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# The effects of a changing climate on root respiration of woody plants in sugar maple forests and northern peatlands

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# THE EFFECTS OF A CHANGING CLIMATE ON ROOT RESPIRATION OF WOODY PLANTS IN SUGAR MAPLE FORESTS AND NORTHERN PEATLANDS

By

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This thesis, “The Effects of a Changing Climate on Root Respiration of Woody Plants in Sugar Maple Forests and Northern Peatlands,” is hereby approved in partial fulfillment of the requirements for the Degree of MASTER OF SCIENCE IN FOREST ECOLOGY AND MANAGEMENT.

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## Abstract

Global climate change might significantly impact future ecosystems. The purpose of this thesis was to investigate potential changes in woody plant fine root respiration in response to a changing climate. In a sugar maple dominated northern hardwood forest, the soil was experimentally warmed (+4 °C) to determine if the tree roots could metabolically acclimate to warmer soil conditions. After one and a half years of soil warming, there was an indication of slight acclimation in the fine roots of sugar maple, helping the ecosystem avoid excessive C loss to the atmosphere. In a poor fen northern peatland in northern Michigan, the impacts of water level changes on woody plant fine root respiration were investigated. In areas of increased and also decreased water levels, there were increases in the $CO_2$ efflux from ecosystem fine root respiration. These studies show the importance of investigating further the impacts climate change may have on C balance in northern ecosystems.

# Chapter 1

## Thesis Introduction

The Intergovernmental Panel on Climate Change (IPCC) predicts that by 2100, the planet as a whole will be from 2-4°C warmer, with significant local and regional changes in water availability due to altered precipitation regimes (IPCC 2007). Greenhouse gases are one of the main contributors to climate change, with these gases affecting the radiative balance of this planet, generally causing more energy to be reemitted toward the surface of the earth causing a general warming of the planet. The response of the autotrophic portion of this planet to climate change is not fully understood, and the purpose of this thesis is to improve our understanding of how root systems of woody plants might respond to climate change and how this will affect ecosystem carbon balance and possible feedbacks to atmospheric $CO_2$ and climatic forcing.

This study chose to specifically investigate root respiration of plants as the way to determine the effects of climate change on these systems. Respiration is the use of photosynthate to create energy and carbon skeletons. Respiration occurs in all living tissues of the plant and the energy created through this process is used in creating new tissue, maintaining tissues, and conducting transport of ions. Respiration is a metabolic process, and thus, is sensitive to temperature and has been found to often respond exponentially to increased temperatures (Tjoelker et al. 2001). The fine roots (<1 mm) of woody perennials are very active. For example, the very fine roots (< 0.5 mm) in surface

soil (0-10 cm soil depth) have been found to contribute 53% to ecosystem root respiration (Burton et al. 2011).

If climate change occurs during the next century, and global temperatures rise, then we could see exponential increases of root respiration, in accordance with values of $Q_{10}$ in the range of 2 to 3 ($Q_{10}$ is the relative increase in respiration for every 10 °C increase in temperature) (Piao et al. 2010). This exponential increase in respiration would represent an increased return of photosynthate to the atmosphere as $CO_2$ (a greenhouse gas). A positive feedback loop could then occur with this increase in atmospheric $CO_2$ increasing global temperatures more, and thus causing respiration rates to increase further. This enhanced respiratory release of $CO_2$ also would represent less C that the plant can use for biomass production, and thus could affect net primary productivity (NPP). However, if the plants can acclimate, that is metabolically down-regulate respiration as temperatures rise, they can mitigate C loss from the plant to the atmosphere. The following chapters will discuss two experiments conducted to observe changes in fine root respiration in two very different ecosystems. The research described in Chapter 2 was conducted in a sugar maple (*Acer saccharum* Marsh.) dominated northern hardwood forest in northern Michigan where the soil was experimentally warmed to mimic climate change. The degree to which sugar maple root respiration can metabolically acclimate to these increased temperatures was observed in heated soil both with and without a the use of water addition to alleviate drier soil conditions associated with increased temperatures. Chapter 3 describes research conducted in a sphagnum dominated poor fen located in northern Michigan, with black spruce (*Picea mariana* (Mill.) B. S. P.), tamarack (*Larix*

*laricina* (Du Roi*)* K. Koch), cranberry (*Vaccinium* spp.), and leatherleaf (*Chamaedaphne calyculata*) plants. This fen was altered by a failed agriculture attempt that was put in place in the early 1900's. As a result of this abandoned effort, the site has a series of levees and ditches to control and drain water coming into the fen. This situation provided an opportunity to observe the effects of water table on changes in the woody vegetation component in this peatland, and how root respiration is affected by altered aeration that is representative of possible impacts of climate change on water table depth.

# Chapter 2

## Short-term responses of woody fine root respiration to warmer soil in a sugar maple dominated northern hardwood forest exhibits metabolic acclimation


### *Abstract*

Climate change will potentially impact C cycling in terrestrial ecosystems during the next century. Plant respiration uses a significant portion of $CO_2$ fixed during photosynthesis, and predicted warmer future temperatures could result in an exponential increase in plant respiration, increasing the amount of photosynthate returned to the atmosphere as new $CO_2$, and decreasing the amount of C sequestered in new plant biomass. One way a plant may counteract this C loss is through metabolic acclimation, a physiological down-regulation of respiration at increased temperature. This study examined root respiration in an experimentally warmed sugar maple dominated northern hardwood forest in the Upper Peninsula of Michigan, United States. The objective was to determine if fine roots of these trees had the capacity to acclimate to warmer soil temperatures (+4 °C) and minimize the C loss from the ecosystem. This study was conducted from 2009-2011, and included a pre-treatment period from May 2009 through June 2010, with the initiation of treatments during late summer of 2010 and continuing throughout the growing season of 2011. Root respiration was measured biweekly throughout the growing season, at both ambient soil temperature for the sample date and at a reference temperature of 18°C. The pre-treatment period found no inherent differences between any of the future treatment

plots. Part of the experimental design consisted of an additional treatment of heat and water (ambient +30%), intended to maintain adequate soil moisture content for heated soil experiencing increased evaporative demand. The heat + water treatment allowed us to assess whether apparent acclimation due to soil warming was due to increased temperature or simply a reduction in respiration associated with drier soil conditions. During the treatment period we found down-regulation of metabolic capacity (respiration rate at the 18°C reference temperature) for the plots receiving the heat treatment. Much of this was due to drier soil conditions caused by heating, but when soil moisture effects were accounted for, there was still down-regulation of root respiration with heating, indicating a slight degree of acclimation. The combined effects of dry soil conditions and acclimation resulted in average root respiration for the heat and heat + water treatments being 6 and 26% greater, respectively, than in the control, which is far less than the 48% increase that would have resulted if a simple exponential increase had occurred for the 4°C increase in soil temperature.

## *Introduction*

Climate change and its potential impacts on terrestrial ecosystems are a growing global concern. The Intergovernmental Panel on Climate Change (IPCC) predicts that many regions of the planet will warm significantly by 2100, while on the other hand, some regions will actually become cooler (Christensen et al. 2007). Additionally, some regions of the planet are predicted to receive more annual precipitation, while other regions might receive less annual precipitation (Christensen et al. 2007). The region of the upper Great

Lakes, including the Upper Peninsula of Michigan, is predicted to experience 3.5°C increase in temperature by 2100 with a possible slight decline in growing season precipitation (Christensen et al. 2007). Understanding how these changes will alter productivity and C cycling in terrestrial ecosystems will help humans make management decisions to either mitigate changes or prepare for a different planet.

The terrestrial portion of the planet sequesters 1.0 ± 0.8 Pg C/yr (House et al. 2003). From 30% - 80% of this is used during plant tissue respiration annually and returns to the atmosphere (Atkin and Tjoelker 2003; DeLucia et al. 2007; Litton et al. 2007; Luyssaert et al. 2007). The total soil carbon efflux portion of the carbon cycle has been found to be 60-80% of total ecosystem respiration, of which 30-60% of soil carbon efflux is attributed to root respiration (Bowden et al. 1993; Epron et al. 1999; Nakane et al. 1996; Pregitzer et al. 1998). Plant autotrophic respiration of $CO_2$ from forests is 45-60 Pg C/yr (Atkin and Tjoelker 2003; Luyssaert et al. 2007), which is currently six to seven times the annual C release from fossil fuel combustion (Piao et al. 2010). The fine roots (<1 mm) of woody perennials are very active contributors to ecosystem respiration. In northern hardwood forests, very fine roots (< 0.5 mm) in surface soil (0-10 cm soil depth) contributed 53% to ecosystem root respiration, and those to a depth of 50 cm contributed 69% of ecosystem root respiration (Burton et al. 2011). Plant tissue respiration has been found to increase exponentially in response to immediate increases in temperature (Piao et al. 2010; Ryan et al. 1997; Tjoelker et al. 2001) with a $Q_{10}$ often between 1.8 and 2.9 (Piao et al. 2010). ($Q_{10}$ is the increase in respiration rate for every 10°C). If this response to temperature holds true for a long-term climatic warming, net primary productivity

(NPP) could be affected, as exponentially more photosynthate would be used for respiration and lost as $CO_2$ at higher temperatures, with less left for NPP. This could lead to faster $CO_2$ build up in the atmosphere, as C that would have normally been sequestered in plant biomass was released through autotrophic respiration enhancing the greenhouse effect. A positive feedback loop could occur where increased temperatures would cause more $CO_2$ to return to the atmosphere, causing even higher global temperatures (Woodwell and Mackenzie 1995).

However, this positive feedback loop could be lessened if the plants acclimated to these warmer temperatures by reducing metabolic activity of existing tissues or by creating new less metabolically active tissues when ephemeral components, such as leaves and fine roots, are replaced. Acclimation to warmer temperatures has been found to occur in some plant tissues and the sensitivity of respiration to temperature can decline with warmer temperatures (King et al 2006). Atkin and Tjoelker (2003) found that $Q_{10}$ values for plant respiration are not constant, but decline linearly with increasing temperatures. They state that respiration is limited at low temperatures by maximum enzymatic activity, but shifts to substrate limitations at higher temperatures, thus affecting $Q_{10}$ values. If substrate limitation moderates the increase in respiration with climatic warming, then it may be possible to maintain or increase NPP. The presence and ranges of acclimation are still unknown for many types of plant tissues, but Tjoelker et al. (2001) found that an increase of 1°C ambient temperature could reduce the $Q_{10}$ value for foliar respiration by 0.04. However, the long-term scale of acclimation to temperature changes may be lower than the short-term scale (Tjoelker et al. 2008). Atkin et al. (2000a) found acclimation

occurred in snow gum leaves (*Eucalyptus pauciflora*) within one day to changes in temperature. Ryan et al. (1997) state that scientific analysis on plant tissue respiration should be investigated with different tree organs (i.e. leaf, stem and root). Piao et al. (2010) ponder what fractions of the total plant tissue respiration are leaf, stem and root. Additionally, they ask if each tree organ (leaf, stem and root) shows similar temperature sensitivity, and if acclimation is possible for these different plant tissues. Atkin et al. (2000b) synthesized several studies across different species of plants where acclimation of root respiration does occur. These species where acclimation occurs due to changing growth temperatures are; *Plantago lanceolata, Zostera mariana, Citrus volkameriana, Festuca ovina, Juncus squarrosus, Nardus stricata, Bellis perennis, Poa annua* and *Holcus lanatus*. Bryla et al. (1997) found growth in different moisture regimes affected temperature acclimation, in which *Citrus volkameriana* root respiration exhibited temperature acclimation when growing in wet soils, but showed no acclimation when growing in dry soils. Though the mechanisms that may cause temperature acclimation in roots are unclear, Atkin et al. (2000b) suggests that the main factor for a short-term response of respiration to temperature is a change in the demand for ATP at warmer temperatures, while at low soil temperatures, the response of respiration to temperature is controlled by enzyme activity. Aktin et al. (2000b) states that a method to determine acclimation is to compare measurements at a common measuring temperature on plant species grown with different growing temperatures. This study chose 18°C as the common reference temperature to assess acclimation, because 18°C is typically close to the soil temperature during the warm portion of the growing season (Figure 2.1).

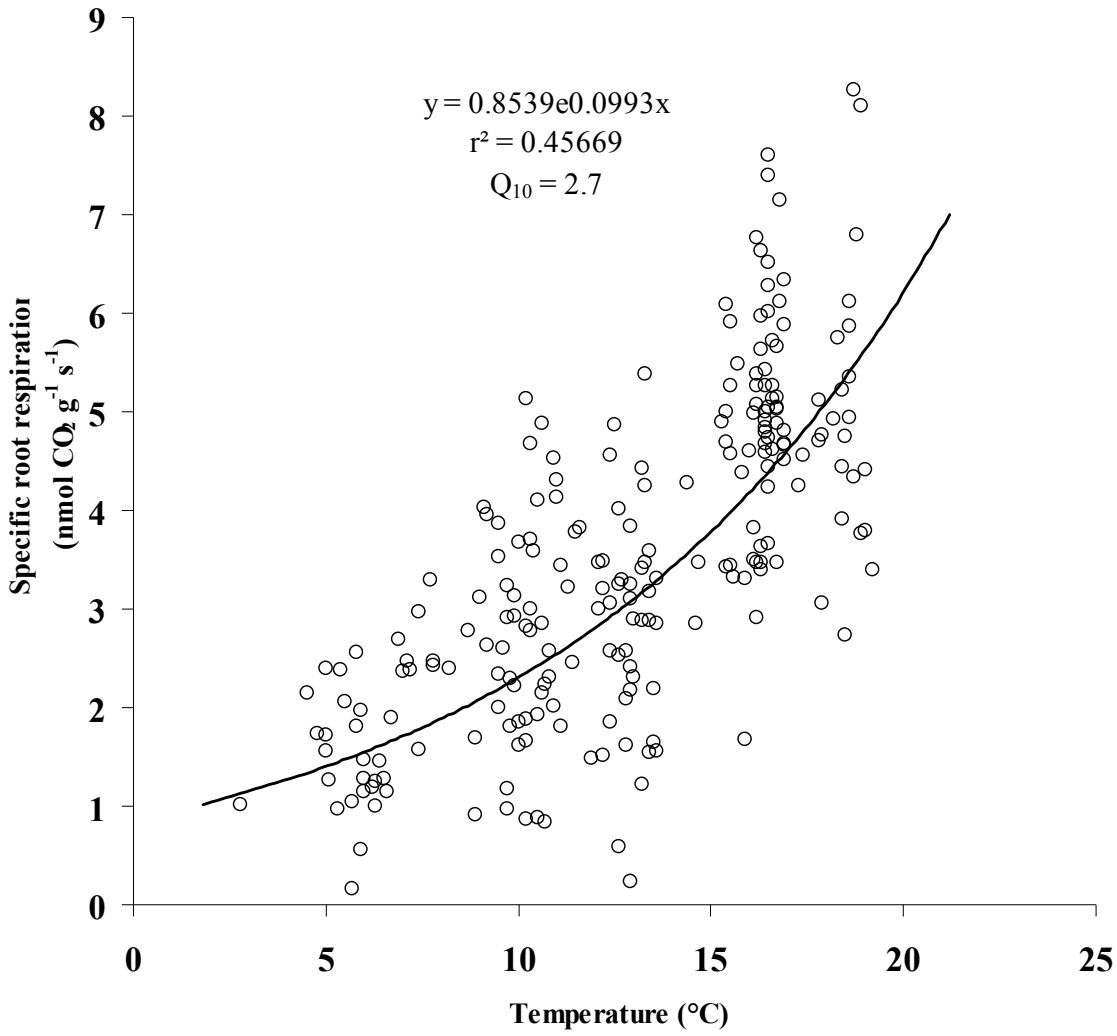


Figure 2.1. Temperature response curve for specific root respiration at ambient soil temperature May 2009 through August 2011

There are several scenarios that can occur with metabolic acclimation of fine root respiration to temperature at the ecosystem level. There could be no metabolic acclimation, in which the trees would either lose an increased amount of C to respiration or need to undergo other adjustments to mitigate the increase in carbon loss associated with increased temperatures (i.e. reduce root biomass). There also could be acclimation by adjusting metabolic capacity of plant cells found in the fine roots. For example, this metabolic adjustment could be a reduction in the number of mitochondria in each cell, which would lower the amount of respiration taking place. Another scenario would be the number of cell mitochondria remaining unchanged, but the rate at which each cell undergoes respiration decreasing. Plant mitochondria can be likened to the power stations of cells. The first acclimation scenario (a reduction of mitochondria) could be similar to a city reducing the number of power stations, but running all the power stations at an unchanged rate. The second acclimation scenario (a reduction in the rate at which the cell undergoes respiration) could be imagined as the city maintaining the same number of power stations, but just reducing the output of each station slightly. Both scenarios would reduce the amount of $CO_2$ leaving the power station and entering the atmosphere. An indicator of this metabolic change could be sugar maple trees growing in warmer conditions creating new fine roots with lower N concentration.

Acclimation, or other responses of the tree to limit C loss, would help mitigate any negative effects of increased temperature on NPP and maintain a forest's carbon sink

strength. Additionally, NPP could increase as global $CO_2$ levels rise and plants undergo $CO_2$ fertilization thus increasing plant water use efficiency (Amthor 1995; DeLucia et al. 1999), and increased temperatures could also create a longer growing season (Menzel and Fabian 1999; Tucker et al. 2001). This situation would allow trees to capture more C by starting photosynthesis earlier in the year. However, to conduct this photosynthesis the trees would have to be supplied with adequate water and nutrients that would allow them conduct photosynthesis and respiration. Atkin and Tjoelker (2003) further postulate that water availability could have an effect on the ability of plant tissue respiration to acclimate to warmer temperatures.

The objective of this study was to see if the fine roots (<1 mm) in a sugar maple dominated northern hardwood forest could metabolically acclimate to increased soil temperatures, avoiding excessive C loss to respiration. This study was located in the Upper Peninsula of Michigan. The soil was experimentally warmed (+4°C) with the use of infrared heating lamps in a factorial combination with water additions intended to maintain the soil moisture in a subset of heated plots at an equivalent level to that found on unheated control plots. This water addition was intended to allow the effects of warmer soil on plant respiration to be separated from effects created by co-occurring drier soil conditions. Specific hypotheses included:

## Hypothesis 1

*The specific root respiration of sugar maple will increase exponentially with seasonal increases in temperature, with no seasonal acclimation (i.e. down-regulation) during warm periods of the year.*

## Hypothesis 2

*There will be no short-term acclimation of fine root respiration in response to experimental soil warming.* As a result, in the days to weeks after the initiation of treatments specific root respiration from the heat plus water addition plots will be significantly higher than the control plots at ambient temperature, and similar to the control plots at the reference temperature of 18°C. After the initiation of treatments the specific root respiration at ambient temperature will be the highest for the heat plus water addition, intermediate for the heat addition, and lowest for the control and water addition plots.

## Hypothesis 3

*There will be long-term acclimation of fine root respiration in months to years after the initiation of experimental warming.* This will be the result of new fine roots being constructed with changes in root N content. As a result, there will be less fine root N in the heat plus water addition, intermediate lessening of fine root N in the heat only and the water only addition, and no change in root N for the control plots after the presence of acclimation occurs when compared to the other treatments.

## *Materials/Methods*

### Location

This study was conducted at Michigan Technological University's Ford Forestry Center (FFC) in Baraga County, Michigan (46° 38' 26.17" N 88° 29' 00.94" W, 400 m elevation) during the growing seasons of 2009 through 2011. Mean annual temperature in this region is 4.9 °C, with a growing season average temperature of 15°C across 134 growing season days. This area receives on average 879 mm of annual precipitation, with 401 mm of precipitation during the growing season (Burton et al. 2011). During the pretreatment measurement year of 2009, the MAT was 4.0 °C with monthly average temperature ranging from 16.9 °C in August to -15.2 °C in January. This pretreatment time period also accumulated 915.2 mm of annual precipitation. The MAT in 2010 was 6.2 °C with a monthly average ranging from 20.2 °C in July to -8.5 °C in January. The site received 697.7 mm of precipitation in 2010 (Table 2.1).

