

The Effects of Wildfire on Hydraulic Properties in Conifers

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Environmental Science

in the

College of Graduate Studies

University of Idaho

by

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January 2007

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Abstract

Wildfires are a natural and ubiquitous component of forested ecosystems in the northwestern United States. However, wildfires can have potentially dangerous impacts on the hydraulic properties of vegetation, which can ultimately lead to mortality or a prolonged state of decline. Water use efficiency (WUE), or an estimate of the amount of carbon fixed per unit of water loss, is an indication of tree physiological status. WUE can be assessed with carbon isotope analysis. This replicated experiment analyzed physiological data from live conifers found in areas of moderate burn severity and compared them to the same species in neighboring unburned controls. Leaf specific conductivity (K_L), stomatal conductance (g_s), soil water potential ($\Psi_{predawn}$), and ^{13}C values ($\delta^{13}\text{C}$) were measured on burned and unburned trees from three different wildfire sites located in central Idaho. Finally, $\delta^{13}\text{C}$ was assessed for the understory shrubs that survived the wildfires and compared with neighboring controls. Leaf specific conductance did not vary significantly with treatment or throughout the summer. Both moisture content ($\Psi_{predawn}$) and diurnal patterns of stomatal conductance were not affected by the burn treatment; however, time was a significant effect in influencing these variables throughout the summer. The $\delta^{13}\text{C}$ values of the wood formed in the burned trees did not differ from adjacent controls, indicating there were no shifts in WUE due to the fire. Although it appeared that there was no difference in the hydraulic properties of the burned and unburned trees, the leaf area in the moderately-burned trees was reduced, signifying that the internal conductance of the burned trees was reduced. By reducing leaf area the burned trees could maintain g_s , K_L , and $\delta^{13}\text{C}$ values that were similar to the conifers in the adjacent unburned plots.

The shrubs located within the burned plots were significantly more enriched in ^{13}C than their adjacent controls, indicating an increase in WUE. In conclusion, the internal hydraulic properties of the partially-burned conifers were not impacted by the wildfires and there were no changes in WUE. However, the understory shrubs in the partially-burned treatments increased their WUE, which may have been due to an increase in photosynthetically active radiation, PAR, reaching the surface and available nitrogen in the soil which ultimately can lead to an increase in photosynthetic capacity in the understory. In addition to this, the $\delta^{13}\text{C}$ of soil-respired CO_2 was studied from severely-burned, moderately-burned, and unburned plots at each of the wildfire sites in order to see if it reflected injury of the aboveground vegetation. While there was no difference between the severely-burned and moderately-burned plots, both of these plots differed significantly from the unburned control plots, indicating that damages to the aboveground vegetation was detectable in the belowground $\delta^{13}\text{C}$ values of soil-respired CO_2 .

Dedication

To my parents, Ray and Klaudia, for their constant support and advice throughout my life and my academic accomplishments. You have helped me discover that learning is an unending process that occurs in more than just the classroom.

Acknowledgements

I am deeply thankful to my major professor, Dr. Kathleen Kavanagh, for giving me the opportunity to work as a part of her lab crew and for all of her advice, patience, and direction throughout the course of this project.

I appreciate all of the helpful comments and assistance provided by my committee members: Dr. Theresa Jain, Dr. Paul McDaniel, and Dr. Charles Harris. I am also deeply indebted to Dr. Chris Williams and Ann Abbott for all of their statistical advice.

My gratitude also extends to Robert D. Stickrod II of the Idaho Stable Isotopes Lab for his technical advice and punctual analysis of my isotopic data. I sincerely thank all of the other students who have aided me in field sampling: Nick Norton, Irish Bob, Ben Austin, and in particular Rob Vaughn for his help in the field and knowledge of soil classification. I want to thank Steve Best and Rob Pangle, who provided me with feedback and motivation throughout this process. Finally, my gratitude extends to Aki Koyama for his incredibly hard work, helpful input, and humor throughout this study.

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List of Symbols

(ΔP) – delta pressure

$(\delta^{13}C\text{‰})$ – delta ^{13}C value

(c_i) – internal concentration

(K_L) – leaf specific conductance

(Ψ_{Leaf}) – leaf water potential

$(\Psi_{Leaf-min})$ – minimum leaf water potential

$(\Psi_{predawn})$ – predawn leaf water potential

(Ψ_{soil}) – soil water potential

(Ψ) – xylem pressure potential

(g_s) – stomatal conductance

(E_{Flux}) – transpiration rate

(PAR) – photosynthetically active radiation

(VPD) – vapor pressure deficit

(WUE) – water use efficiency

Glossary

Cavitation – the breaking of a water column within a plant when air seeps into a tracheid and reduces flow rates

(ΔP) – the difference in water pressure between two ends of a stem

Delta ^{13}C value ($\delta^{13}\text{C}\text{‰}$) – a ratio of ^{13}C to ^{12}C isotopes; a sample is ‘enriched’, ‘heavier’, or ‘less negative’ if has more ^{13}C to ^{12}C when compared to another sample

Embolism – an air bubble trapped inside a tracheid that prevents the flow of water

Heterotrophic community – a microbial community that relies on organic matter for food

Internal concentration (c_i) – a measure of the CO_2 concentration within a leaf

Leaf specific conductance (K_L) – a measure of the internal resistance to water transport within a plant

Leaf water potential (Ψ_{Leaf}) – a measurement of the water status within a leaf

Minimum leaf water potential ($\Psi_{\text{Leaf-min}}$) – the threshold water potential for a leaf, below which it can not survive

Predawn leaf water potential (Ψ_{predawn}) – a measurement of the water status within a leaf during the nighttime, typically stomata are closed and transpiration rates are negligible thus Ψ_{predawn} should reflect the soil water status around the plant

Resinosis – the flow of resin or pitch in response to a wound or infection

Saprophyte – an organism that commonly feeds on dead organic material

Soil water potential (Ψ_{soil}) – the ability of water to move through the soil

Stomatal conductance (g_s) – a measurement of the width of the stomatal aperture

Stomata – pores on a leaf that regulate water vapor loss and CO_2 gain between the leaf and the atmosphere

Tracheid – a conduit/vessel within the xylem of conifers for transporting water and nutrients

Transpiration rate (E_{Flux}) – a measurement of the rate at which water vapor is lost into the atmosphere through the stomata of plants

Vapor Pressure Deficit (*VPD*) – the difference between the actual water vapor pressure in the atmosphere and the saturated vapor pressure at a particular temperature, or a measure of how dry the air is

Water Use Efficiency (*WUE*) – a measure of the amount of water lost by a plant in relation to the amount of carbon gained

Xylem – the portion of a stem that transports water and nutrients to the canopy; the sapwood

Xylem pressure potential (Ψ) – the absolute pressure of the xylem minus the absolute atmospheric pressure; the pressure gradient that drives water from the roots through the canopy

Preface

In this thesis I combine knowledge from plant physiology, fire ecology, biogeochemistry, and silviculture to identify if the disturbance caused by wildfire resulted in physiological alterations occurring in the hydraulic systems of lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), and spirea (*Spiraea betulifolia* var. *lucida*). I also traced the effects of this disturbance to belowground processes. The study was conducted in three wildfire sites that occurred late in the summer of 2003 in central Idaho.

The thesis contains four chapters and an appendix. Chapter 1 includes the introduction, a brief literature review, and research objectives. Chapter 2 describes the results of the impact of the wildfires on the trees and shrubs. Chapter 3 summarizes the impact of the wildfires on soil-respired CO₂. Chapter 4 summarizes the results and provides suggestions for future research. Next is the complete list of references for the whole thesis. Finally, the appendix contains tables and graphs that further describe the study plots and wildfire sites.

Chapter 1

Hydraulic Conductance and Tree Productivity in Conifers

1.1 Introduction

Wildfire is one type of abiotic disturbance that is capable of killing trees immediately or sending them into a state of decline. Frequently, wildfires leave behind many partially-burned and damaged trees, which may exhibit scorched crowns and/or boles. Although many of these trees may have large portions of their canopies that still retain their green needles, giving one the impression that they have successfully survived the fire, they actually may have suffered severe unseen damages, such as cambial mortality, and xylem cavitation, the blocking of xylem tracheids by air pockets. While it is obvious that a severely damaged crown can lead to a decrease in photosynthesis and energy production (Van Wagner, 1973; Peterson and Arbaugh, 1986), less obvious damage to the cambium or phloem may similarly impact tree productivity and survival (Hare, 1965; Ryan, 2000). In addition, damaged roots lead to a reduction in the amount of nutrients and water input to the canopy, thus limiting photosynthesis (Hungerford et al., 1991; Coomes and Grubb, 2000). However, no one has explored the possibility that xylem cavitation and the subsequent disruption of nutrients and water transport in the xylem may also be a cause of post-fire decline and mortality. By understanding how damage to a tree's xylem and the subsequent alteration of its internal hydraulic properties affect productivity and growth rates, modelers may be able to predict long-term mortality rates or fluctuations in water relations within a catchment more accurately. Ultimately, managers may utilize that information to guide their actions across the landscape. For

instance, they may discover that the burned trees suffered no internal damages and thus they may choose to harvest them later when they are larger and commercially more valuable. On the other hand they may realize that mortality within the damaged trees is imminent and therefore harvest immediately in order to reduce the risk of insect outbreaks occurring.

Damage to the xylem via cavitation can send trees into a state of decline and delayed mortality (Tyree and Dixon, 1986; Tyree and Sperry, 1988). Fires commonly cause injuries to a tree's bole near the ground surface by disrupting flow rates through the xylem. High heat intensities can cause the epithelial cells of the resin ducts to rupture and cause resinosis. Ultimately this will increase stem resistance to water flow within the xylem and can trigger a number of feedback effects that limit productivity by reducing transpiration (E), (i.e., the rate of water lost from a plant to the atmosphere), stomatal conductance (g_s), (i.e., the width of a stomatal pore opening), and carbon assimilation (Ryan, 2000). Cavitation also reduces water flow, thus it may also trigger feedbacks that lower xylem pressure potentials and limit productivity to the point where mortality may be imminent (Meinzer et al., 2001).

Wildfire also impacts evapotranspiration rates within disturbed sites by altering the amount of moisture that is available to post-fire surviving vegetation (Swanson, 1981; DeBano et al., 1998). For instance, by reducing the amount of vegetation on the ground, fire can actually increase the amount of available moisture in the soil (DeBano et al. 1998), since less water would be transpired. On the other hand, factors such as a reduction in overstory canopy, reduced organic material in the soil and a blackened surface on the ground could actually decrease the available soil moisture by increasing

radiation absorption at the surface, increasing evaporation rates, and reducing water-holding capacity within the soil (Swanson, 1981). As a result, vegetation must maintain a particular threshold of hydraulic properties with the available water that they have access to in order to maintain essential minimum levels of productivity or else they will die (Bond and Kavanagh, 1999).

Depending on the amount of damage sustained by vegetation and the alteration in available moisture, surviving vegetation may actually benefit from the impacts of the wildfire or be sent into a state of decline. As forestry management plans incorporate prescribed fire and wildland fire use increasingly in the future, the need to understand and accurately model the growth and survival of burned trees will rise also. Therefore, it is necessary that modelers and managers have an understanding of the relationships between fire injury and tree stress physiology (Ryan, 2000). The objective of this study was to determine whether or not wildfires had impacted the hydraulic properties within surviving trees' xylem.

1.2 Effects of Cambial Mortality on Tree Productivity

Bole damage and in particular cambial death play an important role in determining post-fire mortality in trees (Ryan and Reinhardt, 1988). Past studies have revealed that the exposure of physiologically active plant tissues to temperatures of 60°C for only short periods of time is lethal (Hare, 1961). However, the rate of tissue necrosis will vary with temperature and duration to exposure (Hare, 1961; Dickinson and Johnson, 2004). The amount of exposure and subsequent injury that is sustained by these tissues is largely due to the overlying bark thickness, which is linked to tree size and species (Ryan

and Reinhardt, 1988). Although thick bark may prevent extensive cambial damages, a possibility exists that even partial cambial death may lead to serious internal injury and eventual decay (Gara et al., 1985). Consequently, damaged trees may fall into decline as they exhaust their carbohydrate reserves. Ultimately, once trees begin utilizing more carbohydrates during respiration than they can produce via photosynthesis mortality becomes imminent (Waring, 1987).

1.3 Effects of Cavitation on Hydraulic Conductance and Tree Productivity

Productivity in Trees and Ecosystems:

Trees create carbohydrates via photosynthesis in the green needles of their canopies. However, carbohydrates are required in all parts of the tree from the canopy to the stem and roots. In fact, the carbohydrates are even transported to mutualistic mycorrhizae and microbes in the surrounding soil (Högberg et al., 2001). Högberg et al. (2001) found that carbohydrates formed in the canopies of trees 20-25 m tall were made available for root/rhizosphere respiration in 1-4 days. In addition, researchers have determined that photosynthates, created in the canopy, fuel at least 65% of the total soil respiration (Ekblad and Högberg, 2001). Due to this rapid translocation of carbohydrates, there is a strong link between the productivity of the trees within an ecosystem and the productivity of the rest of that system as well.

The carbohydrates are transported throughout the tree in the phloem where they are used in forming defensive compounds, performing cellular maintenance, enhancing growth and seed production, or as stored energy reserves. When carbohydrate production becomes compromised by some type of disturbance, the allocation of these sugars may be

redirected to ensure that the most critical functions within the tree, which are cellular maintenance and transpiration, can be carried out. Otherwise, the trees die when they are unable to produce enough sugars from photosynthesis to replace the carbohydrates that are utilized in respiration (Ryan, 2000).

Consequences of a Damaged Hydraulic System:

Just as the phloem is critical for distributing energy in the form of sugars throughout the tree, the xylem is critical in distributing water, minerals, and nutrients from the roots to the crown in order to perpetuate transpiration and growth within the tree (Figure 1).

