

PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSES OF PINE AND WILLOW SAPLINGS TO POST-FIRE SALVAGE LOGGING

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Abstract

With global warming, forest fires may be increasing in frequency, and subsequently post-fire salvage logging may become more common. The ecophysiological impacts of this practice on tree saplings remain poorly understood. In this study, I examined the physiological and morphological impacts of increased light intensity, due to post-fire salvage logging, on the conifer *Pinus contorta* (pine) and deciduous broadleaf *Salix lucida* (willow) tree and shrub species in the Crowsnest Pass region of southern Alberta. Photosynthetic gas-exchange and plant morphological measurements were taken throughout the summer of 2013 on approximately ten year-old saplings of both species. Neither species exhibited photoinhibition, but different strategies were observed to acclimate to increased light availability. Willow saplings were able to slightly elevate their light-saturated rate of net photosynthesis (A_{\max}) when exposed to higher photosynthetic photon flux density (PPFD), thus increasing their growth rate. Willow also exhibited increased leaf inclination angles and leaf mass per unit area (LMA), to decrease light interception in the salvage-logged plot. By contrast, pine, which exhibited lower A_{\max} and transpiration (E), but higher water-use efficiency ($WUE = A_{\max}/E$) than willow, increased the rate at which electrons were moved through and away from the photosynthetic apparatus in order to avoid photoinhibition. Acclimation indices were higher in willow saplings, consistent with the hypothesis that species with short-lived foliage exhibit greater acclimation. LMA was higher in pine saplings growing in the logged plot, but whole-plant and branch-level morphological acclimation was limited and more consistent with a response to decreased competition in the logged plot, which had much lower stand density.

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List of Abbreviations and Symbols

A_{max}	Light-saturated photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
c_i/c_a	Ratio of internal to atmospheric carbon dioxide concentration
E	Evapotranspiration ($\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$)
F_v/F_m	Chlorophyll fluorescence (variable/maximum)
g_s	Stomatal conductance ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)
LBL	Leaves per unit branch length ($\# \text{ cm}^{-1}$)
LCI	Leaf clumping index ($\text{cm}^2 \text{ cm}^{-1}$)
LAR	Branch leaf area ratio ($\text{cm}^2 \text{ g}^{-1}$)
LMA	Leaf mass per unit area (g m^{-2})
LMF	Leaf mass fraction
PAR	Photosynthetically active radiation ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
PI	Plasticity index
PPFD	Photosynthetic photon flux density ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
SL	Salvage logged
TLA	Total projected leaf area (cm^2)
UL	Unlogged
VPD	Vapour pressure deficit (kPa)
WUE	Water use efficiency (mmol mol^{-1})
%N	Percent nitrogen content (μg of nitrogen/total μg foliar material $\times 100$)
$\delta^{13}\text{C}$	Stable carbon isotope composition (‰)
Φ	Quantum yield (mol mol^{-1})
ΦPSII	Quantum yield of photosystem II electron transport
‰	Parts per thousand

1.0 Introduction

Woody plants are known to exhibit both physiological and morphological acclimation to environmental conditions, including light availability (Niinemets *et al.*, 2001; Valladares *et al.*, 2002). In the Rocky Mountain region of western Canada and the northwestern United States, a variety of disturbances can expose seedlings to higher light intensity. These disturbances include fire and pine beetle infestation, which have increased in frequency over the past few decades, as a consequence of climate warming (Carroll *et al.*, 2003; Flannigan and Van Wagner, 1991; Westerling *et al.*, 2006). Because of the economic implications of such disturbances, salvage logging is a common practice in the region. Salvage logging is understood to cause a variety of impacts, including trampling and compaction by machinery, reduced sprouting rates, more variable microclimate, and increased light availability (Lindenmayer *et al.*, 2008). However, there is a paucity of data demonstrating the impact of salvage logging on the physiological acclimation of saplings to increased light intensity. In this study, I examine the impact of salvage logging on the physiological and morphological acclimation of the two dominant species in the Crowsnest Pass region of the eastern slopes of the Albertan Rocky Mountain region: *Salix lucida* (pacific willow) and *Pinus contorta* (lodgepole pine).

1.1 Increased Frequency of Natural Disasters

Natural disturbances in forest ecosystems, such as wildfires, floods, and insect attacks, heavily affect the plant community and ecosystem as a whole, resulting in widespread tree mortality and initiating secondary succession (McIver and Starr, 2000).

Such disturbances can be enhanced by climate change. For example, Mountain Pine Beetle (*Dendroctonus ponderosae*; Hopkins) range expansion is being made possible by increasing temperatures in areas of higher altitude and latitude, allowing the beetle to colonize areas that were previously unsuitable (Carroll *et al.*, 2003). Similarly, increased drought frequency may augment forest fire activity (Flannigan and Van Wagner, 1991). For example, the wildfire season has increased in length by 78 days in the western United States as a consequence of a warming climate (Westerling *et al.*, 2006). As frequency of these disasters is increasing, it is, thus, important to understand the physiological impacts of fire disturbance and subsequent salvage logging on the resulting forest succession.

1.2 Salvage-Logging in Response to Natural Disasters

Economic loss results from natural disturbance, as valuable resources are consumed. Wildfires burn an average of 2.8 million hectares of land in Canada every year (Flannigan *et al.*, 2005), while the current Mountain Pine Beetle epidemic has affected 18.1 million hectares of forested land in British Columbia alone as of 2012 (British Columbia Ministry of Forests, 2012). Managing forested ecosystems after these disturbances is increasingly important, especially with the anticipated increase in natural disturbances in future years (Westerling *et al.*, 2006; Carroll *et al.*, 2003; Flannigan and Van Wagner, 1991).

To retain some economic value from large-scale ecological disturbances, salvage logging is often performed before the standing dead trees have weathered and decomposed (Shore *et al.*, 2004; Morissette *et al.*, 2002). Around the globe, salvage logging is often carried out in response to natural disturbances, such as forest fires, and it

is widely practiced in North America (Lindenmayer *et al.*, 2008). The process of salvage logging is usually expedited compared to regular logging processes, occurring within 12 to 24 months after a disturbance in order to salvage the wood before it decays or dries (W. Aebli, personal communication, August, 2013). Logging begins immediately after government approval is granted following a natural disaster, as the wood loses value with time and soon becomes unsalable. Following salvage logging, government regulations require the logging company to employ reforestation methods, such as helicopter-based broadcast seeding or natural revegetation (W. Aebli, personal communication, August, 2013). The latter method is often employed in fire disturbed stands. Small, accessible sections of forests may also be logged for personal use by the general public, such as for firewood (W. Aebli, personal communication, August, 2013). Salvage logging is also carried out to decrease the risk of future forest fires (Ne'eman *et al.*, 1997) and pest infestation (Lindemann and Baker, 2001), or to increase sapling regeneration rates (Lain *et al.*, 2008).

1.3 Potential Environmental Consequences of Salvage Logging

The concept that salvage logging is beneficial for ecosystems affected by a disturbance has recently been challenged, and it has been suggested that salvage logging may actually be detrimental to a disturbed ecosystem. Salvage logging increases the amount of fine and coarse downed woody fuel loads, augmenting the risk of future forest fires (Donato *et al.*, 2006), disturbs the nutrient cycle of the ecosystem by altering the microenvironment and forest cover (Foster and Orwig, 2006), and depletes soil of nutrients by removing nutrient rich plant material (Brais *et al.*, 2000). Further, the use of

machinery for logging mechanically disturbs surviving or regenerating understorey plants (Fernandez *et al.*, 2008) and reduces the species richness of the understorey vegetation (Jonášova and Prach, 2008; Purdon *et al.*, 2004). These effects are similar to those found in traditionally logged ecosystems, except that the forest was disturbed prior to logging, which can exacerbate the impact. For example, forest fires expose mineral soil through the combustion of soil organic matter, thereby leaving forests more vulnerable to soil compaction and the degradation that results from salvage logging (McIver and Starr, 2000).

Salvage logging operates on the assumption that a forest ecosystem affected by disturbances is damaged and not as ecologically useful as an undisturbed forest. However, fires and insect infestations of moderate intensity are part of a normal process of ecosystem renewal (Attiwill, 1994; Kauffman, 2004). These disturbances are a critical part of many ecosystems, and many species within these ecosystems are adapted to certain disturbances common to that ecosystem (Bergeron *et al.*, 1999; Pahl-Wostl, 1995). Furthermore, trees that are killed in natural disturbances add to the heterogeneity of the ecosystem, providing structural variation that may be used for shelter by a range of biota, a substrate for flora and fungi growth, and a source of nutrient cycling as the dead trees are eventually recycled by the ecosystem (Martin *et al.*, 2006; Lindenmayer *et al.*, 2006). It is also important to note that while a large portion of the overstorey may be killed during natural disturbances such as insect infestations, rarely is the entire overstorey killed, and the surviving trees add to the functioning of the ecosystem (Brown *et al.*, 2010). The understorey vegetation and seed bank also survive many disturbances,

and may benefit from overstorey tree death, due to increased light availability and reduced competition for nutrients (Lentile *et al.*, 2007).

This combination of dead and surviving trees, understorey vegetation, and seed banks results in a heterogeneous combination of biological legacies. Biological legacies are any organisms, structures, or patterns that have survived from the ecosystem prior to a disturbance and add to the diversity of the disturbed ecosystem (Lindenmayer *et al.*, 2006). Even disturbances as destructive as stand-replacing fires leave biological legacies, and it is from these legacies that colonization and revegetation stems (Turner *et al.*, 2003). Furthermore, disturbances increase biodiversity and ecosystem heterogeneity (Lindenmayer *et al.*, 1999; Jonášova and Prach, 2008; Turner *et al.*, 2003). This increased biodiversity improves the health of the ecosystem and provides a greater range of species interactions. It is, therefore, important to consider all aspects of the ecosystem and the effects that salvage logging may have on them.

One area of research that has not been significantly addressed is the effect of salvage logging on the light regime, and the subsequent effects on forest regrowth. Natural disturbances open the forest canopy and increase incoming solar radiation (Boon, 2009; Burles and Boon, 2011). However, compared to a cleared forest stand, the standing dead trees reduce incoming solar radiation as well as wind speed and air temperature (Burles and Boon, 2011). Burned forests must, therefore, be treated as having distinct microclimates from either healthy or clear cut forest stands, as the partial coverage provided by the standing dead trees affects the light intensity reaching the growing understorey, as well as alters the temperature and humidity within the forest. This creates

a unique ecosystem in which the growing plants are exposed to different growth conditions with increased light availability compared to an undisturbed site, but a lesser amount of solar radiation than a cleared site.

Partial thinning of the overstorey, as opposed to clear cutting, has been shown to provide the greatest benefit to the overall growth of select understorey species (Krasowski and Wang, 2003). This may be similar to disturbed forest ecosystems, in which the dead overstorey remains and provides partial shading. The partial shading provided by the standing dead trees may, therefore, benefit the understorey by reducing the solar radiation compared to an open site, as the associated increase in light intensity and temperature may subsequently result in photoinhibition in the forest understorey (Houter and Pons, 2005). Currently, there is a gap in the literature regarding the physiological and morphological acclimation of saplings of key forest species to changes in light availability in post-fire, salvage-logged environments. In particular, little research has been done on post-fire salvage-logged ecosystems on the eastern slopes of the Rocky Mountains of southern Alberta. Studies on plant acclimation to changes in light intensity would contribute to our understanding of the effects that salvage logging has on the forest community, provide indications of subsequent plant health and form, and provide some insight, at the leaf-level, of how changes in light intensity may affect photosynthesis processes and, thus, forest regrowth.

1.4 Altered Light Regimes and Plant Morphology

Light availability plays a significant role in plant growth and development, as plants develop to both utilize the increased irradiance, as well as avoid damage from the elevated light levels when they are too high. In higher light environments with adequate water availability, plants take advantage of the elevated irradiance by increasing their relative growth rate (RGR). The distribution of growth also changes, as plants grown in elevated irradiance have greater leaf thickness and leaf dry mass per unit area (Walters, 2005). Further, there is greater leaf nitrogen content per unit area in sun grown plants (Gratani *et al.*, 2006), but the nitrogen invested in leaf chlorophyll is reduced (Bilger and Björkman, 1990; Demmig-Adams, 1997; Matsubara *et al.*, 2009). The ratio of chlorophyll a to chlorophyll b is also greater in light-acclimated plants due in part to a reduction of chlorophyll in the light harvesting complexes (Lichtenthaler and Babani, 2004). This helps plants grown in high light environments to avoid damage to their photosystems.

To further reduce light capture, plants will exhibit changes such as higher branch and leaf inclination angles and increased leaf clumping. This is done to decrease the amount of solar radiation striking the photosynthetically active leaf area (Valadares and Niinemets, 2008; Terashima and Hiosaka, 1995). Similarly, plants grown in low light environments tend to increase light capture. For example, leaf inclination angles of *Arisaema heterophyllum* were found to differ between forested low light conditions, with flatter angles to maximize light capture, and deforested high light conditions, with higher angles to avoid excess irradiance (Muraoka *et al.*, 1997). Similar results were observed in

Buxus sempervirens, which also altered leaf angle as well as branch angle to avoid excess irradiance in high light conditions, as well as increasing leaf mass per unit area (LMA) and its leaf clumping as other means of acclimating to a higher light environment (Letts *et al.*, 2011). Variation in light availability was also shown to affect the width of the needles of *Picea abies* (Niinemets and Kull, 1994), as well as the leaf area, and specific leaf area (SLA) of *Isatis tinctoria* (Monaco *et al.*, 2005).

1.5 Altered Light Regimes and Plant Physiology

When plants are grown in high light environments, they acclimate to utilize the increased light availability for carbon assimilation. Plants grown in full sun can acclimate to high irradiance through physiological and morphological adjustments that allow for greater light use during photosynthesis, as well as to avoid damage related to excessive light. This occurs largely as a result of the increase in leaf thickness, which allows for a larger portion of chloroplasts per unit leaf area, as well as compounds required for carboxylation, such as enzymes involved in the Calvin cycle (Evan and Seemann, 1989; Lambers *et al.*, 2008). With the increase in maximum photosynthesis, there is also greater respiration and an increase in the light-compensation point.

Shade-grown plants, by contrast, attempt to capture as much light as is possible, and allocate a greater proportion of carbon to the spongy mesophyll, which increases light absorbance due to greater internal light scattering (Vogelmann *et al.*, 1996). Further acclimation to high light availability can be seen through higher electron transport rates (ETR; Rodríguez -Calcerrada *et al.*, 2007) and through an increase in the quality and

number of leaf pigments involved in photoprotection (Bilger and Björkman, 1990; Galmes *et al.*, 2007).