Table 2.1. Thirty year average temperature and precipitation data from NOAA, and on site precipitation data from a rain gauge in Alberta, MI for 2009 and 2010

| | | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temperature (C) | Thirty Year Average | -12.0 | -9.6 | -3.9 | 3.4 | 11.2 | 16.1 | 18.9 | 17.9 | 12.9 | 6.9 | -1.4 | -8.7 | 4.3 |
| | 2009 | -15.2 | -9.2 | -4.5 | 3.4 | 9.9 | 14.9 | 15.5 | 16.9 | 16.4 | 4.1 | 3.7 | -8.2 | 4.0 |
| | 2010 | -8.5 | -8.1 | 1.7 | 7.6 | 13.6 | 15.8 | 20.2 | 20.1 | 11.3 | 8.1 | 0.8 | -7.8 | 6.2 |
| Precipitation (mm) | Thirty Year Average | 46.0 | 32.5 | 55.1 | 54.4 | 84.8 | 88.6 | 99.8 | 99.1 | 93.0 | 79.0 | 69.3 | 46.2 | 847.9 |
| | 2009 | 57.7 | 71.9 | 15.2 | 105.4 | 34.0 | 79.5 | 75.7 | 167.1 | 70.1 | 147.1 | 16.5 | 74.9 | 915.2 |
| | 2010 | 57.2 | 64.5 | 2.3 | 9.9 | 58.7 | 61.7 | 100.6 | 25.4 | 189.5 | 49.8 | 45.5 | 32.8 | 697.7 |
| Precipitation (mm) | Actual Rain Gauge | | | | | | | | | | | | | |
| | 2009 | - | - | - | - | - | 43.2 | 55.4 | 104.1 | 66.5 | 135.6 | 20.1 | 54.6 | 479.6 |
| | 2010 | 32.3 | 39.9 | 2.3 | 25.7 | 33.8 | 102.6 | 106.7 | 57.4 | 179.8 | 38.1 | 47.2 | 41.1 | 573.0 |
| | 2011 | 41.9 | 14.0 | 26.9 | 77.7 | 46.2 | 87.4 | 18.0 | 39.6 | - | - | - | - | 145.0 |
| | Average | 37.1 | 26.9 | 14.6 | 51.7 | 40.0 | 77.7 | 60.0 | 67.1 | 123.2 | 86.9 | 33.7 | 47.9 | 399.2 |

Sugar maple dominates the overstory (>5.0 cm dbh), contributing 89.3% (21.7 $m^2$ $ha^{-1}$) of the overstory basal area. American elm (*Ulmus americana* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), ironwood (*Ostrya virginiana* (Mill.) K. Koch) and yellow birch (*Betula alleghaniensis* Britton) comprise the remainder. Dominant trees in the overstory are at least 100 years in age. Understory species consist of young sprouts and seedlings of overstory trees with the addition of black cherry (*Prunus serotina* Ehrh.), which rarely competes successfully in the overstory at this location. The herbaceous layer consists of American fly honeysuckle (*Lonicera canadensis* Bartram ex Marsh.), common lady fern (*Athyrium filix-femina* (L.) Roth), spinulose shield fern (*Dryopteris carthusiana* (Vill.) H.P. Fuchs), wild leek (*Allium burdickii* (Hanes) A.G. Jones), dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.), trillium (*Trillium* spp. L.) and yellow trout lily (Erythronium americanum Ker.).

The soil at the site is classified as a Kallio cobbly silt loam (Coarse-loamy, mixed, superactive, frigid Oxyaquic Fragiorthods), which consists of a cobbly silt loam to silt loam to a depth of 41 cm below soil surface, where deeper soil consists of sandy loam to 86 cm turning to gravely loam at the deepest depths of 152 cm.

Disturbance in this forest is historically windthrow and single-tree death (Goodale and Aber 2001; Lorimer 2001). However, since the heavy logging and subsequent clear cutting and fires in the late 19$^{th}$ century that occurred in this area, the canopy is more evenly aged and singletree death is the most common form of disturbance today. This

area also occasionally experiences instances of periodic ice damage (Goodale and Aber 2001), defoliation by insects (Kulman 1971) and canopy dieback of sugar maple (Duchesne et al. 2003).

## Experimental Design

Twelve 10 m by 10 m research plots were established in 2009. These were divided into three blocks of four plots based on geographic separation, with each of four treatments randomly assigned to one plot in each group. Experimental treatments included a control (no treatment), soil warming (+4 °C) by infrared lamps, water addition (ambient + 30% of average ambient), and soil warming plus water. The water additions are intended to offset the increased evaporative water loss due to warming. Wooden boardwalks were installed throughout the plots to minimize disturbance and soil compaction during installation of equipment and sample collection.

Sixteen infrared heating lamps (model MRM1215 heaters, Kalglo Electronics Co., Bethlehem, PA) were suspended 1.5 m above the soil surface for each of the heated plots with the use of a ¾" stainless steel conduit framework. Each heated plot has four rows of IR lamps spaced 2.5 m apart, with each row containing four heaters, also spaced 2.5 m apart. The lamps were spaced so that their infrared beams would overlap slightly on the surface of the soil to ensure adequate and even distribution of radiation. The infrared heating lamps were manually adjusted to 80% power to allow the soil to a depth of at least 5 cm to increase in temperature by at least 4°C. The lamps were kept on throughout

the snow-free season, from early May to mid-November and stayed on 24 hours per day to follow diurnal fluctuations. Measurements on site indicate the actual heated area slightly exceeded the targeted 10 m by 10 m area and soil temperature slowly declined for up to 2 meters outside of the plot edge where soil temperatures equaled the temperature found on the control plots (Table 2.2 and Figures 2.2 & 2.3).

Table 2.2. Temperature differential along transects (n = 24) conducted from inside (-0.05) and outside the 10 m by 10 m treatment plots for the heated treatments (heat and water + heat). Average plot temperature at the same time was 22.0 C (n = 120).

| Transect (m) | Temperature (°C) |
|---|---|
| -0.5 | 21.3 |
| 0 | 20.2 |
| 0.5 | 19.5 |
| 1 | 18.9 |
| 1.5 | 18.3 |
| 2 | 18.3 |

Figure 2.2. The heated footprint illustrated in snow reflects the complete dispersal of heat evenly across the 10 m by 10 m treatment plot. Note the heat extends beyond the 10 m by 10 m plot (Photo by M. Jarvi).

Figure 2.3. Partial heating extended beyond the 10 m by 10 m plots for up to 2 meters (Photo by M. Jarvi).

Soil and air temperature and soil moisture were monitored with data loggers recording at 30-minute intervals. At plot center soil temperature at depths of 1, 5 and 15 cm and air temperature at 1 m were monitored (Hobo U12 4-external channel outdoor/ industrial data logger with TMC6-HA probes, Onset Computer Corporation, Bourne, MA). Volumetric soil moisture and soil temperature were also recorded at 2, 5 and 10 cm below soil surface under heater rows and 2 and 5 cm depths halfway between heater rows in locations approximately midway from plot center to plot edge (Em50 data loggers with 5TM temperature/moisture probes, Decagon Devices Inc., Pullman, Washington). Additionally, on plots receiving warming, soil moisture was monitored at 2 and 5 cm below the soil surface directly under and halfway between heater rows near the plot edge (Hobo U12 4-external channel outdoor/industrial data logger with TMC6-HA probes, Onset Computer Corporation, Bourne, MA).

Ambient precipitation was measured with a weighing rain gage (Model 5-780, Belfort Instrument Co., Baltimore, MD) located in an open area 150 m from the experimental plots. Precipitation used for the water addition plots was captured with the use of three-1,900 L tanks and gutter systems on rooftops of buildings at the Ford Forestry Center, in close proximity to the study site. Water was distributed to the plots with the use of four sprinkler heads (5000 series rotor, Rainbird Corporation, Tucson, AZ) per plot that oscillated 90° from each corner of the plot. The sprinkler head output was adjusted so that there was a slight overlap of water at the center of the plot to ensure even distribution of water. Water addition schedules were arranged to supplement natural rain events when possible, to allow for natural wetting and drying cycles on watered plots.

## Root Respiration

Fine root respiration (<1 mm diameter) was measured periodically over three growing seasons from 2009 through 2011 using an open-system infrared gas analyzer (IRGA, CIRAS-1 and CIRAS-2 portable gas analyzers, PP Systems, Haverhill, MA) at both ambient soil temperature and a constant reference temperature of 18 °C. Measurements at the reference temperature were used to assess changes in respiratory capacity over time and across treatments, and have been found to be a reliable test of acclimation to experimental warming (Atkin et al. 2000a). Excised fine root samples were obtained with the use of a 5 cm diameter by 10 cm deep soil core. Three cores per plot were taken from the center 5 m by 5 m portion of the plot to maximize the likelihood of sampling roots that were connected to trees that had a vast majority of their root system located in treated soil. The roots were hand cleansed of soil, and approximately 2 g fresh weight of fine roots (<1 mm diameter) were placed in a respiration cuvette attached to the IRGA operating in an open system (Burton and Pregitzer 2003; Burton et al. 2011). Respiration rates were recorded after allowing fifteen minutes for readings to stabilize. The cuvette bases were placed in a water bath to maintain the respiration samples at the desired target temperatures. Respiration was analyzed at a $CO_2$ concentration of 1000 $\mu l\ l^{-1}$, which Burton et al. (1997) found approximates the soil $CO_2$ concentrations typically found near the soil surface of sugar maple dominated northern hardwood forests. The samples were subsequently dried at 65 °C for 48 hours in the lab to obtain dry weights of roots. The samples were then ground to a fine powder (8000M Mixer/Mill, Spex SamplePrep LLC,

Metuchen, NJ) and analyzed for nitrogen (N) concentration with an elemental analyzer (Carlo Erba NA 1500 NC, CE Elantech, Lakewood, NJ).

Root respiration was measured every two to three weeks during three time periods: pretreatment, post-installation of experimental infrastructure (post-installation) and treatment. The pretreatment period from May 2009 to June 2010 was used to determine if there were any underlying differences between the plots before any heating and water infrastructure was built and before any treatments were started. The post-installation period from July 2010 to September 2010 was used to determine if any changes in root respiration had occurred due to installation of the infrastructure that supports this experiment. The treatment period from September 2010 to August 2011 was the period of time after the initiation of treatments.

## Statistical Analyses

All statistical analyses were conducted with R (2.12.0, R Development Core Team, Vienna, Austria). Non-linear regression was used to develop temperature response curves of specific root respiration at ambient soil temperature using data from the pretreatment period for all plots, plus data from control plots from the post-installation and treatment periods. This non-linear regression was used to develop the $Q_{10}$ for specific root respiration applicable this forest. Seasonal acclimation was assessed from this data by plotting specific root respiration at the reference temperature of 18 °C against the applicable ambient soil temperatures for those sample dates. A strong negative

correlation would indicate that as seasonal temperatures increased, the roots acclimate to warmer temperatures by down-regulating specific root respiration. Repeated measures analysis of variance (ANOVA) was used to test the effects of soil warming and water additions on fine root respiration rates across time. Separate analyses were performed for the pretreatment, post-installation and treatment periods and for ambient and reference temperatures. The pretreatment and post-installation periods used date (repeated measure) and future treatment as factors in the ANOVA. The treatment period used a two-factor (heat and water) repeated measures (date) ANOVA.

## *Results*

### Pretreatment

The purpose of the pretreatment period was to compare future treatment designations to determine if there were any pre-existing differences. This period was also used to determine if there was any seasonal acclimation of root respiration, with a down regulation of specific root respiration as soil temperatures warmed. There were thirteen sample dates during the growing season within the pretreatment sample period occurring from 27 May 2009 to 30 June 2010. Repeated measures ANOVA indicated no significant differences between the plots and future treatment designations at both ambient ($P = 0.84$) and reference ($P = 0.86$) soil temperatures (Table 2.3, Figure 2.4 & 2.5). There are significant differences among sample dates at ambient ($P = <0.001$) and reference ($P = <0.01$) measurement temperatures. We found that the specific root respiration at this site does indeed increase exponentially with temperature, and subsequently used all pretreatment data, and all treatment data for the control plots to

develop a temperature response curve (Figure 2.1). This temperature response curve was fitted with a trend line using non-linear regression (Equation 2.1), where $R_t$ is specific root respiration and T is ambient soil temperature. This fitted equation was then used to develop the $Q_{10}$ for this site, which was 2.7 (Equation 2.2) (Figure 2.1).

Eq. 2.1: $R = 0.8539 * e^{0.0993 * T}$

Eq. 2.2: $Q_{10} = e^{(0.0993 * 10)}$

$Q_{10} = 2.7$

Table 2.3. Repeated measures ANOVA results for the pretreatment period (May 2009- June 2010).

| Treatment Period | Temperature | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|---|
| Pretreatment | Ambient | **Between** | | | | | |
| | | Treatment | 3 | 0.99 | 0.33 | 0.28 | 0.84 |
| | | Residuals | 8 | 9.37 | 1.17 | | |
| | | **Within** | | | | | |
| | | Date | 11 | 183.32 | 16.67 | 14.22 | <0.001 |
| | | Treatment x Date | 33 | 30.39 | 0.92 | 0.79 | 0.78 |
| | | Residuals | 88 | 103.16 | 1.17 | | |
| | Reference | **Between** | | | | | |
| | | Treatment | 3 | 2.67 | 0.89 | 0.25 | 0.86 |
| | | Residuals | 8 | 28.11 | 3.51 | | |
| | | **Within** | | | | | |
| | | Date | 11 | 101.10 | 9.19 | 3.10 | <0.01 |
| | | Treatment x Date | 33 | 51.87 | 1.57 | 0.53 | 0.98 |
| | | Residuals | 88 | 260.50 | 2.96 | | |

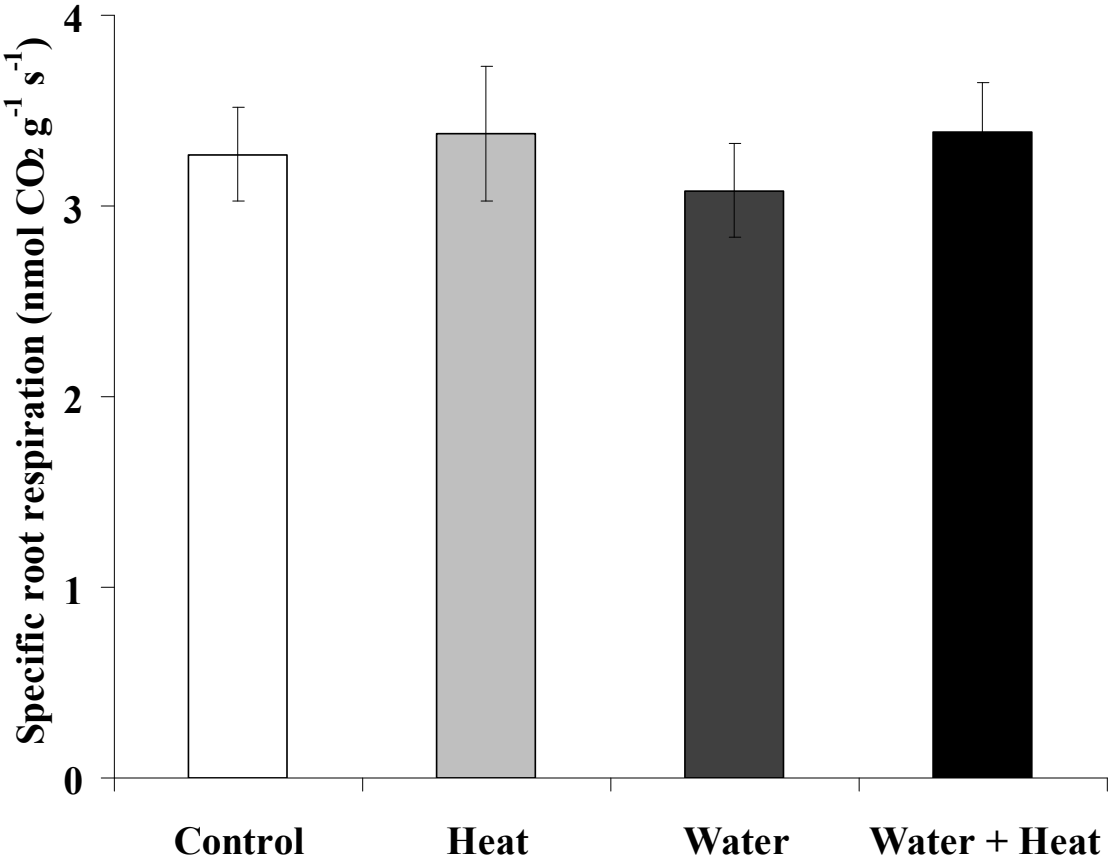


Figure 2.4. Average specific root respiration by treatment at ambient soil temperature (average 12.3°C) for the pretreatment period of 2009-2010 (n = 13). Error bars are standard error of the mean.

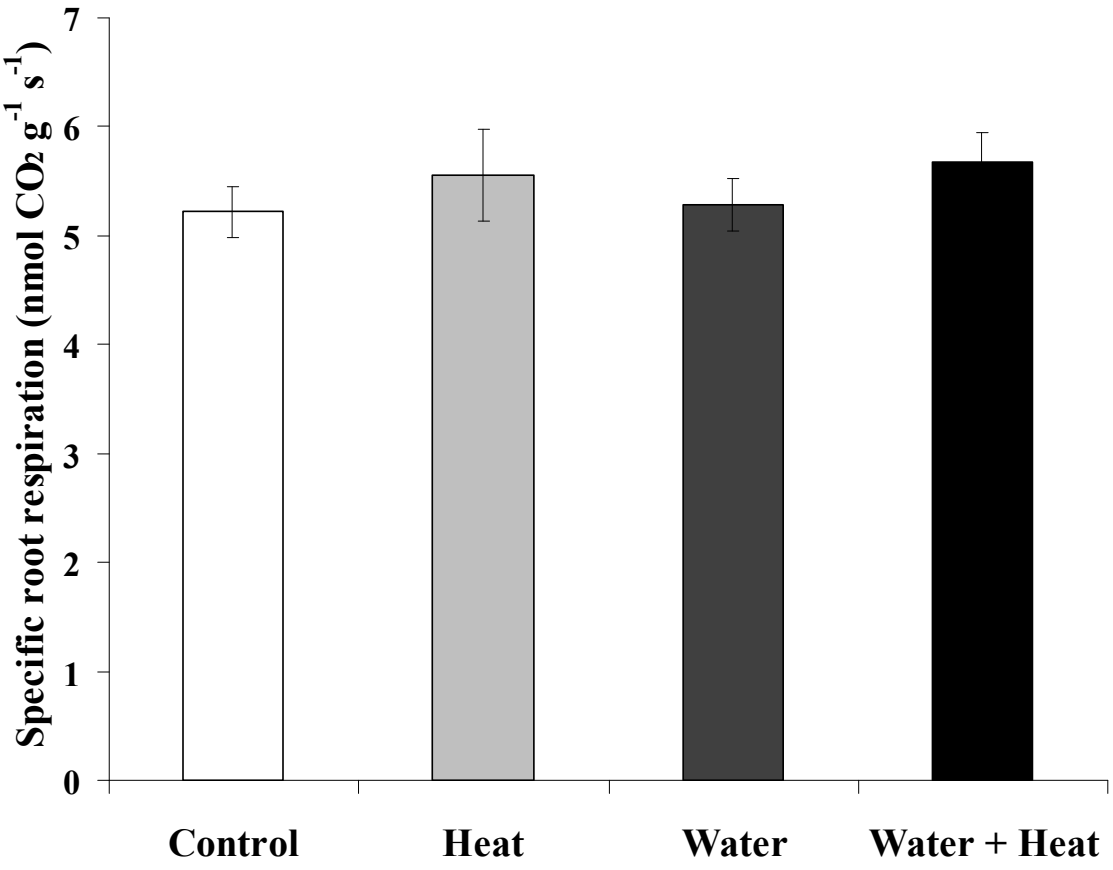


Figure 2.5. Average specific root respiration by treatment at the 18°C reference temperature (average 17.9°C) for the pretreatment period of 2009-2010 (n = 13). Error bars are standard error of the mean.