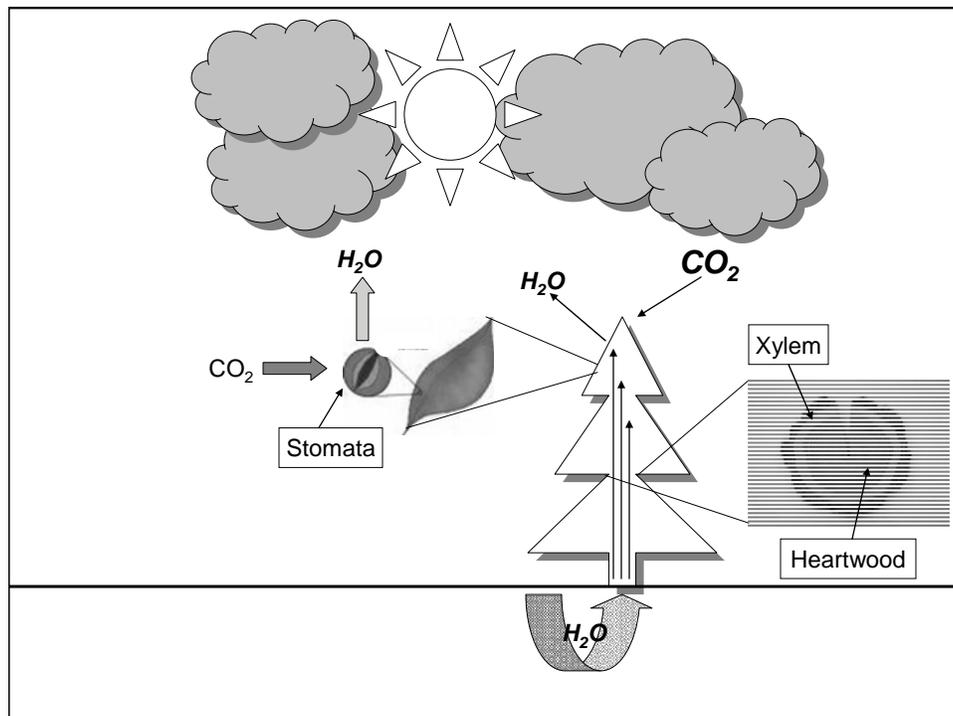


Figure 1: The Hydraulic Pathway. Water is absorbed through roots in the ground. Then it is transported through the bole of the tree in the xylem up to the leaves in the canopy. Leaf specific conductance, K_L , is a measure of the resistance to water transport within the xylem of the bole and the leaves. Plants use water, CO_2 , and sunlight to create sugars via photosynthesis inside the leaf. As water vapor escapes to the atmosphere, CO_2 enters the leaf through pores called stomata. Stomatal conductance, g_s , controls the amount of CO_2 that enters the pore and the amount of water that escapes the pore.

Wildfire may also damage trees by causing excessive cavitation within the plants' xylem. Cavitation disrupts the water flow in the xylem, disturbing the movement of nutrients and water from the roots to the canopy. Xylem cavitation occurs when air seeps through pit membranes and enters the functioning conduits, resulting in decreased xylem pressures from the "embolized" air-filled conduits (Tyree and Sperry, 1988; Sperry et al. 2003). As the xylem pressure continues to become more negative, cavitation increases and the newly formed air embolisms cause a decrease in hydraulic conductance within the tree (Zimmermann, 1983; Tyree and Ewers, 1991; Sperry and Sullivan 1992; Sperry et al. 2003; Figure 2). Decreasing hydraulic conductance highly influences plant water status, particularly if it lowers leaf specific conductance (K_L), which ultimately influences stomatal conductance (Tyree et al., 1993; Bond and Kavanagh, 1999; Hubbard et al., 2001).

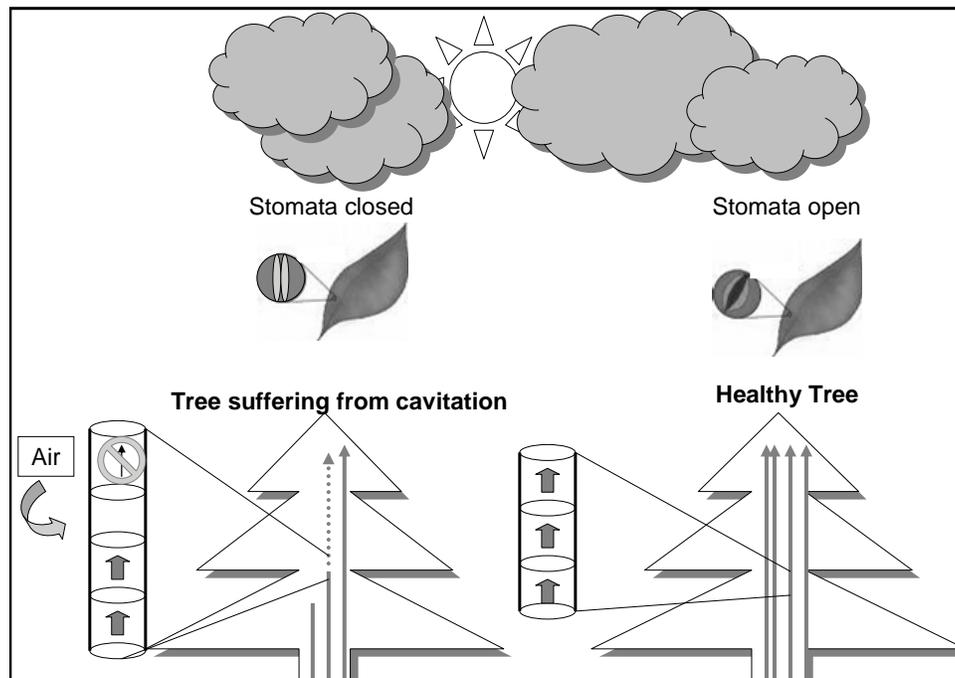


Figure 2: Xylem cavitation. A healthy tree transports water through tracheids in the xylem to leaves in the canopy. However, when cavitation occurs air seeps into the tracheid, thus breaking the water column to the canopy and reducing the amount of water supplied to the foliage. Damaged trees are more sensitive to changes in VPD and will close their stomata earlier in the day in order to conserve water resources and maintain leaf water potentials above their critical threshold.

K_L is a measure of the internal resistance within the plant to transporting water (Zimmermann, 1983). K_L influences stomatal conductance (g_s), by increasing the stomatal sensitivity to changes in whole-plant hydraulics (Addington et al., 2004). Therefore, as K_L decreases, the resistance to water movement increases and the efficiency of a tree to transport water to and through its foliage is reduced. Ultimately, the tree's transpiration and photosynthetic rates decline as well (Sperry et al., 1988; Hacke et al. 2000).

Decreases in K_L may result from a number of different factors. Some of these include a loss of functioning roots (often a direct effect due to fire), reduction in the diameter of hydrogels within the water-transporting tracheids (Zwieniecki et al., 2001),

xylem cavitation, or insufficient sapwood area to support the leaf area (Waring et al., 1982). Frequently, these factors work together synergistically to decrease a tree's resilience (Sperry et al., 1993; Ryan, 2000).

Stomata regulate gas exchange between the tree and the atmosphere. Stomatal conductance (g_s) controls the rate of water loss in a leaf by closing to adjust the transpiration rate (Sperry et al. 2003). Stomata also control CO₂ uptake. When g_s is high, CO₂ more readily enters the leaf (Larcher, 1963; Lawlor, 2002; Romero and Botía, 2006).

Stomatal closure occurs when the water supply does not meet atmospheric demand, thus stomata respond directly to changes in K_L . However, the critical mechanism by which plant cells detect changes in water status remains unknown (Jones, 1998; Luan, 2002). Past experiments have shown that stomatal response can occur within minutes of hydraulic manipulations on coniferous seedlings, via disturbances such as defoliation, root pruning, freezing/thawing of stems, or even the induction of xylem cavitation (Hubbard et al., 2001).

Gas exchange and productivity within the canopy are ultimately influenced by the shifts in K_L .

$$E_{Flux} = K_L(\Delta P) \quad (1)$$

where E_{Flux} is equal to transpiration, a measure of volume flow rate in (mmol/m²/s); K_L is leaf specific conductance, expressed in units per leaf area per second (mmol/m²/s); and ΔP is the change in pressure in the soil and the xylem that drives flow measured in (MPa) (Bond and Kavanagh, 1999; Hubbard et al., 1999).

When trees cannot supply adequate water to meet transpirational demands the trees reduce leaf area. This reduction can be accomplished by leaf fall or branch isolation. As a result, loss of K_L can result in branch mortality also referred to as branch segmentation (Sperry et al., 1993; Tyree et al., 1993). For instance, one experiment revealed that in Douglas-fir the smaller, distal branches may be more vulnerable to cavitation than were the thicker, proximal branches (Sperry and Ikeda, 1997). Consequently, the remaining leaves on the surviving branches must not fall below their minimum leaf water potential or else they will decline in vigor and also die (Tyree and Sperry, 1988; Jones and Sutherland, 1991).

Interestingly, undergoing partial defoliation may actually be beneficial. Once canopy transpiration is reduced, the remaining foliage may actually experience an increase in xylem pressure potential (Ψ), (i.e., the pressure gradient that drives water from the roots through the canopy), g_s , and transpiration (E) at the leaf-level; thus there will be more water available in the soil for the remaining foliage to fix carbon used in photosynthesis. Therefore, Ψ as well as g_s and E at the leaf-level may actually increase after a fire (Ryan, 1990).

Stomatal Responses to Water Stress:

Stomata, the pores on a leaf, allow air (CO_2) to enter the leaf for photosynthesis to occur. Carbon from the CO_2 within the air is used in creating carbohydrates in conjunction with water supplied from the soil, which exits the leaf via transpiration. As a result, stomata must carefully balance the production of photosynthates while avoiding dehydration induced damages such as excessive cavitation and disturbance to cellular

water relations (Tyree and Sperry, 1988; Sperry and Pockman, 1993; Jones and Sutherland, 1991; Hubbard et al., 2001).

Past studies have revealed that trees control their stomatal conductance in order to maintain a constant minimum leaf water potential, according to the following:

$$E_{Flux} = K_L(\Psi_{leaf} - \Psi_{soil}) \quad (2)$$

where E_{Flux} is transpiration rate; K_L is leaf specific conductance; Ψ_{leaf} is the leaf water potential and measured in (MPa); and Ψ_{soil} is the soil water potential and measured in (MPa). Stomatal conductance is regulated in conifers in order to avoid xylem dysfunction and embolism as a result of dropping below the $\Psi_{Leaf-min}$ (Tyree and Sperry, 1988). Interestingly enough, this set minimum value is the same for both healthy and declining trees of the same species (Sperry et al., 1993). However, the point in the day when trees must regulate their stomata in order to maintain their $\Psi_{Leaf-min}$ varies based directly on the tree's physiological properties and also indirectly by environmental conditions such as the vapor pressure deficit (VPD). Transpiration is determined by the following equation (Warren and Adams, 2006)

$$E_{Flux} = g_s(VPD) \quad (3)$$

where E_{Flux} is transpiration rate; g_s is stomatal conductance and measured in (mmol/m²/s); and VPD is the vapor pressure deficit. As the Ψ_{Leaf} becomes more negative and xylem water tension increases, stomatal closure is initiated in order to maintain the water potential at or above $\Psi_{Leaf-min}$. This increases resistance within the hydraulic pathway (i.e., reduced K_L) from the soil to the atmosphere via the tree and results in earlier diurnal variations in water potential within the tree and thus stomatal closure (Warren et al.,

2001). Consequently, stomata are greatly affected by climatic conditions associated with time, both diurnally and seasonally (Prior et al., 1997; Salleo et al, 2000). For instance, stomatal conductance typically decreases throughout the day as temperature increases and relative humidity decreases. Similarly, as the climate becomes drier throughout the summer, the point in the day when stomatal conductance is highest, will occur earlier and earlier in the day.

Damaged and declining trees have greater stomatal sensitivity to shifts in VPD (Hubbard, 2001; Salleo et al., 2000) and therefore may close their stomata earlier on in the day compared to healthy unaffected trees. Since the trees cannot maintain high transpiration rates without dropping below their $\Psi_{Leaf-min}$, they must curtail their transpiration rates by decreasing their stomatal conductance, thus causing them to close their stomata, reducing water loss and water stress. However, this ultimately reduces the tree's photosynthetic rates since CO_2 uptake is also reduced. As a result, the tree's water use efficiency (WUE), which is a measurement of the amount of water lost in relation to carbon fixed by a plant, will increase. This occurrence is most noticeable during the summer or during periods of drought (Jones, 1974; Romero and Botía, 2006). Generally, at these times soil moisture is low and the VPD is high. As a result of these added pressures on the limited water resources, trees must decrease their stomatal conductance earlier in the day in order to survive and avoid additional xylem cavitation with critically low leaf water potentials (Ψ_{Leaf}) (Oren et al., 2001; Lawlor, 2002).

Carbon isotope values and WUE:

Carbon-13 discrimination ($\delta^{13}C\text{‰}$) is another method for evaluating g_s and thus water use efficiency (WUE) within trees. WUE is a ratio of the amount of water lost relative to the amount of carbon gained by a plant. Typically, carbon occurs with 12 neutrons; however, the heavier form of carbon, ^{13}C with its extra neutron, is also present in the atmosphere. Although it comprises only about 1.1% of all the atmospheric carbon dioxide on Earth, it is still measurable, even in plant tissues. The $\delta^{13}C$ variable is a measurement of carbon isotope ratios that are expressed relative to a standard (R_{standard}). Pee Dee belemnite (PDB) is the standard used for carbon isotopes. $\delta^{13}C$ is expressed in units per mil (‰), and is useful in studying CO_2 effluxes within disturbed ecosystems and is determined as follows (O’Leary, 1981; Ehleringer et al., 2000):

$$R = \frac{{}^{13}CO_2}{{}^{12}CO_2} \quad (4)$$

$$\delta^{13}C(\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000\text{‰} \quad (5)$$

where, $\delta^{13}C$ is the isotopic discrimination label of a sample and measured per mil (‰); R_{sample} is the ratio of ^{13}C to ^{12}C in a sample; and R_{standard} is the ratio of ^{13}C to ^{12}C in the PDB standard.

Discrimination against the heavier carbon isotope can occur in plants during photosynthesis. The molecular shape of the ^{13}C atom reduces its diffusivity by 4.4‰ (Farquhar et al., 1982). Once the heavier isotope is inside the leaf, further discrimination occurs during the incorporation of CO_2 by the enzyme Rubisco - ribulose biphosphate carboxylase (Farquhar et al., 1982; Ehleringer et al., 2000). Due to these forms of

discrimination, organic material produced from C_3 photosynthetic matter is more depleted (i.e., -27‰)

Typically, the effects of fractionation in C_3 plants, such as conifers, range from -21‰ to -30‰ (Ehleringer et al., 2000). In fact, over 90% of all C_3 species have isotopic compositions that fall between -22 and -30‰ (Farquhar et al., 1982). Since organic matter is depleted in ^{13}C when compared to the atmosphere standard, the $\delta^{13}C$ values of organic material are negative. Values that are less negative (i.e., close to zero) are 'heavier' or enriched in ^{13}C ; whereas, values that are more negative are 'lighter' or depleted in ^{13}C (O'Leary, 1981). Consequently, as these values are recorded in organic tissues they may be compared to one another through time and used to draw conclusions about a plant's productivity levels.

The impact of stomatal conductance (g_s) on ^{13}C discrimination:

As stomatal conductance decreases, the trees become less discriminate in choosing which carbon (C) molecules they use to form carbohydrates. As discussed above, under optimal conditions plants will favor CO_2 with ^{12}C atoms compared to those with ^{13}C atoms. However, when trees are damaged or undergoing drought conditions and they must close their stomata earlier in the day, less discrimination against ^{13}C occurs. As a result, stressed trees, which typically have lower stomatal conductance values than healthy trees, will show a higher proportion of ^{13}C to ^{12}C (McDowell et al., 2003). Consequently, anything that reduces the internal concentration of CO_2 (c_i) causes less discrimination; therefore this includes photosynthetic efficiency.