However, the light acclimation capacity of some plants is limited, resulting in photoinhibition above certain threshold radiation intensities and durations.

Photoinhibition is the reduction in photosynthetic ability as a result of excess irradiance, and often occurs as a result of the photosynthetic machinery, primarily the photosystem II reaction centre, being damaged (Lambers *et al.*, 2008). When light levels are too high for all the absorbed photons to be utilized in photochemistry, plants must dissipate the excess energy through non-photochemical means, such as through heat or fluorescence. Since some plant species that typically grow in open, high light environments are able to utilize more solar radiation for photosynthesis and have greater means to dissipate excess solar radiation than other, more shade-loving plant species, logging may create conditions favouring one species over another in the salvage-logged sites. By increasing understorey light availability and intensity, salvage logging may upset the natural competitive dynamics of the ecosystem. For example, shade tolerant species, such as subalpine fir, may be negatively impacted by the additional light caused by salvage logging, causing a shift towards more light tolerant species, such as lodgepole pine (Astrup *et al.*, 2008; Collins *et al.*, 2011).

1.6 Lost Creek Fire

The Lost Creek Fire of 2003 occurred in the Rocky Mountain region of southwestern Alberta in the Oldman River Basin, near Crowsnest Pass, Alberta. The wildfire was highly destructive, consuming over 21 000 ha of land as it burned

uncontrollably for 26 days (Silins *et al.*, 2009). Post-fire logging occurred in the years following the burn, involving large equipment such as skidders and feller bunchers. Members of the general public also harvested the dead standing trees by foot (W. Aebli, personal communication. August, 2013), as is the case at the study site selected for this investigation.

1.7 Objectives

This thesis addresses the effects of post-fire salvage logging on the photosynthetic characteristics, plant morphology, and leaf traits of pine and willow in a forest on the eastern slopes of the Rocky Mountains in Southern Alberta. Specifically, it characterizes the change in microclimate caused by post-fire salvage logging and examine how the increased irradiance associated with salvage logging influences leaf physiology and plant morphology of the two dominant plant species. I hypothesized that plant physiological acclimation to higher light intensity would be observed in the salvage logged plot. Specifically, I anticipated increased light-saturated photosynthesis rate (A_{\max}) and light utilization, based on measures such as electron transport rate. I expected higher water-use efficiency at a given temperature and VPD at the salvage-logged plot, due to acclimation to water stress and higher leaf temperature. I further speculated that photoinhibition would become prevalent in plants grown in the salvage-logged ecosystem, particularly towards the end of the growing season, due to lower water availability and reduced cloudiness. Morphologically, I hypothesized that plants grown in the salvage-logged plot would avoid light interception through traits such as more vertically-oriented leaves and branches, as well as leaf clumping, but reduced leaf area relative to leaf mass. Further, I

anticipated that willow would exhibit greater acclimation to the increased light intensity in a salvage-logged ecosystem than pine as pine needles must maintain greater leaf longevity and therefore a more conservative acclimation.

2.0 Methods

2.1 Study Site

The study was conducted within two adjacent plots at a forested site in the front ranges of the southwestern Rocky Mountains of Alberta (Figure 1). The forest was burned in the 2003 Lost Creek Fire. The study site is located near Crowsnest Pass, Alberta, Canada (49°33' N 114°28' W), approximately 5.2 km southwest of the town of Blairmore, Alberta, at an altitude of 1550 m in the Subalpine natural sub-region of Alberta (Archibald *et al.*, 1996). The field site consisted of a forest fire disturbed plot in natural revegetation for ten years (UL), and a post-forest fire salvage-logged plot in natural revegetation for ten years (SL). The plots shared a similar overstorey species assemblage of pine prior to the forest fire (W. Aebli, personal communication. August, 2013).

The town of Coleman (49°38' N 114° 35' W), at an elevation of 1341 m, is the nearest Environment Canada (EC) station to the field sites with long-term temperature records. The mean annual temperature (1981-2010) at Coleman is 3.6°C, with a mean maximum temperature of 9.7°C and minimum of -2.4°C. For the summer (June, July and August), the average, maximum, and minimum temperatures are 13.5°C, 21.2°C and 5.7°C, respectively. The average annual precipitation at Coleman is 582.1 mm, with 69.5% (404.8 mm) of that being rain and 30.5% (177.3 cm) snow. These data, however, are likely very different from those of the field site, as there is an elevation difference of 209 m. Further, observational data throughout the field campaign suggests that the field site and Coleman frequently experience different meteorological conditions.

The selected post-fire SL plot was not a part of the commercial logging that occurred throughout much of the burned forest. Instead, the SL plot had been cut by individuals on foot for private use (W. Aebli, personal communication. August, 2013). This was done to focus on the effects of the altered light regime on the plant community, as the combination of forest fires and clear cutting may accelerate soil erosion and soil compaction, resulting in increased surface runoff (Fernandez *et al.*, 2007). The use of heavy machinery and the removal of vegetation from salvage logging increases bulk density through soil compaction and promotes the loss of nutrient-rich topsoil (Harvey and Brais, 2002). The net result is an increase in surface runoff (Edeso *et al.*, 1999) and soil drying, due to the absence of snags (Purdon *et al.*, 2004). Soil compaction and erosion tend to result in decreased soil moisture, which can create conditions of drought for plants, particularly in higher light environments due to the increased temperatures and evaporation (Valladare and Pearcy 1997; Feng and Li, 2007). It was, therefore, necessary to use a site that had not been logged mechanically in order to single out the effects of the altered light intensity on the microclimate from the reduced canopy coverage on the forest regrowth. Drought stress may still be present, but this is more likely to be the result of the increased solar radiation, temperature, and wind, as opposed to soil compaction from logging.

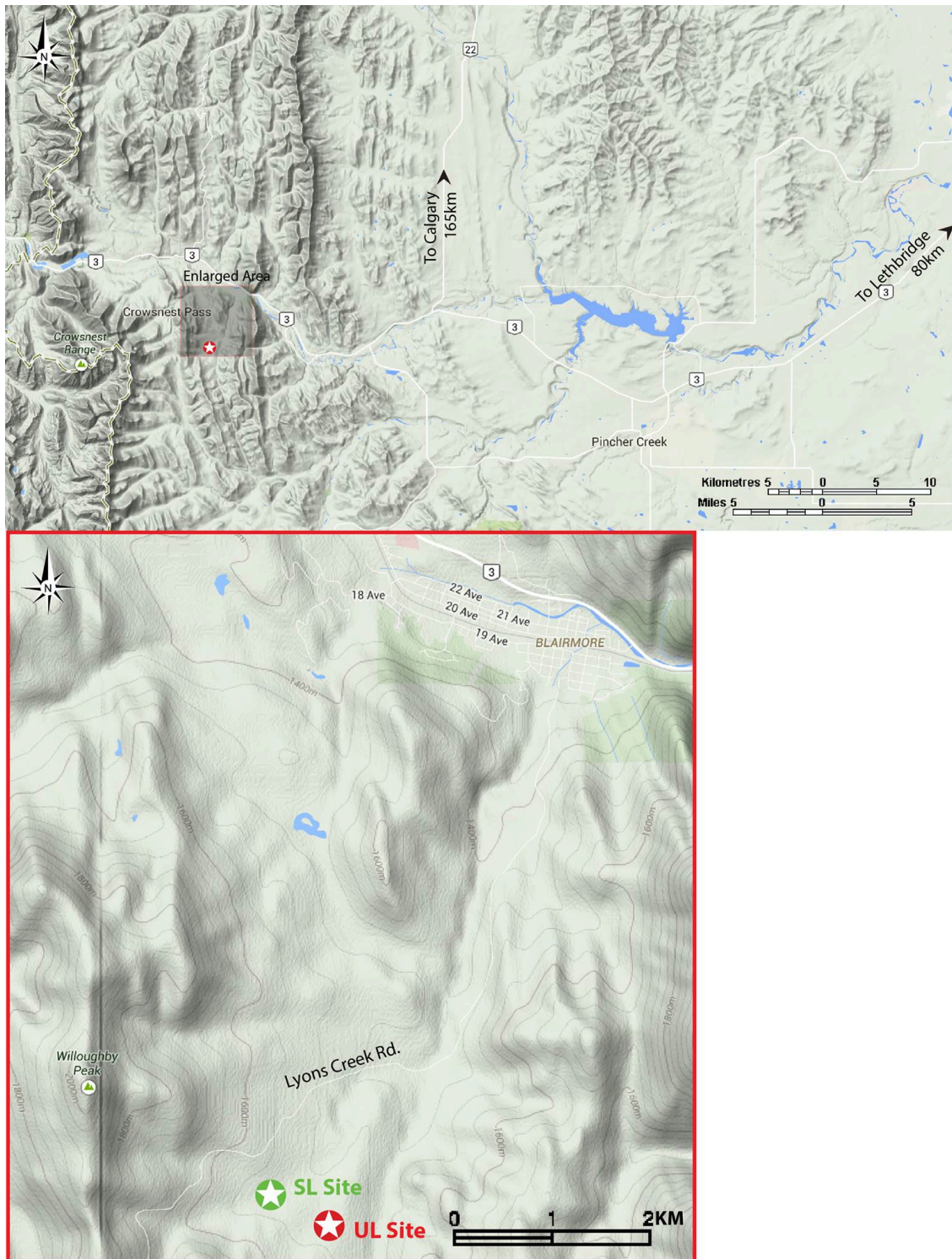


Figure 1. Salvage-logged (SL) and unlogged (UL) plot locations in southern Alberta, Canada.

The current dominant species in the forest regrowth are *Pinus contorta* Douglas ex Loudon ssp. *latifolia* (Engelm. ex S. Watson) Critchfield and apparently the shining or Pacific willow, *Salix lucida* Muhl. ssp. *lucida* var. *latifolia* (Andersson) Andersson (Figure 2). *Pinus* species are tall evergreen trees with clustered needles, and cones that mature in the second season. *P. contorta*, or lodgepole pine, has straight and slightly spread leaves that are approximately 3-6 cm long. The cones spread at right angles to the branches and have scales without prickles. Pine is very common in the southern Rocky Mountains (Looman and Best, 1987), and it is fire successional, often characterized by strong seeding in disturbed habitats which results in dense, slow growing stands (Kral, 1993)

Salix, or willow, is a genus of deciduous trees and shrubs with up to 400 species and two sexes that is native to western and northern North America. Leaves alternate on stems, and unisexual flowers are produced on separate plants (Looman and Best, 1987). Many *Salix* species will vary phenotypically in response to moisture, nutrients, shade, and wind, and often undergo hybridization (Argus, 2008). As a result of this intraspecific variation, identification is difficult.



Figure 2. Foliage of pine (left) and willow (right) at the field site.

2.2 Meteorological Data

One HOBO meteorological station (HOBO U30, Onset Computer Corporation, USA; Figure 2) was installed in both the logged and unlogged catchment sites. Average daytime photosynthetic photon flux density (PPFD), soil moisture, air temperature, relative humidity and dew points were recorded at both plots from Julian day 159 to 231, 2013. PPFD was measured with a factory calibrated quantum sensor (S-LIA-M003, Onset Computer Corporation, USA) installed at the top of each of the 2 towers, 2 m in height. Precipitation was measured only in the salvage-logged plot with a HOBO data Logging Rain Gauge (S-RGB-M002, Onset Computer Corporation, USA). Air

temperature and relative humidity were measured at 1m and 20 cm above ground with two temperature and relative humidity sensors (S-THB-M002, Onset Computer Corporation. USA). Soil moisture was measured using soil moisture probes (HOBO EC-5, Onset Computer Corporation. USA) buried 15 cm into the ground at each station. Measurements were taken every five minutes and recorded to a connected data logger. Mean daytime temperatures and PPFD were then determined from the hours of 05:00 to 21:00. Average soil moisture, maximum VPD and total rainfall per day were also calculated.

Additional PPFD measurements were taken to create a more spatially varied understanding of the differences between the two plots the following year on Julian day 245 at approximately solar noon (between 13:00 and 14:00) under overcast conditions. Measurements were taken simultaneously using both a PPFD sensor connected to a data logger in a completely open nearby site as well as a hand held PPFD sensor that was used at fifteen distinct point locations within each plot; PPFD measurements were then used to determine the relative light availability (%PPFD) by dividing the measured light intensities at each plot by the related light intensities taken at the open site at the same time.

2.3 Sampling Design

Within each plot, a total of fifteen plants of each species were randomly selected and marked for physiological analysis, with an additional ten plants selected for a total of twenty five plants per plot for morphological analysis. Plants were sampled repeatedly on

east-facing branches for ecophysiological measurements, and sampled repeatedly on a south-facing branch for morphological measurements.

Measurements were conducted during three distinct campaigns throughout the summer of 2013, the first from June 18th to June 28th, the second from July 23rd to August 7th and the last from August 19th to September 3rd. Measurements were alternated daily from salvage-logged (SL) and unlogged (UL) plants, and between pine and willow plants, to limit measurement condition effects, including developmental, time of day, and day of year effects. All measurements were taken between 08:00 and 15:00 hours.

2.4 Ecophysiological Measurements of Plant Photosynthesis

Photosynthetic gas exchange was measured using the LI-COR 6400XTR Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NB, USA) equipped with the LI-COR 6400 Leaf Chamber Fluorometer. One healthy leaf from an east-facing branch from each selected willow plant was chosen at each measurement period, for a total of 15 leaves per plot. In the case of pine plants, needles on an east-facing branch from each were selected to fill the sensor head as much as possible with no overlapping needles. Following the measurements, needles were cut to the area of the chamber with a 2 cm² sharpened copper tube and then the leaf area was measured with a portable area meter (LI-3000C, LI-COR Biosciences, Lincoln, NB, USA). Needle area was input manually into the data output and gas exchange calculations accounted for the needle area measured. Willow leaves always filled the sensor head, thus eliminating the need to adjust for measured leaf area.

Leaves from the same branches were used for measurements at each of the three campaigns to remain consistent and avoid effects of aspect differences. Prior to each set of ecophysiological measurements, leaves were allowed to equilibrate in the sensor head to the highest light level (PPFD of 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$, leaf temperature of approximately 22°C, a relative humidity between 50% and 80% and a target VPD of 1 kPa) for twenty minutes, to ensure leaves had reached a steady state gas exchange rate. Measurements were then conducted at PPFD intensities of 2000, 1500, 1000, 650, 400, 200, 100, 80, 50, 20, and 0 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Leaves were equilibrated for each of the light intensities. Measurements taken included photosynthesis rates, to create light response curves, as well as transpiration (E), stomatal conductance (g_s) and the ratio of internal to atmospheric carbon dioxide concentrations (c_i/c_a) at a PPFD of 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Water-use efficiency (WUE; A/E) was then determined at light saturation.