We used plotted specific root respiration at the reference temperature against ambient soil temperature for each sample date and fit a correlation to that data to determine if seasonal acclimation occurs on the site. Seasonal acclimation does not occur ($P = 0.47$, $r = -0.15$), with the fine roots of sugar maple showing little reduction in metabolic capacity, as indicated by specific root respiration at the reference temperature of 18°C, when considering periods of adequate soil moisture. When all time periods, including periods of drought, are used in the analysis there is a slight reduction of metabolic capacity with warmer soil temperature ($P = 0.09$, $r = -0.33$) (Figure 2.6).

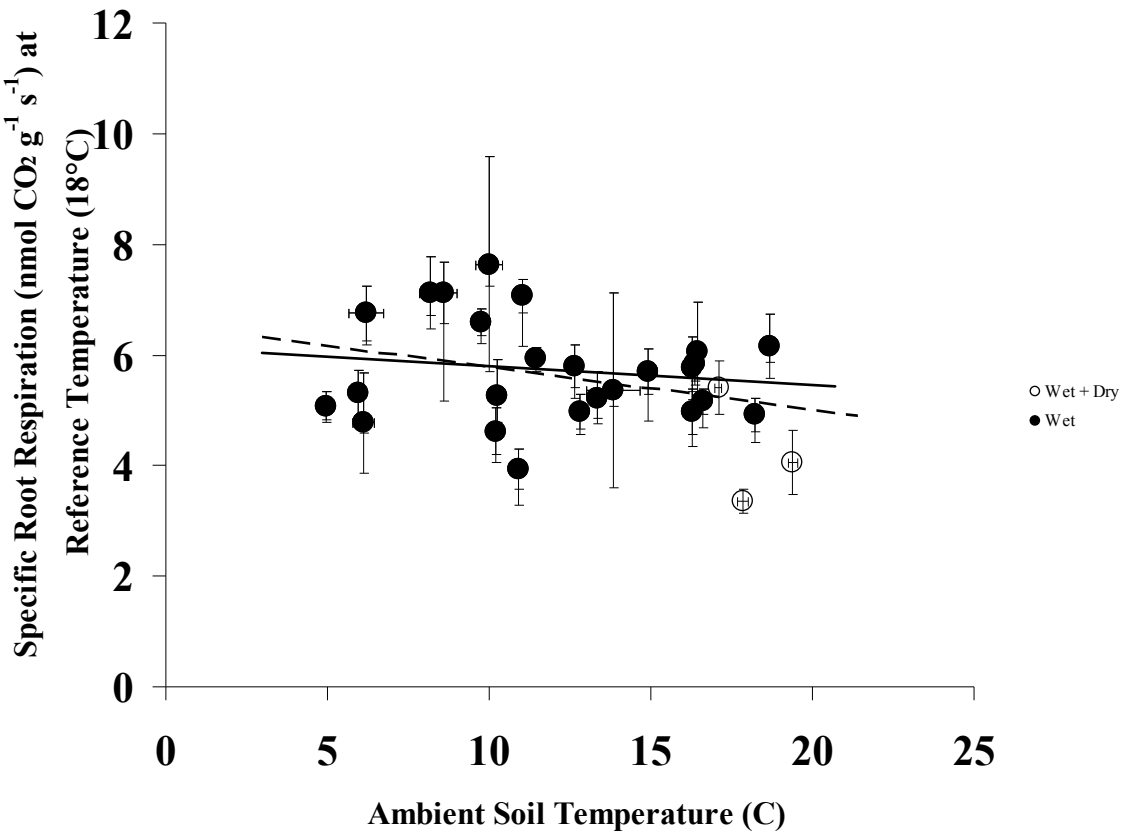


Figure 2.6. Specific root respiration at reference temperature plotted against the ambient soil temperature for each sample date to assess seasonal temperature acclimation. All pretreatment and post-installation plots and dates, with control plots from the post-warming dates used in the analysis. The closed circles and solid regression line indicate periods of adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$) (n = 25). The open circles indicate dry periods (<0.20 $cm^3$ $cm^{-3}$), and the dashed regression line is for all data (both wet and dry periods n = 28). Pearson's correlation for the wet period is -0.15 ($P$ = 0.47), and for the wet and dry period is -0.33 ($P$ = 0.09). Error bars are standard error of the mean for the twelve samples taken on each measurement date.

## Post-installation

The post-installation period occurred from 23 July 2010 to 13 September 2010 and consisted of four sampling dates. Repeated measures ANOVA indicated no significant differences among the future treatment designations after potential disturbance on the site during the construction of the infrastructure to support the experiment $P = 0.94$ at ambient temperature and $P = 0.94$ at reference temperature (Table 2.4, Figures 2.7 & 2.8). There was a significant measurement date effect ($P = <0.001$) at ambient soil temperature.

Table 2.4. Repeated measures ANOVA table for post-installation (2010).

| Treatment Period | Temperature | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|---|
| Post-installation | Ambient | **Between** | | | | | |
| | | Treatment | 3 | 0.86 | 0.29 | 0.14 | 0.94 |
| | | Residuals | 8 | 16.82 | 2.10 | | |
| | | **Within** | | | | | |
| | | Date | 3 | 45.72 | 15.24 | 13.71 | <0.001 |
| | | Treatment x Date | 9 | 17.18 | 1.91 | 1.72 | 0.14 |
| | | Residuals | 24 | 26.69 | 1.11 | | |
| | Reference | **Between** | | | | | |
| | | Treatment | 3 | 1.57 | 0.52 | 0.13 | 0.94 |
| | | Residuals | 8 | 31.26 | 3.91 | | |
| | | **Within** | | | | | |
| | | Date | 3 | 6.35 | 2.12 | 1.15 | 0.35 |
| | | Treatment x Date | 9 | 14.40 | 1.60 | 0.87 | 0.57 |
| | | Residuals | 24 | 44.34 | 1.85 | | |

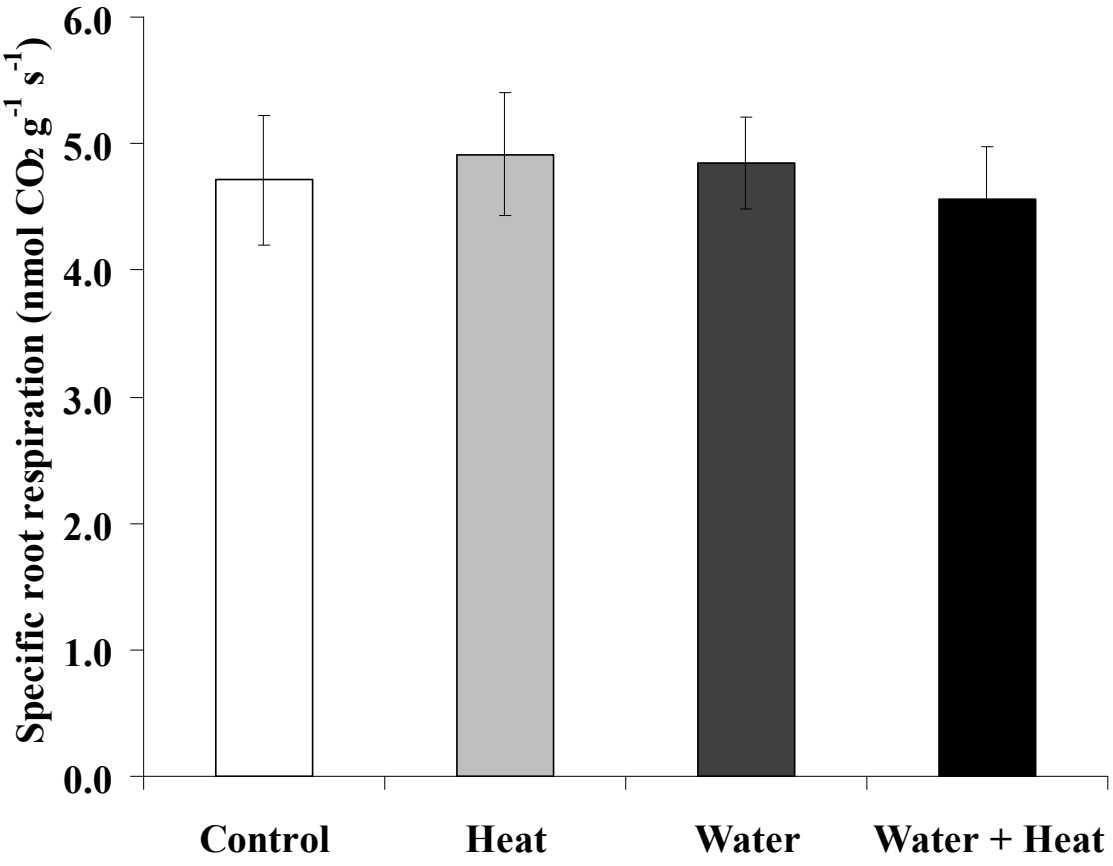


Figure 2.7. Average specific root respiration across treatments at ambient temperature (average 16.1°C) for the post-installation period of 2010 (n = 4). Error bars are standard error of the mean.

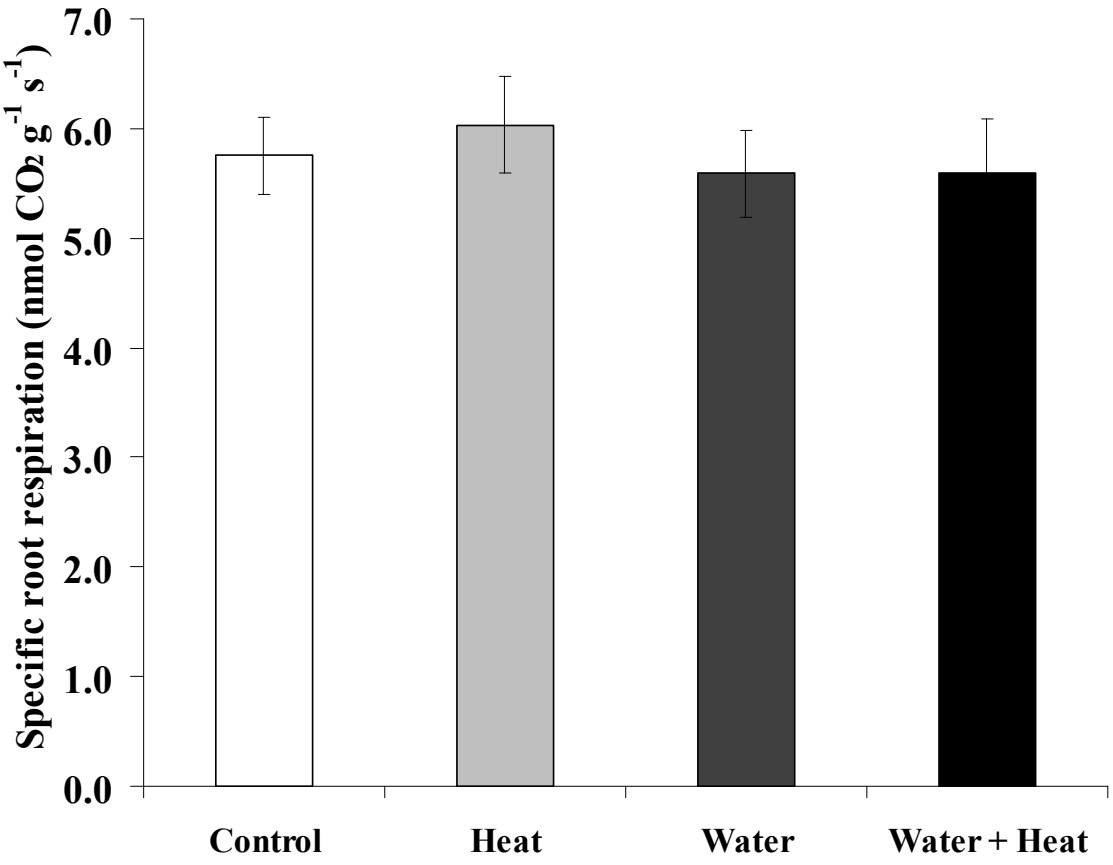


Figure 2.8. Average specific root respiration across treatments at reference temperature (average 18.0°C) for the post-installation period of 2010 (n = 4). Error bars are standard error of the mean.

## Treatment period

### All dates analyzed

The treatment period included 11 sample dates from 20 September 2010 to 12 November 2010 for the 2010 growing season, and from 13 May 2011 to 23 August 2011 for the 2011 growing season. There was a significant measurement date effect at ambient ($P$ = <0.001) and reference ($P$ = <0.001) temperatures during this period (Table 2.5). For root respiration measured at ambient soil temperature, a significant date x heat interaction ($P$ = 0.03) occurred and a slight water x date interaction occurred ($P$ = 0.07). At the reference temperature, there was a significant heat effect on root respiration (P =0.01) (Table 2.5, Figures 2.9 & 2.10).

### Dates with adequate soil moisture (>0.20 $cm^3\ cm^{-3}$)

Adequate soil moisture occurred for eight of the eleven treatments period sample dates, with 15 July 2011, 1 August 2011, and 23 August 2011 excluded due to dry soil conditions on the heated plots (Table 2.6, Figures 2.11, 2.12, 2.13). There was a heat effect on root respiration at ambient soil temperature for these dates ($P$ = 0.03) and a slight heat effect for root respiration at the reference temperature ($P$ = 0.07) (Table 2.6). There were also significant differences among sample dates in root respiration at both the ambient soil temperature ($P$ = <0.001) and reference temperature 18°C ($P$ = <0.01).

Table 2.5. Repeated measures ANOVA table for the treatment period (all dates 2010-2011).

| Treatment Period | Temperature | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|---|
| Treatment (all dates) | Ambient | **Between** | | | | | |
| | | Heat | 1 | 3.66 | 3.66 | 1.83 | 0.21 |
| | | Water | 1 | 7.46 | 7.46 | 3.73 | 0.09 |
| | | Heat x Water | 1 | 0.69 | 0.69 | 0.35 | 0.57 |
| | | Residuals | 8 | 15.99 | 2.00 | | |
| | | **Within** | | | | | |
| | | Date | 10 | 87.09 | 8.71 | 10.79 | <0.001 |
| | | Heat x Date | 10 | 17.70 | 1.77 | 2.19 | 0.03 |
| | | Water x Date | 10 | 14.78 | 1.48 | 1.83 | 0.07 |
| | | Heat x Water x Date | 10 | 3.75 | 0.37 | 0.46 | 0.91 |
| | | Residuals | 80 | 64.56 | 0.81 | | |
| | Reference | **Between** | | | | | |
| | | Heat | 1 | 42.37 | 42.37 | 14.30 | 0.01 |
| | | Water | 1 | 1.73 | 1.73 | 0.58 | 0.47 |
| | | Heat x Water | 1 | 4.44 | 4.44 | 1.50 | 0.26 |
| | | Residuals | 8 | 23.71 | 2.96 | | |
| | | **Within** | | | | | |
| | | Date | 10 | 157.28 | 15.73 | 9.58 | <0.001 |
| | | Heat x Date | 10 | 17.58 | 1.76 | 1.07 | 0.39 |
| | | Water x Date | 10 | 19.73 | 1.97 | 1.20 | 0.30 |
| | | Heat x Water x Date | 10 | 4.62 | 0.46 | 0.28 | 0.98 |
| | | Residuals | 80 | 131.30 | 1.64 | | |

Table 2.6. Repeated measures ANOVA table for the treatment period (adequate soil moisture dates 2010-2011).

| Treatment Period | Temperature | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|---|
| **Treatment (adequate volumetric soil water (>0.20 $m^3$ $m^{-3}$) dates)** | **Ambient** | **Between** | | | | | |
| | | Heat | 1 | 11.33 | 11.33 | 7.49 | 0.03 |
| | | Water | 1 | 2.62 | 2.62 | 1.73 | 0.22 |
| | | Heat x Water | 1 | 0.74 | 0.74 | 0.49 | 0.50 |
| | | Residuals | 8 | 12.10 | 1.51 | | |
| | | **Within** | | | | | |
| | | Date | 7 | 66.48 | 9.50 | 12.16 | <0.001 |
| | | Heat x Date | 7 | 1.72 | 0.25 | 0.32 | 0.94 |
| | | Water x Date | 7 | 4.37 | 0.62 | 0.80 | 0.59 |
| | | Heat x Water x Date | 7 | 2.49 | 0.36 | 0.45 | 0.86 |
| | | Residuals | 56 | 43.74 | 0.78 | | |
| | **Reference** | **Between** | | | | | |
| | | Heat | 1 | 17.59 | 17.59 | 4.47 | 0.07 |
| | | Water | 1 | 0.20 | 0.20 | 0.05 | 0.83 |
| | | Heat x Water | 1 | 4.81 | 4.81 | 1.22 | 0.30 |
| | | Residuals | 8 | 31.45 | 3.93 | | |
| | | **Within** | | | | | |
| | | Date | 7 | 42.88 | 6.13 | 3.21 | 0.01 |
| | | Heat x Date | 7 | 7.24 | 1.03 | 0.54 | 0.80 |
| | | Water x Date | 7 | 15.13 | 2.16 | 1.13 | 0.36 |
| | | Heat x Water x Date | 7 | 3.30 | 0.47 | 0.25 | 0.97 |
| | | Residuals | 56 | 106.90 | 1.91 | | |

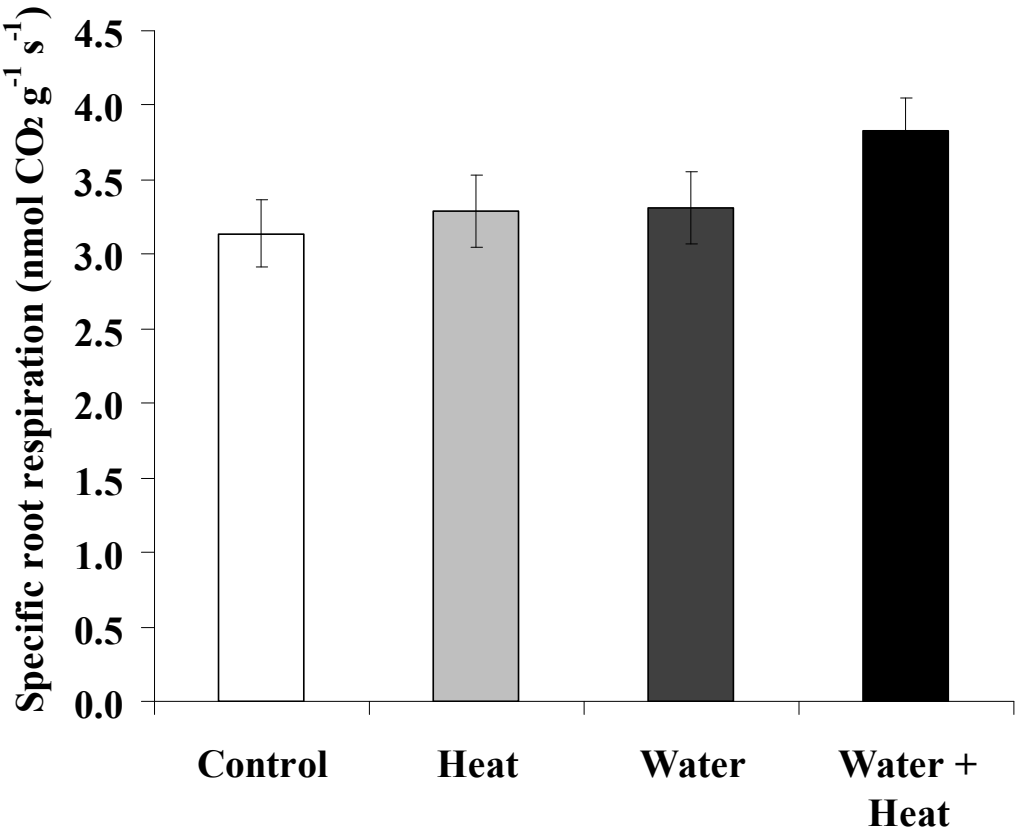


Figure 2.9. Average specific root respiration by treatment at ambient temperature (average 13.8°C) for the treatment period of 2010-2011 for all dates (n = 11). Error bars are standard error of the mean.