The impact of photosynthetic capacity on ^{13}C discrimination:

Nutrients such as nitrogen (N) have been found to greatly impact photosynthetic capacity in C_3 plants (Field and Mooney, 1983; Evans, 1989). When water and photosynthetically active radiation (PAR) are not limiting, increases in leaf N content correlate with increases in photosynthesis. Although these increases ultimately plateau, the increasing photosynthetic capacity of a plant results in rises in CO_2 assimilation per unit leaf area. Since the amount of available N in forested ecosystems typically increases after a fire (Schoch and Binkley, 1986; Kutiel and Naveh, 1987), some plants may actually benefit by increasing their N use efficiency and ultimately their photosynthetic capacity.

This shift in N use efficiency and photosynthetic capacity may be evident in a plant's isotopic compositions as well. As photosynthesis increases, the corresponding rise in CO_2 assimilation may cause the internal gas concentration (c_i) to be depleted much faster, thus increasing the plant's $\delta^{13}\text{C}$ label (Farquhar, 1982).

Since the carbohydrates that are formed in the foliage are also used in making the wood of a tree, the isotopic signature of each growing season may be examined by analyzing each of the tree's growing rings. Therefore, the impacts of past disturbances may be evaluated long after they actually occurred (Francey and Farquhar, 1982).

Foliage can be extremely sensitive to environmental shifts that influence isotopic discrimination. However, it is important to note that reductions in CO_2 assimilation do not always correspond to enrichment in ^{13}C . For instance, foliage that is lower in the canopy tends to be shaded by the surrounding trees and their canopies. As a result of this shading and low irradiance levels, the foliage that is lower in a canopy intercepts less

light and photosynthesizes less. Ultimately this reduction in photosynthesis and the water loss that corresponds with it allow the stomata to stay open longer and their isotopic signatures become more negative as they utilize a higher proportion of ^{12}C (Farquhar et al., 1982).

Trees and plants in the understory tend to follow this same pattern caused by low irradiance levels; however, in a closed canopy system the understory plants are also subjected to atmospheric values that are more negative (i.e., ^{13}C depleted) due to the isotopic signature of the respired CO_2 of the understory that is trapped under the canopy. The respired CO_2 of the overstory canopy and the soil is naturally more negative than the atmosphere. Therefore, the CO_2 that is assimilated in understory plants will already be depleted compared to the atmosphere (Farquhar et al., 1982).

The key principles to remember are that any factor that directly affects leaf metabolism by reducing CO_2 assimilation rates, should increase c_i and increase discrimination against ^{13}C . On the other hand, when CO_2 assimilation is reduced due to a reduction in stomatal conductance, c_i will decrease and decrease discrimination against ^{13}C , because there is less $^{12}\text{CO}_2$ to choose from (Farquhar et al., 1982). Since stomatal conductance is largely a function of climatic conditions and the available water resources, the effects of a drought on a tree and its stomatal conductance would appear to be quite similar to cavitation within a tree and might amplify the effects of cavitation as well. Burn severity may also influence the degree of cavitation within a tree because it impacts the amount of available water resources as well as damaging the internal components of the tree.

1.3 Burn Severity Classification:

Burn severity classification is useful in categorizing the post-fire effects on a burned ecosystem. Often there is great confusion and ambiguity associated with the terms “fire severity”, “fire intensity”, and “burn severity”. These terms have different meanings to people with various backgrounds and consequently they are often used to describe different processes unknown to a specific audience. The terms “fire severity”, “fire intensity”, and “burn severity” all have distinctly different meanings among scientists, managers, and the general public. This study will use terms according to the Fire Disturbance Continuum in which *fire severity* and *fire intensity* refer to first-order fire effects which occurred *during* the combustion process of the actual fire. Typically, *fire intensity* is characterized by flame lengths (m), the rate of spread (m/s), or the amount of energy created by the fire (btus). *Fire severity* relates to the direct effects on the environment including: killing and consuming of vegetation and organic debris and the effects of heating soils. It also signifies the proportion of tree crowns that are consumed during the fire compared to their pre-fire condition (Jain, 2004).

On the other hand, *burn severity*, which is primarily used in describing the plots of this study, refers to environmental characteristics and fire effects that are evident *after* the fire, flames, and smoldering have ended (i.e. the post-fire environment). The post-fire environment is the result of not only the fire itself but also any other disturbance that may have occurred afterwards and further contributed to the condition of that area, such as a rain event that strips away loose soil (Jain, 2004). All of the trees and plots that were sampled were in the wildfire sites and were evaluated based on their burn severity. For each wildfire site, 3 plots were delineated based on their burn severity classification:

unburned controls, moderately/partially-burned plots, and severely-burned plots which experienced stand-replacing fires.

1.4 Objectives

We hypothesize that trees with a damaged xylem after a fire will increase their water use efficiency due to increased stomatal closure. The increase in WUE will be evident in increased midday stomatal closure and less negative $\delta^{13}C$ values in wood formed after the fire relative to unburned controls. In order to test this hypothesis, we put forward the following objectives. First, we investigated the differences in $\Psi_{predawn}$, g_s , and K_L between the plots for the damaged trees and the unburned controls. A significant difference in $\Psi_{predawn}$ would show us that the amount of water resources varied among the treatments. Significant differences in g_s would indicate that trees with a lower midday g_s may have been damaged internally and thus are more sensitive to changes in VPD or the amount of available water resources in the soil. Differences in K_L would show us that either water transport through the xylem was reduced to avoid further cavitation or it was enhanced in order to maintain productivity levels within the remaining canopy and to avoid mortality.

Next, by analyzing $\delta^{13}C$ labels, we examined the differences in the water use efficiencies between these plots following the occurrence of the wildfires in damaged trees as well as understory shrubs. This data would be used to crosscheck the results of the g_s data and identify the labels associated with the overstory conifers and the understory spirea. By synthesizing these results we hoped to determine if the damages to the burned trees were great enough to cause mortality. Finally, we investigated the $\delta^{13}C$

labels of soil-respired CO₂ in severely-burned plots with 100% tree mortality as well as in the moderately-burned plots with damaged trees and the unburned controls. These results would indicate where the bulk of the carbon-13 signal was coming from that the belowground communities were predominantly using.

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Chapter 2

The Effects of Wildfire on Hydraulic Properties in Conifers

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2.1 Abstract

Wildfires are a natural and ubiquitous component of forested ecosystems in the northwestern United States. However, wildfires can have potentially dangerous impacts on the hydraulic properties of vegetation, which can ultimately lead to mortality or a prolonged state of decline. This replicated study analyzed physiological data from a number of partially-burned conifers found in burned areas of moderate burn severity and compared them to neighboring unburned controls throughout the growing season. Since this study focused on analyzing physiological measurements that influenced the water use efficiency of conifers, measurements of leaf specific conductivity (K_L), stomatal conductance (g_s), soil water potential ($\Psi_{predawn}$), and ^{13}C discrimination ($\delta^{13}\text{C}$) were collected from three different wildfire sites located in central Idaho in order to monitor any changes in the tree performance of mature coniferous trees as a result of the fires. Finally, $\delta^{13}\text{C}$ was assessed for the understory *Spirea betulifolia* shrubs that survived the wildfires and compared with neighboring controls. Leaf specific conductance did not vary significantly with treatment or throughout the summer. In addition to this, neither midmorning nor midday stomatal conductance (g_s) was impacted by the burn treatment or by time throughout the summer. Although there was no difference in soil moisture contents ($\Psi_{predawn}$) between the treatments, $\Psi_{predawn}$ was influenced significantly by time and became drier throughout the summer. ^{13}C discrimination did not vary with treatment

or by year for the conifers. Although leaf area within the partially-burned trees was reduced, there was no shift in g_s , K_L , or $\delta^{13}C$, indicating that hydraulic conductance within the partially-burned trees was reduced. Consequently, the reduction in leaf area compensated for the loss of hydraulic conductivity and allowed the partially-burned trees to maintain a constant g_s , K_L , and water-use efficiency throughout the summer. On the other hand, the shrubs located within the burned plots were significantly more enriched in ^{13}C than their adjacent controls. In conclusion, our research showed that the internal hydraulic conductances of the partially-burned conifers were reduced by the wildfires, yet those trees were able to maintain productivity levels by reducing their leaf area. However, the understory shrubs in the partially-burned treatments increased their water-use efficiencies, which may have been due to an increase in photosynthetically active radiation, PAR, reaching the surface and available nitrogen in the soil which ultimately can lead to an increase in photosynthetic capacity in the understory.

2.2 Introduction

Disturbances, such as wildfire, play a major role in shaping forest structure by causing tree mortality. In low to moderate severity fires, there is a mixture of tree conditions that can range from immediate mortality to improved vigor. Interestingly, some of the surviving trees may actually benefit from fire due to a reduction in forest density while others are damaged significantly and eventually die (Ryan, 1990; Ryan, 2000). Understanding the causal mechanisms for this longer-term mortality is important to modeling the impacts of fire severity on tree survival.

Damage that can cause long-term mortality includes crown scorch, root mortality, cambium and phloem mortality, and xylem cavitation. While it is obvious that a severely

damaged crown can lead to a decrease in photosynthesis and energy production (Van Wagner, 1973; Peterson and Arbaugh, 1986), less obvious injuries to the cambium or phloem may also have a similar impact on tree productivity and survival (Hare, 1965; Ryan, 2000). In addition, damaged roots can lead to a reduction in the amount of nutrients and water input to the canopy, thus potentially limiting photosynthesis (Hungerford et al., 1991; Coomes and Grubb, 2000). However, no one has explored the possibility that xylem cavitation and subsequent disruption of nutrients and water transport in the xylem may also be a cause of post-fire decline and mortality.

Cavitation occurs when air is pulled into tracheids, creating a void in the water transporting conduit that prevents the flow of water upward through the stem to the canopy (Tyree and Ewers, 1991). Trees avoid cavitation by closing their stomata (Sperry et al., 2003). The “set point” at which stomata close (i.e., the minimum leaf water potential; $\Psi_{Leaf-min}$) is just above the tension that will cause xylem cavitation (Tyree and Sperry, 1988). If this $\Psi_{Leaf-min}$ is exceeded, then cavitation may occur within the bole of a tree. In addition to this, the more that this minimum threshold is exceeded, the more excessive cavitation will be (Zimmerman, 1983). Plants regulate their stomata throughout the day as atmospheric conditions change and also throughout the season as available water resources and climatic conditions shift.

When the heat from a fire sweeps through the canopy, causing the air to rapidly dry out, the sudden change in vapor pressure deficit, VPD, may result in Ψ_{Leaf} that exceeds the cavitation threshold, thus damaging the xylem and causing long-term reductions in K_L . K_L is a measure of the internal resistance within the tree to transporting water (Zimmermann, 1983). K_L directly influences stomatal conductance, (g_s), by

increasing stomatal sensitivity to changes in whole-plant hydraulics (Addington et al., 2004). Therefore, as K_L decreases, the resistance to water movement increases and the efficiency of a tree to transport water to and through its foliage is reduced. K_L can be described mathematically as (Jones and Sutherland, 1991; Dewar, 1995; Whitehead, 1998; Bond and Kavanagh, 1999):

$$K_L = E/(\Psi_{soil} - \Psi_{Leaf}) \quad (6)$$

where E is the transpiration rate and measured in (mmol/m²/s); K_L is equal to leaf specific conductance and expressed in units per leaf area; and $(\Psi_{soil} - \Psi_{Leaf})$ is the absolute difference between soil and leaf water potential in (MPa).

Consequently, if the reduction in K_L is great enough, then stomatal closure may be triggered (Hubbard et al., 2001). While stomatal sensitivity may be measured directly with a porometer, it is also reflected in the ratio of ¹³C:¹²C found within tree tissues (Francey and Farquhar, 1982). Stomatal closure reduces the internal CO₂ concentration (c_i), leading to less discrimination against ¹³C. As a result, trees with a reduction in K_L accumulate higher concentrations of ¹³C to ¹²C in their tissues in relation to atmospheric concentrations (Cowan and Farquhar, 1977; Farquhar et al., 1982; McDowell et al., 2003; Sala et al., 2005).

Cernusak and Marshall (2001) found that there was a strong positive relationship between carbon isotope composition and the loss of conductivity due to xylem embolism. While foliage can be used to compare recent shifts in a plant's isotopic composition, tree-rings provide a more comprehensive record of the tree's lifespan, allowing one to compare values from past years. In addition to this, foliar C isotope values are influenced by the specific location and shading that the foliage is subjected to within the canopy

(Duursma and Marshall, 2006). Therefore, foliar discrimination has the potential to vary widely within the canopy of a single large tree, depending on how high a needle is in the canopy or how exposed to the sunlight it is.

On the other hand, isotopic discrimination ratios obtained from tree-rings provide a more inclusive record of the canopy at the annual time period because each tree-ring is made from cellulose that is derived from the canopy as a whole rather than just one needle or branch. As the wood is forming, cellulose becomes immobile within the cell walls in the current year's tree-ring, providing an annual snapshot of the tree's carbon-13 discrimination (McDowell et al., 2003), which allows one to compare shifts in WUE of years within the same tree.

Our objective was to determine if trees surviving a wildfire had suffered damage to their water conducting systems. We accomplished this by measuring predawn leaf water potential Ψ_{Leaf} , diurnal g_s , K_L , and carbon-13 ratios over a range of time scales. We hypothesized that trees with a damaged xylem after a fire would increase their WUE due to increased stomatal closure and therefore have less negative $\delta^{13}C$ values in wood formed after the fire relative to unburned controls. We repeatedly monitored these trees in order to see if any differences in the hydraulic properties of the two treatments became exacerbated as water resources became more limiting throughout the growing season. A significant difference between the treatment and the control would indicate a reduction in productivity levels within the damaged trees and an increase in their susceptibility to insect or disease outbreaks.

2.3 Materials and Methods

Sample Collection

To understand how fire affects hydraulic characteristics, this replicated study was conducted in three areas in central Idaho, which burned during the summer of 2003. The wildfire sites included the Canyon Creek fire, the South Fork of the Salmon River fire, and the Hall fire.

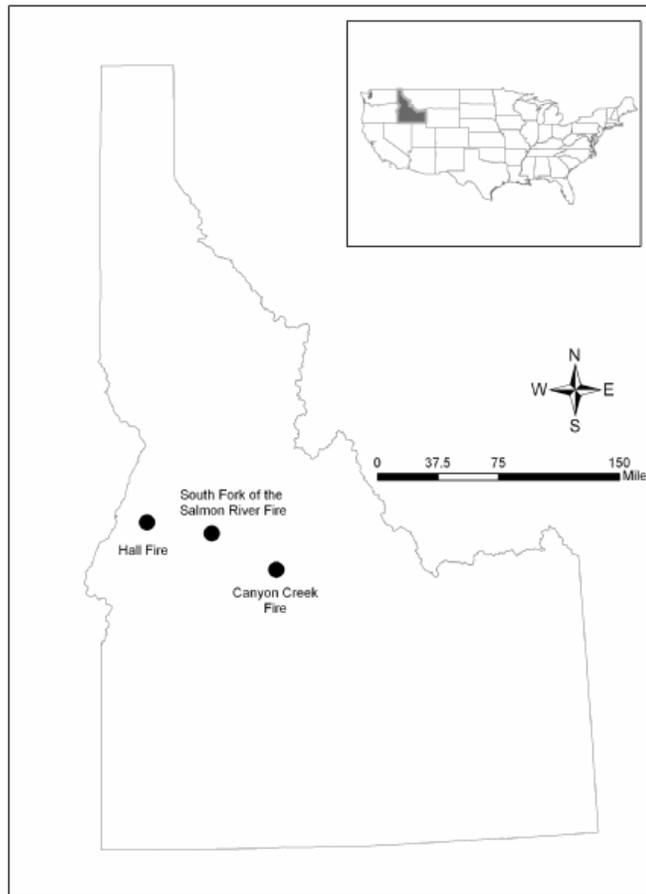


Figure 3: Map of wildfire study sites in Idaho.