2.5 Light Response Curves

The LI-6400 XTR leaf photosynthesis data points at the 11 measured light intensities were fit to a nonrectangular hyperbola in SYSTAT (San Jose, USA) using the equation below to give a light response curve with rates of net photosynthesis (A_{max}) versus photon flux density (I).

Equation 1

$$A_n = \frac{(\Phi I + A_{max} - \sqrt{((\Phi I + A_{max})^2 - 4\theta\Phi_{max})})}{2\theta} - R_d$$

Where:

Φ = quantum yield (mol mol^{-1})

A_{max} = light-saturated photosynthesis rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$)

θ = curvature (varies from 0 – 1)

R_d = respiration rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$)

Light response curves were created for every leaf measurement and then averages of the parameters were taken for each species in each plot for the three measurement campaigns.

2.6 Chlorophyll Fluorescence

Chlorophyll fluorescence was measured simultaneously with photosynthetic gas-exchange, in order to determine the quantum efficiency of photosystem (PS) II (ΦPSII) and the electron transport rate (ETR) at $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. ΦPSII and ETR were calculated through the following equations, respectively:

Equation 2

$$\Phi\text{PSII} = \frac{(F_m' - F_s)}{F_m'}$$

Where:

F_s = Steady state fluorescence

F_m' = Light adapted maximum fluorescence

$$ETR = 0.5 \times PPFD \times \text{Leaf Absorption} \times \Phi PSII$$

Chlorophyll fluorescence measures of the maximum quantum yield of PSII (F_v/F_m) were taken on June 30th, August 6th and August 7th, and August 28th in the field using the LI-COR 6400XTR Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NB, USA) equipped with the LI-COR 6400 Leaf Chamber Fluorometer (LI-COR Biosciences, Lincoln, NB, USA). Leaves were dark-adapted overnight and were kept under dark conditions while they were placed in the sensor head with no actinic light source. Upon reaching a steady state, the dark-adapted leaves were then exposed to an intense saturating pulse of light and the fluorescence response was measured. This provided the maximum quantum efficiency of photosystem II through the ratio of variable fluorescence to maximal fluorescence ($F_v/F_m := (F_m - F_o)/F_m$; Baker 2008).

2.7 Carbon Isotope Composition ($^{13}\text{C}/^{12}\text{C}$) and Total Leaf Nitrogen Content

Upon completion of ecophysiological measurements of photosynthetic gas exchange, leaves were collected and refrigerated until the end of the field campaign. At this point the foliar material was oven dried at 60°C for a minimum of 48 hours. Leaves were then crushed and ground into a powder with a mortar and pestle and stored in glass vials prior to analysis. The powder was then sent to the UC Davis Lab and was combusted in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (UC Davis Stable Isotope Facility, Sercon Ltd., Cheshire, UK)

The carbon isotope composition ($\delta^{13}\text{C}$) and total nitrogen content were measured, and from this the %N ($\mu\text{grams of nitrogen/total } \mu\text{grams foliar material} \times 100$) was determined. The stable isotope ratio of carbon is expressed using delta notation (δ) in parts per thousand (‰) in the following equation, where R is the ratio of heavy isotope (^{13}C) to the light isotope (^{12}C), with the standard being the international standard Pee Dee Belemnite (PDB):

Equation 4

$$\delta^{13}\text{C} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

The mass spectrometer was calibrated using peach leaves as the working standard. The precision was determined by taking the standard deviation of 14 replicate measures and was calculated to be 0.04‰. Replicate willow leaves were also used for a total of 12 measures, and the standard deviation was 0.03‰.

Based on the reported $\delta^{13}\text{C}$ and c_i/c_a ascertained through gas exchange measurements and isotope analysis, expected measures of c_i/c_a and $\delta^{13}\text{C}$ were also calculated. This was done using the following equation (Flanagan *et al.*, 1997):

Equation 5

$$\delta^{13}\text{C}_{\text{leaf}} = \delta^{13}\text{C}_a - a - (b - a) \cdot c_i/c_a$$

Where:

$\delta^{13}\text{C}_a$ = leaf source CO_2 (-8‰)

$\delta^{13}\text{C}_a$ = atmospheric source CO_2

a = $^{13}\text{CO}_2$ diffusion rates relative to $^{12}\text{CO}_2$ (4.4‰)

b = enzymatic discrimination during carboxylation (27‰)

c_i/c_a = ratio of internal to ambient CO_2

The expected values give us a greater understanding of what occurred in the life history of the leaf prior to the gas exchange measurements being taken. The expected values were compared to the measured values using Student's t-test.

2.8 Whole Plant and Leaf Morphology

Total height, ground level stem diameter, and crown width were measured throughout the study, to determine the net plant growth of each species. Height and crown width were measured with a measuring tape and ground level stem diameter was measured with a digital calliper (Procise, The Innovak Group, Canada).

Branch diameter and branch and leaf inclination measures were taken for both plant species during the second measurement campaign from July 23rd to August 7th. One south facing branch was selected for measurements of branch diameter and inclination and leaf inclination. Branch diameter was taken at the base with a digital calliper. Both branch and leaf inclination angles were measured relative to the horizontal using an angle locator (Magnetic angle locator, Johnson. USA). As pine shoots had both previous year and current year growth units, angles of both current and past year growth inclination angles were measured separately. Willow branches were only measured on current year shoots, so past year angles were not measured. Leaf inclination angles for pine were

measured relative to the horizontal at five equidistant points along the top of the selected branches. Leaf inclination angles for willow were measured on the first five mature leaves at the end of the current year growth on the selected branches.

The number of new growth units per plant was counted and the length of apical growth unit was measured for willow during the second measurement campaign, and during the third measurement campaign for pine as a result of time constraints. On the final day of the second campaign, one south-facing branch on 15 of the 25 willow plants was severed at its base, refrigerated, and returned to the lab. The leaves were separated from the stem and measured with a leaf area meter (LI-3000C, LI-COR, Lincoln, NB, USA) to determine their total projected leaf area (TLA). The branch length of the stems was measured and used to determine the leaves per unit branch length (LBL), defined as the ratio of branch length to the number of leaves, and the leaf-clumping index (LCI), defined as the ratio of branch length to TLA.

All plant material was then oven dried at 60°C for 96 hours before being weighed to determine their leaf mass per unit area (LMA). This was calculated by the following equation:

Equation 5

$$LMA = \frac{\text{total leaf dry weight}}{TLA}$$

The branch leaf area ratio (LAR) was determined for each sample by dividing its TLA by the total branch dry weight, including all leaves and stems (Letts, *et al.*, 2011). Leaf mass fraction (LMF) was determined by dividing the total leaf dry weight by the total branch dry weight. Due to time restraints, the same measurements were conducted for pine on the final day of the third campaign.

Additional measurements of stand density were taken the following year on Julian day 245. Five 25 m² plots within the SL plot were randomly selected and the number of willow and pine saplings was counted and then converted to a standard unit of measurement. Due to the density of the forest regrowth in the UL plot, three subplots of 1 m² were sampled within each plot, to determine the average number of saplings per plot.

2.9 Plasticity Index and Statistical Analysis

Indices of phenotypic plasticity were generated in accordance with previous studies (Valladares *et al.*, 2000; Letts *et al.*, 2011). A plasticity index (PI) was calculated for variables of each species where the differences appeared to be significant. PI values were calculated as the difference between the minimum and maximum mean values for each light treatment divided by the maximum mean value; this was done for each species.

Ecophysiological data were analyzed using IBM SPSS Statistics Data Editor using a repeated measures analysis of variance (ANOVA). Variables were analyzed by comparing the SL to UL values for each species that taken during each measurement campaign, which was considered to be a comparison in the seasonal variation. Variables were also compared as a whole data set comparing the seasonal averages using Students T-test. In order to compare species, another set of repeated measures analysis of variance test was conducted comparing the two species within each treatment. Morphological data was analyzed with Students T-test comparing SL and UL within individual species. Microclimatic data were also analyzed using Students T-test comparing averages between the SL and UL plots.

3.0 Results

3.1 Environmental Parameters

Daily mean PPFD showed a similar temporal pattern at the UL and SL weather station sites, with incoming PPFD attenuated by the canopy at the UL plot, resulting in an average PPFD of $536 \pm 22 \mu\text{mol m}^{-2} \text{s}^{-1}$, compared to the SL mean of $733 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ (t-test, $p < 0.01$; Figure 3). The additional PPFD measurements further illustrated the difference in light intensity between the SL and UL plots. On average, 83.4% of the incoming light reached the PPFD sensor at the SL plot, compared to only 53.3% at the UL plot (ANOVA, $p < 0.01$).

Daily temperature exhibited similar trends in both plots at both 20 cm and 1 m heights (Figure 4). There was no significant difference in the temperature variation of the UL and SL plots at either 20 cm (t-test, $p = 0.31$) or 1 m (t-test, $p = 0.35$), with means ranging between 13°C and 14°C. Significantly lower minimum temperatures were observed at the SL plot relative to the UL plot (4.8 ± 0.6 and $6.0 \pm 0.7^\circ\text{C}$, respectively; t-test, $p = 0.02$). Differences were not significant at 100 cm, and maximum values did not differ at either 1 m or 20 cm (t-test, $p = 0.09$ and $p = 0.32$, respectively). Mean daily VPD was greater in the SL at a height of 20 cm, with a mean value of $0.53 \pm 0.04 \text{ kPa}$ compared to $0.33 \pm 0.02 \text{ kPa}$ in the UL plot (t-test, $p < 0.01$) but exhibited no difference at 1 m (t-test, $p = 0.20$; Figure 4).

Total precipitation was $107.2 \pm 0.9 \text{ mm}$ at the field site between June 8 and August 17 (Figure 6), which is below the mean of 133.9 mm for the 72 day period, based on linearly prorated values of mean June, July and August precipitation for Coleman, AB

(176 mm). Mean volumetric soil moisture was higher at the SL plot (0.216 ± 0.003 m^3/m^3) than at the UL plot (0.184 ± 0.007 m^3/m^3 ; t-test, $p < 0.01$).

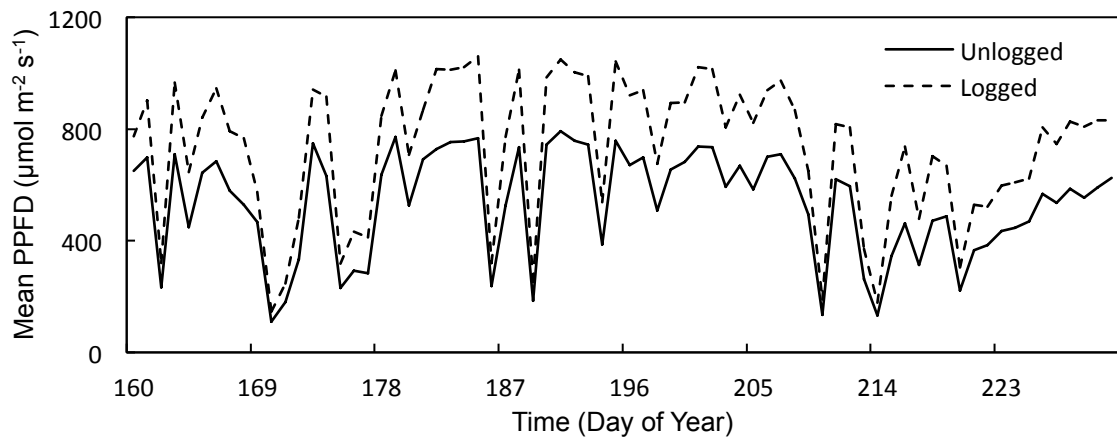


Figure 3. Variation in mean daily photosynthetic photon flux density (PPFD) between logged (dashed) and unlogged (solid) plots from June 9 to August 23, 2014.

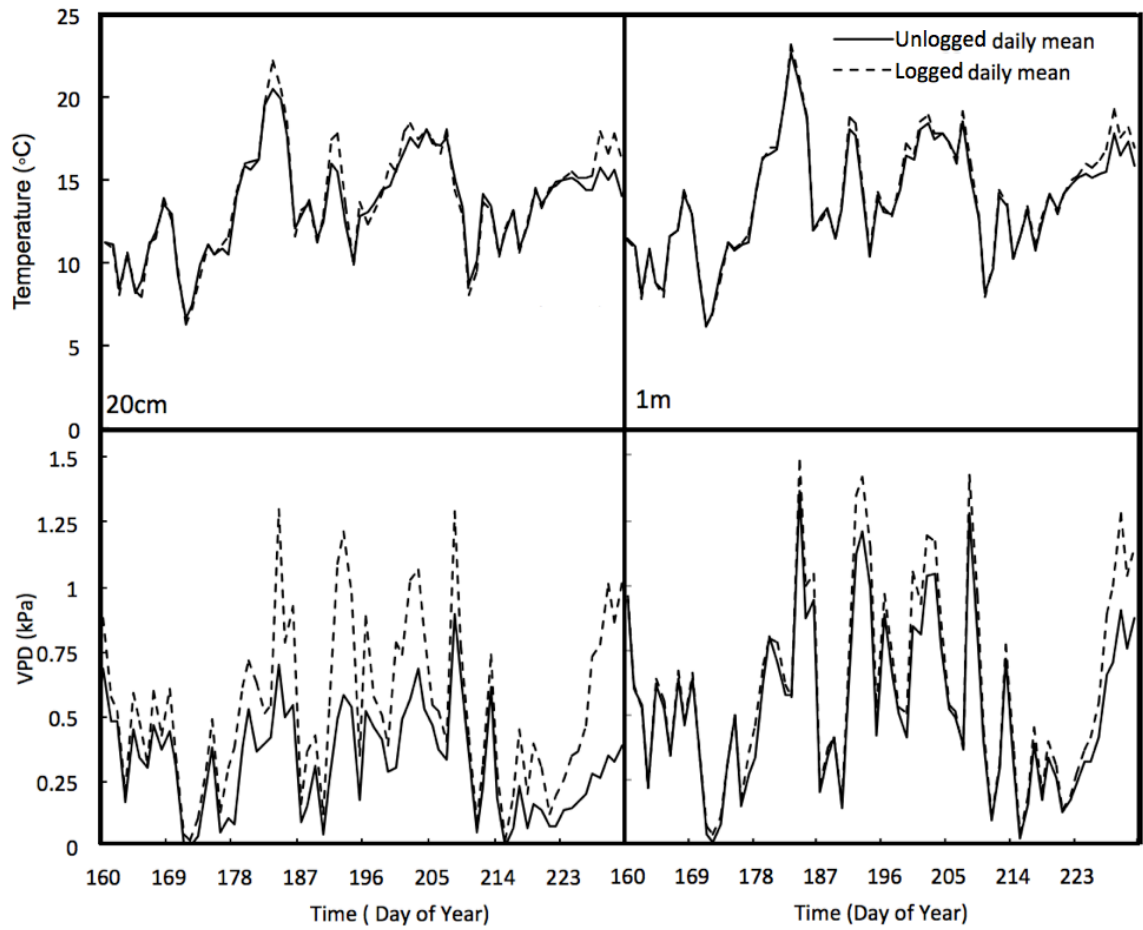


Figure 4. Mean daily air temperature and vapour pressure deficit (VPD) at heights of 20 cm (left) and 1 m (right) in the logged (dashed) and unlogged (solid) plots from June 9 to August 23, 2014.