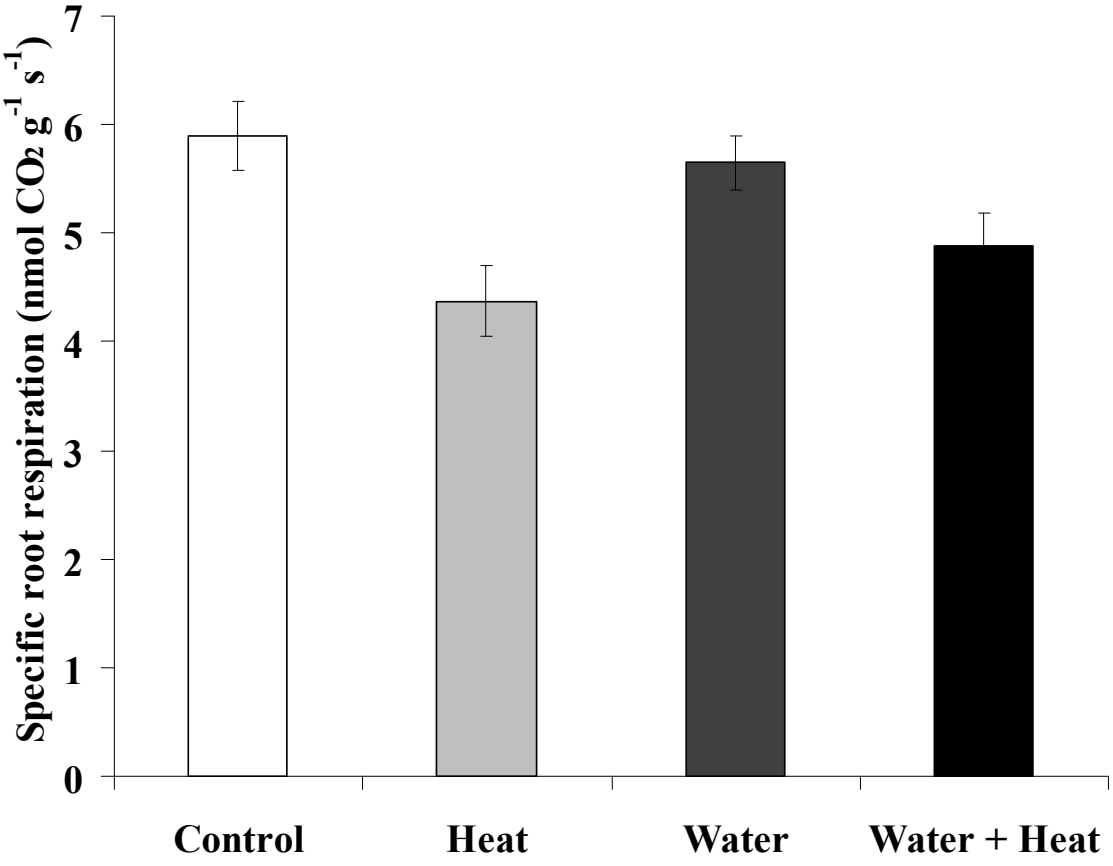


Figure 2.10. Average specific root respiration by treatment at reference temperature (average 18.0°C) for the treatment period of 2010-2011 for all dates (n = 11). Error bars are standard error of the mean.

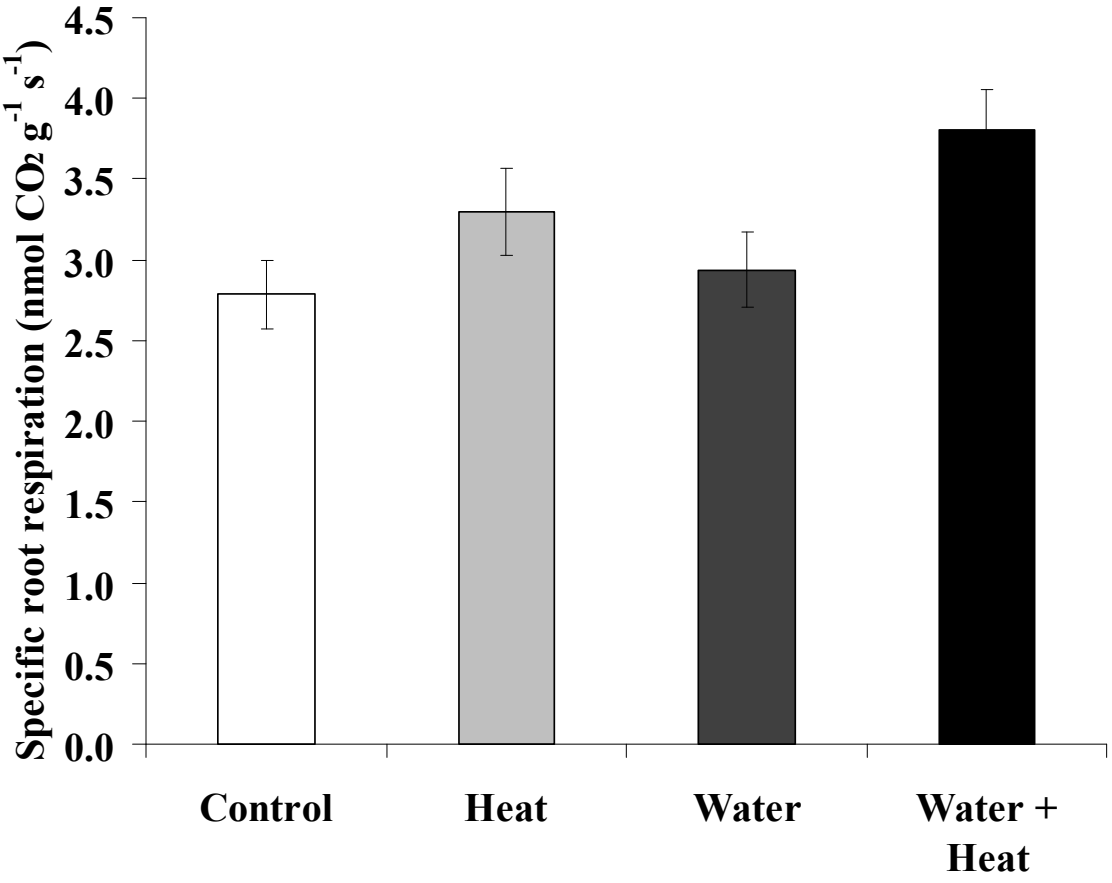


Figure 2.11. Average specific root respiration by treatment at ambient temperature (average 12.8°C) for the treatment period of 2010-2011 for all dates with adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$) (n = 8). Error bars are standard error of the mean.

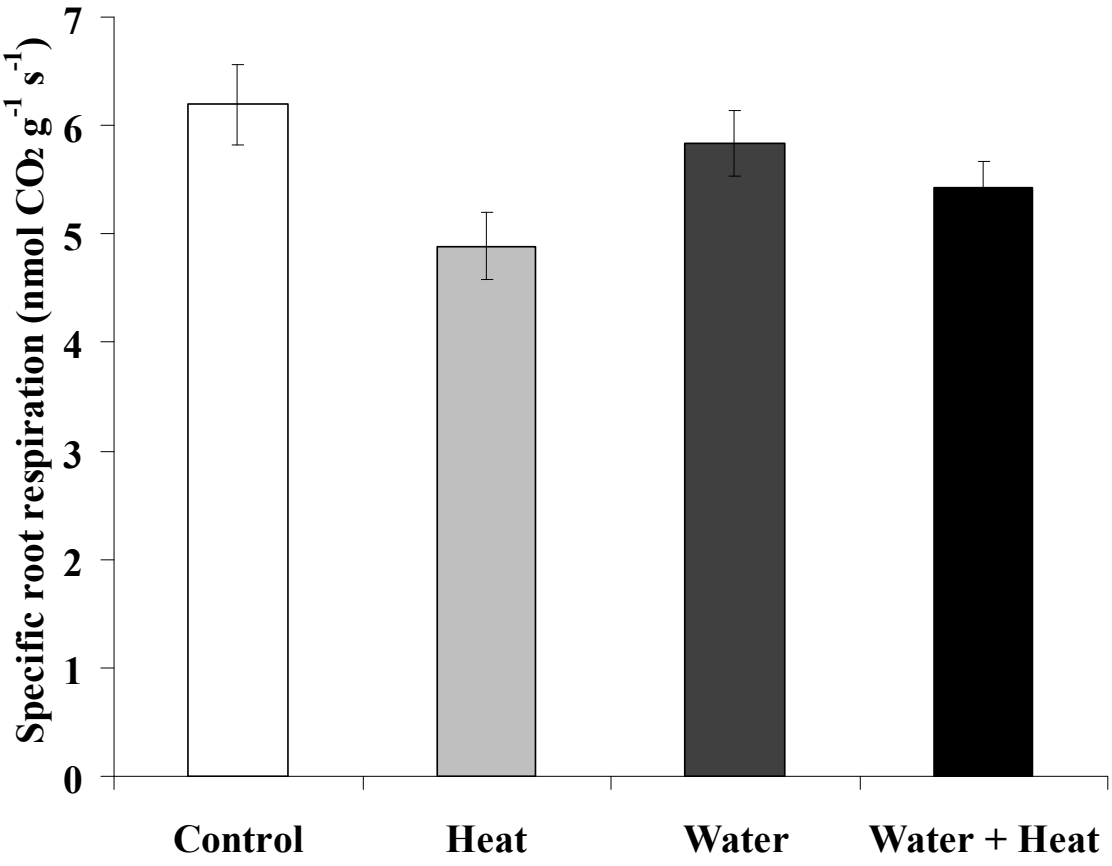


Figure 2.12. Average specific root respiration by treatment at reference temperature (average 17.9°C) for the treatment period of 2010-2011 for all dates with adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$) (n = 8). Error bars are standard error of the mean.

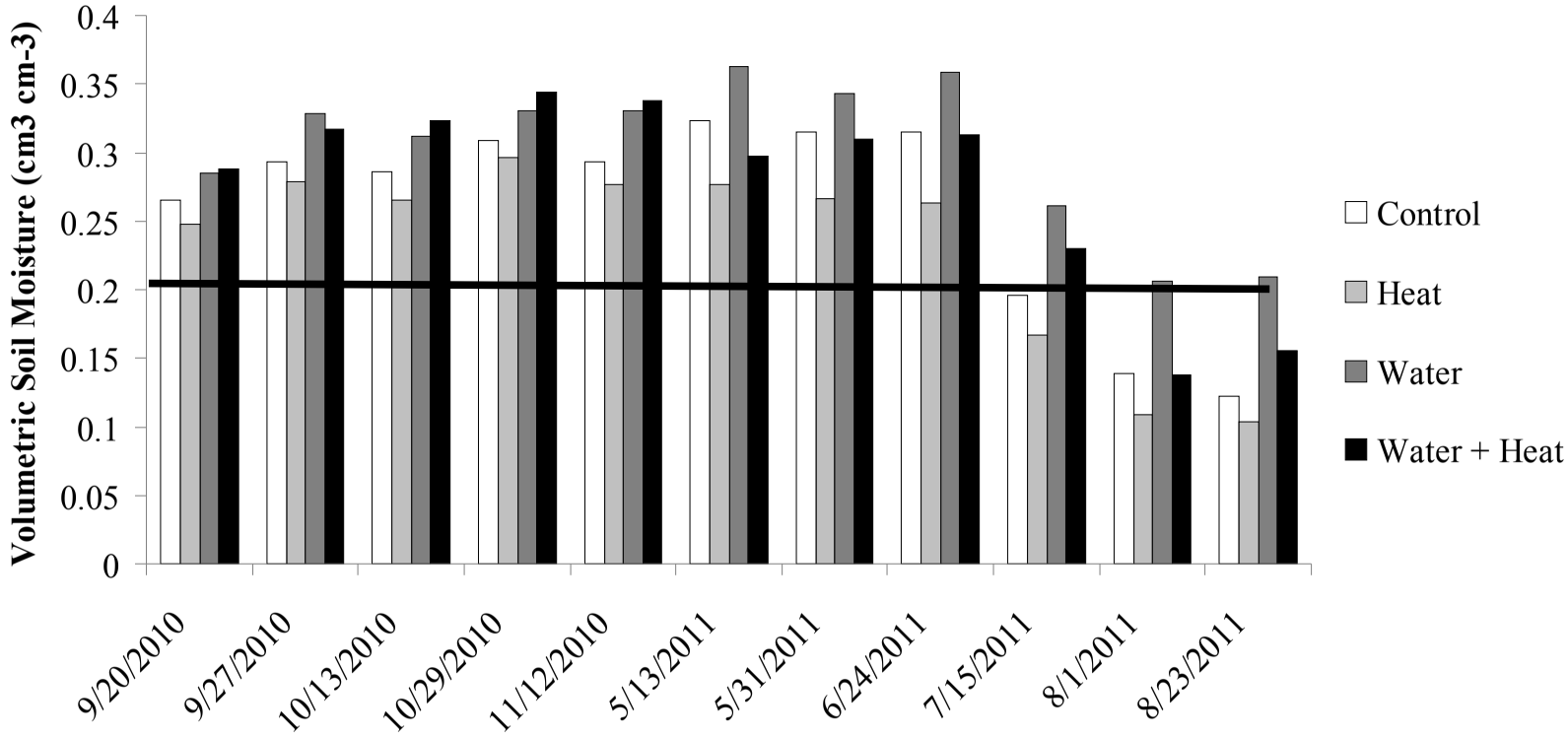


Figure 2.13. Volumetric soil moisture across dates for the treatment period. Open bars are control plots, light grey bars are heated plots, dark grey bars are water plots, and black bars are water + heat plots. The solid line is the cut-off for adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$), and everything below is considered dry soil conditions that can limit root respiration.

## Root N

There were no statistical differences for N concentration (g $kg^{-1}$) of the fine roots between the plots for the period of time before the initiation of treatments (both pretreatment and post-installation periods) ($P = 0.60$). Additionally, there was no significant difference in fine root N during the treatment period ($P = 0.93$) (Figure 2.14).

## Root respiration and soil moisture

All treatments have a positive relationship of fine root respiration at reference temperature to volumetric soil moisture ($cm^3$ $cm^{-3}$) ($P = <0.001$, $r = 0.57$). There is an indication that the heated plots (heat and water + heat) have lower metabolic capacity (respiration at 18 °C reference) at a given volumetric soil moisture level than the non-heated plots (control and water) (Figure 2.15).

## Root respiration and root N

Fire root respiration at reference temperature has a positive relationship to root N (g $kg^{-1}$) for the non-heated plots (control and water), but there is an inherent decrease in respiration at a given root N concentration for the heated plots (heat and heat + water) (Figure 2.16).

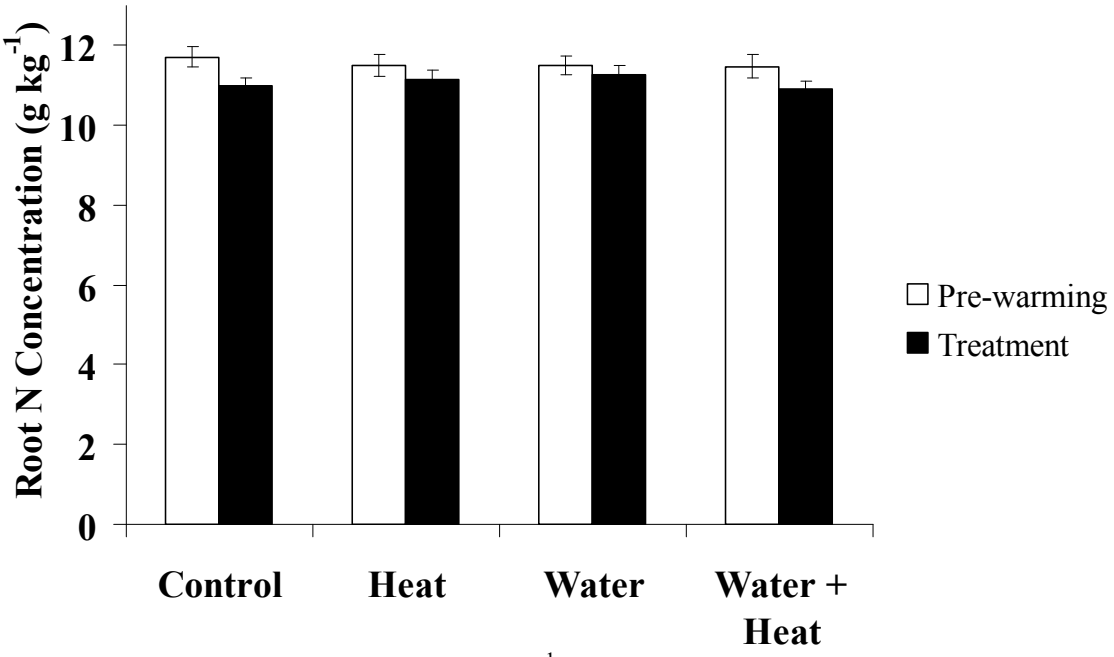


Figure 2.14. Root N concentration (g $kg^{-1}$) for pre-warming ($P$ = 0.60 for treatment effects) (pretreatment & post-installation) and treatment periods ($P$ = 0.90 for treatment effects).

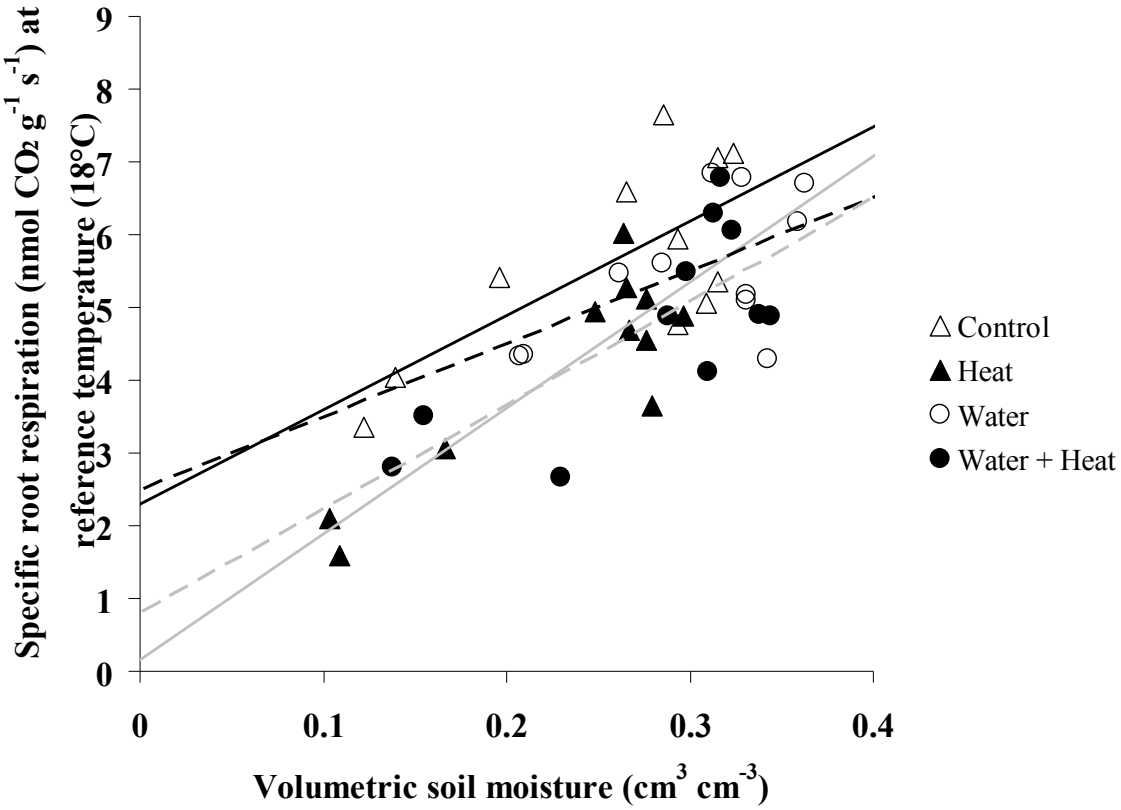


Figure 2.15. Relationship of specific root respiration at reference temperature to volumetric soil moisture by treatment for the treatment period. The solid black line is the fitted regression for control treatment, the grey solid line is the fitted regression for the heat treatment, the dashed black line is the fitted regression for the water treatment, and the dashed grey line is fitted regression for the water + heat treatment.