At each wildfire site 2 - 30x30m plots (one moderately-burned, and one unburned control) were established for sampling. These subsample plots were located as closely as possible to one another in order to reduce any potential effects that soil heterogeneity, aspect, slope, or other site features may have on the different treatments. All of the trees

that were selected for sampling in the moderately/partially-burned plots were burned to varying degrees. However, trees were selected within these plots based upon the similarity of their post-fire burn severity (i.e., percentage of intact green crown and bole scorch characteristics; Table 2) as well as their growth characteristics (height and DBH). All of the moderately-burned plots had less leaf area per square meter than adjacent controls except for the moderately-burned plot at the Hall fire, which also had an uncharacteristically higher basal area than its adjacent control plot (Table 1).

Table 1: Descriptions of the wildfire sites that occurred in central Idaho during the summer of 2003. ^a Indicates a predominant species that fell within the plots but was not included in the study. Habitat types were determined according to the habitat guide for central Idaho (Steele, 1981). ^b and ^c indicate the control and moderately-burned plot respectively.

	Hall Fire	Canyon Creek Fire	South Fork of the Salmon River Fire
National Forest-Ranger District	Payette N.F. – Council R.D.	Boise N.F. – Lowman R.D.	Boise N.F. – Cascade R.D.
Burn Area (ha)	764	2,244	2,698
Elevation (ft)	4,800	5,418	5,205
Slope (°degrees)	25°	32°	0°
Aspect	Southwest	West	N/A
Habitat Type	<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceous</i> - <i>Pinus ponderosa</i> phase	<i>Pseudotsuga menziesii</i> / <i>Acer glabrum</i> - <i>Acer glabrum</i> phase	<i>Pinus contorta</i> / <i>vaccinium caespitosum</i>
Dominant Species	<i>Pinus ponderosa</i> var. <i>ponderosa</i> ^a & <i>Pseudotsuga menziesii</i> var. <i>glauca</i>	<i>Pseudotsuga menziesii</i> var. <i>glauca</i>	<i>Pinus contorta</i> var. <i>latifolia</i>
Tree Age	75-98	76-121	52-92
DBH (cm)	35-60	41-68	18-21
Height (m)	24.5-34.6	23.4-35	12.6-21
LAI^b	4.89	3.90	2.47
LAI^c	6.04	2.01	1.98
Basal Area (m²/ha)^b	33.68	31.67	10.8
Basal Area (m²/ha)^c	43.13	17.48	6.64

Table 2: Detail of burn severity on individual trees within the partially-burned plots.

Site	Tree ID	Green Crown (%)	Brown Crown (%)	Black Crown (%)	Tree Crown (%)	Bole Scorch height (ft, in)		Scorch around base (%)
						Low side	High side	
Hall	HAB1	95	5	0	63	0	7'	65
	HAB2	90	10	0	70	6"	5'	100
	HAB3	95	5	0	64	0	2' 6"	80
	HAB4	95	0	5	60	6' 6"	22'	100
	HAB5	90	10	0	60	2"	4'	100
Canyon Creek	CAB1	100	0	0	68	0	6' 6"	60
	CAB2	70	30	0	65	3'	20'	100
	CAB3	95	5	0	71	0	10'	70
	CAB4	80	20	0	58	4'	24'	100
	CAB5	65	35	0	59	0	10'	85
S. Fork Salmon	SFB1	95	5	0	35	6"	1'	100
	SFB2	100	0	0	36	2"	6"	100
	SFB3	75	25	0	30	2"	6"	100
	SFB4	100	0	0	28	6"	1' 6"	100
	SFB5	95	5	0	36	1'	2'	100

Five trees of the same species were sampled at each burn site as well as their corresponding unburned control for a total of 10 trees at each of the three wildfire locations. The sampled trees were all visually inspected and free of evidence of pathogenic invasion and insect infestation (such as gall rust or bark beetles) in order to control for confounding variables that might further influence conductance values within each tree.

All water potential (Ψ) values were measured on excised foliage using a pressure chamber. Predawn measurements of leaf water potential were collected at approximately 4a.m. and used to determine the soil water availability (Ψ_{soil}). At that time the tree foliage is theoretically in equilibrium with the soil moisture, since the stomata on the needles are closed and there was no light for photosynthesis. Although nocturnal transpiration can influence Ψ_{Leaf} when VPDs are high enough, typically nighttime VPDs are low at elevations as high as our wildfire sites and therefore the effect of nocturnal transpiration is generally negligible. During the second data collection period (July 29th -

31st) the predawn stomatal conductance measurements indicated that there may have been considerable nocturnal conductance that may have distorted Ψ_{Leaf} . However, the VPD data indicate that nighttime VPDs were actually fairly low, ranging from 0.06 – 0.4 kPa, and thus the high predawn stomatal conductance measurements may have been due to instrument error as a result of dew on the foliage. Therefore, we did not see any need to adjust Ψ_{Leaf} since VPDs were so low when the predawn samples were collected. However, all of the measurements were corrected for the effects of gravitational potential, based on the height of the canopy from which the sample was taken. By using the gravimetric correction (0.01 MPa/m) the predawn Ψ_{soil} values could be accurately adjusted. Predawn leaf water potential was also used to test the hypothesis that *soil moisture availability would increase in the burned sites relative to unburned controls.*

A Li-Cor 1600 Steady State Porometer (Lincoln, NE) was used to determine diurnal stomatal conductance (g_s) and transpiration (E), in order to test the hypothesis that *midday stomatal conductance would be reduced in burned areas relative to controls.* Foliar samples were collected approximately 4 times a day from 4a.m. to about 4p.m. or whenever transpiration rates became negligible from each of the burned and unburned control sites. Since leaf age can influence stomatal conductance all samples were taken from one-year old needle tissues. Foliar samples were shot down with a shotgun from the southerly aspect of each tree's crown within the middle to upper third of the canopy and immediately sampled. Afterwards, the samples were taken back to the lab where their leaf area was determined by using ImageJ software (<http://rsb.info.nih.gov/ij/>). To test the hypothesis that *K_L in the surviving trees would be reduced relative to unburned controls* foliar samples were analyzed for E and Ψ_{Leaf} . Together these data were used to

calculate K_L as indicated in equation 6. Leaf water potentials were determined by using a pressure chamber (Model 670, PMS Instruments, Corvallis, OR).

Hobos (Model H8, HOBO Computer, Bourne MA) were placed within shaded sections of the canopies of the unburned controls in order to collect detailed air temperature and relative humidity measurements that would be used in calculating VPD throughout the duration of the project (Figure 1). VPD and g_s were used to adjust E_{Flux} for the canopy and ultimately calculate K_L . Since there was such great similarity in climatic conditions of the different wildfire sites, we assumed that there was no difference in the climatic conditions between the burned and unburned plots within each wildfire site. Therefore, it was only necessary to install one Hobo sensor per site.

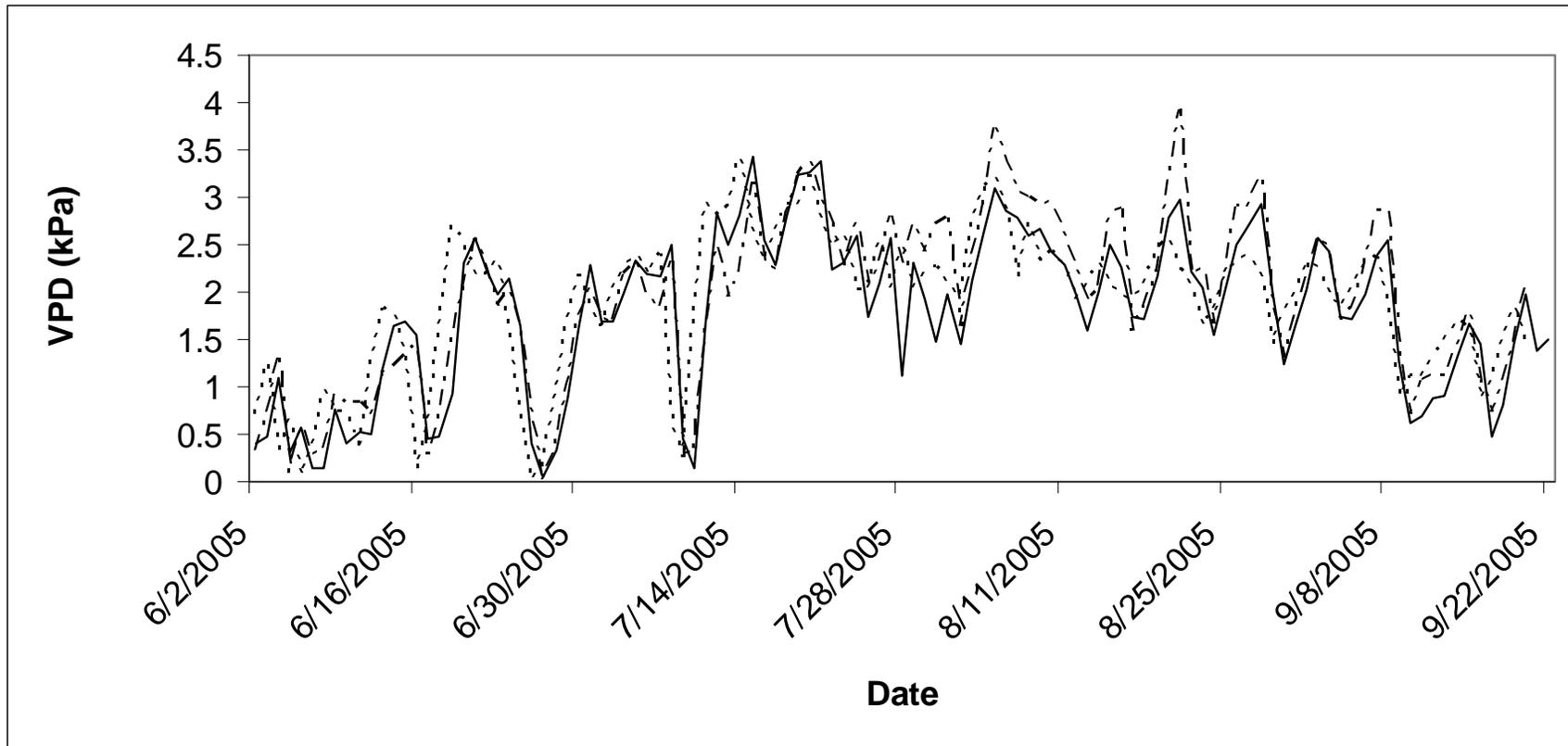


Figure 4: Average daytime VPD at each of the wildfire sites, collected from a half hour after dawn to a half hour prior to dusk. The dotted line, dashed line, and solid line correspond to the Canyon Creek, Hall, and South Fork of the Salmon River wildfires, respectively.

In order to test the hypothesis, *decreased stomatal conductance will lead to decreased carbon isotope discrimination (i.e., increased WUE) in healthy vegetation within the burned sites relative to the unburned controls*, two tree cores were collected from each of the four cardinal directions (a total of eight cores) and pooled together for each tree in order to account for circumferential variability in $\delta^{13}C$ (Leavitt and Long, 1986). The tree cores were then separated by year for the three years post-fire and analyzed for $\delta^{13}C$ with an isotope ratio mass spectrometer at the University of Idaho Stable Isotopes Laboratory (Moscow, ID; precision estimate $\leq 0.1\text{‰}$). The $\delta^{13}C$ of the wood material represents the water use efficiencies, WUE, for the trees during the year in which the fires occurred and two growing seasons afterwards, thus reflecting any long-term impacts the damaged trees may have sustained. In addition to this, foliage from six different spirea, (*Spiraea betulifolia*), shrubs in each plot was collected and analyzed for $\delta^{13}C$.

All wood and foliage samples were dried in an oven at 70°C for approximately 48 hours. Annual growth rings were separated with a scalpel and all eight samples were pooled together for each tree. The samples were diced to less than 1.0mm² and then ground with a Wig-L-Bug grinder (Dentsply/Rinn; Elgin, IL, USA) for approximately 60 seconds or until the samples were fine enough that they could be passed through a 0.2mm-mesh. Finely milled and mixed samples ensure homogeneity and increase the likelihood of getting an isotopic signal that is representative of the growth ring rather than a signal that is dominated by one larger piece of wood (Borella et al., 1998). Harlow et al. (2006) found that bulk wood material accurately represents the $\delta^{13}C$ of wood samples, therefore no extractions were conducted on our samples (Harlow et al., 2006). Finally,

the ground samples were then weighed to $1.0\text{mg} \pm 0.1$, packed in tin cups and then analyzed in the isotope mass spectrometer for $\delta^{13}\text{C}$.

Isotopic composition (δ) was determined by following the equations as used in Ehleringer et al., (2000):

$$R = {}^{13}\text{CO}_2/{}^{12}\text{CO}_2 \quad (7)$$

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\text{‰} \quad (8)$$

Isotope ratios are denoted by the delta notation (δ), which measures the molar ratio of heavy to light isotopes (i.e., ${}^{13}\text{C}:{}^{12}\text{C}$) per mil (‰) within a sample (R_{sample}) and is compared to a Pee Dee Belemnite standard (R_{standard}).

Statistical Analysis

A linear mixed-effects repeated measures ANOVA with SAS software (SAS v9.1; SAS Institute, Cary, NC) was used to construct models for our statistical analyses. PROC MIXED was used because it can account for the random error associated with our sites. It is capable of handling missing data, which occasionally occurred during this study due to instrumentation malfunctions. Another benefit of the mixed effects model was that it provided for analysis of multiple comparison of both the *between* and the *within subjects* factors (Littell et al., 1996). Therefore, Ψ_{Predawn} , g_s , K_L , and $\delta^{13}\text{C}$ could be compared between the partially-burned and control treatments as well as being compared through time. Since we wanted to look at the effects on conifers in general, the species effect was not included in the model. Site was coded as a random effect, since the aim of this study is to make inferences about the effects of wildfires in other areas that are similar to our study sites. The treatment plots were considered the experimental unit and the trees within them were subsamples; therefore, the variation, or observational error,

among the samples actually reflects the homogeneity within the subsample unit.

