

Transpiration Response of Residual Lodgepole Pine After Partial-cut and Strip-shelterwood
Harvesting in Alberta's Southern Rocky Mountains

by

Samantha Karpyshin

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Department of Renewable Resources
University of Alberta

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Abstract

Forest harvesting reduces forest canopy cover which can reduce evapotranspiration and affect the hydrologic regime of watersheds. Prior research has shown while transpiration is reduced by the removal of trees, it can also affect soil moisture and meteorological variables (e.g. temperature, wind, RH) governing water use of un-harvested residual trees. While this may increase transpiration of residual trees after harvesting, this has not been documented in older mature forests that would typically be harvested. Thus, the net affect of harvesting on total transpiration in harvested watersheds remains unclear. This study explores the transpiration response of mature (> 50 years) lodgepole pine (*Pinus contorta*) where transpiration, soil moisture, and meteorological conditions were evaluated for two growing seasons after partial-cut (PC) and strip-shelterwood (SC) harvesting. While transpiration was greatest during the non-moisture limiting, early growing season compared to the moisture limiting, late season in all stands, transpiration was 60 % greater in residual trees in the PC stand and ~ 40 % greater in the SC stand compared to the reference (un-harvested) stand. Atmospheric moisture demand increased by ~ 10 %, while the shallow soil moisture storage increased by ~ 50 % in the SC stand and in the deeper soil layers by 40 % in the PC stand compared to the reference stand. Spatial patterns in transpiration strongly mirrored the spatial and temporal patterns in these above-ground (atmospheric moisture demand) and below-ground (soil moisture) controls regulating transpiration after harvesting. When changes in post-harvest transpiration rates were scaled up to larger spatial scales, results suggest that increased transpiration by residual trees may compensate for the reduction of transpiration by trees removed during harvesting. This is an important finding, as area harvested may not serve as a direct proxy indicator of potential hydrologic change.

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Chapter 1: Thesis introduction

Watersheds situated along the eastern slopes of the Rocky Mountains in southwestern Alberta are critical to the water supply of the moisture-limited prairie provinces (Andrews et al. 2012). These headwater catchments are the primary source of domestic and irrigation water supply, and also support economic activities such as forestry, cattle grazing, and recreation (Andrews et al. 2012; Alexander and Edminster 1981; Winkler et al. 2017). The quality, quantity, and timing of water supply in snow-melt dominated, forested watersheds are of increasing concern given the diversity of land uses, increasing population demand, and forest ecosystem vulnerability to climate change (Winkler et al. 2017). Water yield is susceptible to changing climate conditions with greater concentrations of carbon dioxide and increasing air temperatures leading to summer drought, lower winter snowpack, and timing of spring snow melt (Andrews et al. 2012; Fahey and Knight 1986). These climate-induced processes also put forested ecosystems at risk because of increased frequency of droughts, insect outbreaks, and wildfire (Andrews et al. 2012). A decline in forest viability is a widespread concern both from a commercial and an ecological sustainability perspective. Forest growth requires sufficient water (roots access to water, water movement from root to shoot) to transpire, enabling photosynthesis and carbon assimilation (Maherali et al. 2004). In a climate that is becoming warmer, potential reductions in precipitation or balance of snow/rain and periodic summer droughts, maintaining sufficient water to sustain forest health is a concern (Andrews et al. 2012).

Forest management can be used as a tool to manage watersheds for sustainability of critical water “values” while concurrently producing economic benefits for society (Swanson 1985). One potential objective of contemporary forest management may be to improve growth rates of residual stands by increasing growing space and availability of limiting resources for growth (e.g. water, light, nutrients), while extracting a viable, commercial resource (Thorpe and Thomas 2007). Historically, management goals have been primarily focused on sustainability of timber supplies, while contemporary forest management has included broader ecosystem-based objectives including wildlife habitat, forest health, and other factors needed for environmental, social, and economic sustainability (Thorpe and Thomas 2007).

Forest harvesting can affect the sustainability of water resources such as the volume of water produced, the timing of flows, peak flows, and low flows (Bosch and Hewlett 1982; Stednick 1996). In snow-dominated regions, removing part of the forest canopy often increases snowpack depth or water equivalent which has been the focus of extensive research as a primary driver of disturbance effects on streamflow (Pomeroy et al. 2012; Stednick 1996). This includes potential changes in streamflow volume, timing of snowpack melt, effects on peak flows or flooding, and effects on low flows; most of which may negatively affect channel integrity and stream ecology (Winkler et al. 2017). In order to minimize the likelihood of these potential impacts, forest management plans in Alberta for example often limit the proportion of watershed area harvested to minimize the likelihood of potential impacts to water resources consistent with the provincial Water Act (Alberta Government 2016).

However, forest harvesting has also been shown to increase water use by un-harvested residual trees (Bladon et al. 2006; Lagergren et al. 2008; Reid et al. 2006). Removal of the forest canopy has been shown to increase both micrometeorological variables regulating tree water use such as wind or air temperatures, or soil moisture availability to the tree rooting system (Lagergren et al. 2008; Bladon et al. 2006). However, because of high variability of such responses among tree species, climatic regions, and harvest types, the potential role of these factors in overall transpiration dynamics across harvested watersheds remains highly uncertain. High variability in tree species-specific physiological responses such as stomatal response to water limitation, stand age, and variable root and leaf structure all play a role in how a residual stand might respond to the removal of forest canopy and introduction of new environmental conditions (Rudnicki et al. 2004; Lopushinsky and Klock 1974; Yoder et al. 1994). For example, changes in sun radiation and wind regimes have the potential to reduce rather than increase transpiration where “thinning shock” results from harvest-induced changes (Staebler 1956). Such responses are understood to result from increased atmospheric drought causing water stress, cavitation of xylem tissue, or loss of sapwood permeability (Lagergren et al. 2008; Reid et al. 2006; Maherali et al. 2004; Wullschleger et al. 2000; MacKay et al. 2012; Sparks et al. 2001). Thus this information is needed to address broader uncertainty on impacts of forest harvesting on water resources needed by forest managers (Zhang and Wei 2014).

The physiological response of residual stands after forest harvesting is of particular importance for forest watershed managers. Research literature generally concludes that changes

in catchment scale evaporative losses (of which transpiration is a key component) after harvesting is proportional or linearly related to the area cut (i.e no change in transpiration of residual forest). Winkler et al. (2017) and Bosch and Hewlett (1982) concluded that approximately every 10 % increase in area harvested correspond to approximate increases in annual water yield of 25-36 mm and 40 mm, respectively. However, estimates from such meta-analyses are highly variable across hydrologic regions ranging from very high to no reported water yield increase (Bosch and Hewlett 1982; Stednick 1996). Increased transpiration by residual trees may partially compensate for the reduction in transpiration losses after harvesting, however little quantitative information exists on the importance of this process to overall changes in watershed scale evaporative processes after harvesting. While several studies have shown increased transpiration of juvenile or younger residual trees (< 50 years old) after partial-cut harvesting in Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and Lodgepole pine (Lagergren et al. 2008; Bladon et al. 2006; Reid et al. 2006; Simonin et al. 2007), no studies, to my knowledge, have documented such changes in mature (> 50 years old) trees. This represents an important knowledge gap because mature forests are the primary focus of forest harvesting operations.

Accordingly, the broad goals of this study were to explore the change in evaporative fluxes, specifically the transpiration response, of residual, mature trees after harvesting. The specific research goals were to first evaluate the short term (two to three year) transpiration response of mature lodgepole pine to alternative retention harvest strategies (strip shelterwood (SC) and partial-cut (PC)) and compare these to an otherwise similar uncut reference stand (Figure 1-1). The second objective was to determine how these two harvest strategies might affect the spatial patterns of soil moisture and microclimate variables regulating atmospheric moisture demand.

Chapter 2 of this thesis outlines research evaluating the transpiration response of a mature lodgepole pine stand in PC, SC, within SC, and reference stands during the growing season (May – August) of 2017 and 2018. Specific study objectives were to a) evaluate the influence of PC and SC harvesting on shorter term diurnal patterns of transpiration; b) evaluate the differential effects of PC and SC harvesting on broader seasonal patterns (early- and later growing season) of water use across two full growing seasons; c) evaluate relationships between key tree and stand attributes with these transpiration responses; and d) use these relationships to evaluate how

changes in transpiration of un-harvested residual trees are likely to affect total evaporative flux by transpiration at larger watershed scales.

Chapter 3 reports on research evaluating the spatial patterns of rooting zone soil moisture (edaphic / below ground) and atmospheric demand (atmospheric / above ground) conditions created by the two alternative harvest strategies (PC and SC). Specific study objectives were to: a) evaluate the influence of PC and SC harvesting on seasonal patterns of microclimate variables governing atmospheric demand for moisture (above-ground controls) and soil moisture content and soil water potential (below-ground or edaphic controls); and b) evaluate the relationship between harvest associated changes in above- and below- ground controls and the transpiration response of PC and SC residual stands, and c) to explore the combined effects of both atmospheric and edaphic factors after harvesting to shed light on the relative influence of these controls on post-harvesting transpiration.

Chapter 4 outlines a synthesis of results of these studies in the context of forest management practices in Alberta.

Table and Figures

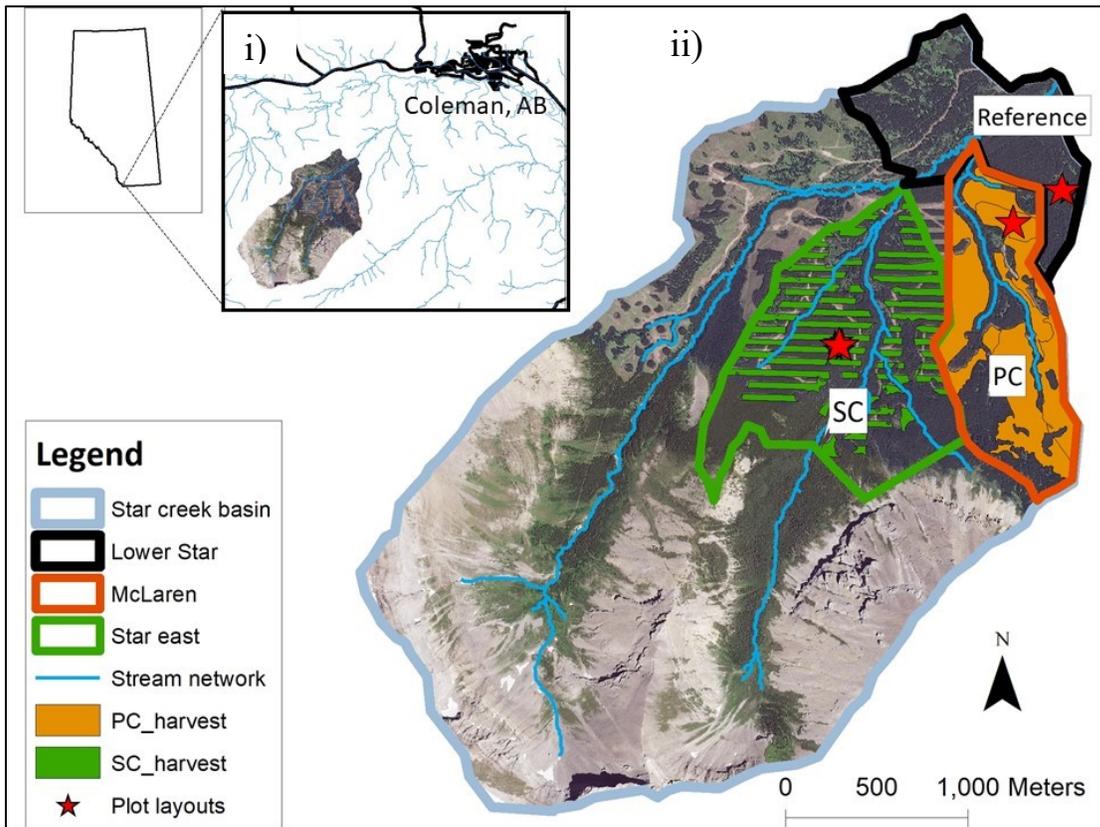


Figure 1-1. i) Map of Star creek basin in the headwaters of the Oldman river basin in southern Alberta, Canada. ii) Map of the two harvest treatments and reference site in Star creek. Harvest treatments are the strip-shelterwood (SC) and the partial-cut (PC). Red stars indicate location of study plots.