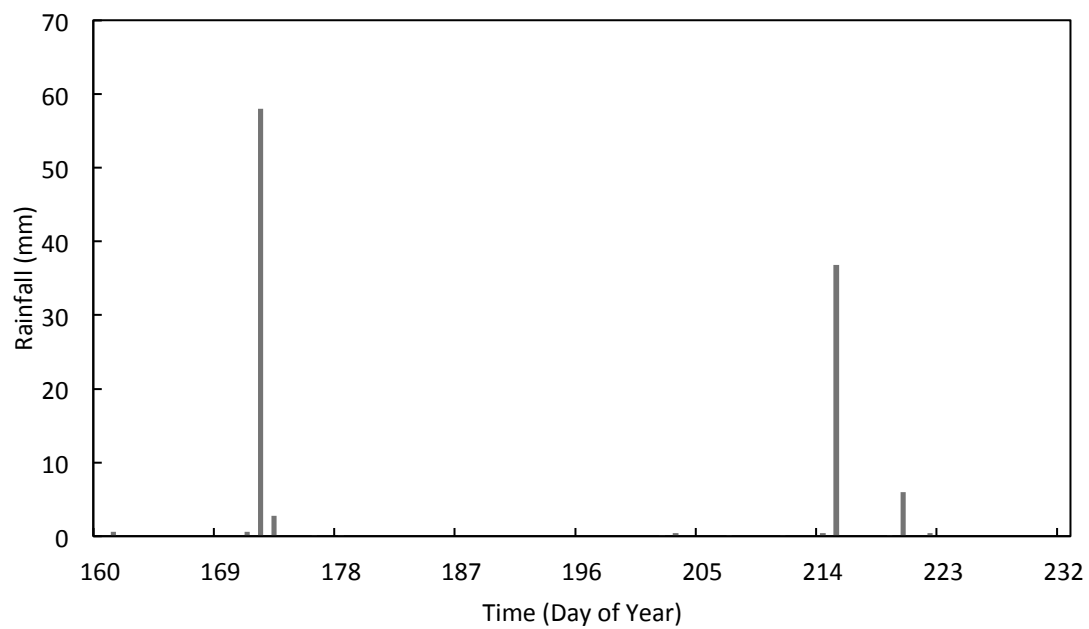


Figure 5. Total daily precipitation at the study site from June 8 to August 17.

3.2 Stand Density, Tree Characteristics, and Net Growth

Stand density measurements showed significant differences in the number of saplings growing back in each plot. The SL plot had an average of 1.3 live pine and 2.1 live willow saplings m^{-2} , which were both significantly lower than the 14 pine and 5.8 willow saplings m^{-2} in the UL plot (ANOVA, $p=0.02$ for both; Table 1; Figures 6 & 7).

Net growth in willow was similar between the two plots (Table 1), with no significant difference in the change in height between the SL and UL (t-test, $p=0.14$). There was also no significant difference in crown width between the SL and UL plots (t-test, $p=0.36$). Stem diameter, however, was significantly higher in the SL plot compared to the UL plot (t-test, $p<0.01$).

Net height was similar in the pine in both plots (t-test, $p=0.36$) and crown width similarly showed no significant change, but tended to be higher in the SL plot than the UL plot (t-test, $p=0.07$). Stem diameter was greater in the SL plot in both willow and pine (t-test, $p<0.01$ and $p=0.03$, respectively; Table 1).

There was a greater number of new growth units on willow saplings in the SL plot (t-test, $p<0.01$), as well as significantly greater apical growth length in the SL willow saplings (t-test, $p=0.01$). Pine exhibited a trend towards a greater number of new growth units in the SL with (t-test, $p=0.09$) but there was no significant difference between SL and UL pine in apical growth length (t-test, $p=0.61$).



Figure 6. Photographs of two separate locations within the logged plot. Top photograph depicts a logged section with a section of unlogged forest directly behind it, and the lower picture illustrates a logged section further from an unlogged section.



Figure 7. Photographs of two separate locations within the unlogged plot. The first photo was taken from deep within the UL plot, while the bottom photograph illustrates the outer edge of the unlogged plot.

Table 1. Tree characteristics and net growth measures taken for willow and pine in both logged and unlogged plots. Values represent means with standard errors, p-values and plasticity indices (PI) for measures that differed between the unlogged and logged plots at $p < 0.10$.

	Measurement	Logged	Unlogged	Significance	PI
Willow	Stand Density (saplings m^{-2})	2.1 ± 0.4	5.8 ± 0.8	0.02	0.91
	Height Increment (cm)	39.3 ± 3.4	31.5 ± 4.0	0.14	-
	Crown Width Increment (cm)	24.3 ± 3.5	19.3 ± 4.1	0.36	-
	Stem Diameter Increment (mm)	2.3 ± 0.4	0.9 ± 0.2	<0.01	0.60
	# New Growth Units	113 ± 19	29 ± 6	<0.01	0.74
	Apical Growth Length (cm)	62.0 ± 4.6	45.3 ± 4.3	0.01	0.27
Pine	Stand Density (saplings m^{-2})	1.3 ± 0.2	14 ± 1.0	0.02	0.64
	Height Increment (cm)	7.8 ± 1.2	6.4 ± 1.0	0.36	-
	Crown Width Increment (cm)	8.2 ± 1.5	4.7 ± 1.0	0.07	0.43
	Stem Diameter Increment (mm)	2.2 ± 0.3	1.5 ± 0.2	0.03	0.34
	# New Growth Units	31 ± 5	22 ± 3	0.09	0.30
	Apical Growth Length (cm)	33.6 ± 2.1	32.1 ± 2.0	0.61	-

3.3 Branch Morphology

Both willow and pine illustrated significant variations in branch morphology (Table 2). Willow had significantly higher branch LAR in the UL plot than the SL plot, and LMF in the UL plot was nearly double that of the SL plot. Branch diameter showed a trend toward slightly higher values in the SL plot, though the results were not significant (t-test, $p=0.09$), and there was no significant difference in either new growth inclination (t-test, $p=0.93$) or LCI (t-test, $p=0.15$; Table 2). The number of leaves per branch also exhibited differences between the two plots, illustrated by the significantly greater LBL in the UL plot (t-test, $p<0.01$).

Pine also demonstrated significant branch morphology variation, though the results were wholly dissimilar to those seen in willow. There was a significant difference in new growth inclination, but in favour of the UL plot (t-test, $p<0.01$). There was, however, no significant difference between the two plots in the old growth inclination (t-test, $p=0.12$). LCI showed a significant difference between plots; however, it was greater in the UL, which was unexpected (t-test, $p=0.05$). Branch diameter was significantly higher in the SL plot than the UL plot (t-test, $p=0.05$) and there was no significant difference between SL and UL branch-LAR in pine (t-test, $p=0.19$), LMF (t-test, $p=0.27$) or LBL (t-test, $p=0.62$; Table 2).

Table 2. Branch morphology measures taken for willow and pine in both logged and unlogged plots. Values represent means with standard errors, p-values and plasticity indices (PI) for measures that differed between the unlogged and logged plots at $p < 0.10$.

	Measurement	Logged	Unlogged	Significance	PI
Willow	New Growth	57 ± 5	57 ± 4	0.93	-
	Inclination ($^{\circ}$)				
	Branch LAR ($\text{cm}^2 \text{g}^{-1}$)	74.3 ± 3.5	104.0 ± 3.8	<0.01	0.29
	LMF (g g^{-1})	1.82 ± 0.19	3.43 ± 0.38	<0.01	0.47
	LCI ($\text{cm}^2 \text{cm}^{-1}$)	0.21 ± 0.02	0.18 ± 0.01	0.15	-
	LBL ($\# \text{cm}^{-1}$)	119 ± 3	138 ± 3	<0.01	0.29
	Branch Diameter (cm)	4.0 ± 0.2	3.5 ± 0.2	0.09	0.13
Pine	Old Growth	6 ± 3	13 ± 3	0.12	-
	Inclination ($^{\circ}$)				
	New Growth	34 ± 3	50 ± 3	<0.01	0.33
	Inclination ($^{\circ}$)				
	Branch LAR ($\text{cm}^2 \text{g}^{-1}$)	27.4 ± 0.6	35.2 ± 5.8	0.19	-
	LMF (g g^{-1})	2.52 ± 0.10	2.70 ± 0.13	0.27	-
	LCI ($\text{cm}^2 \text{cm}^{-1}$)	0.15 ± 0.01	0.19 ± 0.02	0.05	0.21
	LBL ($\# \text{cm}^{-1}$)	38 ± 1	48 ± 8	0.62	-
	Branch Diameter (cm)	5.0 ± 0.3	4.1 ± 0.3	0.05	0.18

LCI, leaf clumping index; *LAR*, branch-leaf area ratio; *LMF* leaf mass fraction; *LBL* leaves per branch length

3.4 Leaf Morphology

Morphological responses to the change in light regime varied considerably between willow and pine (Table 3). Willow exhibited significant variation in leaf morphology between logged and unlogged plots. Individual leaves had a greater mass per unit area (LMA) in the SL plot than in the UL plot (t-test, $p < 0.01$). Leaves in the SL plot also exhibited greater leaf inclination than leaves found in the UL plot (t-test, $p < 0.01$). Leaves also tended to have greater leaf area in the SL plot compared to the UL plot, though the results were not significant (t-test, $p = 0.07$).

Pine showed less variation in leaf morphology than willow plants. There was no significant difference in leaf area (t-test, $p = 0.13$) between SL and UL plants. There was a tendency for greater LMA in the SL plants than in the UL (t-test, $p = 0.06$). Leaf inclination, however, was significantly greater in the UL plants compared to the SL plot, which was unexpected (t-test, $p < 0.01$).

Table 3. Leaf morphology measures taken for willow and pine in both logged and unlogged plots. Values represent means with standard errors, p-values, and plasticity indices (PI) for measures that differed between the unlogged and logged plots at $p < 0.10$.

	Measurement	Logged	Unlogged	Significance	PI
Willow	Leaf Size (cm ²)	9.5 ± 1.0	7.3 ± 0.6	0.07	0.23
	LMA (g m ⁻²)	84.6 ± 1.9	73.1 ± 1.9	<0.01	0.14
	Leaf Inclination (°)	47 ± 2	39 ± 2	<0.01	0.16
Pine	Leaf Size (cm ²)	0.6 ± 0.04	0.5 ± 0.06	0.13	-
	LMA (g m ⁻²)	261 ± 5	234 ± 13	0.06	0.10
	Leaf Inclination (°)	62 ± 2	69 ± 1	<0.01	0.09

LMA, leaf mass per unit area

3.5 Leaf-level Gas Exchange

Light response curves showed little difference between SL and UL plants of either willow or pine plants (Figures 8 & 9). The seasonal variation, or the difference in the mean values throughout the season, for maximum photosynthetic capacity (A_{max}) showed a tendency to be higher in willows of the SL plot, relative to the UL plot (ANOVA, $p=0.09$). On a seasonal average basis, willow exhibited significantly greater A_{max} values in the SL plot (t-test, $p=0.03$). The seasonal average was $20.5 \pm 0.6 \text{ mmol m}^{-2}$ for the SL willow and $19.0 \pm 0.6 \text{ mmol m}^{-2}$ for the UL willow, resulting in a PI of 0.07. Only area-based A_{max} measures showed any variation, as mass-based measures of A_{max} showed no variation between logged and unlogged sites. Dark respiration (R_d) rates showed little difference, with an average value of $-1.82 \mu\text{mol} \pm 0.15 \text{ m}^{-2} \text{ s}^{-1}$ for SL and $-1.93 \pm 0.15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for UL (t-test, $p=0.31$) and no seasonal variation (ANOVA, $p=0.64$). Quantum yield (Φ) also showed no significant seasonal variation (ANOVA, $p=0.52$), and, taken as a seasonal average, exhibited similar mean values of $0.057 \pm 0.001 \text{ mol mol}^{-1}$ for SL and $0.055 \pm 0.001 \text{ mol mol}^{-1}$ for UL willow (t-test, $p=0.23$; Figure 9).

Pine showed no significant difference in A_{max} , with an average of $14.0 \pm 0.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in SL plants and $13.4 \pm 0.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in UL plants (t-test, $p=0.25$) and no seasonal variation (ANOVA, $p=0.47$). Mass-based measures of A_{max} correspondingly showed no variation between logged and unlogged sites. Similarly, R_d showed no significant variation in the seasonal average between SL ($-0.99 \pm 0.10 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and UL pine ($-0.89 \pm 0.09 \mu\text{mol m}^{-2} \text{ s}^{-1}$; t-test, $p=0.24$) and there was no significant seasonal variation (ANOVA, $p=0.36$). Apparent quantum yield (Φ) also showed little seasonal variation (ANOVA, $p=0.14$). However, taken as an average throughout the season, Φ was

significantly greater in the UL plot with an average of $0.045 \pm 0.002 \text{ mol mol}^{-1}$ compared to $0.040 \pm 0.002 \text{ mol mol}^{-1}$ for the SL pine (t-test, $p=0.05$; Figure 9).

Willow and pine plants differed both in terms of the magnitude and seasonal variation of physiological variables, when compared to each other. In the logged plot, willow had significantly higher A_{max} (ANOVA, $p<0.01$) and Φ (ANOVA, $p<0.01$), and more negative R_d (ANOVA, $p<0.01$). In the unlogged plot, the same patterns were observed, where willow had significantly greater seasonal values of A_{max} (ANOVA, $p<0.01$) and Φ (ANOVA, $p < 0.01$), and a significantly more negative R_d rate (ANOVA, $p<0.01$). Further, the seasonal pattern of R_d differed between the two species, with a steady increase (becoming less negative) in willow, but no significant variation in pine (Figure 9).