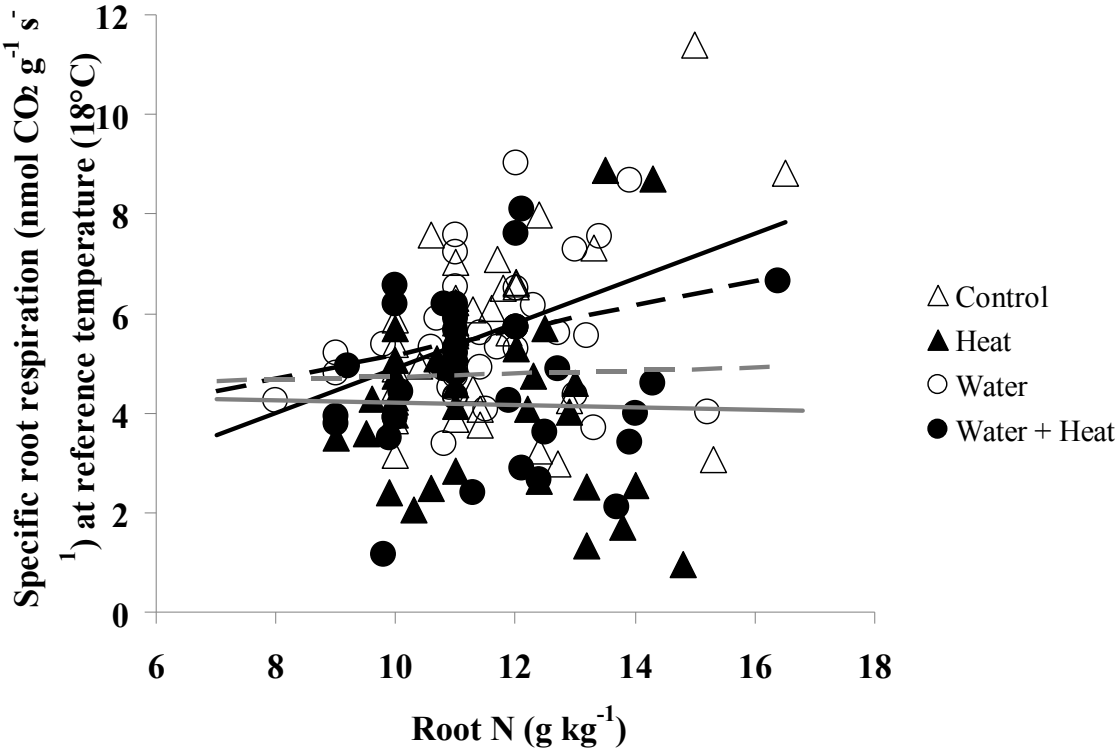


Figure 2.16. Specific root respiration at reference temperature versus root N concentration by treatments for the treatment period. Open triangles are control plots, closed triangles are heated plots, open circles are water plots, and closed circles are water + heat plots. Solid black line is the fitted regression for the control plots, the grey solid line is the fitted regression for the heat treatment, the dashed black line is the fitted regression for the water treatment, and the dashed grey line is the fitted regression for water + heat treatment.

## *Discussion*

The purpose of the pretreatment period of 2009 was to see if there were any underlying differences between any of the groups of plots assigned to the treatments before the initiation of the experiment. We also wanted to confirm that there was an exponential increase in specific root respiration to ambient soil temperatures. We found that fine root respiration increased exponentially with a $Q_{10}$ of 2.7 across a temperature range from 2.8 to 19.2 °C. This temperature range also confirmed that our reference temperature of 18 °C represented the warmer soil temperatures that the fine roots experience in mid-growing season in the top 10 cm of soil. There were no pretreatment differences in fine root respiration among sets of plots intended for the various treatments. The significant effect of measurement date at ambient temperatures ($P$ = <0.001) is due to variation in soil temperatures among dates, affecting root respiration in accordance with the calculated $Q_{10}$ of 2.7. The significant effect of measurement date on specific root respiration at the 18 °C reference temperature ($P$ = <0.01) is likely due to some dates having drier soil conditions, which are known to reduce root respiration rates (Burton et al. 1998).

Seasonal acclimation would be a down regulating of root respiration as soil temperature warmed seasonally. A slight indication of seasonal temperature acclimation exists when all sample periods are considered, but when only sample periods with adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$) are used in the regression analysis there is no seasonal acclimation, as only a non-significant ($P$ = 0.47) minor reduction (3.4%) in specific root

respiration occurs as soil temperatures increases by 13.7°C. Even when all sample periods, including those with dry soil conditions (<0.20 $cm^3$ $cm^{-3}$), are considered, there is still only a 7.8% reduction ($P$ = 0.09) in specific respiration rate at the reference temperature across a 14.4 °C temperature range in ambient soil temperature. This indicates that soil moisture has a fairly important effect on specific root respiration. It is apparent that there is no large down regulation in the respiration of sugar maple fine roots to seasonal changes in soil temperatures.

There was visual evidence suggesting some site disturbance occurred during the construction of the infrastructure that would support the experiment (racks to hold heating lamps, electrical wiring and sprinkler systems to provide the water treatment). We therefore analyzed root respiration for the time from where we finished installing the infrastructure (23 July 2010) to when we began to initiation of treatments (13 September 2010). Root respiration rates remained similar for all treatments in the post-installation period at both ambient soil temperatures ($P$ = 0.94) and the reference temperature ($P$ = 0.94), indicating no effect of installation on root respiration. There was again a significant effect of measurement date at ambient soil temperatures ($P$ = <0.001), and is attributed to variation in soil temperature among sample dates.

The treatment period consists of 11 sampling dates from 20 September 2010 to 12 November 2010, and then again from 13 May 2011 to 23 August 2011. The growing season of 2011 experienced a below average amount of precipitation, and the heated plots (heat and water + heat) experienced very dry soil conditions (<0.20 $cm^3$ $cm^{-3}$) in July and

August (Table 2.1). As a result, separate repeated measures ANOVA were used to assess data from all sampling periods (moist and dry soil conditions) and for only those dates with adequate soil moisture (>0.20 $cm^3$ $cm^{-3}$). There were three sampling dates where the volumetric soil content was considered very dry for the heated plots. These were 15 July 2011 with 0.18 $cm^3$ $cm^{-3}$, 1 August 2011 with 0.12 $cm^3$ $cm^{-3}$, and 23 August 2011 with 0.11 $cm^3$ $cm^{-3}$ (Figure 2.13). When all dates, including those without adequate soil moisture, were included, there was a potential for a significant reduction in metabolic capacity for the heated treatment, as indicated by reduced specific root respiration at the 18 °C reference temperature, $P = 0.01$ (Figure 2.10). This is also illustrated by the lower specific root respiration rates for dry soils for the heated treatment (Figure 2.15). It is evident that at any given soil moisture the plots that receive heat treatments have a lower respiratory capacity than those of the non-heated treatments. This down-regulation of respiration at reference temperature for the heat treatments could be an indication of acclimation. There is a slight down-regulation of respiration at reference temperature for the heat + water treatment at reference temperature when compared to the control treatment.

This apparent acclimation could also be due to the effects of drier soils in the heated treatments, as the effect largely goes away when only dates with adequate soil moisture are assessed (Figure 2.12). Because drought can reduce root respiration, a separate analysis was conducted for dates with adequate soil moisture. For dates where soil moisture was adequate, root respiration was not impacted by the water additions. Root respiration was greater with heat addition at ambient temperature, and marginally lower

metabolic capacity (respiration at reference temperature, P = 0.07) occurred with heat (Figures 2.9 and 2.10). This result strengthens the indication that fine root respiration is indeed sensitive to soil moisture, and when soil moisture is sufficient to meet the increased evaporative demand associated with raised soil temperatures, the fine roots in heated plots respire at a rate similar to that which would be predicted at a temperature of 4°C warmer than the control, using a $Q_{10}$ of 2.7. There is a 4% lower difference between predicted and actual fine root respiration for the water + heat plots when using a $Q_{10}$ of 2.7 and equation 2.1 where there is adequate soil moisture, and a 20% lower difference between predicted and actual fine root respiration for the heat only plots. Still, there is evidence of slight acclimation in the heated plots even when there is adequate soil moisture for the roots (Figure 2.15). The combined effects of dry soils and this slight acclimation result in annual fine root respiration for the heat treatment being 6% greater than the control and that the heat + water treatment being 26% greater than the control. This is less than the 48% that would be predicted for the 4°C temperature increase with a $Q_{10}$ of 2.7. This indicates an ability of these ecosystems to at least partially avoid excessive $CO_2$ loss from root respiration in warmer soil.

Slight acclimation is evident at this site but there is no indication that it is due to changes in root N concentration. There was no significant difference between root N among treatments during pre-warming (pretreatment and post-installation periods), and there were no differences in root N among treatments (Figure 2.14). During the first year and a half of treatment the trees did not construct new fine roots with a lower N concentration that would be indicative of a lower amount of enzyme and protein N as a mechanism to

down-regulated respiration. There is a clear indication that soil moisture affects fine root respiration in all treatments, but there is also an indication that there is a separation of the response of non-heated plots and heated plots, where the heated plots respire at a lower rate at a given soil moisture content (Figure 2.15). Fine root respiration has been found to increase with root N concentration (Reich et al. 2008; Atkinson et al. 2007; Ryan et al. 1996), but there seems to be an interaction going on for the heated plots when compared to the non-heated plots. Even if the heated plots have roots with a higher N concentration, they are not respiring at a higher rate when compared to root respiration for non-heated plots at a given N concentration (Figure 2.16). It seems that soil moisture and/or substrate limitation have more of an effect on specific root respiration for the heated plots.

A long-term response of root systems subjected to soil warming at the Harvard Forest is that of reduced biomass (Melillo et al. 2011). This response could occur in a similar fashion at the FFC center as well after a longer period of treatment. A reduction in root biomass from the trees could result from a number of different scenarios, in which belowground C allocation patterns, related to C sink strength, could play a role. Carbon in plants often is allocated preferentially to the strongest C sinks (i.e. plant tissues that are most active). If total belowground C allocation remains unchanged in a warmer environment, tree fine root biomass might decline as portions of the root system, which are less active, receive insufficient carbohydrates and senesce. Another scenario of reduced root biomass could come from adenylate control of respiration (Atkin et al. 2000b). This scenario would witness a build up of ATP from enhanced respiration at

higher temperature, but the ATP available would be in excess of that needed for metabolic functions (e.g. nutrient uptake and transport). With ATP unused, ADP would not be regenerated. Since ADP is needed for respiration, then this reduction in ADP would ultimately limit the ability of the roots to undergo respiration. Either of these scenarios could possibly positively affect C gain, as it they would cause less photosynthate to be utilized in less active portions of the root system (e.g. those in lower nutrient patches). The result of this scenario may cause a reduction in C allocation to these root segments severe enough to cause senescence, leading to a reducedroot biomass similar to the long-term scenario at Harvard Forest (Melillo et al. 2011). Though reduced biomass would not be metabolic acclimation, it is still a response from the plant that reduces the amount of carbon lost to the atmosphere, allowing more C to be sequestered in production of new plant tissues.

## *Conclusion*

Although seasonal temperature acclimation was not apparent for sugar maple fine roots, there was evidence of metabolic acclimation occurring during the first year and a half of experimental soil warming by 4 °C. The increased evaporative demand associated with these increased soil temperatures also clearly plays a role in reducing root respiration when soils are dry. However, when only periods of adequate soil moisture are examined, a slight down regulation of fine root respiration at a given temperature still occurred. This could be due to substrate limitation due to limitations of the total amount of C being allocated to belowground resource acquisition. There also could be adenylate control

where the amount of ATP created by enhanced respiration at higher temperature exceeds that needed for metabolic processes such as nutrient uptake and transport, leading to a reduction in ADP regeneration, and a feedback that limits respiration rate. Both of these scenarios could reduce fine root respiration, and substrate limitation could have further impacts, leading to reduced root biomass in the future, if C preferentially flows to only the strongest C sinks (i.e. most active portions of the root systems). Root biomass will continue to be measured annually to assess the long-term potential for changes in root biomass to serve as a mechanism for avoiding excessive root system respiration in warmer soil. Additionally, metabolic acclimation related to enzyme limitation through the production of future root cohorts with lower enzyme and N concentration, will continue to be assessed. Acclimation may not be necessary in plant roots if IPCC predictions are correct in modeling future precipitation events. If the plants experience more drought events, root respiration will decrease with these events and thus there will be a reduction in C lost to the atmosphere potentially leaving more C sequestered in biomass. However, the plant might have to undergo other physiological changes in the roots or leaves to counteract the decrease in available water and its effects on both respiration and photosynthesis.

# Chapter 3

## Ecosystem respiration responses to changes in water level in a northern poor fen peatland may be partially attributed to woody fine root respiration

### *Abstract*

Peatlands cover a small portion of the earth's surface, but contain a large proportion of the C sequestered in the world's terrestrial ecosystems. Though much C can be sequestered in peatlands, $CO_2$ (an important greenhouse gas) is expelled from peatlands at during ecosystem respiration. The amount of this gas either entering or leaving the peatland is what allows it to either be a C sink or source in terms of atmospheric greenhouse gases. Future predictions of climate in the world's peatlands are for increased temperatures and changes in precipitation patterns. These changes in climate could have a significant impact on the C cycling within these systems. Presently, drier conditions in peatlands are assumed to increase ecosystem C loss due to lower water levels leading to enhanced decomposition of peat that accumulated over a long time period in saturated conditions. In some cases, this could shift peatlands from atmospheric C sinks to C sources. However, the role which root respiration plays in altered ecosystem respiration is not well understood. Root respiration, being a metabolic process, is highly sensitive to temperatures and increases exponentially with temperature. The purpose of this study was to determine the role in which fine root respiration of woody plants plays

in the C cycle in a northern poor fen located in the Upper Peninsula of Michigan in Seney National Wildlife Refuge, and how this role changes with manipulation of water table depth. The area is a sphagnum dominated poor fen with black spruce, tamarack, cranberry and leatherleaf dominating the woody plant portion of the vegetation. This location includes a water level manipulation that resulted from a failed agriculture attempt that occurred around the beginning of the 20$^{th}$ century. This study utilized three water levels that exist at the site: control, a wet area (where water flowing through the fen has backed up), and a drained area (where water flowing through the fen has not been allowed to fully enter). All three of these water level treatments have areas of hummocks (raised microtopography), and lawns (lowered microtopography), which also influence vegetation present. Fine root respiration was measured three times during the 2011 growing season with the use of an open-system IRGA. Additionally, root biomass was measured in order to calculate ecosystem level root respiration (specific respiration x biomass), allowing us to determine the contribution of fine root respiration to ecosystem C exchange, as measured by eddy covariance. The wet areas had the highest average specific root respiration rate, with the lowest rates occurring in the control. Root biomass was dominated by leatherleaf and cranberry in all areas and microtopological positions. Greatest root biomass occurred within the drained hummocks, with the wet areas having the second highest biomass, and the controls the lowest amount of biomass. Overall the wet areas had the highest ecosystem root respiration (0.33 μmol $CO_2$ $m^{-2}$ $s^{-1}$), the drained areas were similar (0.31 μmol $CO_2$ $m^{-2}$ $s^{-1}$), and the controls were the lowest (0.17 μmol $CO_2$ $m^{-2}$ $s^{-1}$). These rates compare with about 2.3 μmol $CO_2$ $m^{-2}$ $s^{-1}$ of total nighttime ecosystem respiration measured from eddy covariance towers from this location. Woody

fine roots in these peatland systems are an important contributor to ecosystem respiration, and it is clear that changes in ecosystem C exchange as peatland water tables change are not due solely to altered rates of peat decomposition, as significant changes in woody root respiration are also possible.

## *Introduction*

Wetlands worldwide occupy 3% of the world's terrestrial surface; yet they contain about 33%, or about 455 petagrams (Pg), of the world's total soil carbon (about 1395 Pg) (Gorham 1991; Post et al. 1982). Current climate change models predict warmer temperatures globally in the next century, especially at latitudes close to the north and south poles (IPCC 2007). The majority of peatlands are found in the boreal and subarctic regions of the globe, but some peatlands are found in temperate and tropical regions as well (Gore 1983). With global temperatures predicted to increase over the next century, there is a potential for increased evaporation and decreased water levels in northern peatlands (Gorham 1991; Gorham 1995; IPCC 2007). Additional water level changes will occur due to land use change (Armentano and Menges 1986). A decrease in near-surface water levels in peatlands could increase peat decomposition as conditions become more aerobic (Holden 2005; Waddington and Price 2000). Gorham (1991) calculated that long-term drainage of peatlands could cause a release of 0.0085 Pg of $CO_2$-C to the atmosphere, which is a small proportion of the estimated 0.096 Pg C $yr^{-1}$ sequestered by peatlands (Gorham 1991).

Globally C stored in aboveground and belowground vegetation can be highly variable, but can range from 342 g $m^{-2}$ to 6210 g $m^{-2}$ in woody bogs (Grigal et al. 1985), with an average of about 2000 g C $m^{-2}$ (Grigal et al. 1985; Oechel 1989; Olsen et al. 1983). Gorham (1991) used these estimates to conclude that about 98.5% of total peatland carbon is in the form of peat, with the remainder (about 1.5%) occurring in vegetation. Additionally, Moore et al. (2002) examined plant biomass in bogs and fens in Canada and found that aboveground biomass was 487 g $m^{-2}$ in the bog, and 317 g $m^{-2}$ in the poor fen, with belowground biomass averaging 2,400 g $m^{-2}$ in the bog and 1,400 g $m^{-2}$ in the fen. Moore et al. (2002) also further compared fine root (<2 mm) biomass in the bog and fen systems, and biomass averaged 300 g $m^{-2}$ and 450 g $m^{-2}$ respectively.

Comparatively, terrestrial ecosystem soil respiration accounts for 50-70 Pg C $yr^{-1}$ (Houghton and Woodwell 1989; Schlesinger 1977), of which temperate deciduous forests are about 647 g C $m^{-2}$ $yr^{-1}$, temperate coniferous forests efflux rates are 681 g C $m^{-2}$ $yr^{-1}$, and northern bogs and mires efflux rates are 94 g C $m^{-2}$ $yr^{-1}$ (Raich and Schlesinger 1992).

Peatlands are considered a slight carbon sink (Tolonen et al. 1992), or a carbon source if methane ($CH_4$) output overpowers the $CO_2$ sequestration (Whiting and Chanton 2001). Moore et al. (2002) found that there is an annual C sequestration rate of about 60 g C $m^{-2}$ $yr^{-1}$ in a poor fen located in Ottawa, Canada. Other studies have found weaker sinks in peatlands of 23 g C $m^{-2}$ (Gorham 1995) and 2 g C $m^{-2}$ in boreal peatlands of Sweden

(Waddington and Roulet 2000). A more recent study in eastern Ontario found a daytime uptake of 8-12 μmol $CO_2$ $m^{-2}$ $s^{-1}$, and a nighttime efflux of about 4 μmol $CO_2$ $m^{-2}$ $s^{-1}$ from both bogs and fens, calculated from eddy covariance measurements (Humphreys et al. 2006). With climatic warming and decreased water levels in peatlands, there could be a shift from a C sink to a carbon source for some peatlands (Minkkinen and Laine 1998). It has been found that a lowering of the water table in northern peatlands increases annual $CO_2$ emissions (Martikainen et al. 1995). Minkkinen and Laine (1998) found that although the peat surface had subsided about 22 cm in a peatland after 60 years of drainage in Finland, the C density had increased by about 0.026 g $cm^{-3}$, and C stores had increased about 5.9 kg $m^{-2}$ since this drainage occurred. Minkkinen and Laine (1998) concluded that the reduction in peat levels due to oxidation of the peat was of little importance and that the increase in C density and C storage was from a new input of C through NPP of woody trees at their study location. They further speculated that much of this new input of C to the system was through the increase in the fine roots of trees.