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Chapter 2: Transpiration response of residual lodgepole pine after partial-cut and strip shelterwood harvesting in Alberta's southern Rocky Mountains

2.1 Introduction

The hydrological cycle is susceptible to changes in the composition or structure of vegetation, where vegetative controls over evapotranspiration (ET) serves as the link between the hydrologic and carbon cycle (Lagergren et al. 2008). Timber harvesting removes forest cover thereby modifying the water balance by reducing ET which is strongly linked to changes in hydrologic regime including annual water yield (Stednick 1996). Transpiration, as a part of total ET, is directly affected by forest harvesting by removing tree crowns. However, transpiration of the remaining, un-harvested trees or stands may also be affected because depending on the spatial configuration of the harvest, environmental controls such as air temperature, radiation, wind, and soil moisture regulating transpiration of residual trees may also be affected by harvesting. Generalizing harvest effects on transpiration of residual trees are difficult to predict because of a) high variability in stomatal sensitivity of tree species to both soil and atmospheric drought (Lopushinsky and Klock 1974) and b) harvesting effects on environmental controls such as spatial patterns of soil moisture and atmospheric moisture demand (e.g. air temperature, humidity, wind). These generalizations are not well understood particularly across the range of differing harvesting strategies such as clear-cutting, partial-cutting, and shelterwood harvesting.

Lodgepole pine naturally regenerates after wildfire, forming dense, monospecific stands where light competition of shade intolerant trees such as lodgepole pine largely drives forest stand dynamics (Fahey and Knight 1986; Huang et al. 2004). However, availability of water and nutrients can also play important roles where they are limiting. Forest harvesting can benefit residual trees by decreasing tree density and competition for light and limiting nutrients or water (Keyes et al. 2014; Thorpe and Thomas 2007). For example, reducing the forest canopy density reduces canopy interception of precipitation allowing for more precipitation to reach the ground, increasing soil moisture availability. Forest harvesting can also negatively affect residual trees by exposing them to adverse environmental conditions (Staebler 1956). Reducing the forest canopy increases sunlight and wind exposure within the stand creating increased atmospheric demand for moisture potentially resulting in water stress, cavitation of xylem tissue, or loss of sapwood

permeability (Lagergren et al. 2008; Reid et al. 2006; Maherali et al. 2004; Sparks et al. 2001). Greater soil moisture and lower stand competition have been shown to promote improved water relations (access to water) in residual thinned stands of juvenile or early mature lodgepole pine (Reid et al. 2006), Ponderosa pine (Simonin et al. 2007), Scots pine, and Norway spruce (Lagergren et al. 2008). However this high variability in water relations across species precludes drawing more than the general inference that greater access to water has the potential to increase photosynthetic productivity, increasing the growth of residual stands. Exceedingly little information exists on similar effects in older stands that would more typically be the focus of most forest harvest operations. Older stands may lack the ability to adjust to new growing conditions after harvesting (Yoder et al. 1994), but this is not well understood in general and for lodgepole pine in particular.

Partial-cutting (PC) and strip-shelterwood (SC) are two examples of low-intensity forest harvesting strategies which are designed as alternatives to the conventional clear cut method in many regions. In SC, residual blocks of unharvested strips are left on the landscape and in PC, remaining stands are thinned to a prescribed density. While the physiological response of younger (< 50 year), higher density residual trees after PC harvesting has been studied previously, the likelihood or magnitude of potential transpiration responses in mature trees (> 50 year old) remain unclear. As a consequence, predicting larger scale changes in ET after harvesting remains highly uncertain which creates significant challenges in anticipating potential hydrologic changes after forest harvesting.

Accordingly, the broad goals of this study were to evaluate short term (two to three years after harvesting) acclimation of transpiration in mature, residual lodgepole pine in response to spatial patterns of soil moisture and atmospheric moisture demand produced by PC and SC harvests in the forested Rocky Mountain region of south-west Alberta. Specific study objectives were to a) evaluate the influence of PC and SC harvesting on diurnal patterns of transpiration when soil moisture was more readily available and later in the season under greater soil moisture limitations; b) evaluate the differential effects of PC and SC harvesting on broader seasonal patterns of water use across two full growing seasons; c) evaluate relationships between key tree and stand attributes with these transpiration responses; and d) use these relationships to explore if potential changes in transpiration of residual trees is likely to affect total evaporative flux by transpiration at larger watershed scales.

2.2 Materials and Methods

2.2.1 Study area

This study was conducted in Star creek watershed in Crowsnest Pass, Alberta (49°37'N, 114°40'W, ~1600 m elevation). This headwater catchment is north, north-east facing, situated within the Oldman river basin on the eastern slopes of the Rocky Mountains in southern Alberta (Figure 1-1). Star creek is located within the montane and subalpine Cordillera ecozones, with forests primarily dominated by lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Silins et al. 2016; Bladon et al. 2008; Strong and Leggat 1992). The geology and soils of Star creek are characterized by upper Cretaceous sandstone, clayey siltstone and shale formations overlain by well-drained to imperfectly-drained Eutric or Dystric Brunisols (Bladon et al. 2008). Mean annual precipitation and temperature is 882 mm and 4.6°C respectively (Emelko et al. 2016; Silins et al. 2016). From 2006–2016 growing season mean precipitation (mm) was 284 ± 16 (standard error (se)).

Research activities were executed during the snow-free season from May–August in 2017 and 2018 which spans the primary growing season for the majority of tree growth in this region. Growing season precipitation during the two years of study (2017, 2018) was 119 mm and 129 mm, respectively.

Star creek watershed is composed of four sub-catchments – lower Star, Star east, Star west, and McLaren creeks. Three harvest treatments - clear-cut, strip-shelterwood, and partial-cut - were established in Star west, Star east, and McLaren creek sub-catchments (Figure 1-1). The different harvesting strategies were implemented consistent with broad objectives for regional harvesting approaches identified in the C05 Forest Management Plan (2006–2026) (Alberta Government 2016). The selection of harvesting systems was based broad objectives of the C05 Forest Management Plan to “ensure other values (relating to the close proximity of the drainage to the local community and historical uses that include, but not limited to, hiking, mushroom picking, and intrinsic, spiritual and aesthetic values, etc.) were recognized and Elk habitat is favoured” (Alberta Government 2014). The strip-shelterwood cut (hereafter referred to as SC) consisted of 44 ha variable width strip harvest which consisted of clear cutting pure lodgepole pine and mixed conifer into narrow strips (harvested and un-harvested) approximately

35 m wide by 250–450 m long orientated east-west (Figure 2-1). The partial-cut (hereafter referred to as PC) consisted of a distributed (uniform) and small group selection shelterwood harvesting with a harvest target of 50 % distributed removal. This research focused on the transpiration response of trees in strip-shelterwood and partial-cut harvested units only. Harvest treatments were applied during January–July 2015. Harvesting occurred on a gentle north-northeast facing slope (mean slope 13 % (7°)) in stands ranging from 1590–1650 m.a.s.l. SC cuts comprised a total of 44 ha (30 %) in the lower section of the Star east sub-catchment (147 ha). Dispersed and patch-retention PC harvesting was conducted across 58 % (55 ha) of the McLaren sub-catchment (95 ha). This study focused on the dispersed PC region (instead of the patch retention PC) which was harvested with an objective to retain single, dominant trees at approximately 5 x 5 m spacing.

2.2.2 Sampling approach and plot layout

Transpiration response to harvesting was assessed on randomly selected retention trees both in the SC and PC stand. An additional un-cut reference stand was established for comparison in the lower Star sub-catchment (500 m east of PC and 1500 m from SC).

Plots in the SC harvest were designed to capture transpiration response of both exposed trees at the edge of the reserve strip (edge effects) and the middle of the reserve. Within a reserve section, two 35 m long transects were established from the south to the north edge. Transects were 40 m apart and six trees were randomly selected along each transect approximately 7 m apart. Each transect had trees in the following positions- one at the south edge, one interior south edge, two middle, one interior north edge, and one north edge tree (Figure 2-1). The south and interior south trees were considered representative of the southern portion of the SC reserve (Strip S) where the north and interior north trees would reflect the conditions of the northern portion (Strip N). The two middle trees were considered representative of conditions in the interior portion of the reserve (Strip mid).

For the PC and reference stands, six trees with healthy dominant/codominant crowns were randomly selected and established within a fixed radius (10-15 m) of a central location to enable instrumenting all trees for transpiration measurement (Figure 2-1). All trees had a diameter at breast height (DBH) >18 cm.

Three fixed area plots were sampled within reference, PC, and SC stands in August 2018 to determine pre and post-harvest stand density (trees $\text{ha}^{-1} \pm \text{se}$) and basal area ($\text{m}^2 \text{ha}^{-1}$). Pre-harvest density (trees $\text{ha}^{-1} \pm \text{se}$) was 3393 ± 1023 for reference, 1800 ± 136 for PC, and 6147 ± 834 for SC. PC harvest consisted of single tree and group selection harvest to retain 784 ± 61 residual trees ha^{-1} in the dispersed harvest and 1800 ± 136 trees ha^{-1} in unharvested areas, while SC harvest produced alternating residual densities of 0 trees ha^{-1} for the harvested strips and 6147 ± 834 trees ha^{-1} in the uncut reserve strips. Additional group selection harvesting was done in the PC but residual trees in this portion of the PC harvest were not studied here. Pre-harvest basal area ($\text{m}^2 \text{ha}^{-1} \pm \text{se}$) in reference, SC, and PC stands was 65 ± 10 , 58 ± 2 , and 48 ± 6 , respectively. Post-harvest basal area ($\text{m}^2 \text{ha}^{-1} \pm \text{se}$) for PC was 17 ± 1.5 for the dispersed harvest and 48 ± 6 for the unharvested, and SC had alternating basal densities of zero for the harvested strips and 58 ± 2 for the reserve strips.

2.2.3 Tree Characteristics (Tree height, DBH, A_L , SA, A_L :SA ratio, LAI)

Above ground tree characteristics (diameter at breast height (DBH; cm), tree height (m), age (yr), sapwood area (SA; cm^2), leaf area (A_L ; m^2), sapwood area to heartwood ratio (SA:HA; $\text{cm}^2 \text{cm}^{-2}$), leaf area index (LAI; $\text{m}^2 \text{m}^{-2}$), and leaf area to sapwood ratio (A_L :SA; $\text{m}^2 \text{cm}^{-2}$) were either directly measured or inferred for all instrumented sap flow trees. These parameters were based on relationships from destructively sampled trees from a nearby reference area (see below) and provide insight to the hydraulic architecture of the instrumented trees. DBH (cm) was measured 1.3 m from the base of tree using DBH tape (Forestry suppliers, Jackson, MS, USA). Tree height (m) was measured using the Suunto PM-5 inclinometer (Suunto; Vantaa, Finland).

A separate sample of 13 trees, representative of dominant to intermediate canopy position, were destructively sampled from the reference stand in August–September 2017 to develop relationships between leaf area A_L (m^2) with DBH and SA. These relationships were used to estimate A_L for trees instrumented with sap flow sensors. For each tree, the entire crown was divided into equal length positions: upper, middle, and lower, to account for differences in branch morphology and specific weight of needles within crown position (Bladon et al. 2006; Reid et al. 2006). Crown samples were stored in sealed plastic bags in the field and transported to a laboratory and kept in a cool storage area ($\sim 10^\circ \text{C}$). Fresh needles (~ 3.5 g) were randomly

sub-sampled from each of the three crown positions and scanned on a flatbed scanner using WinSeedle (Regent Instruments, QC, Canada) to determine the one-sided projected leaf area (cm^2). All scanned needles were dried until constant weight at 45°C to determine needle specific area ($\text{m}^2 \text{g}^{-1}$) (Bladon et al. 2006). Total leaf area of each crown position (upper, middle, lower) was calculated from the total dry weight (g) of all the needles in that crown position based on the mean scanned leaf area to dry weight ratio from sub-samples above. The total leaf area A_L ; m^2 was calculated for each tree by summing A_L of all three crown positions.