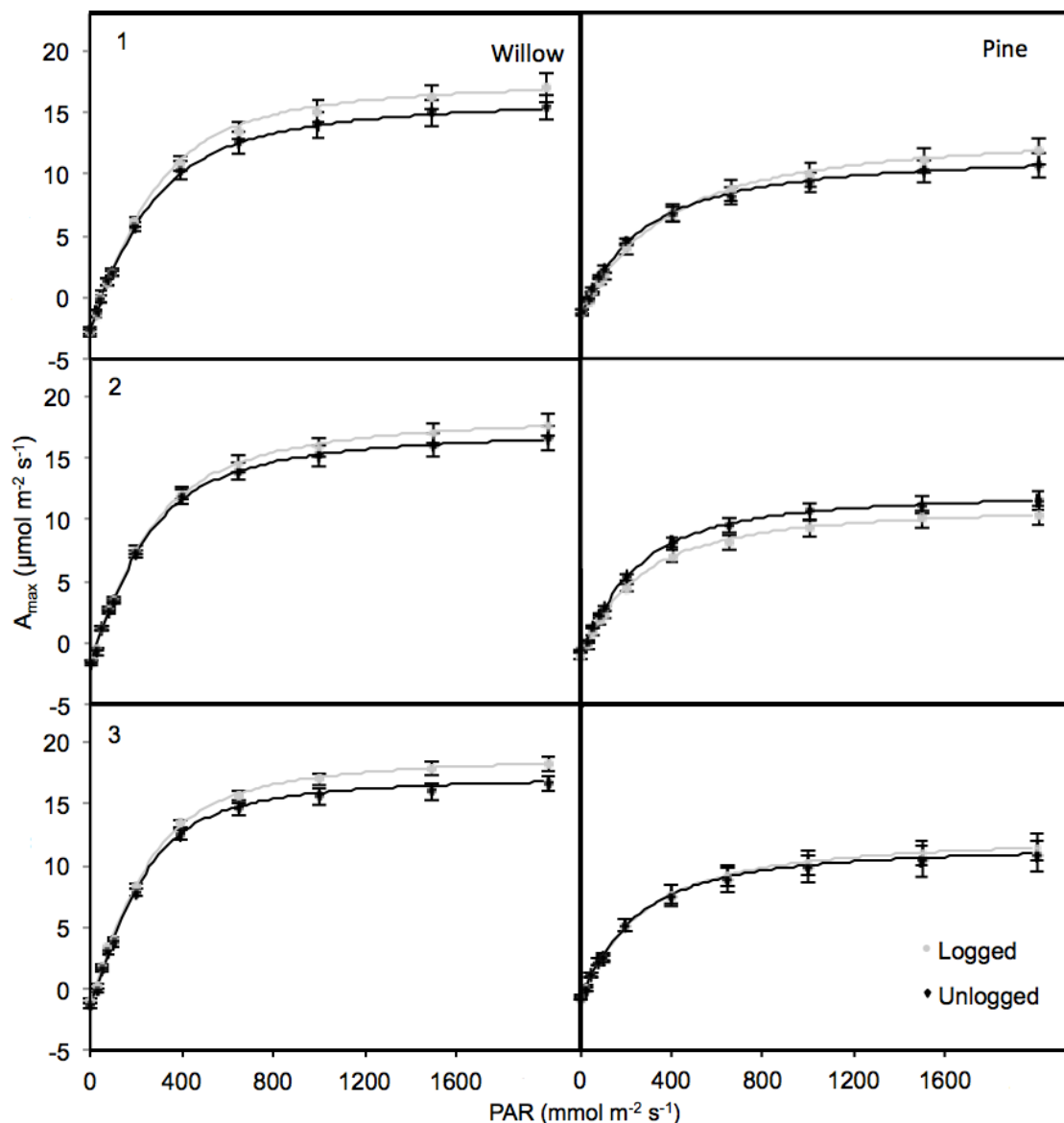


Figure 8. Light response curves of willow (left) and pine (right) in the logged (light) and unlogged (dark) plots for each measurement campaign, using mean values for quantum yield (Φ), light-saturated photosynthesis rate (A_{max}), curvature (θ) and respiration rate (R_d). Measurements were taken in the first time period (1) from June 18th to June 28th, the second (2) from July 23rd to August 7th and the third (3) from August 19th to September 3rd of 2013. Points represent mean values observed at each light level \pm SE, $n=15$.

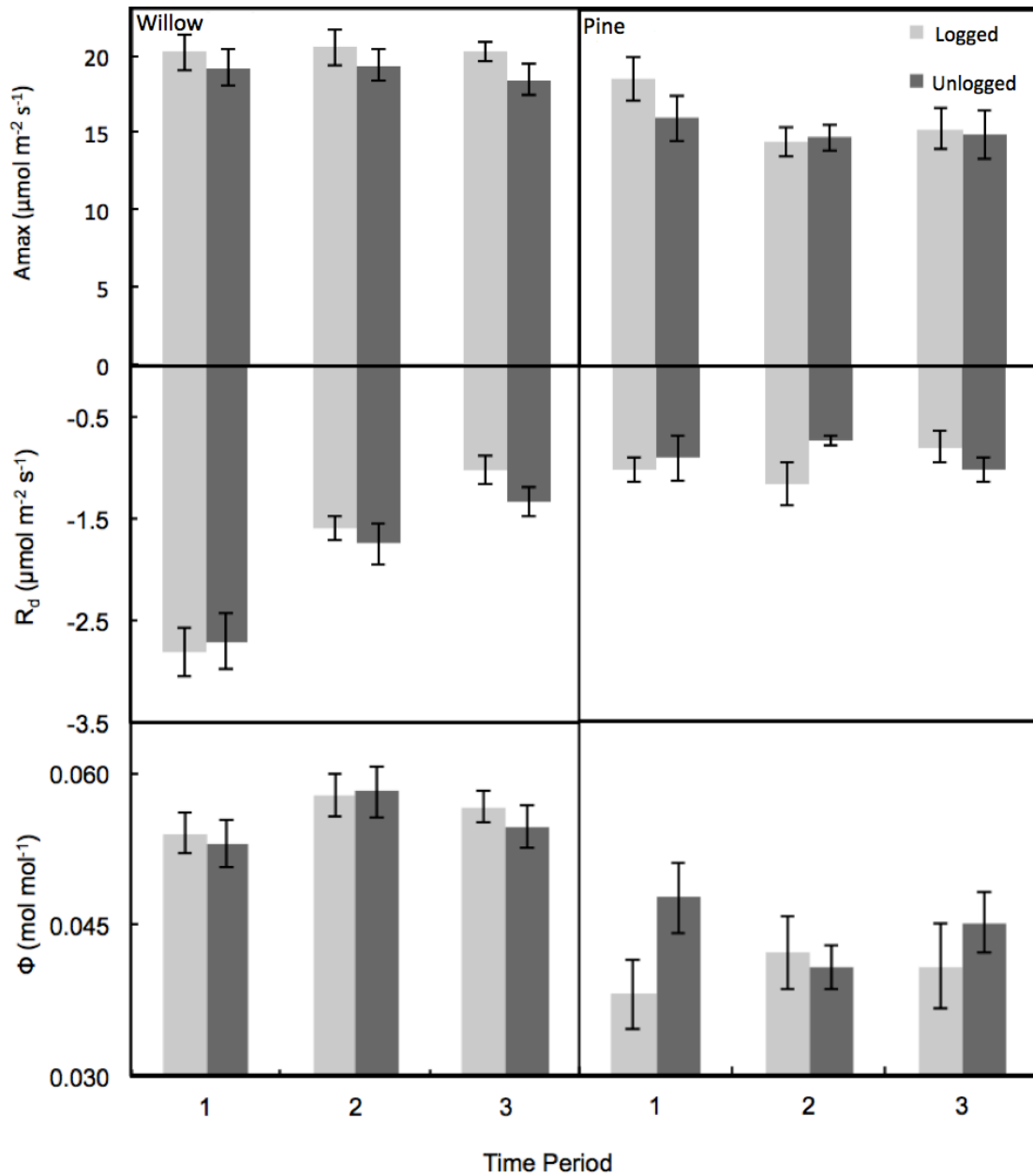


Figure 9. Seasonal changes in light-saturated net photosynthesis (A_{max}), dark respiration (R_d) and quantum yield (Φ) on an area basis for willow (left) and pine (right) plants in the logged (light) and unlogged (dark) plots. Measurements were taken in the first time period from June 18th to June 28th, the second from July 23rd to August 7th and the third from August 19th to September 3rd of 2013. Bars represent mean values taken at each light level \pm SE, $n=15$.

3.6 Water Potential

Willow exhibited significant between-plot differences in water potential that were not observed in pine (Figures 10 and 11). For example, willow showed significantly greater stomatal conductance throughout the season in the UL plot compared to the SL plot (ANOVA, $p=0.01$), with seasonal means of 0.40 ± 0.02 and 0.35 ± 0.02 mol H₂O m⁻² s⁻¹, respectively (t-test, $p=0.01$; PI=0.13). Pine showed no seasonal difference between SL and UL (ANOVA, $p=0.86$), with a seasonal average of 0.14 ± 0.09 mol H₂O m⁻² s⁻¹ (t-test, $p=0.42$). Transpiration rates were similarly greater throughout the season for willow plants in the UL plot relative to the SL plot (ANOVA, $p<0.01$), but this was not the case for pine (ANOVA, $p=0.77$). The seasonal average for willow plants of the UL plot was 4.93 ± 0.21 mmol H₂O m⁻² s⁻¹, compared to 4.12 ± 0.18 mmol H₂O m⁻² s⁻¹ in the SL plot (t-test, $p<0.01$; PI=0.16). Transpiration did not differ significantly between SL (2.23 ± 0.15 mmol H₂O m⁻² s⁻¹) and UL (2.16 ± 0.16 mmol H₂O m⁻² s⁻¹; t-test, $p=0.30$) in pine.

As a result, there was greater seasonal variation in water use efficiency (WUE) in the SL plot than the UL plot for willow (ANOVA, $p<0.01$). The mean WUE was 5.0 ± 0.3 mmol mol⁻¹ in the SL plot and 4.0 ± 0.2 mmol mol⁻¹ in the UL plot (t-test, $p<0.01$; PI=0.19). The seasonal variation in WUE did not differ significantly for pine saplings (ANOVA, $p=0.47$). The seasonal mean WUE of pine saplings did not differ significantly, with values of 6.4 ± 0.5 mmol mol⁻¹ and 6.0 ± 0.3 mmol mol⁻¹ for SL and UL plots, respectively (t-test, $p=0.21$). The ratio of internal to external CO₂ concentrations was greater in the UL than the SL plot for willow plants (ANOVA, $p<0.01$) but the same was not true for pine (ANOVA, $p=0.21$). The seasonal mean c_i/c_a ratio for willow was $0.80 \pm$

0.01 in the UL plot and 0.75 ± 0.01 at the SL plot (t-test, $p < 0.01$), while the corresponding means for pine were 0.61 ± 0.01 and 0.62 ± 0.01 (t-test, $p = 0.24$).

Significant differences were observed between willow and pine in both the UL and SL plots. For example, stomatal conductance and transpiration were significantly higher in willow than in pine at the SL plot (ANOVA, $p < 0.01$; Figure 10). The same was true of c_i/c_a (ANOVA, $p < 0.01$), while pine exhibited higher water use efficiency (ANOVA, $p = 0.02$; Figure 11). Similar differences were observed in the UL plot, with significantly greater stomatal conductance, (ANOVA, $p < 0.01$), c_i/c_a concentration (ANOVA, $p < 0.01$) and transpiration (ANOVA, $p < 0.01$) exhibited by willow, but higher WUE in pine (ANOVA, $p < 0.01$),

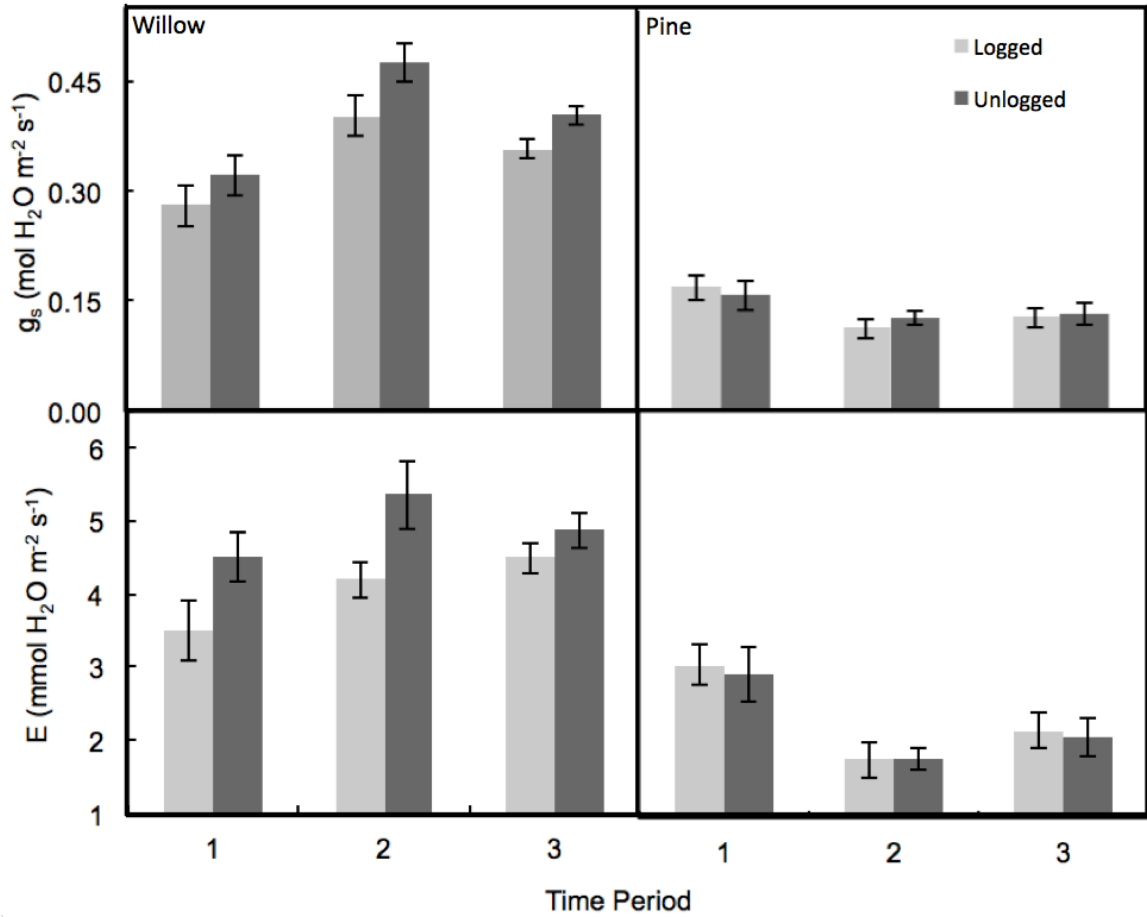


Figure 10. Seasonal values of stomatal conductance (g_s) and transpiration rates (E) for willow (left) and pine (right) plants in the logged (light) and unlogged (dark) plots. Measurements were taken in the first time period from June 18th to June 28th, the second from July 23rd to August 7th and the third from August 19th to September 3rd of 2013. Bars represent mean values taken at each light level \pm SE, n=15.