Consequently, the study was replicated at three sites ($n=3$) and the total number of individuals observed in the study was 30 ($n=30$).

The linear model for these data is:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk} + d_{ijkl} \quad (9)$$

Where:

Y_{ijkl} is the observational vector (i.e., $\Psi_{predawn}$, g_s , K_L , or $\delta^{13}C\%$)

μ is the grand total of the treatment-level population means

α_i is the treatment effect the burn

β_j is the repeated effect of time (i.e., diurnal, seasonal, or annual)

$(\alpha\beta)_{ij}$ is the interaction effect of burn over time

ε_{ijk} is the experimental error associated with the experimental units (i.e., plots)

d_{ijkl} is the observational error associated with the subsamples (i.e., trees)

Source	Df	Df
A	$a-1$	$2-1 = 1$
B	$b-1$	$5-1 = 4$
$(\alpha\beta)$	$(a-1)(b-1)$	$1*4 = 4$
ε	$ab(r-1)$	$2*5(3-1) = 20$
D	$abr(n-1)$	$2*5*3(5-1) = 120$

Table 3: Indicates how the degrees of freedom were calculated, based on the linear model for $\Psi_{predawn}$. The variable 'a' is the number of treatments, 'b' is the number of visits to collect samples at each site, 'r' is the number of sites, and 'n' is the number of trees per experimental unit.

Compound symmetry was used as the covariance structure. Graphical diagnostics were checked in order to ensure normality of the data and the appropriate transformations

were made when necessary. These preliminary tests were also tested for any interaction effects at the ($\alpha > 0.05$) level that may have occurred and impacted the results. However, if there were no significant interaction effects among the variables, then the test for interaction effects was removed and the fixed effects were once again tested for significance at the ($\alpha > 0.05$) level with the pooled error variances and degree of freedom (Kirk, 1995).

Finally, the $\delta^{13}C$ data from the spirea foliage were also analyzed with SAS by using the PROC MIXED function in order to test for any significant difference between the two treatments at the ($\alpha > 0.05$) level. Site was also coded as random and the burn treatment was a fixed effect. However, since foliage was only collected once it was not necessary to include a test for repeated measures effect.

2.4 Results

All of the wildfire sites experienced similar trends in average daytime VPD throughout the summer. Daytime VPD continued to rise after the sensors were installed until September 9th. There were two days, June 28 & July 10, in which daytime VPDs were low enough that the sites may have received some precipitation (Figure 1).

Soil Moisture

Predawn soil water potential in the partially-burned treatments was not significantly reduced compared to the unburned controls. However, predawn water potentials consistently became more negative throughout the summer in both treatments (Figure 5). There was no significant interaction between burn treatment and time ($p = 0.7215$; Table 4a). Therefore, the data could be run in the reduced model without the

interaction test (Table 4b). Consequently, the time effect was highly significant ($p < 0.0001$), but the burn effect was not significant ($p = 0.0504$, Figure 5).

Table 4a: Predawn leaf water potential ANOVA of the preliminary test for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	20	4.11	0.0563
Time	4	20	42.76	<.0001
Burn*Time	4	20	0.52	0.7215

Table 4b: Predawn leaf water potential ANOVA of the pooled model for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	24	4.25	0.0504
Time	4	24	46.85	<.0001

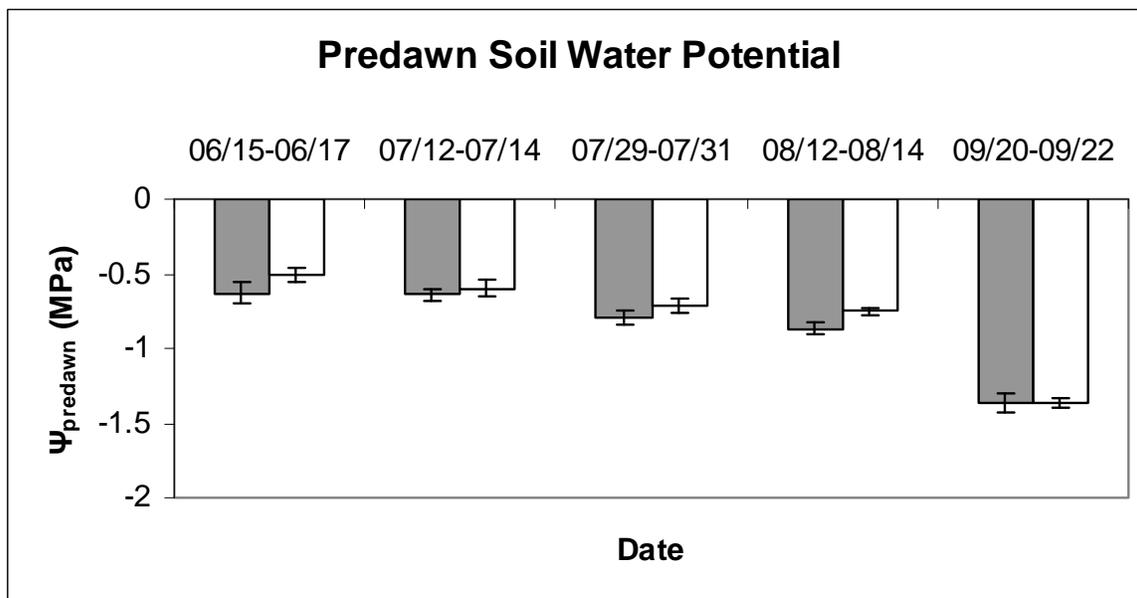


Figure 5: Predawn soil water potential collected throughout the summer. Gray columns and white columns represent the means of the partially-burned and control treatments respectively. Bars represent standard errors.

Stomatal Conductance

Stomatal conductance varied greatly throughout the day and also throughout the summer (Figure 6). Table 5a reveals that during the midmorning measurements, the interaction effect of the burn treatment and time was not significant ($p = 0.6303$). In

addition to this, the results of the pooled model indicate that time did not cause g_s to vary significantly through the growing season ($p=0.8017$), and the burn treatment also did not significantly influence g_s ($p=0.1369$; Table 5b).

Table 5a: Midmorning g_s ANOVA of the preliminary test for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	16	2.26	0.1519
Time	3	16	0.31	0.8169
Burn*Time	3	16	0.59	0.6303

Table 5b: Midmorning g_s ANOVA of the pooled model for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	19	2.41	0.1369
Time	3	19	0.33	0.8017

The interaction between burn and time was not significant ($p=0.8917$; Table 6a) during the midday g_s measurements (Figure 6). The pooled model also indicated that time during the season was not significant ($p=0.9310$) in impacting g_s and neither was burn ($p=0.2404$; Table 6b).

Table 6a: Midday g_s ANOVA of the preliminary test for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	16	1.40	0.2540
Time	3	16	0.13	0.9426
Burn*Time	3	16	0.20	0.8917

Table 6b: Midday g_s ANOVA of the pooled model for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	19	1.47	0.2404
Time	3	19	0.15	0.9310

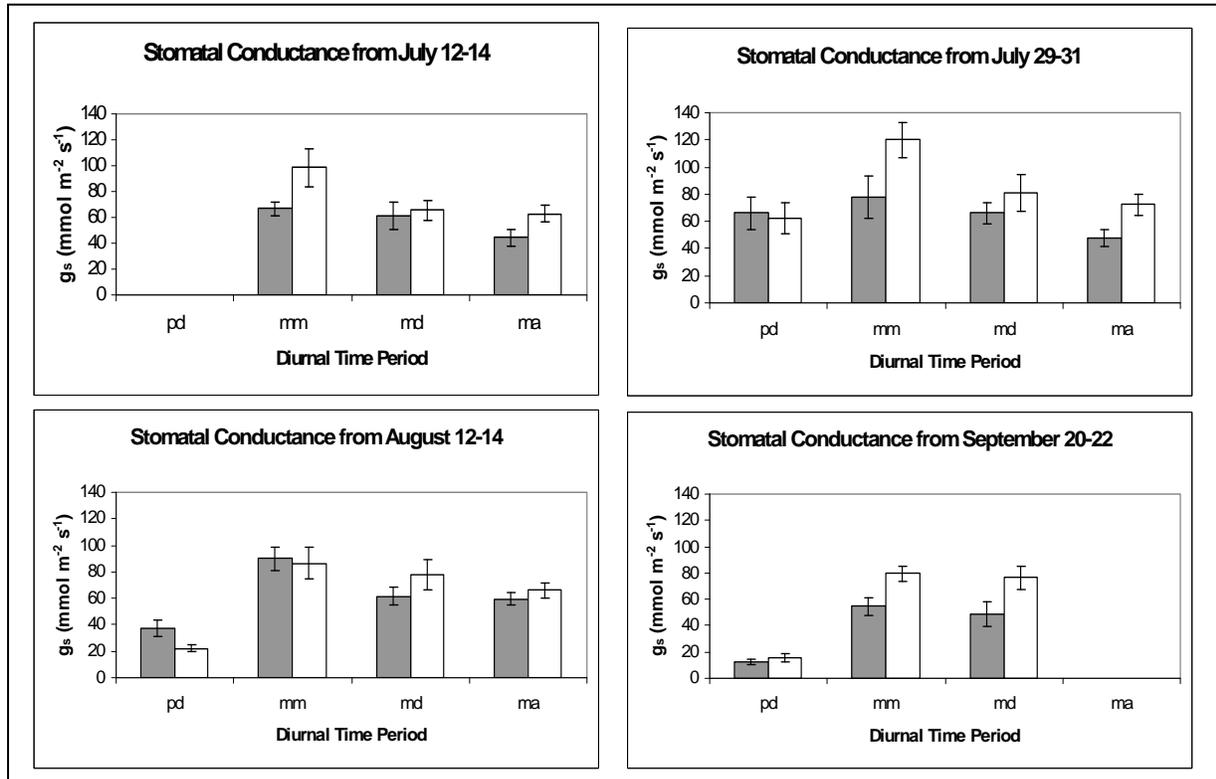


Figure 6: Stomatal conductance collected throughout the summer. Gray columns and white columns represent the means of the partially-burned and control treatments respectively. Diurnal time periods “pd”, “mm”, “md”, and “ma” correspond to predawn, midmorning, midday, and midafternoon, respectively. Bars represent standard errors.

Leaf Specific Conductance

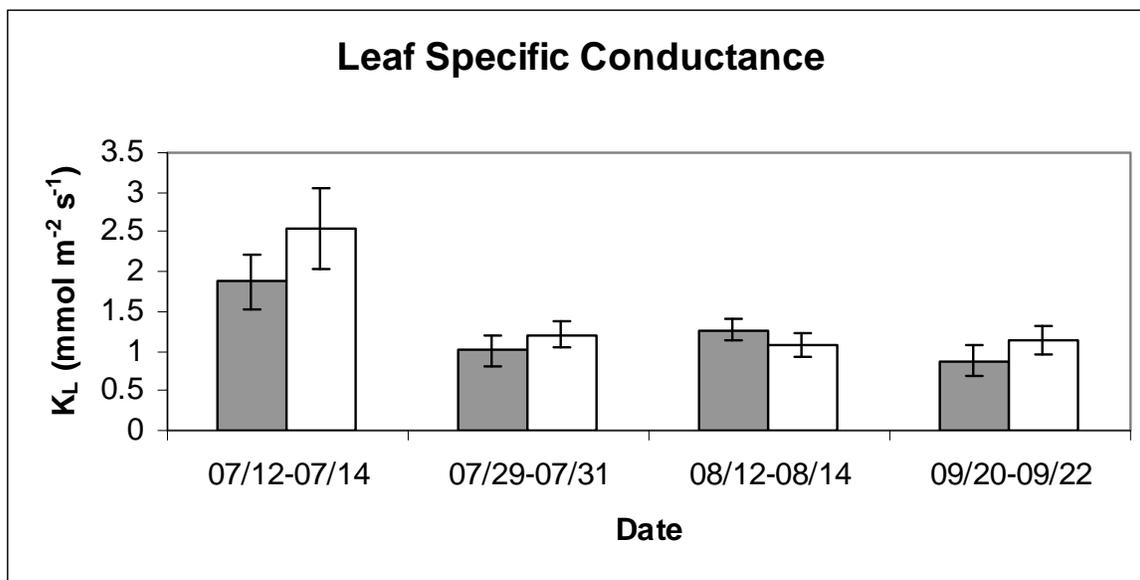
There was no significant interaction between burn and time for K_L ($p=0.8934$; table 7a), the model was run again without the interaction effect. Table 7b shows the results of the reduced model. Interestingly, time did not significantly impact K_L ($p=0.8312$). In fact, with the exception of the first data collection period, the K_L values remained fairly constant (Figure 7). In addition to this, the burn effect also was not significant ($p=0.4101$).

Table 7a: K_L ANOVA of the preliminary test for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	16	0.30	0.4383
Time	3	16	0.26	0.8536
Burn*Time	3	16	0.63	0.8234

Table 7b: K_L ANOVA of the pooled model for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	19	0.71	0.4101
Time	3	19	0.29	0.8312

**Figure 7:** Leaf specific conductance collected throughout the summer. Gray columns and white columns represent the means of the partially-burned and control treatments respectively. Bars represent standard errors.

$\delta^{13}C$

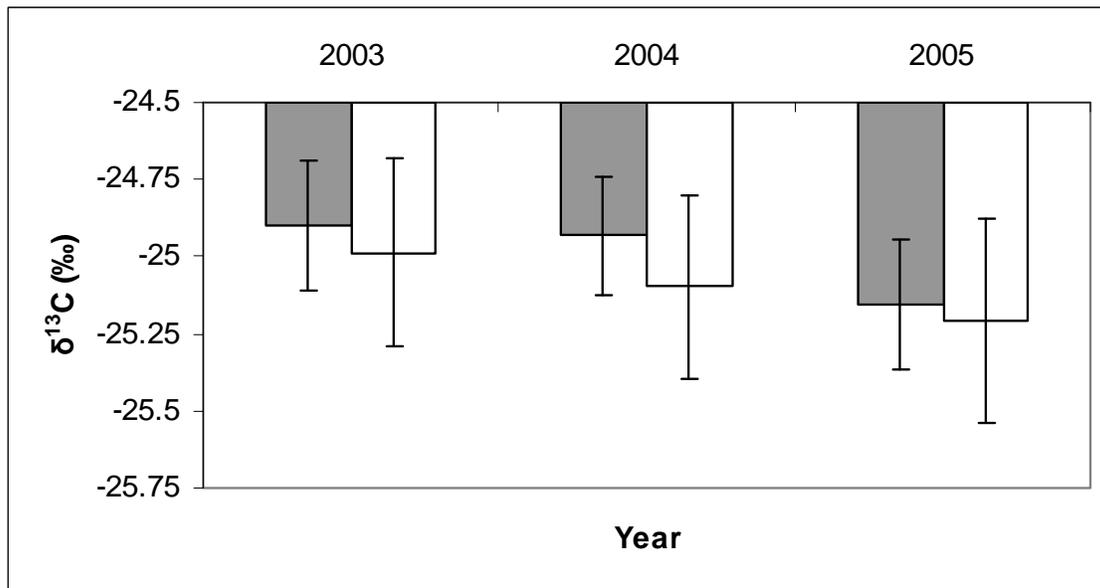
The interaction between treatment and time for $\delta^{13}C$ in wood material was not significant ($p=0.9951$; Table 8a). The results of the pooled test (Table 8b) indicate that neither year ($p=0.8226$) nor burn treatment ($p=0.9080$) were significant in influencing ^{13}C fixation. Consequently, the burn treatment had no effect on the water use efficiency of the affected trees (Fig. 8).