Sapwood area (SA; cm^2) of the 13 destructively sampled trees was determined by collecting two cross sections at DBH height. Cross sections were air dried and sanded from coarse to fine-grit sandpaper finishing with 400-grit sandpaper (Wengert 1976; Yang 1987). Visual discrimination of the sapwood area was achieved by wetting the surface with ethanol and allowing it to evaporate for one minute (Wengert 1976; Yang 1987). Scanning the cross section after one minute exposed the highly permeable sapwood. The SA was delineated and digitally measured using Image J software (National Institute of Health, MD, USA) to determine mean SA from the two cross sections.

Linear relationships between A_L versus DBH and A_L versus SA from the 13 destructively sampled trees were evaluated to enable estimation of A_L of instrumented trees. The relationship between DBH and A_L was somewhat stronger (higher R^2) and was selected to estimate A_L of trees instrumented for transpiration.

At the completion of the study, SA was measured on the sap flow sensor instrumented trees using a non-destructive method. SA and age of the instrumented trees were estimated from extracting two tree cores from the north and south side of the tree. Extractions were done with a 5.15 mm, 10 inch long tree increment borer (Haglof, Sweden). At the time of extraction, sapwood is highly transparent due to its permeability. The extracted tree core was placed on a measuring board to determine the sapwood thickness. Once thickness was recorded, cores were sealed in 6 mm paper straws (Greenmunch, AB, Canada) and returned to lab for 72 hours of drying. Once dried, cores were mounted on wooden blocks and sanded from coarse to fine grit finishing with 400-grit sandpaper to determine the age and annual growth rate of the tree. Tree ring growth rates before and after harvest were assessed from three extracted cores from within the reference, PC, and SC stands. Tree ring growth rates were categorized into two groups: 10 year pre-harvest mean (2004–2014) and post-harvest mean (2016–2017).

Tree characteristics (DBH, heartwood (HA), and sapwood area (SA)) in reference, PC, and SC were recorded and used to derive (A_L , SA to heartwood ratio (SA:HA), A_L to SA ratio (A_L :SA), and LAI) for instrumented trees and stands. Mean SA and HA areas were determined by averaging the SA and HA from the two tree core extractions from each instrumented tree. A_L was estimated from DBH based on the relationship between A_L with DBH (from the destructively sampled trees described above). LAI was estimated from fixed area plots within each treatment based on A_L (m^2) for each tree (estimated using relationships between DBH and A_L for the destructively sampled trees). A_L was summed for all trees in the plot and divided by the plot area to derive LAI (m^2 of leaf area per unit ground area (m^{-2})).

2.2.4 Transpiration

Thermal dissipation probe (TDP) sap flow sensors (Dynamax Inc., Houston, TX) were used to measure the sap flow to estimate transpiration of 24 lodgepole pine in 2017 and 2018 in SC ($n = 12$), PC ($n = 6$), and reference ($n = 6$) stands. Based on measured sapwood from previous sampled trees, 30 mm TDP sensors (TDP-30) were selected for sap flow measurements. The TDP-30 sensor consists of two thermocouple needles (40 mm vertical spacing and 30 mm long) inserted into small holes drilled into the north azimuth of each tree at 1.3 m from the base (Granier 1987). All study areas had TDP installed on the north azimuth to minimize the effect radial position has on sap velocity measurements (Do and Rocheteau 2002). Each TDP-30 was installed to a depth of approximately 25–27 mm in order to capture sapwood and avoid contact with heartwood. The upper needle contains a heater supplying constant 0.2 W creating a thermal gradient between the heated upper needle and unheated (reference) needle. TDP-30 sensors were protected from solar heating with 8 inch foam eggs and reflective thermal insulation wrap. Thermal insulation wrap was secured on the tree with ducttape to ensure that stem flow would not come in contact with heated needle (Dynamax, Houston, TX, USA).

The temperature difference (ΔT ; $^{\circ}C$) between TDP needles was measured every 20 s to calculate and store 10 and 60 min average ΔT using a CR1000 (Campbell Scientific) and an AM 16/32 Multiplexer (Dynamax, Houston, TX, USA). The sap flow measurement system was powered with one 50 Watt polycrystalline solar panel (Matrix Infinity, Canada) and two 12 volt deep cycle batteries (Interstate batteries, Canada) in parallel. Four separate measurement quality

control assessments were conducted for all TDP-30 sensors before installation and concluded that readings were within 5 % of each other and natural thermal gradients were considered negligible (Appendix A).

Sap flow and transpiration was measured using the temperature difference (ΔT ; °C) between the upper and lower TDP needles (Reid et al. 2006; Granier 1987). When vertical sap flow is low (night conditions) the heat dissipation is primarily through conduction resulting in a maximum temperature difference (ΔT_m ; typically 8–10°C) (Dynamax Inc., Houston, TX). The maximum temperature difference ΔT_m was used to calculate sap flow (Equation 2-1). When vertical sap flow is high (mid-day), heat is dissipating more rapidly due to convection and the ΔT decreases. ΔT was measured in all trees in the reference, SC, and PC stands from May 19–August 29 in 2017 and 2018. Sap flow velocity (v_s ; cm s⁻¹) was subsequently determined for each instrumented tree from empirical equations developed by Granier (1987) based on Equations 2-1 and 2-2.

$$K = \frac{\Delta T_m - \Delta T}{\Delta T} \quad [2-1]$$

$$v_s = 0.0119 (K^{1.231}) \quad [2-2]$$

The volumetric rate of sap flow (Q_v ; cm³ h⁻¹) can be estimated for each instrumented tree by multiplying the v_s by the cross sectional area of sapwood (SA ; cm², Equation 2-3). SA was estimated from measured sapwood thickness assuming a circular cross-sectional area for each tree. To compare sap flow amongst other trees, transpiration per leaf area (Q_L ; L m⁻² d⁻¹) was calculated by dividing Q_v by the crown leaf area (A_L) (Equation 2-4) where A_L of each tree was estimated from measured DBH using the empirical relationship between A_L and DBH developed in section 2.2.3. The Q_L allows for direct comparison with trees from reference, SC, and PC stands.

$$Q_v = SA v_s \quad [2-3]$$

$$Q_L = \frac{Q_v}{A_L} \quad [2-4]$$

Transpiration response to both harvesting strategies (SC and PC) was evaluated by comparing transpiration with that of the unharvested reference stand. The transpiration response was also evaluated for the edges of the SC stand (Strip N and Strip S) by comparing transpiration with that of the middle of the reserve uncut unit (Strip mid). Continuous measurements of sap flow normalized by leaf area (Q_L) were measured for reference, PC, SC, and within SC (Strip N, Strip S, and Strip mid) for the whole growing season (134 days in 2017 and 2018). Two time periods in each season (early and late season; prior to and after July 15) were analyzed separately to explore the differential transpiration response to harvesting earlier in the season when soil moisture was less limiting to that later in the season under greater soil moisture limitations.

2.2.5 Scaling transpiration measurements up to the watershed scale

Transpiration for reference, SC, and PC at the plot scale was scaled up to the sub-watershed scale to estimate total transpiration per hectare prior to, and after harvest (Q ; mm ha^{-1}) (Equation 2-5). Total transpiration was estimated from plot scale transpiration (Q_L ; $\text{L m}^{-2} \text{d}^{-1}$) for the whole season, leaf area to basal area ratio ($A_L \text{ BA}^{-1}$; $\text{m}^2 \text{m}^{-2}$) and the pre and post-harvest basal area (BA ha^{-1} ; $\text{m}^2 \text{ha}^{-1}$).

Because transpiration was not measured prior to the harvest (2015), pre-harvest Q for SC and PC was estimated based on measured Q_L in the reference stand in 2017 and 2018 and scaled up using $A_L \text{ BA}$ ratio ($\text{m}^2 \text{m}^{-2}$) and pre-harvest BA ha^{-1} densities of SC and PC, respectively. Pre-harvest BA ha^{-1} for reference, PC, and SC was calculated based upon the fixed area plots described in section 2.2.2.

Post-harvest Q for SC, PC, and reference were estimated based on measured Q_L of each stand type in 2017 and 2018 and scaled up to SC, PC, and reference basal densities, respectively. Mean area-weighted BA ha^{-1} after harvests was estimated across unharvested and harvested areas within SC and PC. For SC, mean post-harvest basal area per hectare was derived by combining the reserve (unharvested) basal area ($58 \text{ m}^2 \text{ha}^{-1}$) and harvested basal area ($0 \text{ m}^2 \text{ha}^{-1}$) multiplied by their respective proportions within the watershed (70 % reserve, 30 % harvested). For PC, the post-harvest basal area per hectare was derived by a similar approach with proportionally weighting (58 % harvested, 42 % reserve) basal area for harvested ($17 \text{ m}^2 \text{ha}^{-1}$) and reserve ($48 \text{ m}^2 \text{ha}^{-1}$) sections of PC.

$$Q = Q_L \frac{A_L BA}{BA ha} \quad [2-5]$$

2.2.6 Data Analysis

Differences in tree growth rates before and after harvest were evaluated using the Kruskal-Wallis rank sum test due to non-normal data with equal variance. Differences in other tree characteristics between harvest treatments were compared using one-way ANOVA with post-hoc comparisons using a LSD test.

Repeated measures ANOVA was used to evaluate differences in seasonal transpiration (early and late) with tree as a random component to account for variation between individual trees within a harvesting treatment. Transpiration variables were not normally distributed therefore a Generalized Estimating Equation (GEE) was used. GEE is an extension of Generalized Linear Models (GLM) and is suited for clustered, correlated responses without any assumption of data normality and homoscedasticity (Zeger et al. 1988). A Gamma distribution and correlation structure (AR 1) for temporally auto-correlated data were used in this analysis.

Variation in transpiration as a function of tree characteristics (height, age, SA, $A_L:SA$, DBH, and A_L), independent of harvesting, were also evaluated. 2017 and 2018 daily transpiration and individual tree characteristics from all study treatments were first evaluated for multicollinearity and removed one at a time until all parameters had a variance inflation factor (vif) of less than 3 (Gareth et al. 2013). Linear mixed models were evaluated with tree as the random component (Pinheiro et al. 2018). To identify tree characteristics that were significantly associated with transpiration, a backward selection approach starting with the full model was used. Once the final model was derived, standardized coefficients of the model were extracted to determine the relative importance of explanatory variables to whole tree transpiration. Standardized coefficients are helpful when variables have different scales of measurement and allows for comparability across variables by standardizing according to common characteristics – means and standard deviations (Kim and Ferree 1981). All analyses were implemented in R (R Core Team 2018), with significance reported relative to $\alpha = 0.05$.

2.3 Results

Growing season precipitation (May 19–August 29) was 119 mm and 129 mm in 2017 and 2018, respectively which was < 50 % of mean historic growing season precipitation from 2006–2016 (284 mm \pm 16 (standard error(se))). Despite similar total precipitation, the temporal pattern of precipitation differed between the two years of study. Early season precipitation (May 19–July 15) was greater in 2018 (103 mm compared to 84 mm in 2017) whereas, late season (July 15–August 29) was greater in 2017 (35 mm compared to 25 mm in 2018).

Winter precipitation (October 1–April 30) was 722 mm and 577 mm in 2017 and 2018, which was above average by 62 % and 29 % of mean historic winter precipitation from 2006–2016 (447 mm \pm 33 (se)).

2.3.1 Tree characteristics

Regressions between leaf area (A_L ; m²) versus diameter at breast height (DBH; cm) ($R^2 = 0.86$, $p < 0.001$) and A_L versus sapwood area (SA; cm²) ($R^2 = 0.84$; $p < 0.001$) (Figure 2-2; 2-3) were derived from the 13 destructively sampled trees.

Annual growth rate (mm yr⁻¹) was assessed from three tree cores from each treatment (Figure 2-4; 2-5). The 10 year mean annual growth rate (mm yr⁻¹ \pm se) prior to harvest (2004-14) for reference, SC, and PC was 0.65 \pm 0.1, 0.82 \pm 0.1, and 1.12 \pm 0.2, respectively. Post-harvest (2016-2017) mean annual growth rate (mm yr⁻¹ \pm se) for reference, SC, and PC was 0.52 \pm 0.1, 1.16 \pm 0.1, and 1.48 \pm 0.5, respectively. Marginally significant increases in annual tree ring growth were observed between the pre to post-harvest period in PC ($p \leq 0.05$) whereas, no significant difference in tree ring growth were evident in trees from SC ($p > 0.05$).