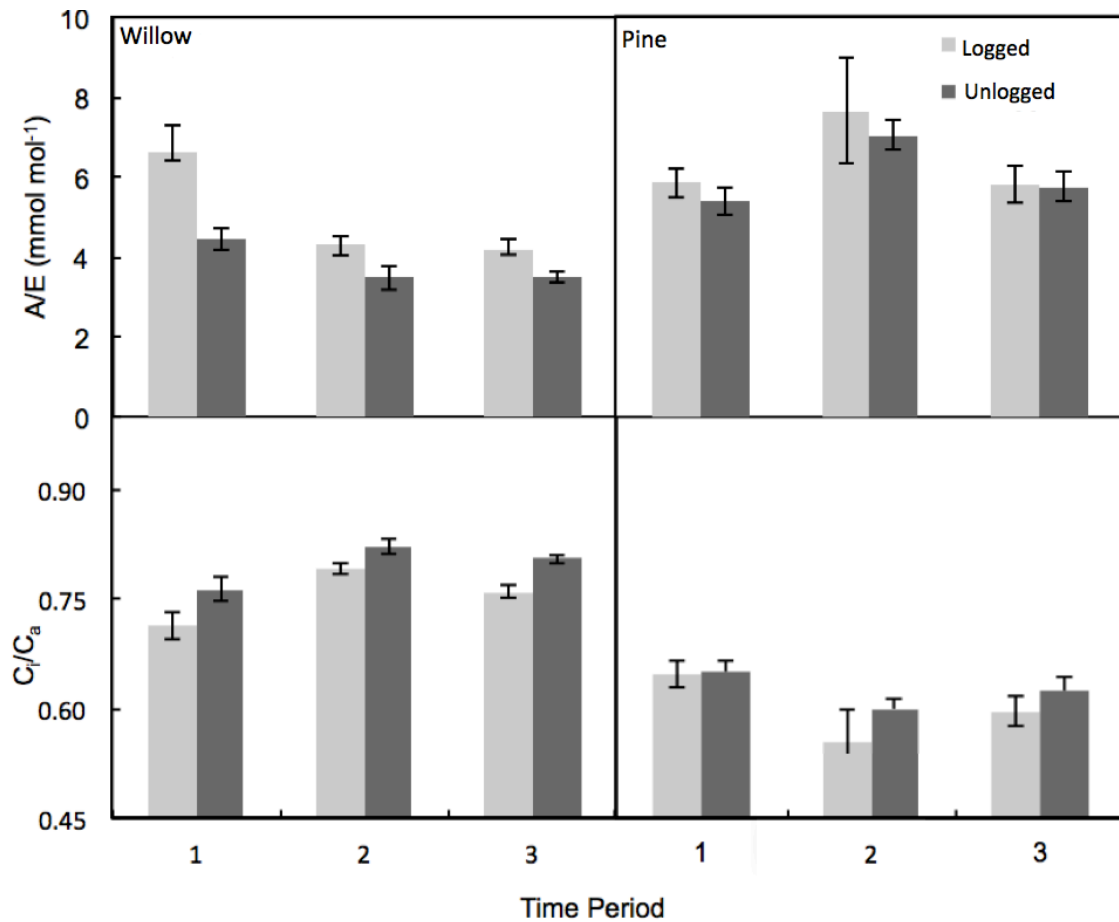


Figure 11. Seasonal changes in water use efficiency (WUE; A/E) and ratios of internal to atmospheric carbon dioxide concentrations (c_i/c_a) for willow (left) and pine (right) plants in the logged (light) and unlogged (dark) plots. Measurements were taken in the first time period from June 18th to June 28th, the second from July 23rd to August 7th and the third from August 19th to September 3rd of 2013. Bars represent mean values taken at each light level \pm SE, $n=15$.

3.7 Chlorophyll Fluorescence

Intrinsic photochemical efficiency (F_v/F_m) chlorophyll fluorescence measurements illustrate the degree to which plants are able to withstand higher light intensities without being photoinhibited (Griffin *et al.*, 2004), with larger F_v/F_m values indicative of greater leaf health. Quantum yield of PSII (F_v/F_m) showed no significant seasonal variation between SL and UL plots in either willow or pine (Figure 12). The seasonal mean F_v/F_m values of willow were 0.810 ± 0.002 and 0.811 ± 0.002 in the SL and UL plots, respectively, while corresponding values for pine were 0.836 ± 0.002 and 0.837 ± 0.002 . Between species, pine illustrated significantly greater F_v/F_m in both the UL (ANOVA, $p < 0.01$) and SL (ANOVA, $p < 0.01$) plots throughout the season. However, values remained within a normal and optimal range throughout the season in both species.

Electron transport rate (ETR) showed no significant between-plot differences throughout the season in willow (ANOVA, $p = 0.17$). By contrast, ETR was significantly higher at the SL plot than in the UL plot in pine saplings (ANOVA, $p = 0.02$). ETR tended to be slightly higher in the SL plot than in the UL plot in willow, with mean values of $128.6 \pm 4.3 \mu\text{mol m}^{-2}\text{s}^{-1}$ and $120.4 \pm 3.5 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively (t-test, $p = 0.07$). ETR differed significantly between the SL and UL plots in pine, with mean values of $121.8 \pm 3.3 \mu\text{mol m}^{-2}\text{s}^{-1}$ and $107.4 \pm 2.8 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively (t-test, $p < 0.01$). In terms of between-species differences, willow exhibited significantly higher ETR than pine in the UL plot (t-test, $p = 0.02$). However, there was no significant difference between the two species grown at the SL plot (t-test, $p = 0.29$).

The quantum efficiency of photosystem (PS) II (ΦPSII) was similar throughout the season in willow (ANOVA, $p=0.12$) and was significantly higher for SL than UL pine saplings (ANOVA, $p=0.02$). The overall mean ΦPSII in willow was 0.149 ± 0.005 at the SL plot, which was significantly greater than the 0.138 ± 0.004 mean observed in the UL plot (t-test, $p=0.04$). Seasonal mean ΦPSII was higher in pine in the SL plot (0.139 ± 0.004) than in the UL plot (0.123 ± 0.003 ; t-test, $p<0.01$). As was the case with ETR, ΦPSII values were higher in UL willow than in UL pine (t-test, $p=0.02$), but there was no significant difference between the two species grown in the SL plot (t-test, $p=0.21$).

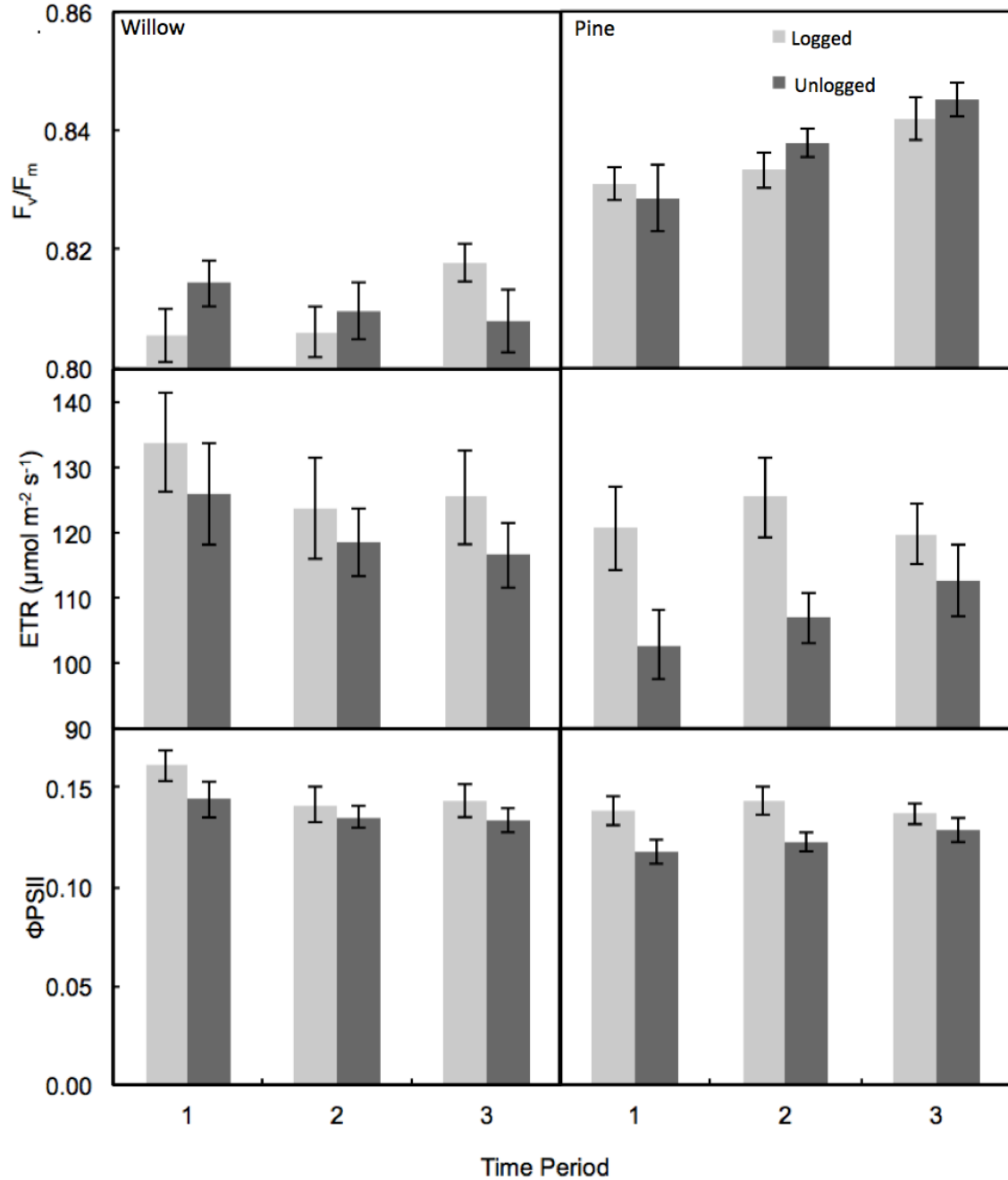


Figure 12. Seasonal values of dark adapted leaf chlorophyll fluorescence (F_v/F_m , variable/maximal), electron transport rate (ETR), and quantum efficiency of photosystem (PS) II (Φ_{PSII}) for willow (left) and pine (right) plants in the logged (light) and unlogged (dark) plots. Measurements were taken in the first time period from June 18th to June 28th, the second from July 23rd to August 7th and the third from August 19th to September 3rd, 2013. Bars represent mean values taken at each light level \pm SE, n=15.

3.8 Leaf Nitrogen and Carbon Isotope Composition ($\delta^{13}\text{C}$)

Leaf nitrogen concentration did not differ significantly between treatment plots in willow saplings, which showed no difference in seasonal variation between treatments (ANOVA, $p=0.11$; Figure 13). Mean leaf N was $2.53\% \pm 0.19\%$ in willows of the SL plot and $2.35\% \pm 0.15\%$ in the UL plot. Pine saplings, however, had significantly greater foliar nitrogen in the SL plot than the UL plot (ANOVA, $p=0.04$), with seasonal averages of $1.19\% \pm 0.04\%$ and $1.01\% \pm 0.04\%$, respectively ($PI=0.15$). There was significantly greater foliar nitrogen in willow than pine in both the SL (ANOVA, $p<0.01$) and UL (ANOVA, $p<0.01$) plots.

Carbon isotope composition ($\delta^{13}\text{C}$) exhibited significant differences both between treatment and between species. The mean $\delta^{13}\text{C}$ of willow was $-27.7\text{‰} \pm 0.2\text{‰}$ in the SL plot and $-28.5\text{‰} \pm 0.2\text{‰}$ in the UL plot (ANOVA, $p=0.02$). Corresponding means in pine were $-29.9\text{‰} \pm 0.1\text{‰}$ (SL) and $-28.9\text{‰} \pm 0.2\text{‰}$ (UL; ANOVA, $p<0.01$). Between species, pine had significantly more negative $\delta^{13}\text{C}$ values in both the UL (ANOVA, $p<0.01$) and SL plots (ANOVA, $p<0.01$).

Expected $\delta^{13}\text{C}$ values were also determined from the measured c_i/c_a values, and were significantly more negative than the measured $\delta^{13}\text{C}$ values (Table 4) for both logged and unlogged willow and pine (t-test, $p<0.01$). Similarly, expected c_i/c_a values were calculated based on the measured $\delta^{13}\text{C}$ values, and were significantly lower than for both logged and unlogged willow and pine (t-test, $p<0.01$).