Table 8a: $\delta^{13}\text{C}$ ANOVA of the preliminary test for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	12	0.04	0.8360
Year	2	12	0.08	0.9206
Burn*Year	2	12	0.00	0.9951

Table 8b: $\delta^{13}\text{C}$ ANOVA of the pooled model for the three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	1	14	0.05	0.8226
Year	2	14	0.10	0.9080

**Figure 8:** Carbon isotope values from bulk wood material. Gray columns and white columns represent the partially-burned and control treatments respectively. Bars represent standard errors.

The $\delta^{13}\text{C}$ values for the spirea shrub foliage did differ significantly between the treatments by approximately 2‰ ($p < 0.0001$; Table 9; Figure 9).

Table 9: Output of ^{13}C in Spireae b. foliage from all three wildfire sites.

Effect	NUM DF	DEN DF	t Value	Pr > F
Burn	1	32	122.75	< 0.0001

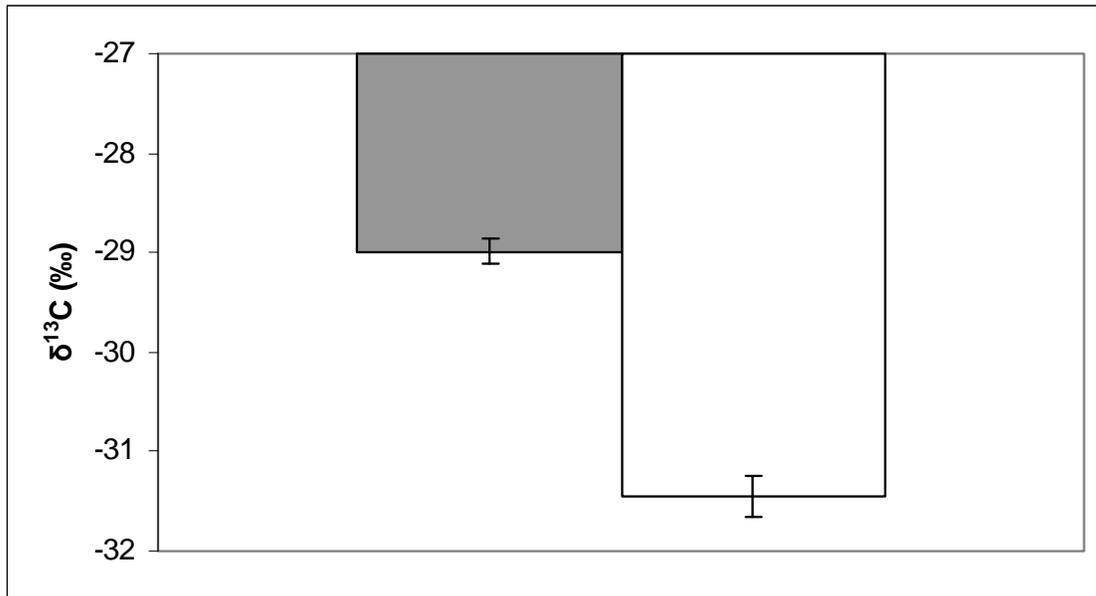


Figure 9: Carbon-13 discrimination from spirea foliar material. Foliage was collected during the 2005 growing season. Gray columns and white columns represent the partially-burned and control treatments respectively. Bars represent standard errors.

2.5 Discussion

The hypothesis, that xylem cavitation reduced stem conductance post-fire, was supported by our findings. Although there were no distinct differences in the treatments for the $\delta^{13}\text{C}$ data for the conifers, nearly all of the burned trees experienced reductions in leaf area after the fire, suggesting that their internal hydraulic conductance was reduced. The reduction in leaf area then allowed the burned trees to supply the remaining foliage with enough water so that they could maintain g_s , K_L , and $\delta^{13}\text{C}$ values that were similar to their adjacent unburned controls. There was no statistically significant difference in predawn leaf water potential between the two treatments. In addition to this, neither midmorning stomatal conductance, midday stomatal conductance, nor leaf specific conductance varied between the partially-burned treatments and the unburned controls for the conifers. As a result, we conclude that the damaged trees experienced a reduction in

hydraulic conductance and consequently they adjusted their leaf area in order to maintain a constant K_L for the remaining foliage.

Nearly all of the moderately-burned trees had brown dead needles at the base of their crowns. This foliage may have been sacrificed by the trees in order for them to maintain Ψ_{Leaf} above their minimum threshold for the remaining foliage. By reducing leaf area, the trees would be able to maintain a constant K_L throughout the rest of the growing season and thus prevent the remaining foliage from becoming water stressed or dehydrated. Pataki et al. (1998) found that increases in G_s , i.e., stomatal conductance for the whole canopy, and hydraulic conductance were linked to reductions in leaf area. Although there were no significant differences in stomatal conductance among the treatments in our study, nearly all of the trees did experience reductions in leaf area and in some cases up to 30% of their total canopy was lost. Conifers are capable of surviving substantial reductions in leaf area; past research has revealed that up to 40% of the live crown could be removed in conifers without reducing diameter growth (Heidmann, 1963; Pearson et al., 1972; Wyant et al., 1986). While our sample trees may not have been damaged to the point of mortality, the hydraulic conductivity of the burned trees must have been reduced during the wildfires. Since the burned trees were able to maintain similar g_s values compared to their adjacent controls, the leaf area reductions allowed the remaining foliage to maintain constant stomatal sensitivity and productivity levels after the fires. However, it is unclear whether the reduction in hydraulic conductivity was a result of cavitation or resinosis within the sapwood.

Although the differences in soil water status were not statistically significant ($p=0.0504$), on average the burned plots were slightly drier than the controls. This may

be the result of an increase in evapotranspiration due to understory and canopy removal and the subsequent increase in radiation reaching the surface in the burned plots.

Nonetheless, the variation in soil moisture does not appear to have been great enough to influence or amplify other hydraulic characteristics (i.e., g_s and K_L) within the partially-burned trees.

The WUE values were not impacted by the effects of the wildfires. Since the wildfires occurred late in the growing season it was assumed that the $\delta^{13}C$ values would be nearly identical for the two treatments for the year 2003, which they were. In addition to this, if the trees were sufficiently damaged by the wildfire, then a significant difference in $\delta^{13}C$ would have been apparent during the 2004 season and most likely would have continued into the 2005 growing season until the damaged trees were able to recover. However, the lack of differences in $\delta^{13}C$ values between the treatments over time suggests that the partially-burned trees remained constant and were not impacted at all by the wildfire. In fact, Figure 8 reveals that the $\delta^{13}C$ values of the partially-burned trees were virtually identical to those found within the control plot. In addition to this, there was only a slight increase in discrimination two years after the wildfires occurred, indicating that the trees may have experienced climatic conditions similar to the previous two years. A reduction leaf area would have prevented the trees from experiencing water constraints for photosynthesis at the leaf level. Consequently, it would have appeared that the burned trees had not adjusted their water use efficiencies at all, because they were able to maintain g_s , K_L , and $\delta^{13}C$ values for the remaining foliage that were similar to the measurements from the unburned trees.

Although we did not find any direct evidence of cavitation, by modeling climatic parameters and leaf properties we were able to estimate potential levels of cavitation experienced by the burned conifers. The temperatures generated by the fires would have caused VPDs at the base of the canopies to rise significantly. According to a fire behavior model developed by Mercer and Weber (1994), extreme estimates of VPDs from a fire with a high intensity of 5000 kW/m² at the base of the canopy could have been as high as 12.7 kPa. The VPDs would exponentially decrease with increasing height in the canopy; therefore only the foliage at the base of the canopy would have experienced such high VPDs. We used a range of VPD values along with g_s and K_L values that we collected during this study in order to model the Ψ_{Leaf} values that the foliage at the base of the canopy would have maintain during the fire. The modeled Ψ_{Leaf} values were then compared to xylem vulnerability curves in order to determine the amount of cavitation that they may have experienced. Using VPDs that ranged from 5.07-12.7 kPa, we found that the foliage at the base of the canopy would have had to maintain extremely negative $\Psi_{Leaf-min}$ values ranging from -2.97 to -3.69 (MPa) for the Douglas-fir and -2.29 to -2.90 (MPa) for lodgepole pine. These $\Psi_{Leaf-min}$ values correlate to 5-10% of the xylem cavitating in the large stems of Douglas-fir trees (Sperry and Ikeda, 1997) and 9-25% cavitation in the bole xylem of lodgepole pine (Wang et al., 2003), indicating that the burned trees most likely had experienced some degree of cavitation.

However, there may have been other factors that played a key role in the survival of these trees both during the fire and post-fire. Xylem vulnerability has been shown to vary not only with species (Bond and Kavanagh, 1999) but also within populations of the

same species (Kavanagh et al., 1999). For instance, coastal mesic populations of Douglas-fir, which cannot exceed Ψ lower than -3.0 MPa, were more vulnerable to cavitation when compared to drier interior populations, which must maintain Ψ above -3.5 MPa (Kavanagh et al., 1999). The Douglas-fir and lodgepole pine used in this study were also from dry interior environments, indicating that perhaps these populations adapted to their environments by reducing their vulnerability to cavitation.

Even brief exposure to these high VPDs may have triggered other mechanisms within the tree to avoid excessive cavitation and mortality. One possible explanation is that the xylem walls in the leaves of the trees may have collapsed in order to prevent embolism. Cochard et al. (2004) found that, as xylem pressure decreases past a certain pressure threshold ($P_{collapse}$), xylem walls in pine foliage collapsed in order to avoid or delay the risk of cavitation within the tree. Wall collapse dramatically reduced xylem conductance and also was rapidly reversible upon rehydration. In addition to this, Hacke et al. (2001) found a correlation between xylem vulnerability to cavitation and wall collapse. Therefore, the xylem collapsing mechanism may have been used to temporarily reduce the hydraulic stress by decreasing xylem conductance until conditions became favorable and rehydration occurred.

Water storage in the bole and branches is an adaptation that helps the trees overcome hydraulic stress (Holbrook, 1995). Phillips et al. (2003) found that water stored in the xylem accounted for as much as 25% of the total daily water use in large Douglas-fir trees. Perhaps some of the water lost during the fire was replenished by water that was being stored in elastic tissues in the xylem. Therefore, this mechanism

may work synergistically with xylem collapse in order to prevent the damaged trees from exceeding their $\Psi_{Leaf-min}$ and experiencing excessive cavitation.

There also may have been a rain event that caused the fires to stop burning and replenish soil water. Consequently, flow resistance within the plants would have rapidly decreased while stem conductance increased, causing the embolisms to eventually come out of solution (Sperry et al., 2003); thus the effects of cavitation may have been countered so that there were no long lasting damages to the hydraulic structure of the tree.

On the other hand, there was a distinct difference between treatments in the $\delta^{13}C$ values for the spirea foliage in the shrub understory. The shrubs in partially-burned plots were enriched in ^{13}C when compared to the unburned controls, indicating that the partially-burned shrubs increased their water-use efficiencies. Since the soil moisture measurements accessed by pine and Douglas-fir roots did not statistically differ between treatments, the difference in WUE may be the result of shifts in photosynthetic capacity within the spirea shrubs in the burned plots. Unlike the conifers, the shrubs in the burned plots experienced an increase in foliar nitrogen concentration (Koyama, 2006) as well as an increase in PAR due to the canopy reduction. Together these factors would also increase photosynthetic capacity and ultimately, decrease c_i , the internal CO_2 concentration within the leaves of the shrubs. As c_i is drawn down in the foliage then the shrubs would become enriched in ^{13}C .

In conclusion, there was no evidence that the partially-burned trees suffered sufficient damage to cause any prolonged impacts on their internal hydraulic systems. On the other hand, the soil moisture content during the years after the fires was not

reduced enough to amplify any damages that the conifers may have sustained. If the trees had experienced a drought during the growing season immediately after the wildfires occurred, then perhaps some differences in the trees' hydraulic properties may have emerged. On the other hand, the increase in nitrogen and light appears to be responsible for increases in the water use efficiencies of the understory spiraea shrub layer of the burned plots.

Future studies should directly measure cavitation with the aid of acoustic detectors and post-fire with staining the xylem. By doing this one may ascertain with certainty whether a tree's xylem has been impacted or not by the fire. Furthermore, temperature and moisture sensors should be placed at various depths in the soil and also at various heights in the canopy. This would provide the researcher with a deeper understanding of the fire behavior and aid in modeling root mortality and VPDs throughout the canopy at the time of the fire. Then measurements regarding WUE can be collected in order to understand the post-fire impacts on the damaged tree's hydraulic system and subsequent responses.

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Chapter 3

The Impact of Wildfire on Soil-Respired CO₂

3.1 Abstract

Disturbances play a pivotal role in shaping ecosystems and impacting critical ecosystem processes. Wildfire is one type of disturbance that can significantly alter carbon flux dynamics in forested ecosystems. As vegetation is damaged and removed from an ecosystem the carbon cycle may be greatly impacted. We hypothesized that the fire effects on aboveground vegetation would lead to reduced carbon-13 discrimination ($\delta^{13}C$) in the soil-respired CO₂. A replicated experiment was used to examine the impact that wildfires have on ecosystem water use efficiency (WUE) by comparing isotopic signals of soil-respired CO₂. The $\delta^{13}C$ values of three wildfire sites in central Idaho were compared throughout the summer of 2005. At each wildfire site, three treatments were established: a severely-burned plot, a moderately-burned plot, and an unburned control plot. Although there was no difference in the isotopic labels between the severely-burned and moderately-burned plots, each of these plots differed significantly from the unburned controls. The burned plots were enriched in ¹³C compared to the unburned controls, which was most likely due to the enrichment in recently formed carbohydrates from the understory vegetation.

3.2 Introduction

Microorganisms in the soil use carbon (C), created via photosynthesis from neighboring trees, in order to transform organic nitrogen (N) (through decomposition) into inorganic N. Through this process the microbes make N, which is a limiting nutrient for plants, “available” for plant use (Grogan et al., 2000). Consequently, shifts in

belowground carbon pools can greatly impact the rates of gross N cycling processes (Hart et al. 1994).

Soil respiration is comprised of autotrophic and heterotrophic respiration in the soil (Andrews et al., 1999). Autotrophic respiration results from roots that are living in contact with mycorrhizal fungi (Steinmann et al. 2004), while heterotrophic respiration results from microorganisms within the soil, decomposing dead organic material, and their own consumers (Andrews et al., 2000). Ultimately, soil respiration is driven by photosynthesis and the factors which influence it, such as temperature, soil moisture, photosynthetic active radiation (PAR), stomatal conductance, and the microbial community within the soil. Shifts in photosynthesis have an impact not only on the carbon uptake of foliage and plants, but also on the organisms belowground in the soil profile that feed off of the carbohydrates translocated from the canopy (van Veen et al. 1991; Ekblad and Högberg, 2001; Steinmann et al., 2004).