Despite broadly similar pure lodgepole pine stand composition across the study area, mean tree and stand characteristics were moderately variable across reference, PC, and SC stands (Table 2-1). Trees in the PC harvest had the largest DBH, SA, and A_L , whereas trees in the SC were the oldest and had the greatest SA:HA ratios. Trees in the reference stand had the greatest height, A_L :SA and LAI. Significant differences ($p < 0.05$) between DBH, SA, and A_L occurred between SC and PC. Significant differences between height, A_L :SA, and LAI occurred between

reference and SC. Age was significantly different for PC compared to the reference and SC stands.

No significant difference in mean tree or stand characteristics were evident for residual trees across relative positions (north, middle, or south side) within the reserve strip of the SC harvest (Table 2-2).

Sapwood area (SA), leaf area to sapwood ratio ($A_L:SA$), and height were concluded, based on the mixed models, as the main explanatory variables that had an influence on transpiration (regardless of harvest site). The standardized coefficients for SA was 0.39, $A_L:SA$ (0.29), and height (-0.36).

2.3.2 Hourly transpiration

To enable comparing differential patterns of hourly transpiration among stands under similar radiation and atmospheric conditions (air temperature, vapour pressure deficit, etc.) hourly transpiration per leaf area (Q_L ; $L\ m^{-2}\ h^{-1}$) was explored across three days in the early and late season for SC, PC, and reference (Figure 2-6). These six days were representative of days with high solar flux (rain-free) and similar atmospheric conditions. Early season (June 30–July 3) was representative of high soil moisture availability whereas the late season (August 15–18) was representative of similar atmospheric conditions, but with much lower soil moisture availability.

During the early season, Q_L for reference, PC, and SC ranged from $\sim (0-0.045\ L\ m^{-2}\ h^{-1})$. However, onset of early morning transpiration in SC and PC stands began one to two hours earlier (8:00 am versus 9:00/10:00 am) compared to trees in the reference stand. Peak transpiration occurred at 14:00 for reference and between 14:00 and 16:00 for SC and PC. Peak transpiration of trees in SC and PC stands was 33 % and 58 % greater than in the reference stand, respectively. On average, total daily Q_L of trees in SC was 42 % and PC was 83 % greater than in reference stands. In contrast, late season, Q_L for all trees was notably lower than early season transpiration ranging from $\sim (0-0.015\ L\ m^{-2}\ h^{-1})$. Onset of morning transpiration in SC and PC stands began one hour earlier than in reference stands (8:00 am versus 9:00 am). While there was no difference in timing of peak transpiration (14:00) between reference, PC, and SC stands, peak transpiration in SC and PC stands was 25 % and 16 % greater than in reference stands,

respectively. On average, total daily Q_L in SC was 32 % and PC was 23 % greater than in reference stands.

Transpiration per leaf area (Q_L ; $L\ m^{-2}\ h^{-1}$) of trees within the SC (Strip mid, Strip N, and Strip S) during the early and late season is shown in Figure 2-7. While Q_L for all trees ranged from $\sim (0 - 0.043\ L\ m^{-2}\ h^{-1})$ during the early growing season, timing of early morning and late daily water use did not appear to differ within SC. Peak transpiration occurred at 14:00 for Strip mid and either 15:00 or 16:00 for Strip N and Strip S. Peak transpiration was 33 % and 17 % greater for trees in Strip N and Strip S than Strip mid, respectively. On average, total daily Q_L of trees in Strip N was 42 % and Strip S was 20 % greater than trees in Strip mid. During the late season, Q_L was considerably lower than early season transpiration in all trees ranging from $\sim (0 - 0.02\ L\ m^{-2}\ h^{-1})$. Q_L of trees in Strip N and Strip S started one to two hours (8:00 am versus 10:00 am) earlier than Strip mid but peaked at the same time (14:00). However, peak Q_L was 93 % and 24 % greater in trees in Strip N and Strip S than in Strip mid, respectively. On average, total daily Q_L in Strip N was 115 % and Strip S was 37 % greater than Strip mid.

2.3.3 Seasonal transpiration

To enable comparing differential patterns of seasonal transpiration among stands under a variety of radiation and atmospheric conditions (air temperature, vapour pressure deficit, etc.) daily transpiration per leaf area (Q_L ; $L\ m^{-2}\ d^{-1}$) was explored from May 19–August 29 for SC, PC, and reference (Figure 2-8). Mean daily transpiration per leaf area (Q_L ; $L\ m^{-2}\ d^{-1}$) ranged from 0.03-0.48 $L\ m^{-2}\ d^{-1}$ in reference, PC, and SC stands across the two growing seasons (2017, 2018). Transpiration during the initial part of the growing season showed an ascending trend to approximately July 15th (Julian Day 196) and followed by a notable decline after July 15. This ascending and descending time series was categorized as the early (ascending; May 19–July 15) and late (descending; July 16–August 29) growing season. Mean early season transpiration of trees in the PC stand was 68 % and 67 % greater than trees in the reference stand, in 2017 and 2018, respectively, while in the SC stand, transpiration was greater than the trees in the reference stand by 7 % and 40 %, in 2017 and 2018, respectively (Figure 2-9). Early season transpiration in 2017 PC was significantly different from SC and reference, whereas in 2018 reference was significantly different from SC and PC. In contrast, while mean transpiration declined in all trees

after Julian Day 196, trees in the SC stand were able to maintain more consistently greater transpiration than in the reference stand in 2017-2018, whereas transpiration of trees in the PC stand were greater than in the reference stand only in 2018. In the late season, mean Q_L of trees in the SC stand were 77 % and 145 % greater than in the reference stand, in 2017 and 2018, respectively, while transpiration in the PC stand by 7 % and 82 % compared to the reference stand in 2017 and 2018, respectively. In the late season 2017, SC was significantly different from reference and PC, whereas in 2018 all three study sites are significantly different. Mean total growing season transpiration (May–August) in 2017 and 2018 was PC > SC > reference and all study sites were significantly different from one another. Trees in the PC stand transpired 56 % and 70 % more and trees in the SC stands transpired 20 % and 61 % more than in reference stands during 2017 and 2018, respectively.

Trees in different positions within the reserve SC strips showed a similar pattern of ascending and descending transpiration across earlier and latter periods of the growing season (Figure 2-10), where mean Q_L ranged from 0.05–0.52 L m⁻² d⁻¹ across all positions. During the early 2017 season, transpiration of trees in Strip N and Strip S were 32 % and 9 % greater than in Strip mid (Figure 2-11). Strip N was significantly different from Strip S and Strip mid ($p < 0.05$). In contrast, early 2018 season, trees in Strip N and Strip S transpired 10 % and 26 % less than trees in Strip mid, where Strip S was significantly different from Strip N and Strip mid. During the late season (2017, 2018), trees in Strip N transpired 132 % and 136 % more than Strip mid, respectively and mean Q_L of trees in Strip S transpired 53 % (2017) and 24 % (2018) greater than trees in Strip mid. Both years during the late season, had all three study sites average Q_L significantly different from one another. Overall total growing season transpiration (May–August) differed across treatments in 2017 and 2018 where in 2017, the pattern of mean Q_L was Strip N > Strip S ≥ Strip mid compared to Strip N > Strip mid > Strip S in 2018. Both years had mean Q_L significantly different from all positions within SC. Mean transpiration in Strip N was 55 % (2017) and 21 % (2018) greater than Strip mid whereas trees in Strip S transpired 19 % more (2017) but 16 % (2018) less than in Strip mid.

2.3.4 Watershed scale

Because SC and PC harvest strategies produced differing proportions of harvest disturbance at the larger watershed scale (Figure 1-1), an area weighted approach was used to scale measured plot transpiration up to the sub-watershed scale (Table 2-3). Total estimated catchment scale transpiration (Q ; mm ha^{-1}) in the reference, PC, and SC stands from May–August is shown in Table 2-4. The pattern of estimated catchment scale transpiration prior to the harvest from greatest to least was reference > SC > PC. However, if the reduction in total transpiration loss were proportional to relative reduction in basal area due to harvests, the estimated reduction at a catchment scale would have been 38 % and 30 % for PC and SC harvests, respectively. Actual post-harvest transpiration measured in 2017–2018 for both PC and SC were on average 103 % and 99 % the pre-harvest Q , respectively. This suggests that the PC and SC stands are likely compensating for the direct basal area reduction of evaporative losses by transpiration after harvesting by an average of 66 % and 44 %, respectively.

2.4 Discussion

Results of this study clearly showed that transpiration of un-harvested, residual mature lodgepole trees was increased over two growing seasons after harvesting with both distributed single tree PC and spatially discrete SC harvesting strategies. Residual trees showed generally greater transpiration both earlier in the growing season when soil moisture was greater, but also later in the season during two very dry summers when low soil moisture limited transpiration in the un-harvested reference stand.

2.4.1 Hourly–Daily transpiration

The difference in timing of water use, peak transpiration, and total daily water use between reference, strip-shelterwood (SC) and partial-cut (PC) indicates that harvest type influenced tree water use (Figure 2-6; 2-7). While stands in this study were 55–92 years old, hourly transpiration (Q_L ; $\text{L m}^{-2} \text{h}^{-1}$) under clear-sky conditions (both early and late season) were within magnitude of

transpiration of younger, higher density lodgepole pine (Graham and Running 1984; Reid et al. 2006), mature (> 50 year), less dense eastern white pine (*Pinus strobus*) (MacKay et al. 2012; McLaren et al. 2008) and mature, more dense lodgepole pine (Knight et al. 1981).

Harvesting affected the diurnal pattern of transpiration which started one to two hours earlier in the harvested stands (SC and PC) compared to the reference stand in both the early and late season. In the late season, trees on the edge of the un-harvested reserve strips (Strip N and Strip S) began to transpire one to two hours before trees in the middle (Strip mid). This earlier onset of transpiration is consistent with previous studies on partial cutting (Bladon et al. 2006). The increase in direct and diffuse sunlight in the PC and edges of the SC stands would have stimulated onset of photosynthesis and transpiration earlier in the harvested compared to the reference sites (Knight et al. 1981; Williams et al. 1999; Vyse et al. 2006). This was likely a factor partially explaining the greater total daily transpiration I observed in SC and PC stands. In particular, peak transpiration was strongly elevated in the harvested stands (PC and SC) and on the edges of the SC (Strip N and Strip S). This was most likely a response to atmospheric moisture demand and soil moisture availability after harvesting (Chapter 3). Similar increases in post-harvest water use of residual trees have been observed by Reid et al. (2006) with residual lodgepole pine (~ 20–100 %); Lagergren et al. (2008) with Scots pine and Norway spruce (~ 6–27 %); and Bladon et al. (2006) with white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) (marginal to 200 % increase).

Soil moisture was greater in the harvested stands due to the combined increases in throughfall that would occur after canopy removal and reduced total transpiration losses. Soil moisture (0–50 cm) has been observed to increase (4–30 %) post-harvest due to reduced interception (Lagergren et al. 2008; Bladon et al. 2006). In this study, shallow soil moisture (0–20 cm) increased by 50 % in the SC and decreased by 10 % in the PC compared to the reference stand (Chapter 3). While the effects of harvesting in producing both greater daily peak atmospheric moisture demand along with greater soil moisture availability are described in Chapter 3, both of these factors were likely key factors responsible for the greater mid-day transpiration evident in both the PC and SC stands. Wind thrown lodgepole pine trees within the PC stand were examined for rooting depth, which indicated the majority of fine roots were < 20 cm from the surface highlighting the importance of surface soils for tree water relations and photosynthesis (Donner and Running 1986; Lagergren et al. 2008). While surface soil moisture

was slightly lower in PC compared to the reference stand, fine roots near the bottom of this layer would have been able to access the increased soil moisture that was observed in deeper layers (Chapter 3). Within SC, alternating harvested and reserve strips caused a sequential pattern of shading from the residual trees, which was associated with a gradient of increased soil moisture of 18 % from the southern to northern edges of the reserve strip. While both edges of the SC (Strip N and Strip S) generally transpired more than Strip mid, the discrepancy (in peak transpiration and overall daily transpiration) between Strip N and Strip S was likely due to this gradient of moisture.

