residual-SWC correlation (bottom).
Figure 40. AOS Temperature-efflux correlation (top) and residual-SWC correlation (bottom).
Appendix E:
Phenoperiod Temperature-Moisture Efflux Analyses

Figure 41. FAS Phenoperiod 1 temperature-efflux correlation (top) and Phenoperiod 2 temperature-efflux correlation (bottom).
Figure 42. AOS Phenoperiod 1 temperature-efflux correlation (top) and Phenoperiod 2 temperature-efflux correlation (bottom).
Figure 43. FOS Phenoperiod 1 temperature-efflux correlation (top) and Phenoperiod 2 temperature-efflux correlation (bottom).
Appendix F:
Nighttime NEE Comparison with Soil Respiration Measurements

Figure 44. FASET nighttime NEE versus autochamber measured Rs.
Figure 45. Gap-filled Re nighttime data versus autochamber measured Rs, showing that Rs accounts for about 65% of total ecosystem respiration.
Figure 46. C fluxes at FASET. NEE and GPP inverted to facilitate comparison with respiratory effluxes. REgf = gap-filled $R_e$. 
Appendix G: Hydrology

Figure 47. AAS Volumteric SWC versus absolute value of Soil Matric Potential (Kpa). SWC converted to matric potential using the method of Romberger et al. (1986). Note that 1500 Kpa is a typical wilting point for plants.
Figure 48. Data from all working SWC sensors at AOS. SWC increases to above 25% on some occasions. Deeper SM sensor stays uniformly drier than surface during growing season.

Figure 49. Data from all working SWC sensors at FOS. Both 30 and the 60cm do not get as wet, nor dry as fast, as the 5 and 15cm sensors. Surface eventually dries more than deep (30-60cm) sensors.
Figure 50. Data from all working SWC sensors at AAS. Deep SWC does not dry as much, nor get as wet, as surface sensors.

Figure 51. All data from working SWC sensors at FAS. Note different SWC axis scale. FAS is much wetter than other sites. Deep sensor stays driest.