The carbon and nitrogen cycles are intricately linked and critical to the overall productivity of an ecosystem. Since carbohydrates created in the canopy are rapidly translocated for microbial and root respiration, soil-respired CO₂ data were used to gain insight in regard to the recent changes in foliar discrimination throughout the growing season (Ekblad and Högberg, 2001; Högberg et al., 2001; Steinmann et al. 2004; Göttlicher et al. 2006; Keel et al. 2006). Understanding how both of these cycles are affected by wildfire can provide greater insight to the effects of wildfire on vegetation, soil microbial communities, and nutrient cycling.

Past studies have found that disturbances can greatly impact a plant's hydraulic properties (Tyree and Sperry, 1988; Hubbard, 1999; Ryan, 2000). Xylem cavitation and

reduced hydraulic conductivity in a plant can lead to increased stomatal sensitivity (Sperry et al., 1993; Piñol and Sala, 2000). While disturbances such as wildfires may cause damaged plants to increase stomatal sensitivity (Ryan, 2000), thus increasing their water use efficiencies, their overall productivity rates may actually decrease (Jones, 1998). The $\delta^{13}C$ of soil organic carbon reflects the photosynthetic productivity of the aboveground community (Boutton, 1996; Amundson, 1998), and consequently may mirror the impacts sustained by the damaged vegetation.

The isotopic composition of soil-respired CO_2 ($\delta^{13}C$) is determined by following the equations (Ehleringer et al., 2000):

$$R = {}^{13}CO_2/{}^{12}CO_2 \quad (10)$$

$$\delta^{13}C(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\text{‰} \quad (11)$$

$\delta^{13}C$ measures the molar ratio of heavy to light isotopes (i.e., ${}^{13}C: {}^{12}C$) and measured per mil (‰) within a sample (R_{sample}) and is compared to a Pee Dee Belemnite standard (R_{standard}) (O'Leary, 1981; Ehleringer et al., 2000).

During another component of this study, it was found that the surviving conifers within the moderately-burned treatment were not sufficiently damaged to cause any prolonged impacts on their internal hydraulic systems when compared to their unburned adjacent controls (Thompson et al., submitted). In addition to this, there was no significant difference in the predawn leaf water potential, a measure of soil moisture, of the moderately-burned plots when they were compared with their adjacent controls. However, spirea bushes, *Spirea betulifolia*, located in the shrub understory of the moderately-burned treatment plots, were impacted when compared to their adjacent controls. The $\delta^{13}C$ label of the spirea from the foliage within the treatment plots had an

isotopically enriched signal when compared to the spirea from within the control plots, indicating an increase in their water use efficiencies. Our objective was to determine if soil-respired carbon dioxide (CO₂) would reflect the isotopic labels of aboveground vegetation that was impacted by wildfire.

3.3 Materials and Methods

Study Sites and Sample Collection

In order to understand how fire affects soil-respired CO₂, this replicated study was conducted in three areas of central Idaho that recently burned during the summer of 2003. The wildfire sites included the Canyon Creek fire, the South Fork of the Salmon River fire, and the Hall fire.

At each wildfire site three - 30x30m plots (one severely-burned, one moderately-burned, and one unburned control) were established for sampling. The plots were located as closely as possible to one another in order to reduce any potential effects that soil heterogeneity, aspect, slope, or other site features may have on the different treatments. All of the trees located in the severely-burned plots were completely scorched and dead. In addition to this, the surface was burned down to the mineral soil. While many of the saplings located within the moderately/partially-burned plots were completely burned, the larger, more mature conifers were burned to varying degrees and a considerable portion of the plots' surfaces were also burned down to the mineral soil. Burn severity for the trees was based on the percentage of intact green crown and bole scorch as well as the percentage of charred and unburned organic material remaining on the surface of the plot (Jain, 2004).

All sampling plots were located in catchments that drained in a westerly direction. All sites were similar in elevation. The dominant species at these sites were Douglas-fir, lodgepole pine, and ponderosa pine and the habitat types were determined by consulting the habitat guide for central Idaho (Steele et al., 1981).

In order to collect the soil-respired CO₂ samples, steel traps with airtight valves were placed below the organic duff layer, directly on the mineral soil (Figure, 10). Five of these traps were located randomly within each of the 30x30 meter treatment plots. Air samples were then collected through the rubber septa of the airtight valves with a syringe and injected into 15mL glass airtight vials, which were later analyzed by using a continuous flow, isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) at the University of Idaho Stable Isotopes Lab (Moscow, ID; precision estimate $\leq 0.1\text{‰}$). This soil-respired air was collected during each trip in which transpiration and water potential measurements were gathered. By collecting samples throughout the summer as water resources become more limiting, differences in the isotopic labels of the treatments may become more apparent.

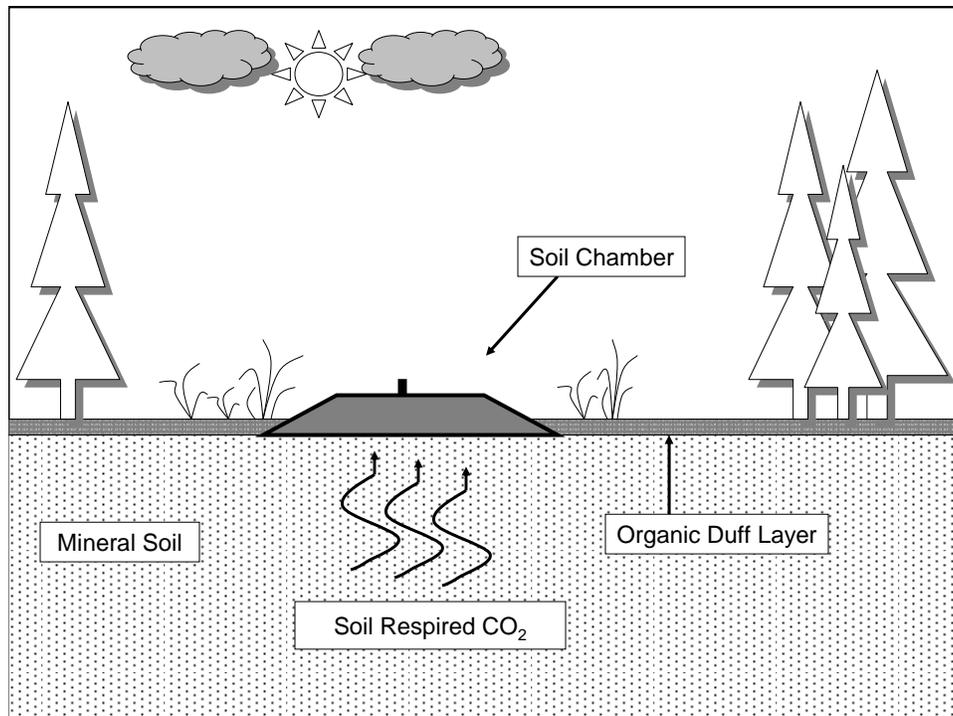


Figure 10: Profile of location of soil chamber on mineral soil that traps soil-respired CO₂.

Soil CO₂ was collected and later adjusted as described below in order to find the true value of the respired-soil CO₂ within the plots. When soils are relatively moist, respiration rates are high and atmospheric intrusion into the pore space in the soil profile is negligible. However, as the soil dries out during the summer, the microbial activity and respiration rates of organisms within the soil also decline. Consequently, a reduction in the amount of respired CO₂ leaving the soil allows the atmospheric CO₂ to penetrate deeper into the soil profile and skew the isotopic ratio. The mixing of the atmosphere, which has a “heavier” and more enriched label of -8‰, would further enrich the typically “lighter” soil CO₂ (-13 to -30‰) (Cerling et al., 1991; Davidson, 1995; Steinmann, 2004). Therefore, since each of the plots within the study sites underwent periods of seasonal dryness during the summer, a Keeling plot was used in order to adjust

their values for the amount of atmospheric mixing that they experienced within the soil profiles.

Finally, after the Keeling plot adjustments, the values had to be corrected for the theoretical minimum isotopic difference between soil CO₂ and soil-respired CO₂. This difference results from the lighter ¹²CO₂ molecules having a higher rate of diffusion through the soil than the heavier ¹³CO₂ molecules. Consequently, the heavier ¹³CO₂ molecules remain in the soil profile and steel chamber longer. As a result, the steel traps, which collect soil CO₂, are theoretically 4.4‰ enriched when compared to the actual soil-respired CO₂ (Cerling et al., 1991; Steinmann, 2004).

Statistical Analysis

Since the soil-respired CO₂ that was collected from the sampling containers was not independent of the gases from other containers found within the same plot, each treatment was only replicated three times, i.e. once per treatment per site. Therefore, the averages of the respired gas samples, found within each plot, were input into the SAS model.

Soil-respired CO₂ measurements were analyzed using the MIXED procedure (PROC MIXED) with SAS software (SAS v9; SAS Institute, Cary, NC). PROC MIXED is capable of handling missing data, which occasionally occurred during this study due to traps being tampered with by wildlife. It is also capable of applying multiple comparison procedures to both *between* and *within subjects* factors. Therefore, transpiration could be compared between the different treatments as well as being compared through time.

A repeated measures analysis of variance was used in order to understand the effect of time on soil-respired CO₂ measurements. This analysis allowed the model to compare differences in measurements for each treatment over seasonal time (Littell, et al., 1996) However, since the measurements of a single subject (i.e., the repeated measures of a single subject) are more likely to be similar than those measurements taken on different individuals, the repeated measures are correlated. Thus, it was necessary to use the proper covariance structure in conjunction with the repeated measures model.

The linear model for these data is:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk} + d_{ijkl} \quad (12)$$

Where:

- Y_{ijkl} is the observational vector (i.e., soil-respired $\delta^{13}C\%$)
- μ is the grand total of the treatment-level population means
- α_i is the treatment effect the burn
- β_j is the repeated effect of time (i.e., seasonal)
- $(\alpha\beta)_{ij}$ is the interaction effect of burn over time
- ε_{ijk} is the experimental error associated with the experimental units (i.e., plots)
- d_{ijkl} is the observational error associated with the subsamples (i.e, gas samples)

Source	Df	Df
<i>A</i>	$a-1$	$2-1 = 1$
<i>B</i>	$b-1$	$5-1 = 4$
$(\alpha\beta)$	$(a-1)(b-1)$	$1*4 = 4$
ε	$ab(r-1)$	$2*5(3-1) = 20$
<i>D</i>	$abr(n-1)$	$2*5*3(5-1) = 120$

Table 10: Indicates how the degrees of freedom were calculated, based on the linear model for soil-respired CO₂. The variable ‘a’ is the number of treatments, ‘b’ is the number of visits to collect samples at each site, ‘r’ is the number of sites, and ‘n’ is the number of trees per experimental unit.

The two covariance structures that were used were compound symmetry (cs) and the unstructured (un) option. The compound symmetry option assumes that correlations between all pairs of measures are the same; whereas, the unstructured option estimates each covariance individually. While the unstructured option may seem to be more realistic it can actually be less powerful than compound symmetry because the more data that are used to determine the correlation structure, the less data there are to estimate the parameters of linear models.

Compound symmetry and unstructured covariance structures were compared using Bayesian Information Criteria (BIC) in order to select the best model. The model that received a lower BIC rating was consequently selected for use. Plots of the residuals were checked to ensure normality of the data and any necessary transformations were made until the model received the lowest possible BIC rating. These full models were also tested for any interaction effects at the ($\alpha > 0.05$) level that may have occurred and impacted the results. If there were no significant interaction effects among the variables,

then the full model was reduced by removing the test for interaction effects and the effects were once again tested for significance.

Finally, a Tukey-Kramer test of multiple comparisons was used in order to understand exactly which treatments were statistically different from one another and which ones were not.

3.4 Results:

The results in Table 10 indicate that both the time of year ($p=0.0006$) and the burn treatment ($p<0.0001$) played significant roles in influencing soil-respired CO₂ labels. In addition to this, the Figure 11 reveals that as the summer progressed, the variations of isotopic labels of the soil-respired CO₂ collected from the different treatments were reduced.

Table 11: Output of soil-respired CO₂ from all three wildfire sites.

Effect	Num DF	Den DF	F Value	Pr > F
Burn	2	38	36.41	<.0001
Time	4	38	6.21	0.0006

The results from the Tukey-Kramer test in Table 11 reveal that there were no significant differences between the severely-burned treatment and the moderately-burned treatment throughout the summer ($p = 0.7324$). However, the unburned control treatment was significantly different from both the severely-burned treatment and the moderately-burned treatment ($p < .0001$) and ($p < .0001$), respectively. Figure 11 reiterates these conclusions.

Table 12: $\delta^{13}\text{C}$ output of the soil-respired CO₂ shows the results of each treatment compared to on another.