Peak daily transpiration was strongly reduced in all trees during the drier, late season conditions reflecting stomatal closure to limit the loss of hydraulic conductivity and cavitation during periodic drought (Brix 1978; Lopushinsky and Klock 1974). However, despite high evaporative demand during the drier late season, trees in both PC and SC stands were able to maintain moderately greater mid-day transpiration rates compared to those in reference stands illustrating the importance of even small increases in soil moisture in harvested sites during this period. In the SC stands, greater soil moisture during dry periods in Strip N (Chapter 3) were associated with notably greater mid-day transpiration of trees in this position.

2.4.2 Seasonal transpiration

Temporal patterns of seasonal water use further illustrate the importance of soil moisture availability as a first order control over transpiration in lodgepole pine. Variation in seasonal tree water use showed a consistent pattern of greater Q_L in all stands during the first half of the growing season when soil moisture after snowmelt would have been the greatest, followed by steadily declining Q_L through late August in both 2017 and 2018. Summer precipitation was well below average in both growing seasons which were both less than 50 % summertime average over the previous 10 years. The strong decline in mean transpiration of all stands during the late season reflected greater water stress and stomatal limitations on Q_L . These observations were consistent with similar late season trends in water use of lodgepole pine shown in previous studies (Lagergren et al. 2008; Reid et al. 2006).

Both PC and SC harvest strategies produced strong variation in the seasonal pattern of transpiration across wetter to drier growing season periods in comparison to reference stands.

Mean transpiration was greatest in the PC stand, followed by SC and reference stands during the early growing season in both years. In contrast, mean Q_L was greater in the SC stand during the drier, late growing season in both years. While late season transpiration was greater in the PC than the reference stand in 2018 which is consistent with previous studies showing higher transpiration after thinning (Lagergren et al. 2008; Simonin et al. 2007), late season water use in the PC stand was slightly lower than in the reference stand in 2017. In particular, trees situated in the cooler, more sheltered conditions in Strip N maintained both the greatest transpiration and showed the least late season decline in Q_L than trees in any of the other stand conditions (Figure 2-8; 2-10). Greater late season soil moisture availability in the shallow rooting zone was particularly evident in the Strip N position (Chapter 3) which was likely a key factor in maintaining late season root water uptake in both years.

Pre-harvest tree and stand characteristics including sapwood area (SA), leaf area (A_L), and density can also exert considerable influence on tree water relations. In this study the PC stand had the greatest mean SA , low $A_L:SA$ ratio, and the lowest density which would have promoted greater potential water supply per unit canopy leaf area (Dawson 1996; Simonin et al. 2007). However, strong harvest associated increases of Q_L in the PC stand was only evident during the early portion of the growing season when soil moisture was more readily available. Similarly, greater late season Q_L was also associated with greater SA , and A_L as well as increased soil moisture on the northern side of the strip throughout the growing season. In contrast, while the reference stand had the greatest leaf area index (LAI ; $m^2 m^{-2}$), tallest height, and the second highest tree density (Table 2-1), this likely resulted in greater snow/rainfall interception (Kranabetter and Coates 2004; Vyse et al. 2006) which limited soil moisture availability thereby imposing greater below-ground limitations on Q_L .

The trees in the PC and SC stands transpired the most during the early and the late season, respectively. The greater sapwood and leaf area of the younger PC stand (average age 55 years) promoted the greatest transpiration when soil moisture was non-limiting. In contrast, during the drier season, trees in the SC stand (average age 92 years) transpired the most despite having the lowest sapwood and leaf area. This suggests that while hydraulic architecture is an important factor in transpiration dynamics of older pine forests, other factors such as soil moisture can exert the primary control if soil moisture is more limiting.

Stand age was also likely an important factor in this study which included older–mature (55 yr. old in PC) to late mature (82 and 92 yr. old in SC and reference stands, respectively) lodgepole pine stands in contrast to younger stands that would be expected to have greater hydraulic conductance (lower hydraulic resistance (shorter stands)) and xylem permeability (Irvine et al. 2004; Delzon and Loustau 2005). While post-harvest thinning studies have reported persistently elevated transpiration rates after harvesting in juvenile or early mature stands (Reid et al. 2006; Lagergren et al. 2008; Simonin et al. 2007), exceedingly few studies have documented transpiration responses to silvicultural practices in older forests and none (to my knowledge) have explored these in lodgepole pine. Thus, results of this study showing increased Q_L in 55-82 yr. old lodgepole pine stands after SC and PC harvesting strategies across both wetter and drier growing seasons is a novel finding.

2.4.3 Watershed effects and implications for resilience

Results of this study also suggest that watershed-scale changes to evaporative processes are not directly proportional to the basal area removed during harvesting. Residual trees remaining after SC and PC harvests showed greater diurnal and seasonal transpiration compared to those of unharvested reference stands. At larger spatial scales, this would act to largely or entirely compensate for the direct reduction in total transpiration associated evaporative losses after forest harvesting. If transpiration rates of residual trees would have remained unchanged after harvesting, the 30 % and 38 % removal of basal area from each sub-catchment would have reduced total transpiration losses (mm) to 70 % and 62 % of pre-harvest transpiration losses for both years in SC and PC harvested sub-catchments, respectively. In contrast, increased post-harvest transpiration by residual trees resulted in total estimated transpiration losses in the 2017 growing season that were 85 % and 98 % of pre-harvest losses for SC and PC harvests, while losses during the 2018 season were 113% and 108% of pre-harvest losses for SC and PC harvests, respectively.

This is an important finding from several respects. Firstly, because reduction in transpiration and precipitation interception are known to be key causal mechanisms resulting in increased streamflow after harvesting (Bosch and Hewlett 1982; Stednick 1996), these findings provide a clear potential explanation for why many long-term watershed studies have reported

little or no impact on streamflow from harvest associated basal area reduction. Secondly, in an effort to minimize potential harvest impacts on streamflow regimes after forest harvesting, many forest management agencies employ forest management planning procedures to limit the proportion of total watershed area or total basal area harvested within watersheds based on the assumption that changes in streamflow are proportional to these parameters (e.g. equivalent clear-cut area [ECA] frameworks in Alberta and B.C.) (Alberta Government 2016; Winkler et al. 2017). Conversely, results of this study show that the increased transpiration of residual trees can partially or entirely compensate for the reduction in the transpiration component of total evaporative losses. This supports the notion that ECA analyses as proxy indicators of potential hydrologic change may overestimate harvest impacts on evaporative processes governing streamflow where significant residual basal area is retained after harvest.

Both SC and PC harvests resulted in improved soil moisture availability. Given that these are mature lodgepole pine stands, the chances of significant growth release over the longer term are unlikely, however improved water relations would benefit overall growth and stand health.

Among the two harvest strategies, SC improved the moisture regime across the entire strip (though mostly on the northern side) which sustained transpiration rates through to the dry, late season. This would presumably result in improved future water relations, carbon uptake, and growth.

2.5 Conclusion

Diurnal and seasonal transpiration of lodgepole pine increased after two alternative harvest (PC and SC) strategies were employed in mature, moderately dense lodgepole pine. Transpiration rates (both hourly and daily) were higher in the harvested sites and on the edges of the retention strips (SC harvest). This was a product of a moisture legacy, increased sunlight exposure, and less competition created by these harvest strategies. Patterns of seasonal transpiration showed increased transpiration even during very dry late growing season conditions, particularly in the SC stands where melt from increased post-harvest snowpacks maintained a relatively higher level of soil water availability. These findings are unique in showing transpiration responses in mature lodgepole pine stands which have important

implications for understanding potential hydrologic changes at larger watershed scales. Increased transpiration rates after harvesting were estimated to a larger spatial scale and shown to partially compensate for the direct reduction in total transpiration associated evaporative losses after forest harvesting.

Tables and Figures

Table 2-1. Mean tree and stand characteristics for reference, strip-shelterwood (SC), and partial-cut (PC). Values are the average of measurements within each site (\pm standard error): diameter at breast height (DBH), tree height, age, sapwood area (SA), sapwood area to heartwood area (SA:HA), leaf area (A_L), leaf area index (LAI), and leaf area to sapwood area ratio (A_L :SA). The F statistic, p value, and LSD post hoc comparison from ANOVA are shown for each tree or stand variable.

Tree characteristics	reference (n=6)	SC (n=12)	PC (n=6)	F	<i>p</i>	ref:SC:PC
DBH (cm)	24.2 \pm 1.9	20.6 \pm 0.6	26.6 \pm 2.4	4.58	0.022	ab:b:a
Height (m)	20.3 \pm 0.4	17.4 \pm 0.3	18.8 \pm 1.0	7.06	0.0045	a:b:ab
Age (yr)	82 \pm 5.7	92 \pm 1.6	55 \pm 2.0	95.44	<0.001	aa:a:b
SA (cm ²)	237 \pm 33	202 \pm 15	327 \pm 57	4.09	0.032	ab:b:a
A_L (m ²)	32 \pm 5	24 \pm 2	40 \pm 7	4.85	0.02	ab:b:a
SA: HA (cm ² cm ⁻²)	1.9 \pm 0.2	2.5 \pm 0.3	2.0 \pm 0.3	0.99	n/s 0.39	a:a:a
A_L : SA (m ² cm ⁻²)	0.14 \pm 0.01	0.12 \pm 0.01	0.12 \pm 0.01	2.80	n/s 0.08	a:b:ab
<hr/>						
Stand characteristics						
LAI (m ² m ⁻²)	4.0 \pm 0.5	2.4 \pm 0.3	3.0 \pm 0.1	5.13	0.05	a:b:ab
Density pre-harvest (trees ha ⁻¹)	3393 \pm 1023	6147 \pm 834	1800 \pm 136	8.23	0.02	b:a:b
Density post-harvest (trees ha ⁻¹)	3393 \pm 1023	4172 \pm 566	1209 \pm 78	6.90	0.03	ab:a:b

Table 2-2. Mean tree and stand characteristics for within Strip. Strip mid (middle of Strip), Strip N (north side of reserve strip), and Strip S (south side of reserve strip). Values are the average of measurements within each site (\pm standard error): diameter at breast height (DBH), tree height, age, sapwood area (SA), sapwood area to heartwood area (SA:HA), leaf area (A_L), leaf area index (LAI), and leaf area to sapwood area ratio (A_L :SA). The F statistic, p value, and LSD post hoc comparison from ANOVA are shown for each tree or stand variable.

Tree Characteristics	Strip N (n=4)	Strip S (n=4)	Strip mid (n=4)	F	<i>p</i>	N : S : mid
DBH (cm)	21.8 \pm 1.1	19.8 \pm 0.2	20.3 \pm 1.5	0.92	n/s 0.433	a:a:a
Height (m)	18.0 \pm 0.7	17.2 \pm 0.3	16.9 \pm 0.7	0.86	n/s 0.456	a:a:a
Age (yr)	89 \pm 1.0	94 \pm 4.2	91 \pm 2.2	0.64	n/s 0.549	a:a:a
SA (cm ²)	229 \pm 39	192 \pm 7	186 \pm 25	0.77	n/s 0.493	a:a:a
SA:HA (cm ² cm ⁻²)	2.5 \pm 0.5	2.9 \pm 0.8	2.0 \pm 0.4	0.57	n/s 0.587	a:a:a
A_L (m ²)	27 \pm 3	21 \pm 1	23 \pm 4	0.94	n/s 0.426	a:a:a
A_L : SA (m ² cm ⁻²)	0.12 \pm 0.01	0.11 \pm 0.01	0.12 \pm 0.01	0.18	n/s 0.839	a:a:a

Table 2-3. Mean watershed scale stand characteristics prior to and after harvesting used to scale transpiration from stand to watershed scales (mean values \pm standard error).