Early hypotheses suggested that the draining of peatlands will increase their C efflux, potentially causing them to switch from C sinks to C sources. However, since drainage in peatlands can initiate succession towards forest vegetation (Laine et al. 1995), the increase in NPP that Minkkinen and Laine (1998) found with woody trees could alternatively maintain peatlands as a C sink.

The interaction of woody plants and water table depth in a northern poor fen, especially in terms of $CO_2$ efflux associated with fine root (<1mm) respiration, was the focus of this

study. Respiration can be a large determining factor of carbon balance and in many instances is very close to GPP in peatland systems (Gorham 1995; Moore et al. 2002; Waddington and Roulet 2000). As a result, changes in respiration can move peatlands from a C sink to a C source. However, measured increases in $CO_2$ efflux that are presumed to be due to oxidation of peat (heterotrophic respiration) could also be due to enhanced fine root respiration (autotrophic respiration) associated with increased fine root biomass from encroaching trees. Decreased water levels might allow higher peat temperatures and higher levels of oxygen that could favor tree species encroachment into the peatland. In addition, the decomposition of peat due to decreased water levels could provide needed nutrients for plant biomass production and further provide adequate growing conditions for woody plants, helping offset the C loss from peat.

This study was conducted in Seney National Wildlife Refuge (SNWR) in the Upper Peninsula of Michigan during the summer of 2011. A system of ditches and dikes were constructed at SNWR in the early part of the 20$^{th}$ century for agricultural attempts that subsequently failed. The effects of the alterations on water levels have persisted, and provided an opportunity to study effects of water level in a northern peatland system (Figure 3.1). The series of ditches and levees in this study location run parallel with the water flow in some locations which provide a control condition (no water level effect), and the ditch/levee runs perpendicularly to the water flow very close to the control area which backs up the water on one side of the ditch raising the water level when compared to the control, and drains the peatland on the other side of the ditch (Figure 3.1). Fine root respiration rates for woody roots in hummocks and lawns located in different water

levels were sampled three times during the summer of 2011. Woody fine root biomass was also measured during the middle sampling period.

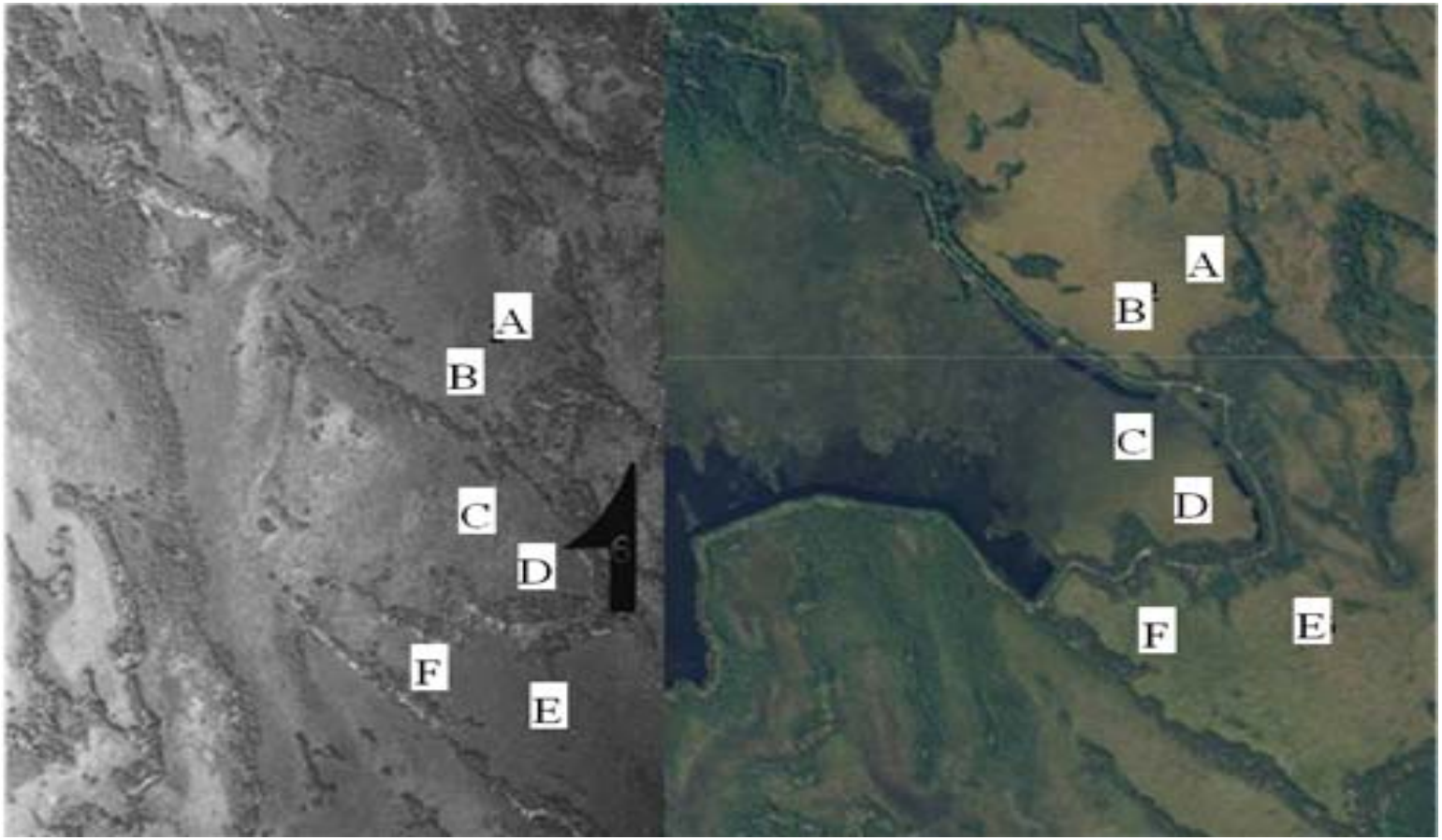


Figure 3.1 Location of six study sites at Seney National Wildlife Refuge. Sites A&B are control, site C&D are wet, and site E&F are drained. The flow of water is from the northwest to the southeast. Note the photo on the left is prior to the construction of the ditches and dikes (early 1900s), and a recent photo is shown on the right.

Specific hypotheses included:

## Hypothesis 1

*Specific root respiration will be highest for the drained hummocks and lawns, with control plots having intermediate specific root respiration rates and the wet plots having the lowest respiration rates for both hummocks and lawns.*

## Hypothesis 2

*The drained plots will have the highest amount of woody fine root biomass (<1mm), the control plots will be intermediate, and the wet plots will have the lowest biomass.*

## Hypothesis 3

*Overall the drained plots will have the highest ecosystem level root respiration (biomass x specific respiration rate), the control plots will be intermediate and the wet plots will have the lowest ecosystem level root respiration.*

## Hypothesis 4

*Decreased water levels will increase decomposition and thus supply woody tree species with more N.* This will cause an increase in root N that will be correlated with increased specific root respiration, such that, the drained plot will have higher root N concentration, the control plots intermediate, and the wet plots will have the lowest root N.

## *Materials/Methods*

### Location

This study was located in a poor fen northern peatland at Seney National Wildlife Refuge (SNWR), in Schoolcraft County, Michigan (46° 11' 26.12" N, 86° 1' 14.59" W). SNWR is located in the Upper Peninsula of Michigan, is managed by the United States Fish and Wildlife Service and encompasses about 38,500 ha. SNWR was established in 1935 after years of logging operations, fire clearing, and finally ditch construction for the purposes of draining the wetland for agriculture had greatly altered the landscape. A water table manipulation resulted from a failed ditching attempt to drain the peatland for agriculture in the early 1900's. The ditches and dikes in this particular location were intended to intercept the water flowing from the northwest and move the water offsite to allow the peat to drain and create an opportunity to farm. For a section of the site, the dike follows the flow of water from the northwest to the southeast. From here the dike turns sharply to the west and runs perpendicularly to the flow of water. This series of dikes creates a control treatment on one side of the dike where the water flows parallel to the dike and is allowed to flow relatively unchanged from the site (plots A and B, henceforth named Control). Plots C and D (henceforth Wet) are located where the dike turns sharply west and collects water flowing from the northwest, and plots E and F (henceforth Drained) are located on the opposite side of the dike where water is drastically cut off from flowing southeast beyond the dike (Figure 3.1). Boardwalks were established on site to

allow access to the area while minimizing impacts on the peatland vegetation and soil. This poor fen has microtopography consisting of hummocks (raised areas) and lawns (lower areas) typical of northern peatlands.

## Root respiration

Woody plant fine root (<1mm) respiration was the focus of this study. Woody species present included black spruce (*Picea mariana* (Mill.) B. S. P.), tamarack (*Larix laricina* (Du Roi*)* K. Koch), cranberry (*Vaccinium* spp.), and leatherleaf (*Chamaedaphne calyculata*). Root respiration was determined for excised fine roots (<1mm) collected using an 11.5 cm diameter peat core to sample a depth of 20 cm at randomly selected locations within each treatment area. Roots were sorted from the peat by hand from 2 cores taken per sample location on each sample date, and approximately 2 g fresh weight of live fine roots of the woody plants was collected. Root samples were measured for $CO_2$ efflux (nmol $CO_2$ $s^{-1}$) after being placed in a cuvette attached to an open-system infrared gas analyzer (IRGA, CIRAS-1/CIRAS-2 portable gas analyzer, PP Systems, Haverhill, MA). Measurements were made at ambient peat temperature for each particular sample location and date, and respiration rates were recorded after allowing fifteen minutes for readings to stabilize. The cuvette's aluminum base was placed in a water bath to maintain the roots at the desired temperature during the measurement period (Burton and Pregitzer 2003; Burton et al. 2011). Respiration was analyzed at a $CO_2$ concentration of 1000 μl $l^{-1}$. The samples were subsequently dried at 65°C for 48

hours in the lab to obtain dry weights of roots for use in determining specific root respiration (nmol $CO_2$ $g^{-1}$ $s^{-1}$). The samples were then ground (8000M Mixer/Mill, Spex SamplePrep LLC, Metuchen, NJ) to a fine powder and analyzed for nitrogen (N) concentration with an elemental analyzer (Carlo Erba NA 1500 NC, CE Elantech, Lakewood, NJ).

## Root biomass

Root biomass was determined for two 11.5 cm by 20 cm deep diameter cores per sample location. The cores were placed on ice for transport and hand sorted in the lab to remove peat, and separate the roots by species and diameter class (<1, 1-2, 2-10 mm). Roots attached to living members of the species in the field were examined to define morphological fine root characteristics that were used to separate species during sorting of bulk root biomass samples in the lab. Samples were then oven dried at 65°C for 48 hours to calculate root biomass (g $m^{-2}$) to a depth of 20 cm.

## Ecosystem root respiration

Ecosystem level root respiration (μmol $CO_2$ $m^{-2}$ $s^{-1}$) was calculated from the product of measured specific root respiration and measured root biomass for both hummocks and lawns at each site, and then weighted for areal proportions of hummocks and lawns particular to this site for comparison with eddy-covariance C exchange rates.

## Statistical Analysis

Statistical analyses were conducted with R (2.12.0, R Development Core Team, Vienna, Austria). Analysis of variance (ANOVA) was used to determine differences among water levels and microtopological positions (hummocks and lawns) for specific root biomass. Repeated measures ANOVA was used to detect the effects of water table elevation (control, wet, drained) and microtopological positions (hummocks vs. hollows) across the sample dates (repeated measure) for specific root respiration, ecosystem root respiration and root N concentration. All tests used an alpha of 0.05. Non-linear regression was used to determine temperature response curves for specific root respiration as a function of ambient peat temperature conducted post-hoc when differences between water levels using analysis of covariance (ANCOVA) were established with temperature as a covariate. Tukey's HSD was used post-hoc to determine differences which combinations of water table elevation and microtopological position differed in fine root biomass.

## *Results*

There were no significant differences in specific root respiration (nmol $CO_2$ $g^{-1}$ $s^{-1}$) among control, wet or drained plots, between microtopological positions (hummock vs. lawn), or their interaction (Table 3.1, Figures 3.2, 3.3).

There were significant differences among sample dates in specific root respiration ($P$ <0.001), and a significant date x water level interaction ($P$ = 0.05) (Table 3.1) that were both likely due largely to differences among sample dates in peat temperature. As a result, there was a significant difference between water levels ($P$ = 0.03) when ambient peat temperature is used as a covariate to predict specific root respiration. In this instance the wet plots were significantly different from the control and the drained plots, with no significant difference between the control and drained plots. Based on these results, non-linear regression was used to fit responses of specific root respiration to temperaturefor the wet plots, and for the control and drained plots combined. $Q_{10}$ values of 2.4 for the control and drained plots, and 1.6 for the wet plots were calculated from these non-linear regression equations (Figure 3.3).

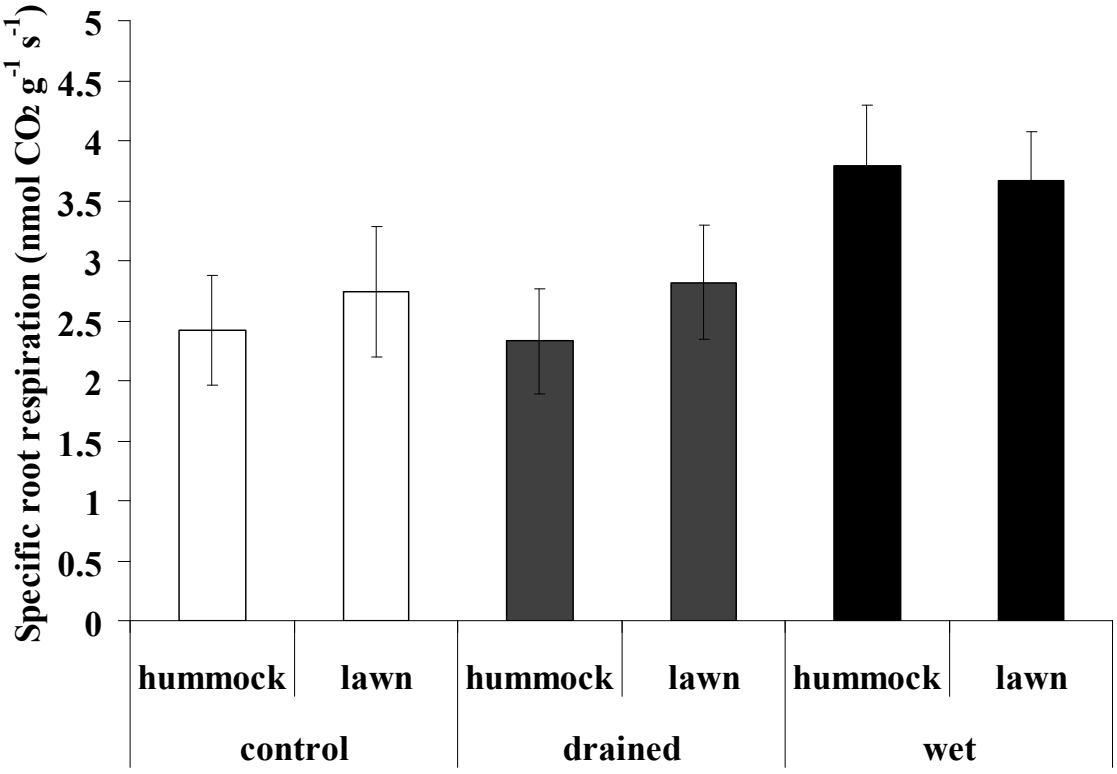


Figure 3.2. Specific root respiration at ambient temperature by treatment (control, drained, wet) and microtopological position (hummock, lawn) with standard error bars.

Table 3.1. Repeated measures ANOVA for the effects of water level and microtopography on specific root respiration in a northern peatland

| Dependent | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|
| **Specific root respiration** | **Between** | | | | | |
| | Water level | 2 | 10.66 | 5.33 | 1.14 | 0.38 |
| | Microtopography | 1 | 0.47 | 0.47 | 0.10 | 0.76 |
| | Water level x Microtopography | 2 | 0.60 | 0.30 | 0.06 | 0.94 |
| | Residuals | 6 | 28.03 | 4.67 | | |
| | **Within** | | | | | |
| | Date | 2 | 17.64 | 8.82 | 16.12 | <0.001 |
| | Water level x Date | 4 | 7.23 | 1.81 | 3.30 | 0.05 |
| | Microtopography x Date | 2 | 0.23 | 0.11 | 0.21 | 0.82 |
| | Water level x Microtopography x Date | 4 | 1.38 | 0.35 | 0.63 | 0.65 |
| | Residuals | 12 | 6.57 | 0.55 | | |

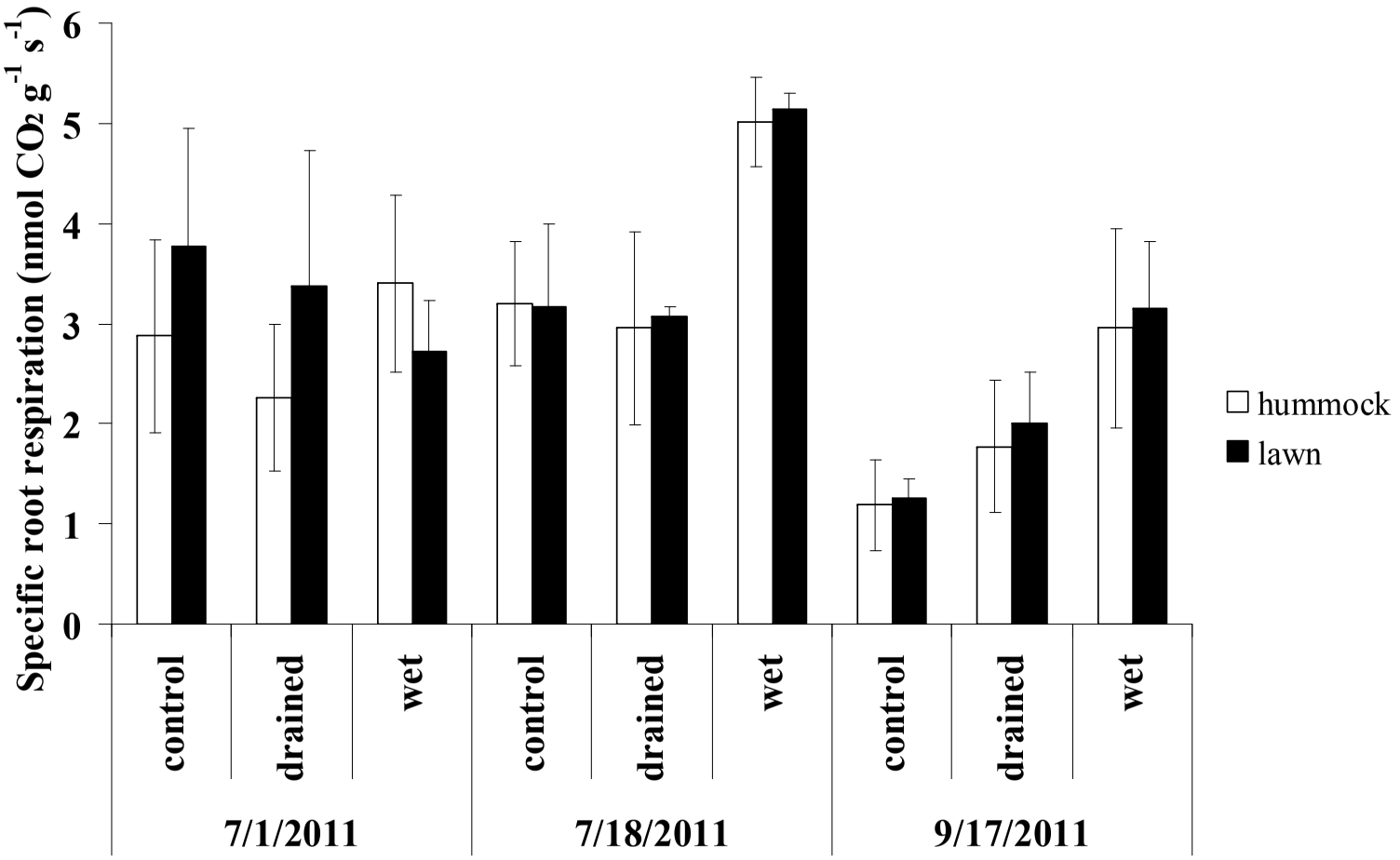


Figure 3.3. Specific root respiration by water level and microtopography across dates with standard error bars.