Effect	Treatment	Treatment	Estimate	Error	DF	t value	Pr > t	Adj P
Burn	Severe	Moderate	-0.1469	0.1946	38	-0.76	0.4548	0.7324
Burn	Severe	Unburned	1.3589	0.1946	38	6.98	<.0001	<.0001
Burn	Moderate	Unburned	1.5058	0.1946	38	7.74	<.0001	<.0001

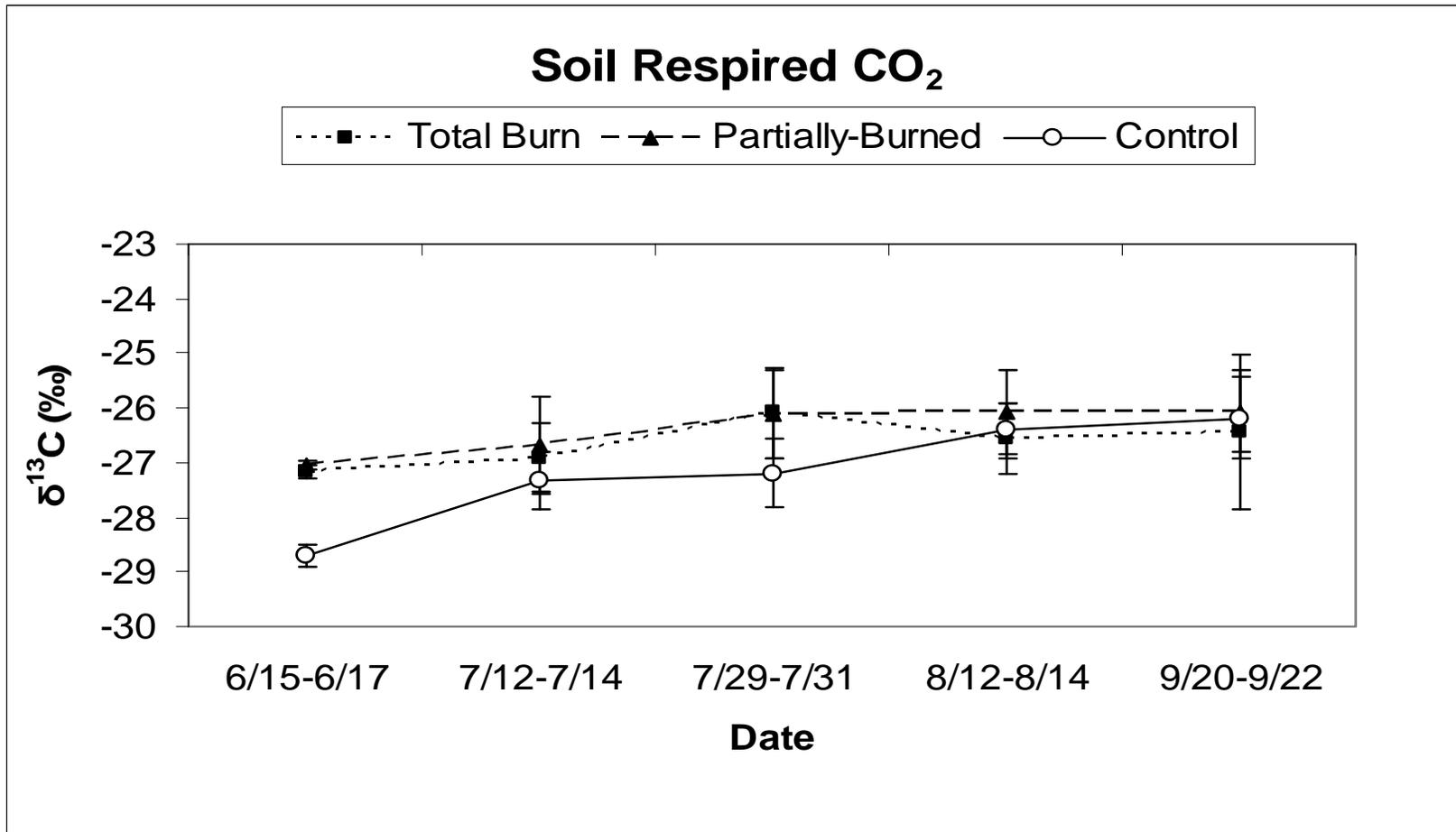


Figure 11: Carbon isotope ratios from soil-respired CO₂. Samples were collected during the 2005 growing season. Error bars represent standard errors.

3.5 Discussion:

Although there was no difference between the two burned treatments, i.e. the severely-burned and moderately-burned treatments, each of the burned treatments were significantly more enriched in ^{13}C when compared to the unburned controls in early to midsummer. This indicates that the soil-respired CO_2 labels from the burned plots were impacted by the disturbance caused by the wildfires.

The physiological measurements of hydraulic conductivity and water-use efficiencies for the conifers in the moderately-burned plots did not vary significantly from the unburned controls; therefore, they could not have been responsible for causing the enrichment in the soil-respired CO_2 collected from the burned treatments. However, the isotopic labels of the understory spirea shrub layer and the soil moisture contents did vary between the two treatments (Thompson et al., submitted). Although these measurements could only be collected from the moderately-burned treatment plots and the control plots, they support the results of the soil-respired CO_2 data. Consequently, it appears that the highly significant differences between the burned treatments and the unburned controls for soil-respired CO_2 are the result of the impacts of the wildfires on the understory vegetation rather than the dominant overstory trees which did not vary in their $\delta^{13}\text{C}$ values.

This conclusion is further supported by the lack of a difference between the soil-respired CO_2 signals in the moderately-burned plots, which retained overstory live trees after the fires, and the severely-burned plots, which retained no living trees at all. If the overstory trees contributed significantly to the belowground soil-respired CO_2 signal,

then the isotopic signal of the moderately-burned plots would appear to be lighter than the signal of the severely-burned plots.

As the fires swept through the burned plots they not only killed vegetation but also reduced the overstory canopy and organic duff layer on the plots' surface. Reductions in these components of the ecosystem allow more radiation to reach the ground, surface temperatures to rise, and ultimately soil moisture content to decrease (Grogan et al., 2000). In addition to this, the soil microbial community may have been seriously altered. The fluctuation of these factors also greatly impacts soil C labels (Fransson et al., 2001; Steinmann et al., 2004). Andrews et al. (2000) found that shifts in soil temperature and community structure of microbial heterotrophs significantly impacted the $\delta^{13}C$ labels of soil-respired CO_2 . Although there was not a significant difference in soil moisture between the controls and the partially-burned plots, a shift in soil temperature or heterotrophic or saprophytic diversity combined with a shift in the isotopic signal in the shrub understory may be responsible for the difference in the soil-respired CO_2 signals in the burned and control treatments.

The control plots clearly show an increase in the aboveground plant WUE throughout the summer, which would have resulted from the decrease in stomatal conductance due to seasonal drought conditions. Consequently, the soil-respired CO_2 signal in the control plots may have been dominated by heterotrophic respiration that relied on recently-formed photosynthates from the canopy. On the other hand, this trend is not as clear in the burned treatments, which had enriched labels and considerably less variability in their $\delta^{13}C$ values throughout the summer compared to the controls.

Therefore, the soil-respired signal in the burned treatments may have been dominated by other microbial communities such as saprophytes.

Future studies may focus on differentiating the contribution of heterotrophic and saprophytic communities on the soil-respired CO₂ label. It would also be beneficial to examine how microbial community composition is altered by wildfire, since this greatly influences the carbon cycle and nitrogen mineralization rates within the soil. If managers can link soil-respired CO₂ label of microbial communities that are poor at cycling nitrogen or other nutrients in the soil, then they may alter their restoration practices in order to hasten the establishment of vegetation within the burned areas and boost productivity levels.

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Chapter 4

Closing Remarks

4.1 Summary and Conclusion

This research was performed in 2005 at various locations in central Idaho where wildfires occurred late in the summer of 2003. We investigated the effects of wildfire on soil-respired CO₂ as well as hydraulic properties and water-use efficiency in damaged conifers, focusing on predawn soil water potential ($\Psi_{Predawn}$), stomatal conductance (g_s), leaf specific conductance (K_L), and carbon-13 isotopic discrimination ($\delta^{13}C$). Conifers from partially-burned areas, located along the perimeters of the wildfires, were selected based on the severity of the damages they sustained to their boles and canopies and then compared with adjacent unburned controls throughout the summer.

We hypothesized that the wildfires would result in xylem cavitation that would force the damaged conifers to alter their hydraulic properties in order to avoid mortality or a prolonged state of decline. Therefore, under this assumption, the damaged trees would adjust their water use efficiencies by modifying their g_s and K_L in order to make a full recovery. We found that while the partially-burned plots appeared to have lower predawn soil moisture contents there was not a statistically significant difference between the treatments. In addition to this, the damaged trees maintained g_s and K_L values similar to their adjacent unburned controls; however, nearly all of the partially-burned trees experienced reductions in leaf area due to a loss of hydraulic conductivity. By modifying leaf area the partially-burned conifers were able to maintain g_s and K_L values similar to their adjacent unburned controls. This indicated that the partially-burned conifers were

not sufficiently damaged by the wildfires to have caused any prolonged effects to their hydraulic systems or water-use efficiencies. Furthermore, we used isotopes from tree rings to crosscheck these findings and discovered that, in fact, there was no difference in water-use efficiencies between the two treatments. Consequently, we concluded that the damaged trees reduced their leaf area in order to maintain a constant K_L and productivity levels within the remaining foliage.

Although there were no differences found between the different conifer treatments, the plots that they were located within were in fact impacted by the wildfires. Carbon isotope analysis of the spirea understory revealed that the understory in the partially-burned plots significantly increased their water use efficiencies. The increases in water-use efficiency may be the result of the increases in nitrogen and PAR reaching the understory, thus raising the photosynthetic capacity within their leaves. In addition to this, it appears that the soil-respired CO_2 label was highly influenced by the shrub signal. Although there was no difference between the severely-burned and moderately-burned soil-respired CO_2 signals throughout the summer, both of these treatments differed significantly from the controls. Both of these treatments were isotopically enriched in ^{13}C compared to the adjacent controls.

4.2 Recommendations for Future Research

As trees become stressed from a disturbance and their productivity levels decrease, the amount of carbon that they fix is reduced. Consequently, if they are unable to produce enough energy to maintain respiration, they will die. This research was used in conjunction with another study to assess the impacts of disturbances in trees' hydraulic

characteristics and ultimately their carbon cycle on the damaged ecosystem's nitrogen cycle too. Despite the fact that we were unable to discern whether the loss in hydraulic conductivity was due to cavitation or resinosis, this methodology can still be used in the future to monitor the effects of disturbance on hydraulic properties. This study should be conducted again using trees that have sustained more damages to their boles and canopies. In addition to this, it would be beneficial to begin monitoring the trees directly during the fire with acoustic recorder in order to monitor cavitation rates directly. Collecting g_s and K_L data at the beginning of the next growing season immediately after the fire may aid in understanding how the damaged trees immediately react to the disturbance. Continuing the study over two or three field seasons would allow researchers to track the recovery or decline of the damaged trees in the context of their changing physiological processes as well as their environment.

Future research should also focus on monitoring a plethora of species other than Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and spirea (*Spireae betulifolia*). Different species will not always react to disturbances in similar ways; therefore, by studying species that infrequently experience wildfires, such as western red cedar or western hemlock, shifts in hydraulic properties and soil-respired CO₂ may actually become more apparent. However, regardless of which species is studied, it is necessary to examine a wide array of physiological data in order to understand what may be attributable to a treatment effect and what may be the result of a difference in environmental characteristics among plots.

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Appendix

This appendix contains supplementary data and graphs that describe the plot characteristics in greater detail. The information on leaf area and basal area per plot give greater insight in regard to the productivity levels within each plot. Finally, the burn severity of the soil within the moderately-burned and severely-burned plots is presented to further describe the impact of the wildfires on these plots.

Leaf area and basal area was based on measurements of the living trees within each plot (Table A). The unburned control plots at the South Fork of the Salmon River and Canyon Creek wildfires had more basal area and leaf area compared to their adjacent partially-burned plots (Figures A & B). On the other hand, the unburned control plot at the Hall fire had less basal area and leaf area compared to the partially-burned plot that was adjacent to it.

Site	Basal Area per plot (m ²)	Basal Area (m ² /ha)	Leaf Area per plot (m ²)	LAI
WLPB	0.597573811	6.639709013	1784.926161	1.98325129
WLU	0.971972799	10.79969777	2219.623369	2.46624819
HAPB	3.882141303	43.13490336	5436.494002	6.04054889
HAU	3.031511632	33.68346257	4397.66718	4.88629687
CCPB	1.573455534	17.48283927	1813.461897	2.01495766
CCU	2.850360702	31.67067447	3507.395531	3.89710615

Table A: Basal area and leaf of trees area per plot. Site prefixes WL, HA, and CC correspond to the wildfire sites Warm Lake, Hall, and Canyon Creek, respectively. Site suffixes PB and U correspond to the partially-burned and unburned plots, respectively.

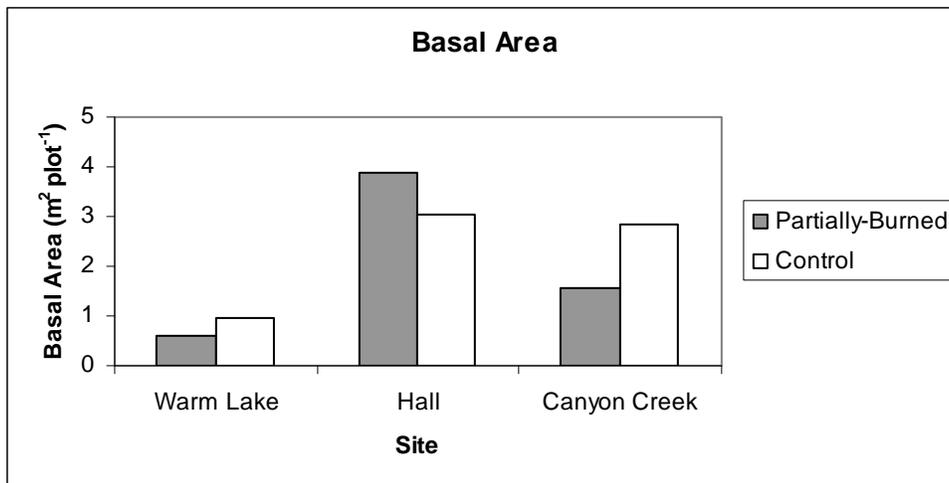


Figure A: Basal area for each plot, based on measurements of living trees.

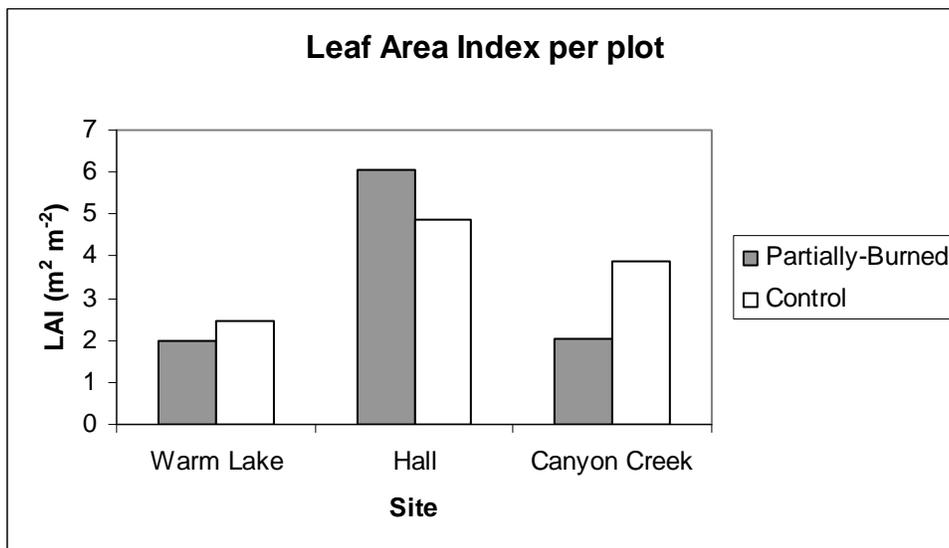


Figure B: Leaf area for each plot, measured in meter² of leaf area per meter² of ground surface.

Burn severity was assessed for each of the partially-burned and severely burned plots and recorded in Table B. The severity was based on the amount of exposed bare mineral soil within each plot. As the litter and humus layer are consumed by fire, the soil moisture capacity may be reduced, causing severely-burned soils to dry out faster than unburned soils that have considerable amounts of litter.

Table B: Detail of burn severity on the soil at each wildfire site.

Site	Total Surface Cover (%)	Partially Burned Plot	Severely Burned Plot
Canyon Creek	Litter/Humus	20	5
Canyon Creek	Bare mineral soil	80	95
Warm Lake	Litter/Humus	35	5
Warm Lake	Bare mineral soil	65	95
Hall Fire	Litter/Humus	25	5
Hall Fire	Bare mineral soil	75	95