Harvest Treatment	Watershed area (ha)	Harvested area (ha)	Pre-harvest basal area ($\text{m}^2 \text{ha}^{-1}$)	Post-harvest basal area ($\text{m}^2 \text{ha}^{-1}$)	Pre-harvest density (trees ha^{-1})	Post-harvest density (trees ha^{-1})
reference	95	0	65 ± 10	65 ± 10	3393 ± 1023	3393 ± 1023
SC	147	44	58 ± 6	40 ± 4	6147 ± 834	4172 ± 566
PC	95	55	48 ± 2	30 ± 2	1800 ± 136	1209 ± 78

Table 2-4. Total scaled transpiration (Q; mm ha⁻¹) for reference, strip-shelterwood (SC), and partial-cut (PC) from May 19–August 29 in 2017, 2018. Estimated pre-harvest Q was based on measured Q_L of reference stands. Estimated post-harvest Q reflects reduction in basal area (BA) (30 % in SC and 38 % in PC) (e.g. reduced Q if directly proportional to reduction in basal area). Actual post-harvest Q were derived from scaled measurements of Q_L in SC and PC stands. Compensatory effect with regards to BA reduction represents percent difference between actual post-harvest Q and estimated post-harvest Q. Compensatory effect with regards to pre-harvest Q represents percent difference between actual post-harvest Q and estimated pre-harvest Q.

	Estimated pre-harvest Q (mm)	Estimated post-harvest Q (mm) if proportional to BA reduction	Actual post-harvest Q (mm)	Compensatory effect with regards to BA reduction (%)	Compensatory effect with regards to estimated pre-harvest Q (%)
2017					
reference	67.1	-	67.1	-	-
SC	59.1	40.8	50.3	23 % ↑	85 % ↑
PC	49.4	30.6	48.2	58 % ↑	98 % ↑
2018					
reference	53.5	-	53.5	-	-
SC	47.1	32.5	53.4	64 % ↑	113 % ↑
PC	39.4	24.4	42.4	74 % ↑	108 % ↑

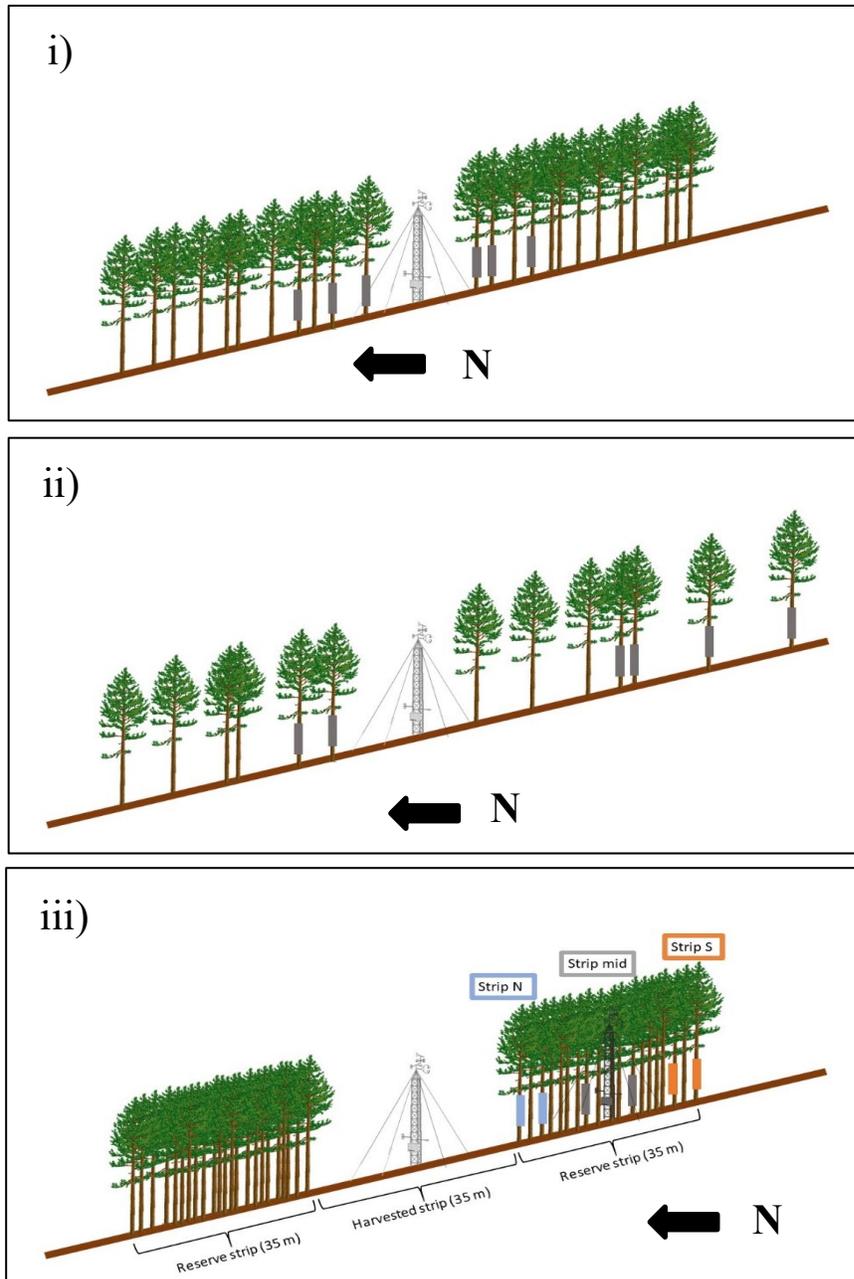


Figure 2-1. Plot layouts for i) reference, ii) partial-cut (PC), and iii) strip-shelterwood (SC). All plots had a north-northeast facing slope with 13 % grade. Each site had a meteorological station recording climate data. Instrumented trees measuring the sap flow are indicated by the grey, blue and orange rectangular boxes.

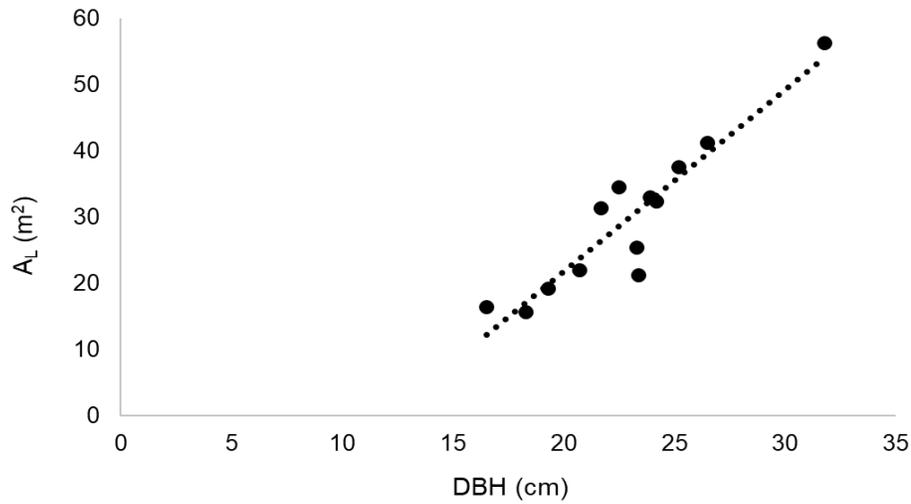


Figure 2-2. Relationship between total leaf area (A_L ; m^2) versus diameter at breast height (DBH; cm) ($y = 2.7322x - 32.766$, $R^2 = 0.8611$, $p < 0.001$) for the 13 destructively sampled trees during August–September 2017.

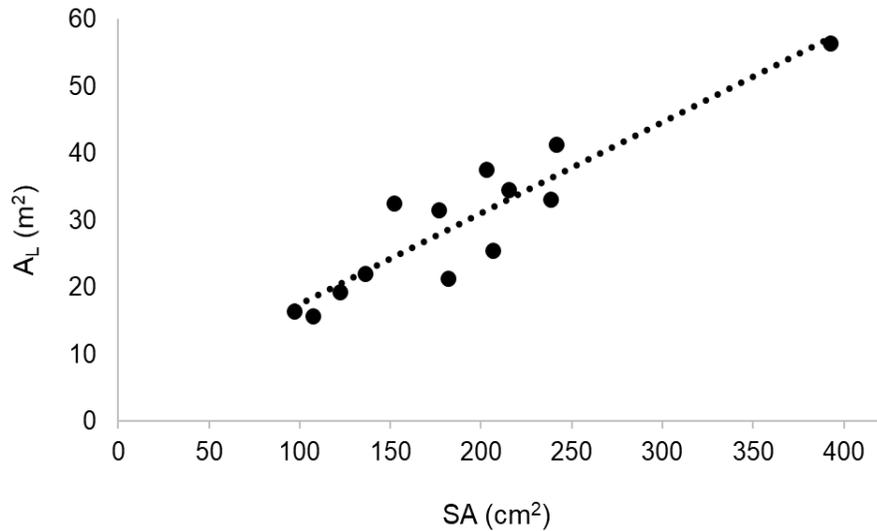


Figure 2-3. Relationship between total leaf area (A_L ; m^2) versus sapwood area (SA; cm^2) ($y = 0.1359x - 3.8717$, $R^2 = 0.8404$, $p < 0.001$) for the 13 destructively sampled trees during August–September 2017.

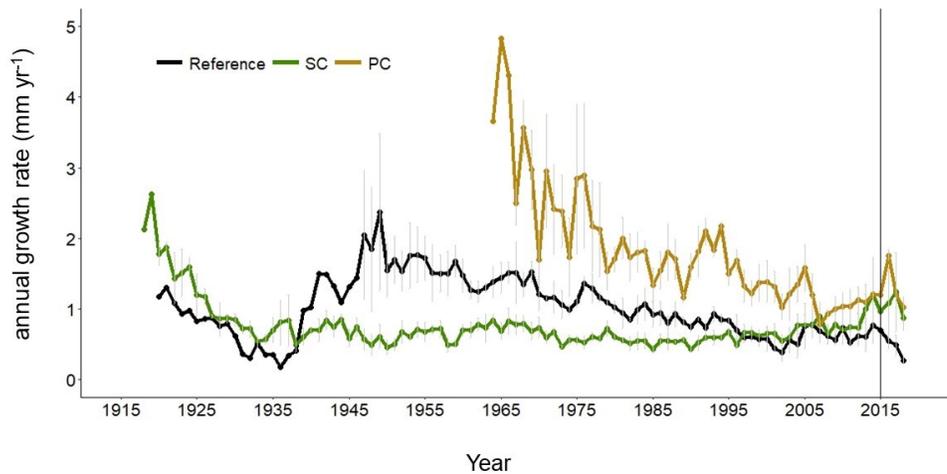


Figure 2-4. Mean annual ring growth (mm yr^{-1}) for reference, strip-shelterwood (SC), and partial-cut (PC). The time series is an average of three cores per site. Error bars represent one standard error. Vertical line at 2015 represents when the harvest was implemented.

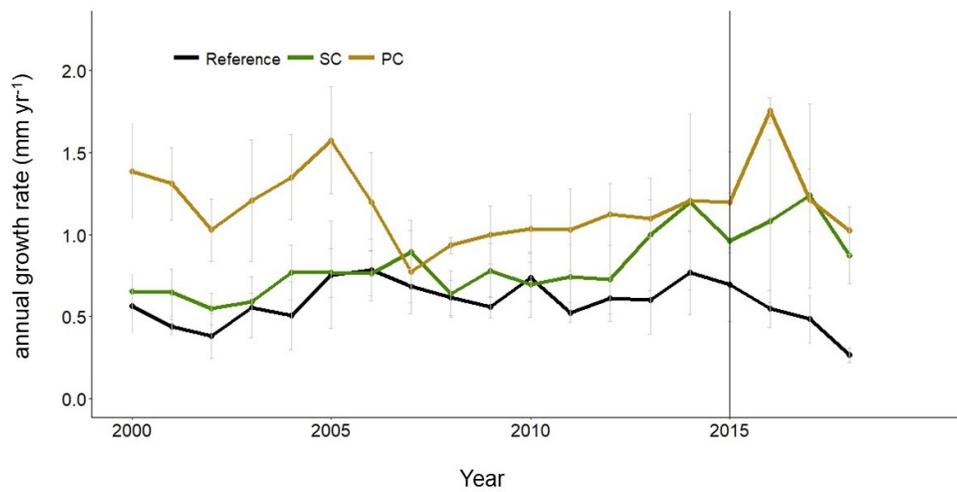


Figure 2-5. Mean annual ring growth (mm yr^{-1}) for reference, strip-shelterwood (SC), and partial-cut (PC). Time series is focused on 2000–2018. Error bars represent one standard error. Vertical line at 2015 represents when the harvest was implemented.