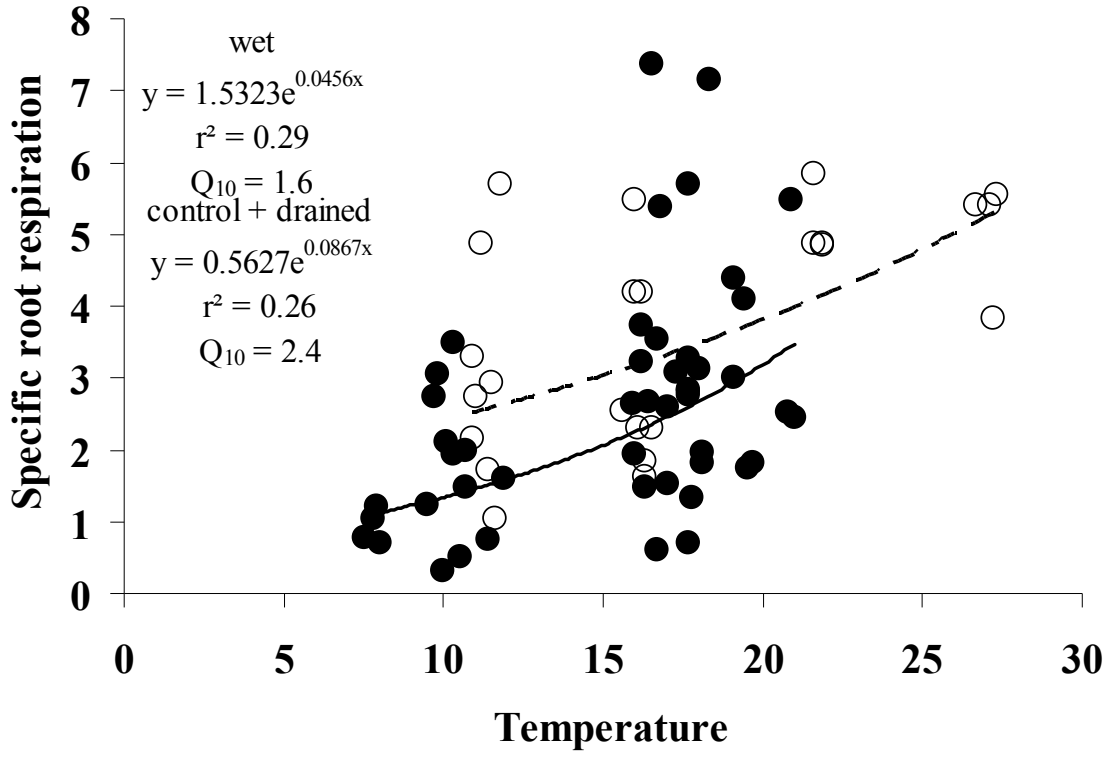


Figure 3.4. Relationships between specific root respiration and ambient peat temperature. The closed circles are control and drained plots, with the solid black line as the fitted non-linear regression. The open circles are the wet plots with the dashed black line as the fitted non-linear regression

Root biomass differed significantly among water levels ($P = 0.01$), and microtopological position ($P = <0.001$). There also was an indication of a potential interaction between water level and microtopological position ($P = 0.07$) (Figure 3.4). The drained plots had a greater total root biomass than the control plots, with an encroachment of black spruce and tamarack roots into the lawn of the drained area, and increased leatherleaf fine root biomass. The wet plots have less of a proportion of black spruce and tamarack roots, but a greater proportion of cranberry roots when compared to the control and drained plots (Figure 3.5).

Ecosystem root respiration, the product of measured specific root respiration and fine root biomass, exhibited no effect for water level ($P = 0.45$), no influence of topological position ($P = 0.80$), and no interaction between the two (Figure 3.6). Repeated measures ANOVA indicated significant difference among sample dates for ecosystem root respiration ($P = <0.001$) and a non-significant date by water level interaction ($P = 0.11$) (Table 3.2, Figure 3.8). Figure 3.9 shows the component of ecosystem level root respiration, as an eddy covariance tower would measure $CO_2$ flux. Ecosystem level fine root respiration has been calculated as a weighted average of contributions from hummocks and lawns, based on transects conducted on site to determine the relative proportions of each found at the site. The areal proportions for the control plots are 50:50 hummocks to lawns, the wet plots are 40:60 hummocks to lawns, and drained plots are 55:45 hummocks to lawns.

A repeated measure ANOVA indicated no significant differences for N concentration of the fine roots by water level and topological position across dates (Table 3.3, Figure 3.10). However, when root N is weighted based on areal proportions of hummocks and lawns, and when microtopography is combined for each water level across dates, there is a trend for wet and drained plots to have higher root N concentration progressing through the growing season, with wet plots having higher root N than drained plots (Figure 3.10).

Table 3.2. Repeated measures ANOVA for the effects of water level and microtopography on ecosystem root respiration in a northern peatland

| Dependent | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|
| **Ecosystem root respiration** | **Between** | | | | | |
| | Water level | 2 | 0.04 | 0.02 | 0.85 | 0.45 |
| | Microtopography | 1 | 0.002 | 0.002 | 0.07 | 0.80 |
| | Water level x Microtopography | 2 | 0.03 | 0.02 | 0.62 | 0.57 |
| | Residuals | 6 | 0.16 | 0.02 | | |
| | **Within** | | | | | |
| | Date | 2 | 0.03 | 0.02 | 12.66 | 0.001 |
| | Water level x Date | 4 | 0.01 | 0.003 | 2.38 | 0.11 |
| | Microtopography x Date | 2 | 0.001 | 0.0003 | 0.20 | 0.82 |
| | Water level x Microtopography x Date | 4 | 0.01 | 0.001 | 0.98 | 0.46 |
| | Residuals | 12 | 0.02 | 0.001 | | |

Table 3.3. Repeated measures ANOVA for the effects of water level and microtopography on root N concentration in a northern peatland

| Dependent | Factor | d.f. | Sum Sq | Mean Sq | F value | P-value |
|---|---|---|---|---|---|---|
| **Root N concentration** | **Between** | | | | | |
| | Water level | 2 | 0.09 | 0.04 | 0.59 | 0.58 |
| | Microtopography | 1 | 0.07 | 0.07 | 0.97 | 0.36 |
| | Water level x Microtopography | 2 | 0.003 | 0.001 | 0.02 | 0.98 |
| | Residuals | 6 | 0.44 | 0.07 | | |
| | **Within** | | | | | |
| | Date | 2 | 0.008 | 0.004 | 0.83 | 0.46 |
| | Water level x Date | 4 | 0.04 | 0.01 | 2.31 | 0.12 |
| | Microtopography x Date | 2 | 0.02 | 0.01 | 2.22 | 0.15 |
| | Water level x Microtopography x Date | 4 | 0.03 | 0.006 | 1.36 | 0.30 |
| | Residuals | 12 | 0.06 | 0.005 | | |

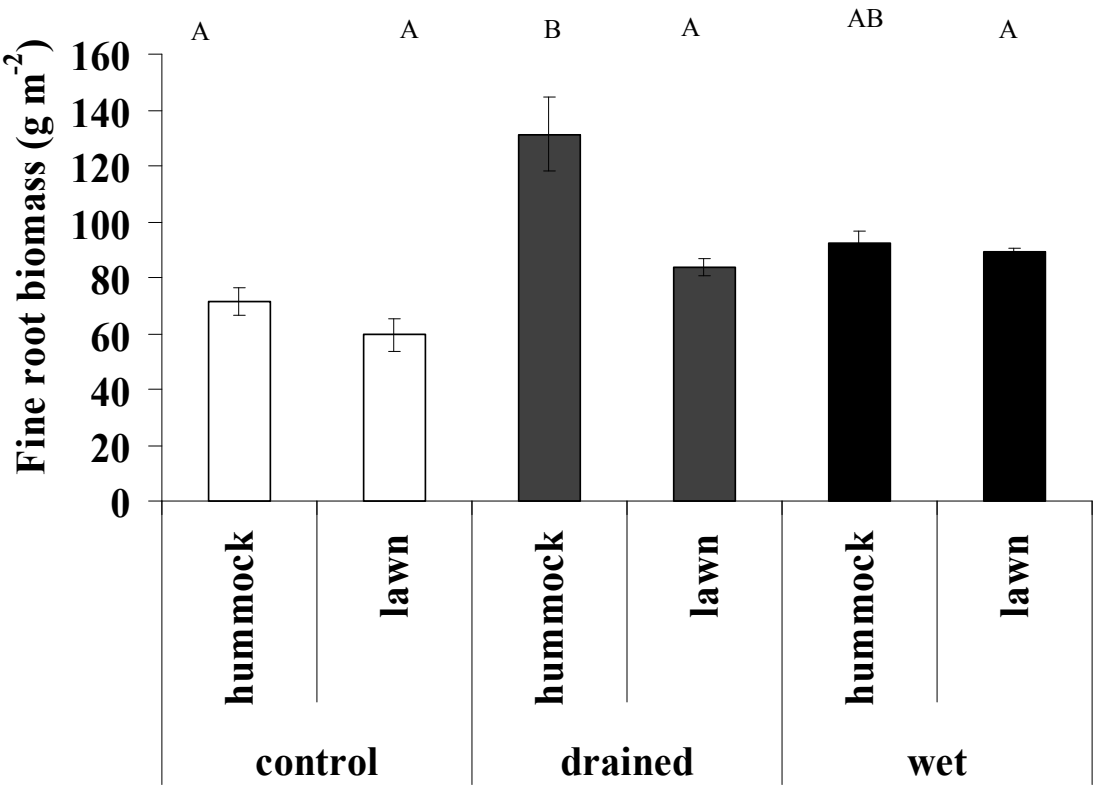


Figure 3.5. Fine root biomass by treatment and microtopological position with standard error bars. Letters above bars indicate Tukey HSD test results.

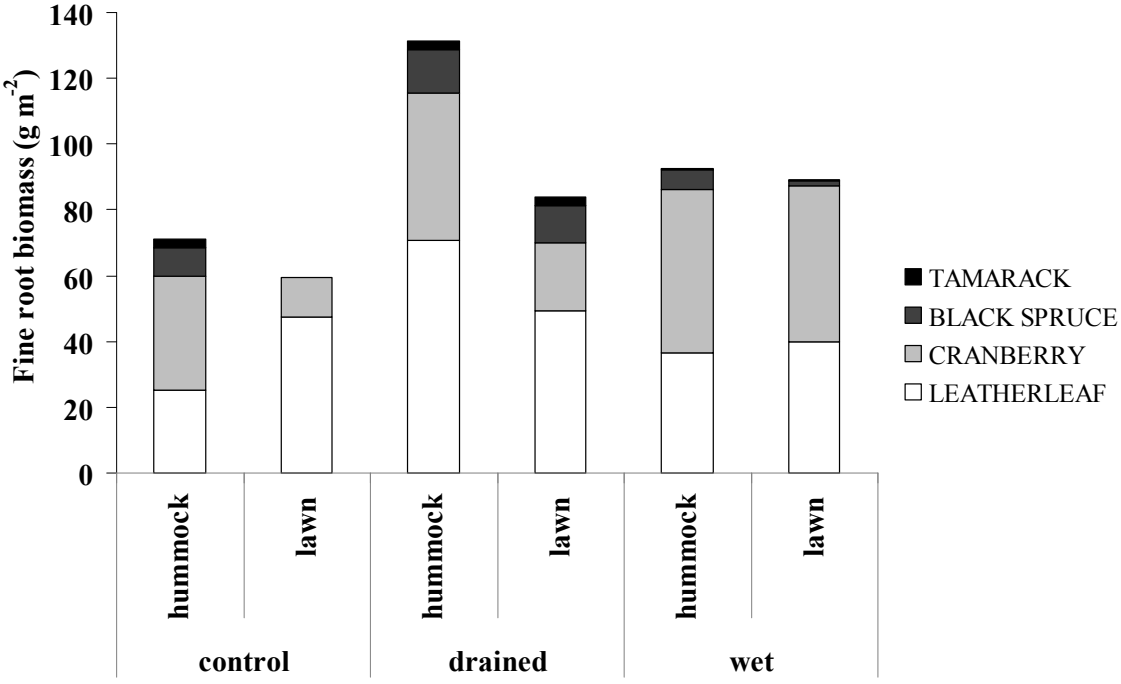


Figure 3.6. Fine root biomass (<1 mm) by species, treatment and microtopological position.

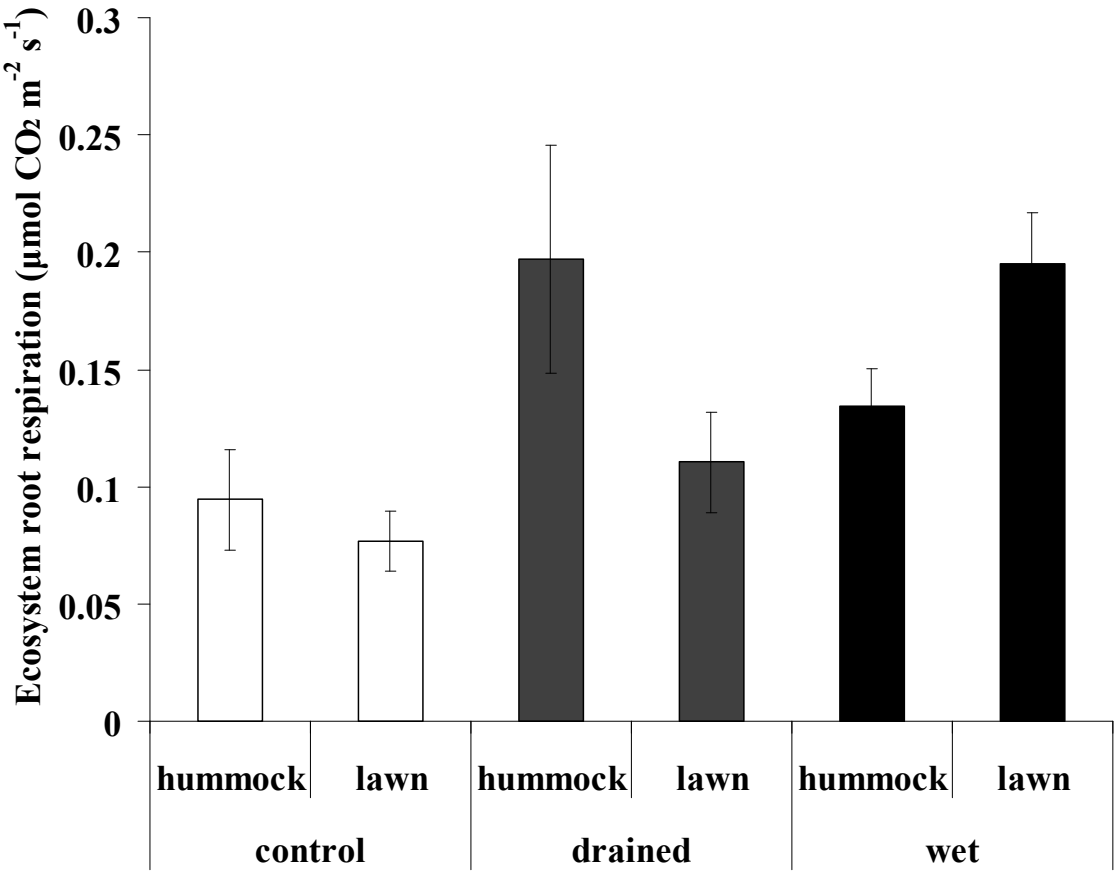


Figure 3.7. Ecosystem level root respiration by water level and microtopological position. Values are averages across all three sample dates.

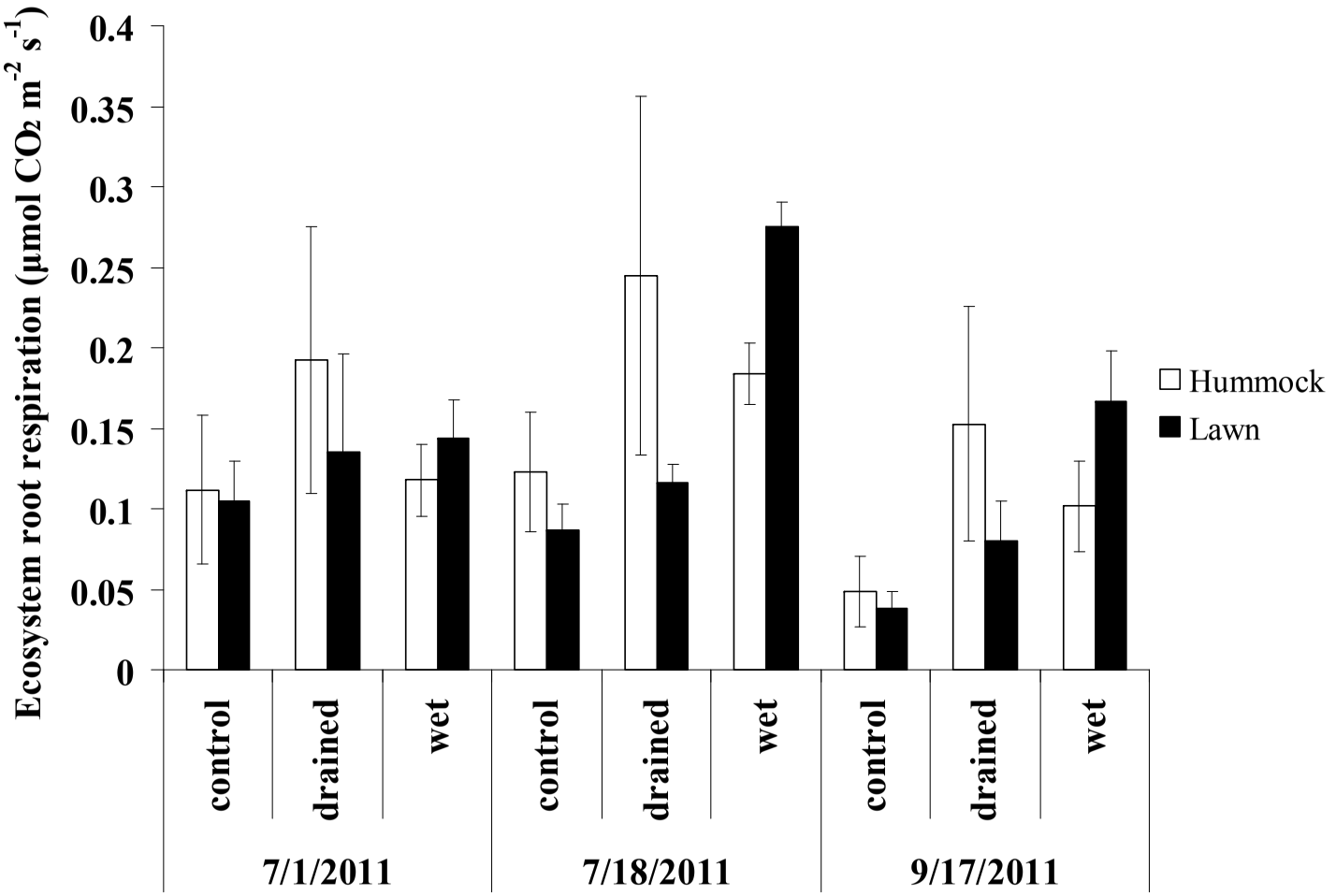


Figure 3.8. Ecosystem root respiration by water level and microtopography across dates with standard error bars. Values are weighted by areal hummock to lawn proportions (Control 50/50, Wet 40/60, Drained 55/45).