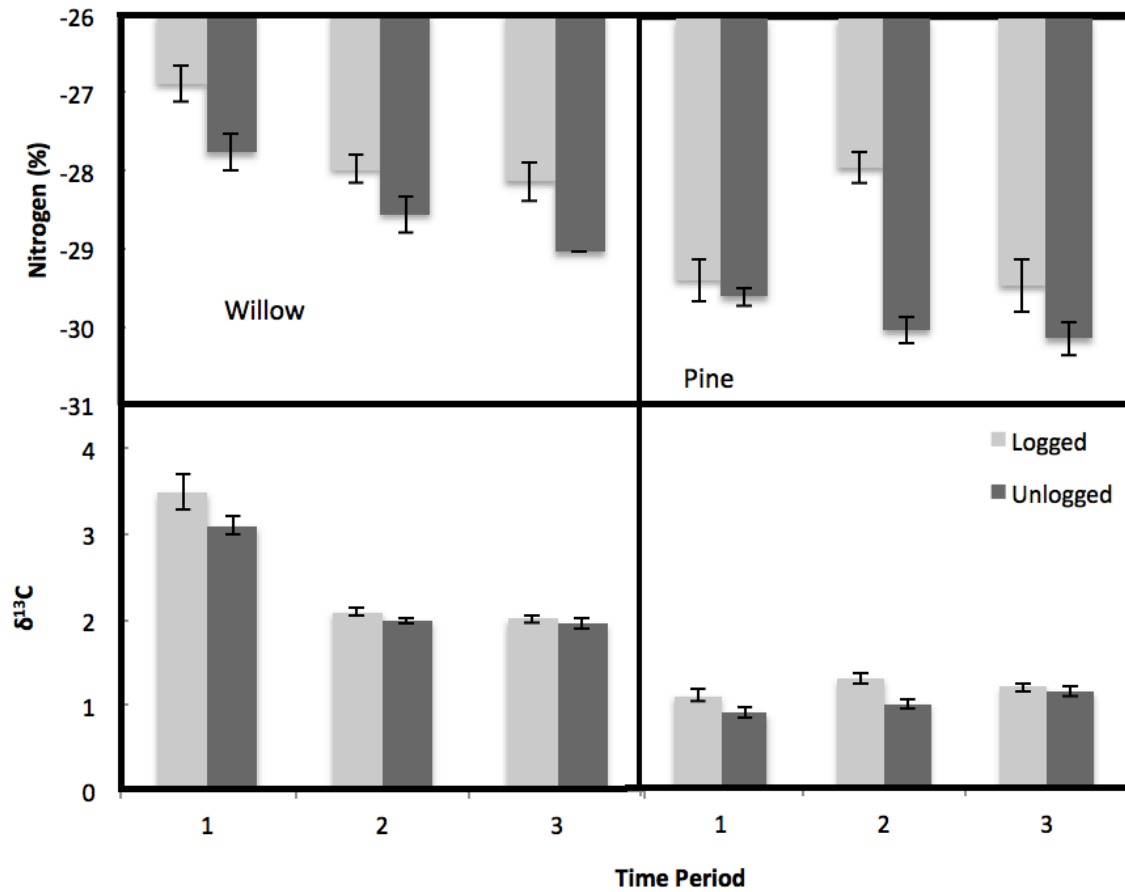


Figure 13. Stable carbon isotope ($\delta^{13}\text{C}$) and leaf nitrogen (%N) composition on a mass basis in willow (left) and pine (right) saplings of the logged (light) and unlogged (dark) plots. Measurements were taken in the first time period from June 18th to June 28th, the second from July 23rd to August 7th and the third from August 19th to September 3rd of 2013. Bars represent mean values taken at each light level \pm SE, $n=15$.

Table 4. Comparison of expected and measured c_i/c_a and $\delta^{13}\text{C}$ values. Values represent means with standard errors and p-values comparing the measured values to the expected values.

	Site	Measurement	Measured Value	Expected Value	Significance
Willow	Logged	c_i/c_a	0.75 ± 0.01	0.68 ± 0.01	<0.01
		$\delta^{13}\text{C} (\text{‰})$	-27.7 ± 0.2	-29.5 ± 0.2	<0.01
	Unlogged	c_i/c_a	0.80 ± 0.01	0.71 ± 0.01	<0.01
		$\delta^{13}\text{C} (\text{‰})$	-28.5 ± 0.2	-30.5 ± 0.2	<0.01
pine	Logged	c_i/c_a	0.62 ± 0.01	0.73 ± 0.01	<0.01
		$\delta^{13}\text{C} (\text{‰})$	-29.9 ± 0.1	-26.2 ± 0.3	<0.01
	Unlogged	c_i/c_a	0.61 ± 0.01	0.78 ± 0.01	<0.01
		$\delta^{13}\text{C} (\text{‰})$	-28.9 ± 0.2	-26.5 ± 0.2	<0.01

c_i/c_a , ratio of internal to atmospheric carbon dioxide concentration; $\delta^{13}\text{C}$, Stable carbon isotope composition

4.0 Discussion

Post-fire salvage logging impacts the reforestation environment in various ways, including altered microclimate, soil condition, nutrient availability, and light intensity (McIver and Starr, 2000; Foster and Orwig, 2008). In this study, I selected an area that had been logged by people on foot, to limit compaction effects on the above variables, and focus primarily on the salvage logging impacts on light regime and the resultant effects on the photosynthetic physiology of saplings. The primary abiotic difference between the two microsites was the far greater solar radiation and PPFD at the SL plot. Temperature variation between the two plots was minimal, and VPD only showed a discrepancy at 20 cm in height. As a result, I was able to analyze the effects that the change in light intensity had on the two major species co-occurring in this habitat.

As would be expected from species of two different plant functional groups, willow and pine exhibited differences in the magnitude of both physiological and morphological variables (Table 5). This is in keeping with previous studies comparing physiological responses between functional groups (Valladares *et al.*, 2000; Wyka *et al.*, 2012). Further, I found both physiological and morphological acclimation to light availability resulting from post-fire salvage logging that was unique to each species. These findings are consistent with my hypothesis that willow would exhibit greater acclimation to increased light availability than pine. This occurs due to the conifer's long leaf lifespan, which requires increased investment into leaf durability and plant structure, such as thicker stems, as opposed to photosynthetic properties such as increasing A_{\max}

(Wyka *et al.*, 2012). This could present significant implications for species assemblages following post-fire salvage logging.

Table 5. Morphological variables and the overall effect that logging has on the variables for each species. ↑ indicates an increase in the SL plot, while ↓ indicates a decrease in the SL plot. – indicates no change. The presence of a *t* represents a trend ($p < 0.1$) as opposed to a significant difference ($p < 0.05$).

	Measured Variable	Willow	Pine
Whole Plant	Height	–	–
	Crown Width	–	<i>t</i> ↑
	Stem Diameter	↑	↑
	# New Growth Units	↑	<i>t</i> ↑
	Apical Growth	↑	–
	Length		
Branch Morphology	Branch Diameter	<i>t</i> ↑	↑
	Old Growth	–	–
	Inclination		
	New Growth	–	↓
	Inclination		
	Branch LAR	↓	–
	LMF	↓	–
	LCI	–	↓
	LBL	↓	–
	Leaf Size	<i>t</i> ↑	–
Foliar Morphology	LMA	↑	<i>t</i> ↑
	Leaf Inclination	↑	↓
Foliar Physiology	A_{max}	↑	–
	R_d	–	–
	Φ	–	–
	E	↓	–
	g_s	↓	–
	WUE	↑	–
	c_i/c_a	↓	–
	F_v/F_m	–	–
	ETR	–	↑
	Φ_{PSII}	–	↑
	$\delta^{13}C$	↑	↑
	%N	–	↑

4.1 Changes in Stand Density and Species Composition

The reduced growth of individuals growing in the UL plots of both pine and willow may be related to increased competition among saplings, due to much higher stand density. Salvage logging appears to affect regrowth, possibly by damaging or reducing the size of the seed bank (Van Nieuwstadt *et al.*, 2001), thereby reducing the number of saplings that emerge and survive (Cooper-Ellis *et al.*, 1999). Similar results have been observed in Oregon, where the natural revegetation of conifers in a post-fire forest was severely reduced in logged plots compared to unlogged (Donato *et al.*, 2006). Consequently, the individual saplings in the SL plot do not have as much competition for limited resources, such as soil moisture and light availability, and are able to grow more rapidly. This can be seen through higher growth rates in both species, as well as reduced leaf and branch inclination angles in pine in the absence of competition for vertical growth to reach canopy levels with higher light intensity.

Furthermore, logging appears to also cause a shift in the species composition between plots. Willow and pine are both sun-loving plant species, though it appears that willow is able to acclimate to the increased light availability to a greater degree than the pine. This is not surprising, given that it has been shown that evergreen conifers acclimate to a lesser degree than deciduous angiosperms (Valladares *et al.*, 2000; Matyssek, 1986) and are, therefore, less likely to take advantage of the increased light availability. As a result, post-fire salvage logging appears to have created conditions that favour the regrowth of willow as opposed to pine, which would normally flourish in the

burned understorey, thus altering competitive dynamics during forest regrowth and potentially altering species composition as the forest matures. Long-term studies are, therefore, required to elucidate the effect of post-fire salvage logging on species diversity and composition after either post-fire logging or natural revegetation.

It is also important to note that grass and weed species, which tend to grow and utilize resources more rapidly than woody species (Letts *et al.*, 2009), were prevalent in the SL plot but absent in the UL plot. These species remove shallow soil moisture, which is necessary for seed germination and early sapling growth. This may also have decreased stand density, by reducing the number of surviving saplings during the first few years of post-fire revegetation. As a result of the introduced grass and weed species, as well as the favoured growth of willow, there was a shift in the species composition of the logged forest (Stuart *et al.*, 1993). This speculation is based mainly on visual observation at the study site and requires verification through further investigation.

4.2 Whole Plant Characteristics and Growth in Willow

Willow demonstrated more vigorous overall growth in the SL plot, as demonstrated by higher stem diameter, apical growth length, and number of new growth units (Table 5). While plant height did not differ between the two plots, I observed evidence of severed old shoots in some willow saplings of the SL plot, indicative of past-year herbivory. New growth of study saplings was not consumed during the current study. Due to the nature of the SL plot, with greater space between plants and few fallen trunks, herbivore access to the succulent vegetation of the SL plot is unrestricted, and this

likely reduced the height of the willow saplings. Crown width of willow did not differ between plots, but pines showed greater width at the SL plot, perhaps due to a lesser need for vertical growth to access higher light intensity. Stem growth, and number of new growth units were higher in the SL plot in both species, while apical growth was higher in willow. Collectively, these results indicate greater above-ground growth of individual saplings at the SL plot, likely due to increased PPFD availability, but perhaps also due to decreased competition.

4.3 Plasticity of Branch Level Morphology in Willow

While greater branch diameter and apical growth lengths were observed in willow saplings growing in the SL plot, there was greater carbon allocation to leaf development relative to branch growth in the UL plot. This is illustrated by the augmented branch LAR, LBL, and LMF values (Table 2). These measures show that UL willow saplings have more leaves per unit branch length, and that the leaves have greater leaf area and mass relative to branch weight. This represents greater investment in light capture efficiency for photosynthesis rather than structural gain and long term growth. This also helps shade-grown willow plants to outcompete neighboring plants by shading them and simultaneously capturing more light. Previous studies have shown that shade-grown plants of species intolerant of low light exhibit a shade avoidance response and experience stem elongation at the expense of structural development (Valladares *et al.*, 2012). Based on the carbon allocation patterns observed in the present study, it appears that light harvesting efficiency may be important for willow saplings growing in post-fire forest understory.

4.4 Plasticity of Leaf Level Morphology and Physiology in Willow

Willow exhibited greater LMA and leaf inclination in the SL than the UL plot. These results are consistent with growth in a high light environment, as they help to reduce light capture efficiency, as greater LMA in leaves results in less surface area on a mass basis for light capture, and increased leaf inclination angles cause lower light interception per unit leaf area, due to the more vertical orientation of the leaves (Letts *et al.*, 2011; Valladares and Niinemets, 2008). Increased LMA also results from the need for increased carboxylation in order to avoid photoinhibition. As photosynthesis requires a large amount of the enzyme Rubisco per unit leaf area, leaves need to house more Rubisco in order to utilize the greater irradiance for photosynthesis in the SL plot (Terashima, *et al.*, 2010). However, while the increased LMA is indicative of greater Rubisco content per unit leaf area, leaf nitrogen content was not significantly greater on a mass basis in the SL leaves. As nitrogen measures in leaves are common gauges for Rubisco content, this may explain the limited variation of A_{max} .

Plants grown in shade typically increase leaf area in order to increase the surface area exposed to the sun for improved light capture efficiency (Monaco *et al.*, 2005). In the current study, leaf and branch morphological measurements demonstrate that shaded UL willows increased proportional allocation of resources to leaf growth, to improve light interception. However, willow tended to have a greater leaf area at the SL plot, likely due to increased overall growth when exposed to higher light availability.

Photosynthetic properties of willow were similar between SL and UL plots, as demonstrated by the similar A_{max} , R_d , and quantum yield. However, there was a slight

difference in A_{max} throughout the season, and, taken as a seasonal average, the SL willow saplings exhibited significantly higher A_{max} . This difference, though small, is in keeping with previous studies on differences in plant photosynthesis in response to light regimes (Rodríguez -Calcerrada *et al.*, 2007; Wayne and Van Auken, 2009). Quantum yield is typically similar between sun and shade leaves, as the efficiency of light reactions in photosynthesis varies little in relation to light interception; however, when leaves are damaged by high irradiance, quantum yield may decrease through photoinhibition (Lambers *et al.*, 2008). The lack of change in quantum yield suggests that increased light availability did not cause photoinhibition.

No between-plot differences were observed in ETR, $\Phi PSII$, or F_v/F_m for willow. This suggests that willow is capable of utilizing the increased light availability afforded through the post-fire logging. Many species exhibit non-photochemical quenching (NPQ) and higher ETR, to increase thermal dissipation and reduce the risk of oxidative damage with increased irradiance (Rodríguez -Calcerrada *et al.*, 2007; Ogren 1991). F_v/F_m provides another measure of photoinhibition, but the invariability in these values further suggests that there was no damage to the photosynthetic apparatus or reduction in photosynthesis as a result of increased irradiance. Given that willow did not exhibit any of these responses, it appears that the increase in light intensity in the SL plot was not detrimental, as there was no decrease in photosynthetic capacity or any indication of other protective mechanisms being utilized to dissipate excess excitation energy. Moreover, there was a small increase in A_{max} in response to increased light availability. This suggests either that willow leaves are capable of withstanding the light intensities observed at the field site, or that morphological acclimations were responsible for

reducing light capture to avoid photoinhibition by increasing their leaf angles (see Letts *et al.*, 2011).

Measures of photosynthetic water-use exhibited larger differences than A_{max} . Willow exhibited lower E , g_s , c_i/c_a , but higher WUE, at the SL plot when exposed to the same PPFD intensity in the leaf chamber. Furthermore, higher $\delta^{13}C$ values were observed at the SL plot, which is supportive of the higher WUE observed through photosynthetic gas-exchange measurement, suggesting less discrimination against ^{13}C by Rubisco. These results are suggestive of slightly greater water stress at the salvage logged plot, as hypothesized, but are not consistent with volumetric soil moisture, which was significantly higher overall at the SL weather station. It is possible that other microclimatological factors, such as higher leaf temperature or wind speed, may have contributed to a modest degree of drought stress. Studies on gaps within forest ecosystems have shown that soil moisture tends to be lower in forested sites as there is a greater number of transpiring trees and multilayered leaf area increasing interception of precipitation (Vilhr and Simončič, 2012; Diaz *et al.*, 2007). This is consistent with my results as there was a significantly greater number of saplings in the UL plot which would be reducing the soil moistures. Acclimation to light availability is known to be influenced by moisture availability (Chapin *et al.*, 1993). In this study, reduced g_s may have mediated the increase in A_{max} in response to increased light intensity.