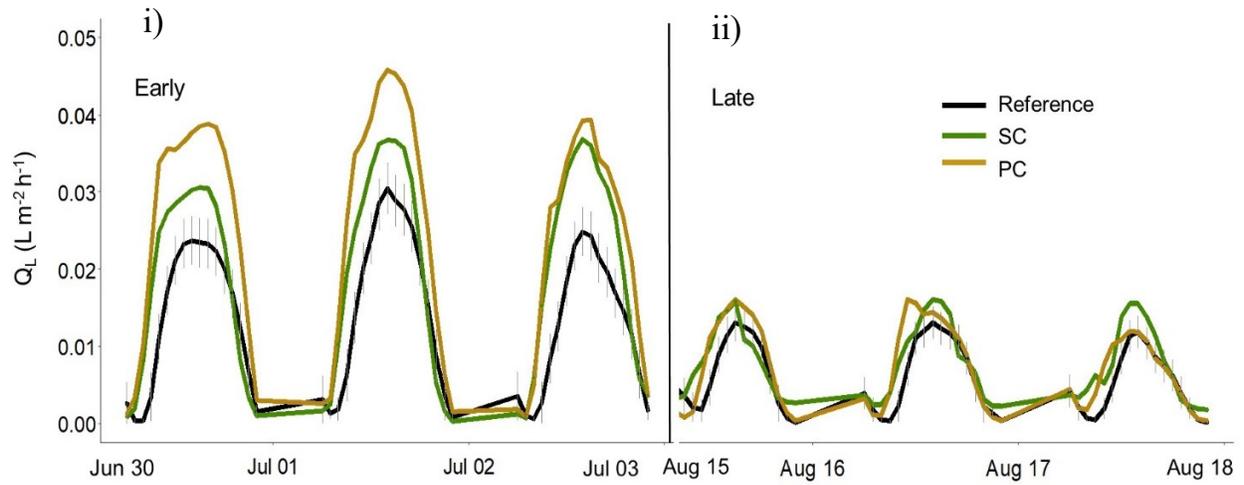


Figure 2-6. Mean hourly transpiration per leaf area Q_L ($L m^{-2} h^{-1}$) (\pm standard error) in 2017 for trees in reference, strip-shelterwood (SC), and partial-cut (PC) stands during two three day periods i) early growing season (June 30–July 2) and ii) late growing season (August 15–18). Standard error presented only in trees in the reference stand for clarity.

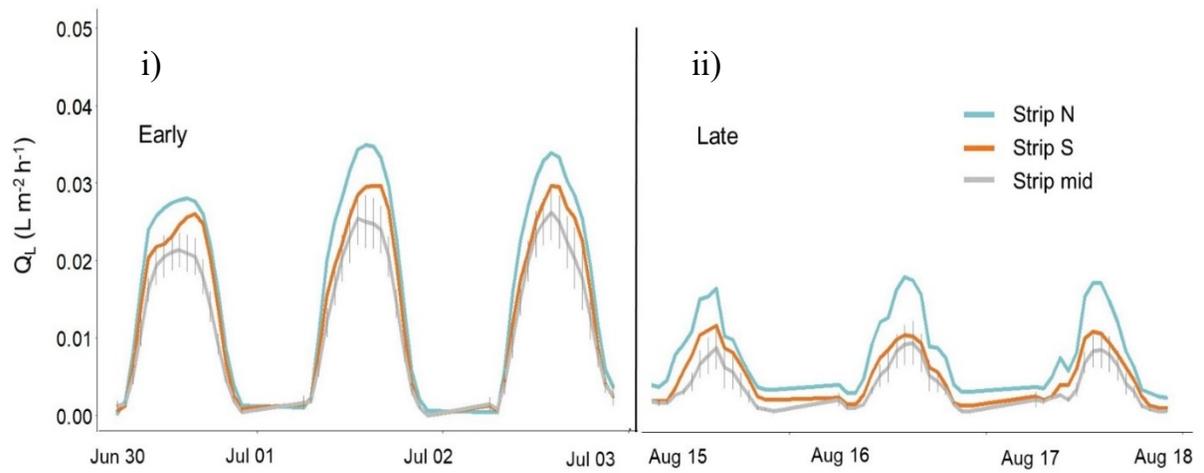


Figure 2-7. Mean hourly transpiration per leaf area Q_L ($L\ m^{-2}\ h^{-1}$) (\pm standard error) in 2017 for trees in strip-shelterwood (Strip mid, Strip N, and Strip S) during two three day periods i) early growing season (June 30–July 2) and ii) late growing season (August 15–18). Standard error presented only in trees in the Strip mid for clarity.

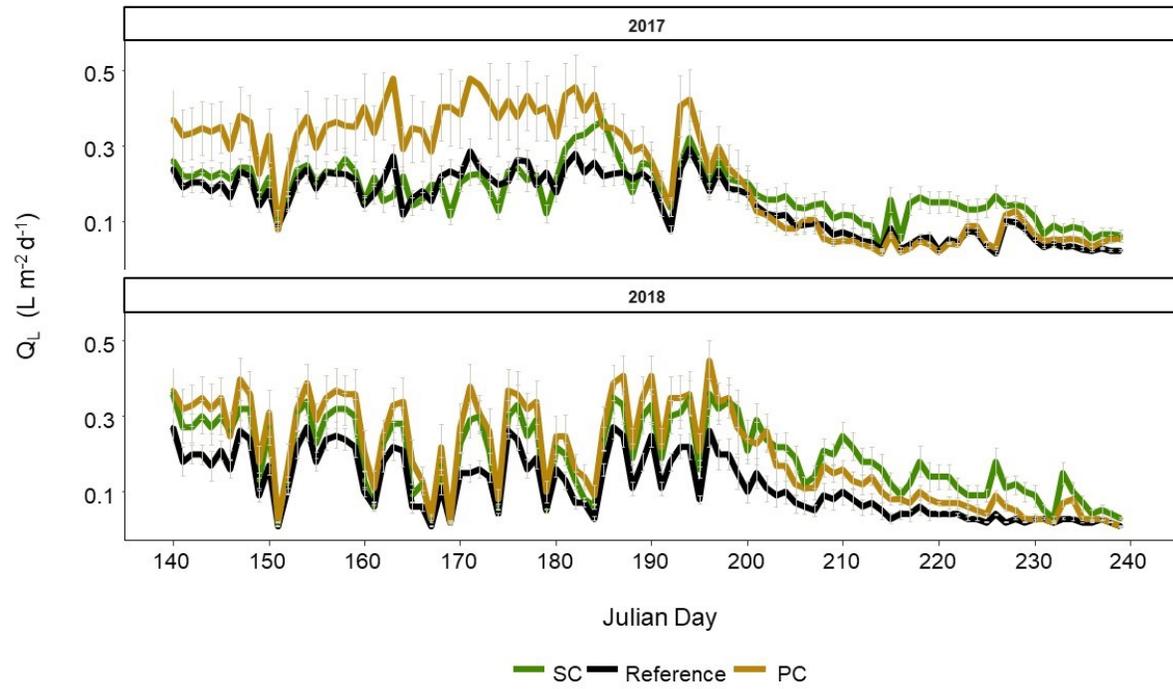


Figure 2-8. Mean daily transpiration per leaf area Q_L ($L\ m^{-2}\ d^{-1}$) (\pm standard error) for reference, strip-shelterwood (SC), and partial-cut (PC) throughout the growing season (Julian Day 139–239) (May 19–August 29) during 2017, 2018.

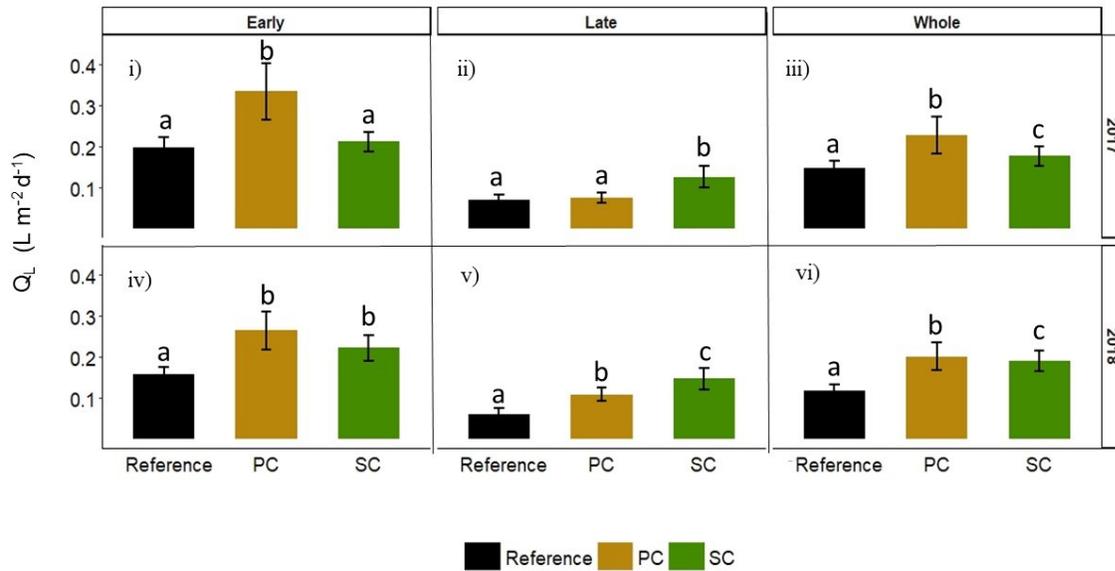


Figure 2-9. Mean daily transpiration per leaf area (Q_L ; $L m^{-2} d^{-1}$) for reference, strip-shelterwood (SC), and partial-cut (PC) during the 2017 i) early (May 19–July 15), ii) late (July 16–August 29), and iii) whole (May 19–August 29) growing season and the 2018 iv) early (May 19–July 15), v) late (July 16–August 29), and vi) whole (May 19–August 29) growing season. Error bars represents one standard error. Different letters are representative of significantly different Q_L ($p < 0.05$).

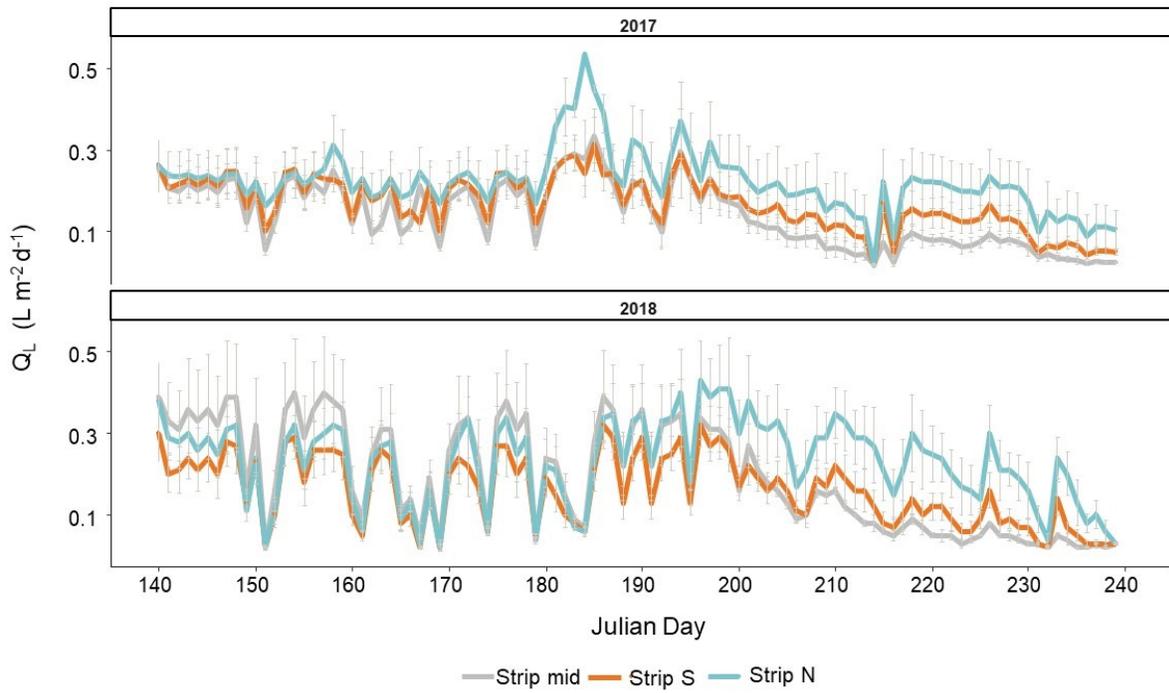


Figure 2-10. Mean daily transpiration per leaf area Q_L ($L\ m^{-2}\ d^{-1}$) (\pm standard error) within strip-shelterwood (Strip mid, Strip N, and Strip S) throughout the growing season (Julian Day 139–239) (May 19–August 29) during 2017, 2018.