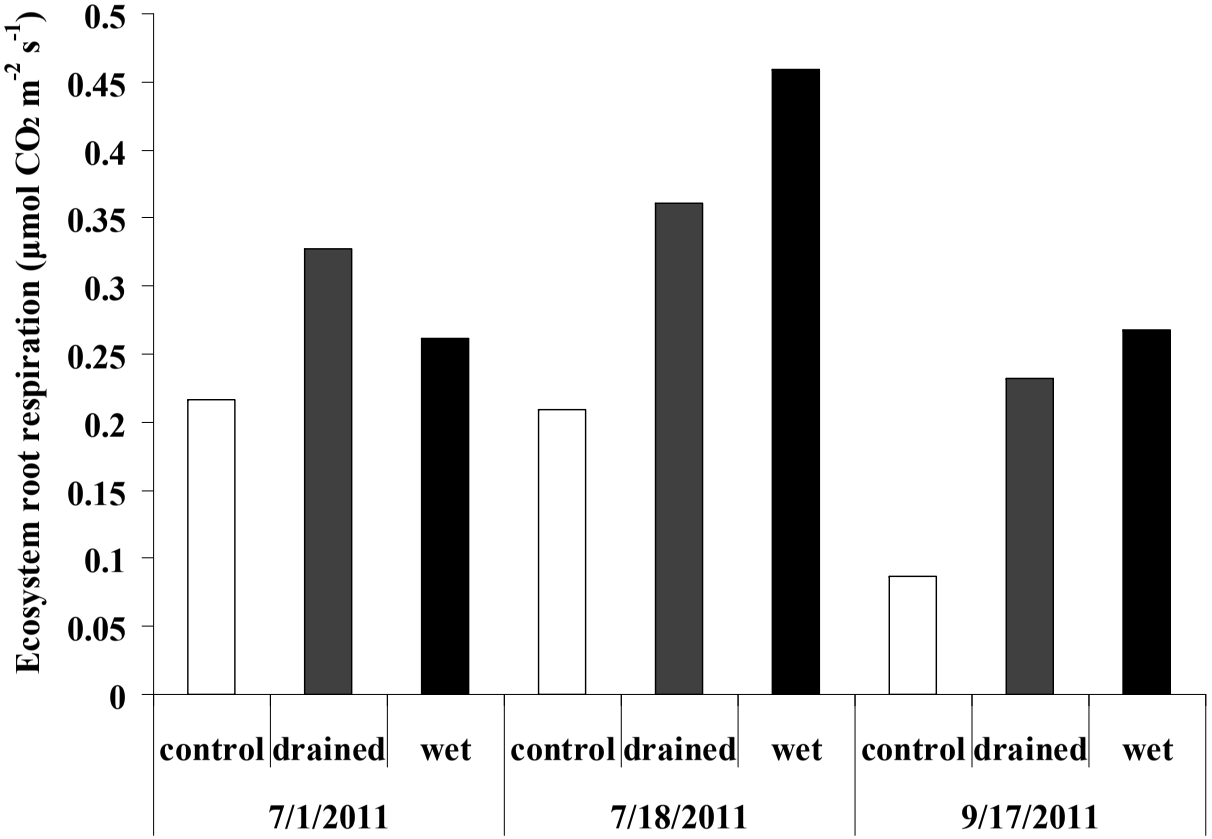


Figure 3.9. Ecosystem root respiration by water level across dates with standard error bars. Values are averages across all dates, weighted by areal hummock to lawn proportions (Control 50/50, Wet 40/60, Drained 55/45).

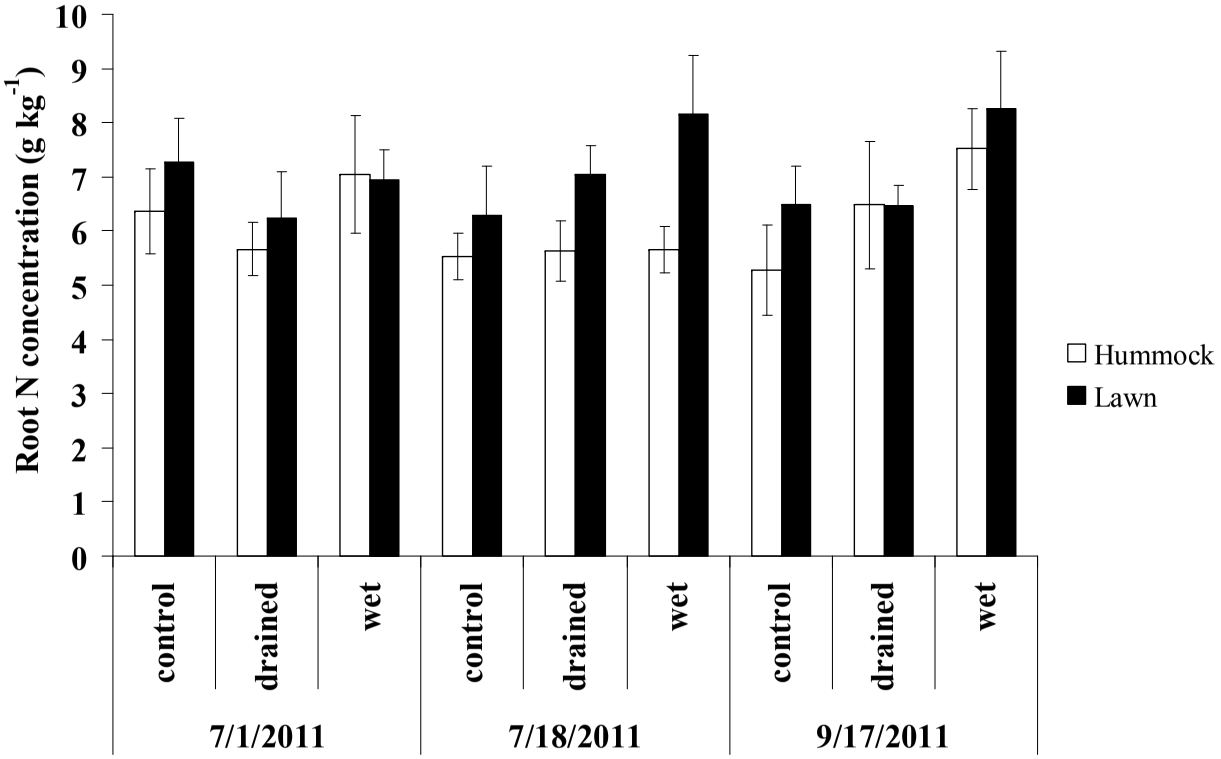


Figure 3.10. Fine root root N concentration by treatment and microtopography across dates with standard error bars.

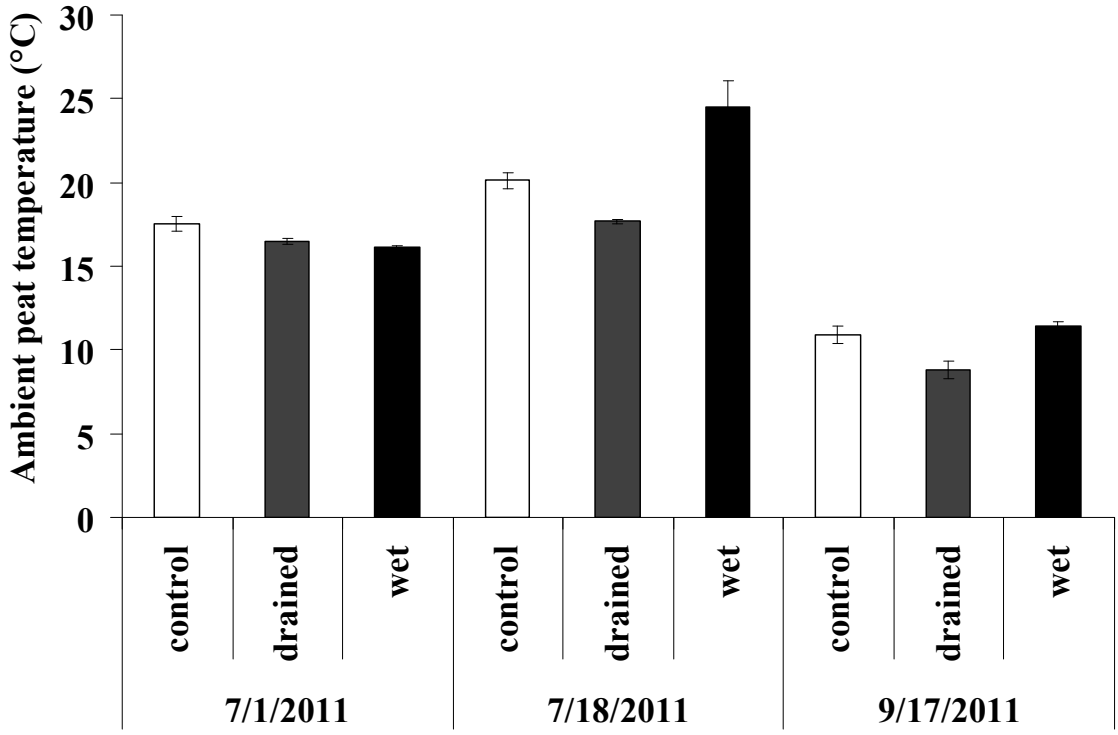


Figure 3.11. Ambient peat temperature (°C) to a depth of 10 cm for treatments and microtopography across dates with standard error bars

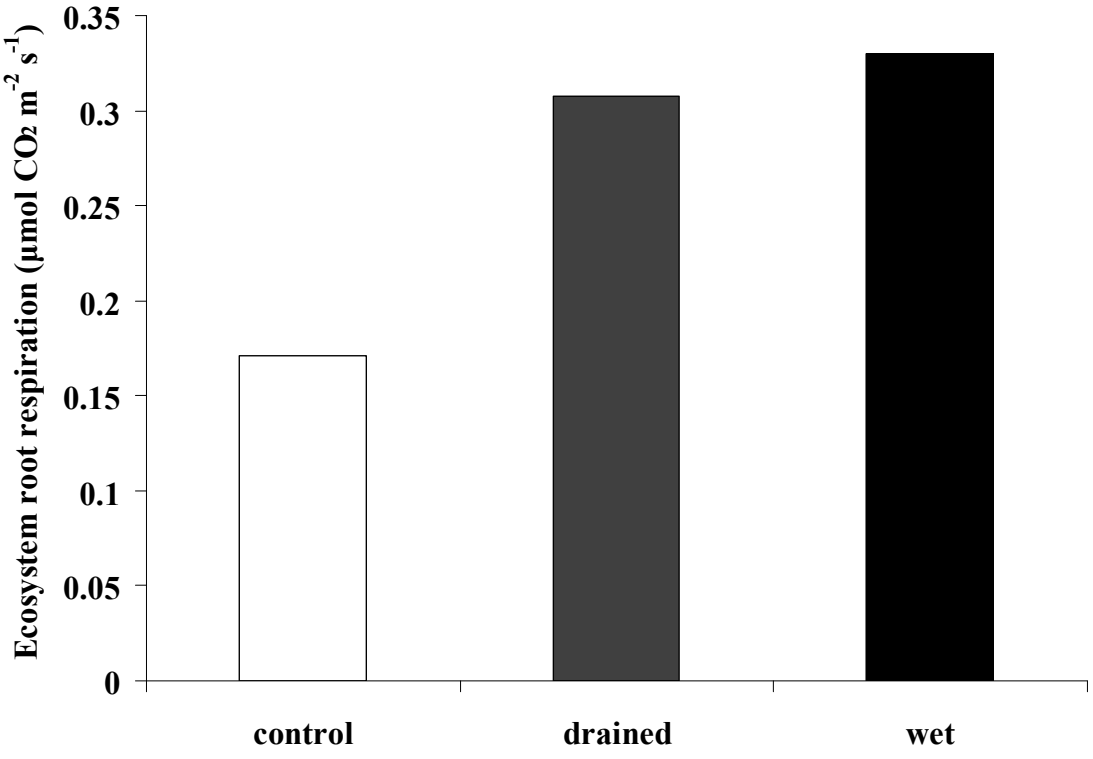


Figure 3.12. Ecosystem level root respiration by treatment.

## *Discussion*

There is a significant water level by date interaction ($P$ = 0.05), indicating that when water levels dropped seasonally for all treatments, beginning with the 18 July 2011 date, specific root respiration was greater for the wet plots (Figure 3.7). Overall, the wet plots seem to have higher specific root respiration rates for the hummocks and lawns than the control and drained plots (Figure 3.2). Evidently, when this peatland dries seasonally, respiration increases in response to increased aeration, in addition to effects of increased temperature. Field observations indicated that water level across the entire site was highest for the 1 July 2011 date, and lowest for the 17 September 2011 date with the 18 July 2011 date occurring just after the water levels began to drop. It seems that during this time period, that the fine roots on the wet plots for the 18 July 2011 date responded to the presence of more aerobic conditions. Additionally, the 18 July 2011 date corresponds to the highest ambient peat temperatures from all three sampling dates, with the wet plots having the highest average temperature of all (24.5°C) (Figure 3.11). Roots in the wet plots may be responding to both increased aeration and increased nutrient availability resulting from enhanced decomposition of the aerated peat by initiating a new flush of fine roots. New fine roots often have higher N concentration and respiration rates (Burton et al. 1996), as we observed for fine roots on this date, especially those from the wet plots. Based of field observations, the 18 July 2010 date had the greatest amount of fine white root tips on the collected samples. In the wet lawn areas where fine root respiration was highest, the roots experienced the greatest amount of water level

decline during this period and are likely responding rapidly to the sudden decrease in water level and associated changes in aeration and nutrient availability.

Cranberry and leatherleaf dominate the fine root biomass for all water levels and microtopological positions. The drained hummocks have higher fine root biomass than the other water levels and microtopological positions (Figure 3.4). Additionally, the drained hummocks and lawns seem to have the highest proportion of black spruce and tamarack roots. However, the wet plots have a larger proportion of leatherleaf and especially cranberry roots in the lawns and hummocks, which seem to be affecting root respiration (Figure 3.5). This domination is further expressed when calculating ecosystem level root respiration as a product of specific root respiration and root biomass and weighted to actual areal proportions of hummock/lawn found on the water levels. The control and drained areas had relatively even proportions of hummock/lawns with 50/50 and 55/45 respectively, but the wet area had a proportion of 40/60. This means when the microtopological positions are weighted to calculate ecosystem root respiration for a given water level, the influence of cranberry and leatherleaf roots is increased, especially in the wet area (Figures 3.5 & 3.6). The wet and drained plots have greater ecosystem level fine root respiration than the control plots (Figure 3.12), which can have implications for interpreting eddy covariance measurements. If one were to see an increase in $CO_2$ flux from studies located in wetlands with water table manipulations, they could misinterpret changes in the flux rate as being largely indicative of changes in peat decomposition. The control plot fine roots respire at a specific respiration rate of 0.171 μmol $CO_2$ $m^{-2}$ $s^{-1}$, the drained plots respire at a rate of 0.307 μmol $CO_2$ $m^{-2}$ $s^{-1}$, and

the wet plots respire at a rate of 0.330 μmol $CO_2$ $m^{-2}$ $s^{-1}$. Within the SNWR site there is an 80% increase in ecosystem level root respiration from the control plot to the drained plot, and a 93% increase in ecosystem level root respiration from the control plot to the wet plot. Compared to nighttime ecosystem respiration from eddy flux towers at the SNWR site, ecosystem fine root respiration contributes an important proportion of the total ecosystem respiration rates. For the dates of our root respiration measurements, nighttime ecosystem respiration rates were 2.4 μmol $CO_2$ $m^{-2}$ $s^{-1}$ from the wet plots, 2.5 μmol $CO_2$ $m^{-2}$ $s^{-1}$ for the drained plots, and 3.1 μmol $CO_2$ $m^{-2}$ $s^{-1}$ for the control plots. Our estimates of fine root respiration would account for 14, 13, and 6% of these values for the wet, drained, and control area, respectively. Though these calculations only represent three sample dates from the warmer part of the growing season, the larger proportional contribution of fine roots to ecosystem root respiration for the drained and wet plots, illustrates the importance of considering root respiration when making inferences regarding changes in C cycling and peat decomposition as peatland conditions are altered.

The large increase in specific root respiration is evident for the wet plots on 18 July 2011, and it is likely due to the combined effects of warmer temperatures (Figure 3.11), and the initiation of new, high N concentration roots just after lowering of water levels associated with low precipitation events during the summer of 2011. During the 17 September 2011 sampling date when water levels were even lower due to prolonged drought (Figure 3.7), specific respiration were again highest for the wet plots, but values for all water levels were lower than in mid July due to decreased peat temperature (Figure 3.11), with the

average temperature of the peat for the control, drained and wet plots at 10.9, 8.8 and 11.5$^{o}$ C respectively.

The increase in ecosystem level root respiration across dates also follows this pattern of decreased water levels and increased peat temperature associated with higher respiration rates for the drained and wet plots on 18 July 2011 especially (Figure 3.9).

## *Conclusion*

As temperatures increase, and precipitation regimes change, C cycling and nutrient availability in peatland systems will change, and if peatland water levels lower, woody plants may encroach. It is expected that lower water levels will enhance peat decomposition, leading to greater $CO_2$ efflux from these ecosystems. However, assumptions that measured increases in C flux from northern peatlands due to shifts in water levels are due primarily to enhanced decomposition could be in error, especially for chamber-based measurements. Our data does support previous studies which show that changes in water levels might increase the C flux from the peatland to the atmosphere. However, we also measured an increase of up to 93% more ecosystem level fine root respiration for areas experiencing water level changes. Up to 14% of the measured ecosystem root respiration from this study area could be attributed to woody fine root respiration during our measurement dates, with the greatest contribution occurring from areas where the water level had been altered. Thus an important proportion of the increase in ecosystem respiration with water level change was not due to altered peat

decomposition, but was instead attributable to increased fine root respiration, which represents a return to the atmosphere of recently fixed photosynthate, rather than old C sequestered in the peat. As a result there must be caution in assuming that a large change in flux of C from a drained peatland is strictly decomposition.

# Chapter 4

## Thesis Summary

An improved understanding of mechanisms by which climate change may alter C allocated to autotrophic respiration of plant fine roots may help future climate change and ecosystem modelers fine-tune their models to better reflect likely real-world ecosystem responses. These improved models may help land managers and policy makers make sound decisions based on actual scientific findings to help mitigate any hardships that might be encountered with changes in our planet in the next 100 years.

In Chapter 2, we show that even after a short-term temperature manipulation (one and half years), the trees were already metabolically adjusting fine root respiration to warmer soil, which at the ecosystem level would help constrain carbon loss from autotrophic respiration. Perhaps with further observation and experimentation, researchers may be able to fully understand the degree to which such acclimation will occur and persist in the roots of sugar maple tree and other trees, and how it will impact the C balance, health and productivity of northern temperate tree species. This may help managers of this forest type make decisions on either continuing management for species such as sugar maple, or favor different species. Further investigation may confirm findings similar to Melillo et al. (2011) in which the trees reduced their root biomass after being subjected to warming at Harvard Forest, MA, effectively reducing C allocated to root respiration, allowing C to be allocated to other uses, such as the observed increase in aboveground productivity.

Chapter 3 shows that changes in water level can dramatically increase woody plant specific root respiration in peatlands, and ultimately ecosystem root respiration. These increases in ecosystem root respiration result in increased peatland $CO_2$ efflux in response to changes in water level, and could be misinterpreted as increased decomposition of peat that has been sequestered for hundreds, if not thousands of years, if details of autotrophic C cycling were not fully understood. At the SNWR, a measureable proportion of the increase in ecosystem respiration measured by eddy covariance towers was actually C that was recently captured through photosynthesis and returned to the atmosphere through root respiration.

These two studies show the importance of investigating mechanistic responses of woody plant root systems to a changing environment. It is very important to utilize these and similar data from other studies to further strengthen the ability of ecosystem process models to predict effects of climate change and integrate the resulting feedbacks to atmospheric $CO_2$ into coupled climate change models.

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