Furthermore, from the calculations used to extrapolate the expected c_i/c_a values from $\delta^{13}C$, it appears that internal carbon concentrations were lower relative to ambient carbon concentrations throughout the leaves lifespans compared to the c_i/c_a values determined through the gas exchange measures (Table 4). Similarly, $\delta^{13}C$ values showed

less discrimination against the ^{13}C isotope throughout the life history of the leaves, and appeared to decrease throughout the season in both willow and pine saplings (Figure 13). This is indicative of greater moisture stress earlier in the season, prior to gas exchange measurements being conducted. While many ecosystems experience water stress later in the summer when ambient temperatures and evapotranspiration rates increase (Smedely *et al.*, 1991), it appears that the logged environment in the current study experienced the opposite trend. This is likely the result of the unusual rain patterns seen in Alberta in 2013, which resulted in significant flooding, though further research needs to be done to examine if these results would appear in drier years.

4.5 Whole Tree Characteristics and Growth in Pine

Pine exhibited indication of increased growth in the SL plot compared to the UL plot, though the differences were not as great as in willow. Stem and branch diameter were greater in pine, and there was a trend toward greater crown width and more new growth units, though these were not statistically significant. Overall, growth increment was lower in pine than in willow. Coniferous trees typically have lower photosynthesis rates, due to increased carbon allocation to cell walls and cuticular materials, which increase leaf lifespan at the expense of photosynthetic productivity (Matyssek, 1986). As stem and branch diameter increments increased (Table 1) it would appear that some growth went to structural support, but the overall growth increment in response to increased light availability was still fairly limited.

4.6 Plasticity of in Branch Level Morphology in Pine

Branch morphology of pine exhibited some confounding results that are not in keeping with the literature on light acclimation. Both LCI and branch inclination angles tend to increase in high light environments in order to reduce light capture (Pearcy *et al.*, 2005; Valladares and Niinemets, 2008). However, these were both greater in the UL plot in pine saplings. This is likely not the result of a change in the light availability afforded to these plants by the logging event, but instead to the greater stand density in the UL plot. As a result, there is greater competition for resources, including light, and thus branches are growing up toward canopy levels with higher light availability, rather than fanning out to increase light interception. Little change was observed in LMF, LAR, or LBL. Collectively, these results suggest limited plasticity in branch morphology of pine as a response to changes in light availability.

4.7 Plasticity of Leaf Morphology and Physiology in Pine

Similarly to willow, LMA was also greater in pine in the SL plot, demonstrating the reduced need for light capture and greater need for more photosynthetic machinery on an area basis to utilize the greater light afforded to the leaf. However, leaf inclination was greater in the UL plot than the SL plot. Similarly to branch inclination angles, this is peculiar as leaf inclination is often greater in high light environments, to reduce light interception (Pearcy *et al.*, 2005; Valladares and Niinemets, 2008; Falster and Westoby, 2003). Again, in the current study these results are likely the result not of the need for plants to reduce light interception, but to outcompete other saplings for light in the UL plot with the decreased space for growth. As can be seen by the greater stand density

measures, there were twice as many willow saplings in the UL plot than the SL plot, and over ten times as many pine saplings in the UL plot than the SL plot. This greater density of saplings, while on the one hand suggesting greater regrowth biomass, on the other hand increases competition for resources in the UL plot. As a result, plants need to grow taller to outcompete their neighbors for sunlight, thus increasing both branch and leaf inclination angles to reach heights with greater light availability.

Evergreen leaves tend to show higher F_v/F_m when they are oriented more vertically than horizontally (Werner *et al.*, 2001). As the needles in the SL plot were not oriented more vertically, nor was there a large change in F_v/F_m or apparent quantum yield, there is no sign of photoinhibition in the SL needles. There was also greater ETR in pine in the SL plot. As pine did not exhibit the same increase in leaf inclinations and LCI in the high light environment as willow did, which will be discussed later, the ETR increase, coupled with greater $\Phi PSII$, suggesting avoidance of oxidative damage as the greater number of excited electrons from the increased light capture are readily moved away from the antennae complex and either utilized for photosynthesis or dissipated through other means. The greater $\Phi PSII$ found in the SL pine indicates that a greater amount of light energy was utilized for photochemical reactions rather than being dissipated through other means (Jiang *et al.*, 2006). Pine was less capable of altering its physiological plasticity in order to utilize the increased radiation for photosynthesis, as seen through the static nature of A_{max} , quantum yield, and R_d . Foliar nitrogen content was also significantly greater in the SL pine. As there was no increase in A_{max} , the greater LMA might suggest instead that the increased nitrogen is being used for cell wall proteins for structural investment as opposed to increased Rubisco content (Letts *et al.*, 2011).

Overall, the invariability in the quantum yield of PSII suggests that photoinhibition did not result from the higher PPFD in the SL plot (Griffin *et al.*, 2004). Also, while there was no difference in stomatal conductance, evapotranspiration, WUE, or c_i/c_a concentrations between plots, $\delta^{13}\text{C}$ values are consistent with greater drought stress in the SL plot as there is less discrimination against ^{13}C .

4.8 Interspecific Differences Between Pine and Willow

Willow and pine belong to different plant functional groups (broadleaf and conifer) and, as a result, exhibit different physiological characteristics from each other. In both SL and UL plots, willow demonstrated a light response curve with higher rates of light-saturated photosynthesis, greater dark respiration rates, and greater quantum yield. All of these characteristics are common to more sun-loving plants and are typical of plants with a shorter leaf life span (Reich *et al.*, 1998; Wullschlegel, 1993). Further, willow saplings had higher plasticity indices for the majority of the morphological measures. While both willow and pine are early successional plant species that utilize the increased light availability after a natural disturbance, willow appears to respond physiologically to utilize the increased light availability compared to pine, which may be for a number of reasons, such as leaf longevity and shade tolerance. Further, willow acclimates its foliage to avoid light interception in higher light environments.

It has been shown that leaf longevity is linked to lower plasticity in response to differences in light availability (Wyka *et al.*, 2012; Wyka *et al.*, 2007; Valladares *et al.*, 2000). This was illustrated in the current study, as a greater number of the measured variables exhibited more plasticity in willow than in pine. Longer leaf life spans are often

covariate to physiological characteristics, such as lower photosynthetic rates (Wullschleger, 1993) and respiration rates (Reich *et al.*, 1993). These differences between long lived conifer needles and short lived deciduous leaves are likely the result of the effect that longevity has on the speed at which a plant is able to track and respond to environmental changes, such as increased light availability (Valladares *et al.*, 2000). By replacing its leaves annually, willow is able create phenotypically different leaves every year that can rapidly respond to the change in the light availability, orienting the leaves higher, for example, every season, or responding to changes in water availability. Further, pine needs to express a more conservative growth rate in order to not over-grow the resources provided by its environment. Pine saplings also need to apply a greater proportion of resources to structural growth, to combat seasonal strains and herbivory over the course of many seasons. As a result, pine cannot express the same rapid growth and photosynthetic response to light that the deciduous willow saplings are able to; the two plant species therefor appear to employ different strategies with regard to resource use.

A previous study comparing evergreen and deciduous conifers (spruce and larch) found similar results (Matyssek, 1986), which is particularly helpful in determining the cause of the interspecific differences, as the deciduous tree, larch, used in the comparison possesses needles rather than leaves. Matyssek (1986) found that leaf longevity is correlated with decreased water demand, slower growth rates, reduced nitrogen use in current year needle growth, and reduced carbon assimilation rates. As a result, it is unsurprising that pine, an evergreen plant species, would similarly show reduced carbon assimilation rates and an even greater reduction in stomatal conductance, and therefore

higher WUE than willow. These characteristics appear to be related to nitrogen content per unit weight, as greater nitrogen content can be correlated with lower LMA, chlorophyll content and subsequently, maximum carboxylation rates (Matyssek, 1986; Reich *et al.*, 1995). This would suggest that the nitrogen use differs significantly between functional groups, with deciduous foliage requiring rapid growth and subsequently fast nitrogen and water use, while conifer leaves require investment into structure for longevity. These results were found in the current study as pine had significantly less nitrogen content on a mass basis than willow did. It has been suggested that leaf anatomy is responsible for poor leaf nitrogen utilization in evergreen conifers as the needles have longer diffusion pathways, thicker cell walls, and lower porosity compared to deciduous angiosperms (Evans and von Caemmerer 1996; Hikosaka and Shigeno 2009; Wyka *et al* 2012). However, confounding these results is the $\delta^{13}\text{C}$ data, in which pine exhibited lower values, signifying greater discrimination against the ^{13}C isotope and therefore greater stomatal conductance and less drought stress, yet has a greater WUE measured through gas exchange than willow does. Given the long leaf lifespan of pine needles, it is possible that water stress may have been experienced at the time of initial leaf growth. However, further research is needed to elucidate the reason for this observation.

It has been formerly demonstrated that plants that are less shade-tolerant afford greater risks regarding their acclimation to low light environments by putting fewer resources to structural support (Valladares *et al.*, 2012). These plants tend to respond to low light by trying to escape the condition and grow taller; however, this creates biomechanically weaker individuals that are thinner and less robust. Plants that are more shade-tolerant are able to afford greater costs as opposed to risks, such as increased

sturdiness through thicker stems, whereas shade-avoidant species will take risks, such as increasing internode lengths to allow for greater light interception (Valladares *et al.*, 2012). These findings were mirrored to a lesser degree in the current study, and would suggest that despite pine being a sun-loving, early successional species, the nature of its long leaf lifespan requires that it also be more conservative in response to light than willow. This was further demonstrated by the greater proportional number of pine growing in the UL plot relative to the SL plot. This is likely due to the nature under which pine reproduces. As it is dependent on forest fires for seed germination (Lotan, 1976), the species is adapted to slightly less light availability due to the overshadowing of the standing dead tree species.

It is also worth noting that, while there were significant between-species differences in light-saturated photosynthetic rates, quantum yield, and dark respiration, there was also a clear between-species difference in the seasonal pattern of dark respiration. While A_{max} and quantum yield remained similar throughout the season, R_d increased throughout the season in willow, but not in pine. This may be explained by previous work done on a mixed conifer forest where similar seasonal variation in leaf respiration was observed. Ubierna and Marshall (2010) demonstrated that foliage respired twice as much in the early portion of the growing season as in late summer, and that this resulted in greater early-season depletion in carbon. This was the result of higher respiration costs in developing leaves than in mature leaves. This has been observed in both coniferous and deciduous leaves (Jurik, 1986). Our results clearly illustrate this trend in the growing deciduous saplings, but show that one-year-old conifer foliage has

matured enough to not exhibit significantly greater respiration at the beginning of the season.

5.0 Conclusion

Willow and pine differed in their responses to a change in light regime. Willow is better able to utilize the increased irradiance, primarily due to its shorter leaf lifespan, which allows it to respond quickly to changes in the environment (Matyssek, 1986; Reich *et al.*, 1998). Willow saplings are able to photosynthesize at greater rates and subsequently grow more in logged environments. As a result, they exhibit greater LMA, stem diameter, apical growth length, number of new growth units, and crown width, as previously observed in studies comparing the growth of understorey plants in a healthy forest to a deforested one (Muraoka *et al.*, 1997). Furthermore, nitrogen use differs significantly between the two functional groups, with conifer needles allocating resources to structural needs, to increase leaf longevity, and deciduous leaves requiring rapid growth and subsequently fast nitrogen and water use (Reich *et al.*, 1995).

In response to increased light availability from logging, there is a positive growth of individual saplings, increased by more in willow than pine saplings. Pine saplings are less able to utilize increased irradiance, as a result of the conservative characteristics that result from leaf longevity, which reduces the rate at which they are able to respond to changes in their environment (Matyssek, 1986). However, there were no signs of photoinhibition or damage as a result of the increased irradiance from cutting. This is likely due to physiological adjustments to energy dissipation, as shown by increased electron transport rates and quantum yield of photosystem II (Jiang *et al.*, 2006). Growth increment also did not increase as much in pine as in willow. However, there was greater stem and branch diameter, and an increase in LMA, in the SL plot, suggesting that they are still able to utilize the greater light availability for increased growth, structural

support, and leaf thickness. These results are similar to previous gap studies, which have found that gap formation increases photosynthesis rates on an area basis and leaf nitrogen concentrations (Jones and Thomas, 2007). Willow saplings of the UL plot exhibited traits that increase light capture efficiency, such as lower leaf inclination (Letts *et al.*, 2012) and exhibited greater investment in leaf growth, as opposed to structural development, to avoid shade and increase light interception (Valladares *et al.*, 2012).

While individual saplings appear to benefit from the increased irradiance, it is important to note that species composition and stand density were severely altered by the effects of salvage logging. In fact it would appear that many of the morphological differences observed in pine saplings were the result of greater competition in the UL plot, including increased new growth and leaf inclination angles and leaf clumping index, which were seen on pine saplings in the UL plot. These traits are more typical of plants growing in high light environments, to reduce light capture (Letts *et al.*, 2012). In this case, however, they are believed to have resulted from the plants' need to compete with other saplings for light, causing them to grow taller and with more foliage to outcompete their neighbors. Willow saplings, by contrast, showed a greater number of leaves per branch length, and greater leaf area relative to the leaf and branch weight at the UL plot, to increase light capture efficiency, which is more consistent with previous observations of plant response to increased light availability (Valladares *et al.*, 2012).

Salvage logging impacts ecosystems and the forest regrowth in a variety of ways. In this study, the focus was on the effect of light regime on willow and lodgepole pine regrowth. We found that stand density was much lower at the SL plot, especially in the case of lodgepole pine, but that individual plants did not exhibit photoinhibition. In

response to increased light availability, ten year-old willow saplings exhibited significantly higher A_{max} , leaf inclination, and LMA. Pine saplings, which generally exhibited lower photosynthetic gas-exchange rates at the leaf level, increased the rate at which electrons were moved through and away from the photosynthetic apparatus, to avoid photoinhibition, but showed less physiological plasticity. While LMA increased, whole-plant and branch level morphological changes were consistent with a response to lower competition, and there was no change in growth increment between plots. Further research is warranted to investigate the implications of these findings on species composition and ecosystem function in forests that have experienced salvage logging.

6.0 References

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