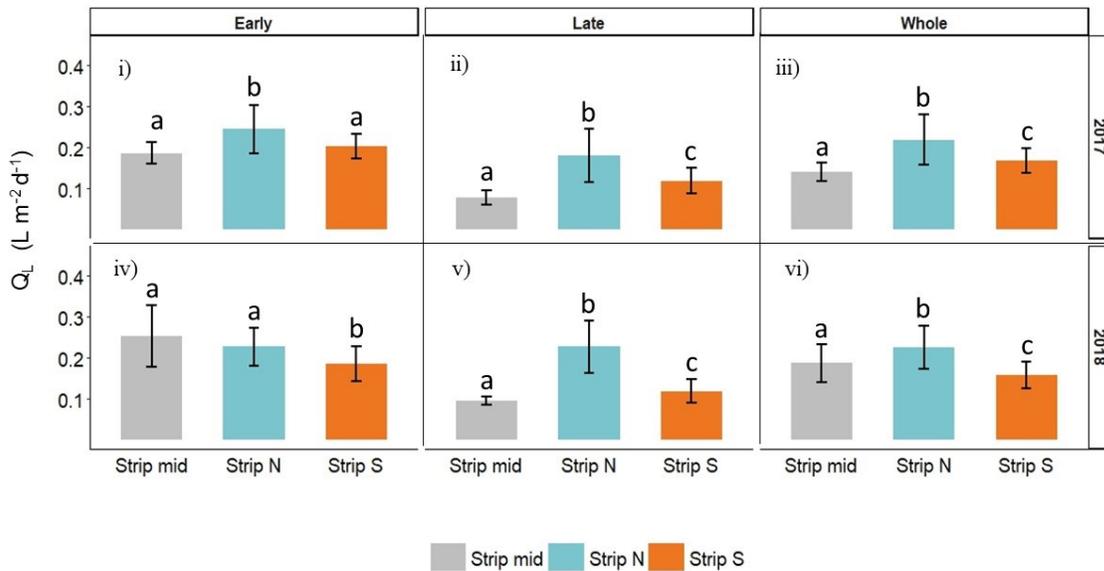


Figure 2-11. Mean daily transpiration per leaf area (Q_L ; $L\ m^{-2}\ d^{-1}$) within strip-shelterwood (Strip mid, Strip S, Strip N) during the 2017 i) early (May 19–July 15), ii) late (July 16–August 29), and iii) whole (May 19–August 29) growing season and the 2018 iv) early (May 19–July 15), v) late (July 16–August 29), and vi) whole (May 19–August 29) growing season. Error bars represents one standard error. Different letters are representative of significantly different Q_L ($p < 0.05$).

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Chapter 3: Effects of partial-cut and strip-shelterwood harvesting on atmospheric variables and soil moisture availability regulating post-harvest transpiration of lodgepole pine.

3.1 Introduction

Interactions between forest vegetation and microclimate play an important role in governing stand growing conditions and the outcome of sustainable forest management strategies to promote stand and forest health (Aussenac 2000). Forest cover modifies climatic parameters within the stand (Aussenac 2000). By removing part or all of the forest canopy, forest harvesting can alter the spatial pattern of microclimate variables such as solar radiation, wind, air temperature, and relative humidity which can affect soil water balance and water relations of the remaining un-harvested residual trees. Forest harvest strategies such as partial-cutting (PC) and strip-shelterwood (SC) may be considered as alternative low-intensity forest management strategies to address broader regional landscape management objectives such as limit impacts of forest harvesting on water resources and wildlife habitat. However, post-harvest changes in microclimate and soil water balance may also alter growing conditions for residual trees. Partial canopy removal may result in decreased competition for nutrients, water, and light within the residual stands, potentially increasing the growth (and economic value) of the remaining trees.

Trees are positioned at the transition point between below- (soil moisture) and above-ground (atmospheric) components of the soil-tree-atmosphere continuum. The growth and transpiration of un-harvested residual trees is largely governed by the extent to which partial canopy removal affects both above-ground microclimate variables such as air temperature, humidity, radiation, and wind and their linkage with below-ground factors regulating soil moisture availability (soil water content and water potential). Partial canopy removal can increase overall evaporative demand for moisture through the combined effects of increased wind penetration into the stand and increased radiation which can potentially result in increased air temperatures and vapour pressure deficits (Bladon et al. 2006; Staebler 1956; Ruel et al. 2001). In contrast, reduced forest canopy density reduces canopy interception of precipitation (rain or snow) resulting in increased precipitation inputs (Aussenac and Granier 1987; Simonin et al. 2007) which along with reduced canopy water uptake can increase soil water availability for residual trees (Lagergren et al. 2008; Bladon et al. 2006). This may be particularly important

for management strategies aimed at limiting hydrologic changes after forest harvesting where changes in microclimate or soil moisture may affect or even compensate for the harvest associated change in watershed evapotranspiration. Generalizing harvest effects on the transpiration and growth of the residual trees is difficult because of the complex interaction between spatial patterns of soil moisture, atmospheric moisture demand (e.g air temperature, humidity, wind), and species-specific stomatal response to these conditions (Lopushinsky and Klock 1974). For example, while moderate research attention has focused on the atmospheric or edaphic influences on the post-harvest transpiration response of juvenile lodgepole pine stands (Reid et al. 2006), far less is known about the combined influence of both above- and below-ground drivers on the post-harvest transpiration response of residual, mature (> 50 years of age) stands. The adaptation of mature lodgepole pine to the new growing conditions after low-intensity harvest strategies has not (to my knowledge) been previously documented. However because mature stands are the primary focus of most forest harvesting operations, this lack of information represents an important knowledge gap needed to inform strategies employing low-intensity harvesting to address broader regional landscape management objectives. This information is also particularly important in developing management strategies to limit the impacts of forest harvesting on water resources.

Accordingly, the broad goals of this study were to evaluate spatial patterns of soil moisture and atmospheric moisture demand two to three years after PC and SC harvesting in mature lodgepole pine stands in the forested Rocky Mountain region of south-west Alberta. Specific study objectives were to: a) evaluate the influence of PC and SC harvesting on seasonal patterns of microclimate variables governing atmospheric demand for moisture (above-ground controls) and soil moisture content and soil water potential (below-ground or edaphic controls); and b) evaluate the relationship between harvest associated changes in above- and below-ground controls and the transpiration response of PC and SC residual stands, and c) to explore the combined effects of both atmospheric and edaphic factors after harvesting to shed light on the relative influence of these controls on post-harvesting transpiration.

3.2 Materials and methods

3.2.1 Study area

This study was conducted in Star creek watershed in Crowsnest Pass, Alberta (49°37'N, 114°40'W, ~1600 m elevation). This headwater catchment is north, north-east facing, situated within the Oldman river basin on the eastern slopes of the Rocky Mountains in southern Alberta (Figure 1-1). Detailed descriptions of forest cover and sub-surface geology are outlined in section 2.2.1. Mean annual precipitation and temperature is 882 mm and 4.6°C, respectively (Silins et al. 2014; Emelko et al. 2016). From 2006–2016 the mean growing season (May–August) precipitation was 284 ± 16 mm (standard error).

This study was conducted during the snow-free season from May–August in 2017 and 2018, which represents, the primary growing season for the majority of tree growth in this region. Growing season precipitation during the two years of study (2017, 2018) was 119 mm and 129 mm, respectively.

Strip-shelterwood (SC) harvesting consisted of alternating harvested and un-harvested (reserve) strips where harvesting comprised 30 % (44 ha) of the lower section of the Star east sub-catchment (147 ha). Dispersed and patch-retention partial-cut (PC) harvesting was conducted across 58 % (55 ha) of the McLaren sub-catchment (95 ha). This study focused on the dispersed PC region, instead of the patch retention PC, which was harvested with an objective to retain single, dominant trees at approximately 5 x 5 m spacing. Plot layouts in reference, SC, and PC are described in section 2.2.2.

3.2.2 Instrumentation

Two meteorological stations were installed on October 2016 in the SC stand – one in the reserve and another in the harvested strip and on May 2017 in the reference and PC stands (Figure 2-1). The meteorological stations in the PC and reference stands were installed within 10 m of sap flow sensor-instrumented trees. In the SC stand, one meteorological station was installed in the middle of the reserve strip (7–17 m from sap flow instrumented trees) and one meteorological station was installed in the harvested strip (17 m from the reserve strip).

Meteorological instruments were mounted below canopy (3 m above ground) and at canopy height (14 m above ground) on a 15 m radio tower. At each meteorological station, similar instrument configurations were set up at both heights, with the exception of net radiation (Q^* ; Wm^{-2}) and shortwave radiation (Q ; $W m^{-2}$), which were installed only at canopy height. Q^* data was collected using a NR-Lite Net Radiometer (Campbell Scientific, Logan, UT, USA). Q was measured with a SP Lite2 Pyranometer (Campbell Scientific, Logan, UT, USA). Air temperature (T_a ; °C) and relative humidity (RH; %) were measured using a CS215 Temperature and Relative Humidity Probe (Campbell Scientific, Logan, UT, USA). T_a and RH were used to calculate ambient vapour pressure (e_a ; kPa), saturation vapour pressure (e_s ; kPa) and vapour pressure deficit ($e_s - e_a$) (D ; kPa). Wind speed (u ; ms^{-1}) was measured using an RM Young Anemometer 05103 (Campbell scientific, Logan, UT, USA). Cumulative precipitation data was collected using a Jarek Tipping Bucket Rain Gauge (Geo Scientific Ltd., Vancouver, Canada) located within a kilometer of the SC, PC, and reference stands.

Each meteorological station was powered with one 30 Watt polycrystalline solar panel (Matrix Infinity, Canada) and one 12 Volt deep cycle battery (Interstate Batteries, Canada). Prior to purchase in July 2016, all meteorological instruments were calibrated at the manufacturer's facility (Campbell Scientific, Logan, UT, USA). The RM Young Anemometer was corrected for the south direction in the field at the time of installation. All atmospheric variables were sampled every 20 seconds and averaged across the hour using a CR1000 datalogger (Campbell Scientific, Logan, UT, USA).

3.2.3 Atmospheric variables

Atmospheric moisture demand (E_o ; $mm d^{-1}$) was calculated in the reference, SC, and PC stands from mean hourly atmospheric variables measured at canopy height from May 19–August 29, 2017 and 2018 using the original Penman-combination equation (Giambelluca and Nullet 1992) (Equation 3-1):

$$E_o = \frac{(\Gamma \Pi) + \gamma((0.263 + 0.138\mu)D)}{(\Gamma + \gamma)} \quad [3-1]$$

Where Γ (kPa °C⁻¹) is the slope of saturation vapour pressure versus temperature curve, Π is net radiation expressed as an equivalent, daily water depth (mm d⁻¹) = 0.0353Q* (W m⁻²) (Giambelluca and Nullet 1992), and γ is the psychrometric constant (0.056 kPa °C⁻¹) (Allen et al. 1998). D is the vapour pressure deficit (mb), and μ (m s⁻¹) is the wind speed. Q* was not collected until 2018, therefore regressions with Q* and Q were used to back-calculate (gap fill) Q* in 2017. For the SC stand, μ and Q* were averaged between the reserve and harvested meteorological stations because I concluded a single measurement of μ and Q* in the centre of the reserve strip did not meaningfully represent conditions across exposed and interior portions of the strip. RH, Ta, and D all showed no significant difference between the SC harvested and reserve strip therefore these atmospheric variables were not averaged, and the reserve strip atmospheric variables were used to best represent what the residual trees were experiencing for atmospheric moisture demand.

3.2.4 Edaphic variables

Daily, depth-averaged (0–20 cm, and 0–60 cm) volumetric soil moisture (θ ; cm³ H₂O cm⁻³ soil) was measured biweekly with the Time Domain Reflectometry (TDR) method (Topp et al. 1980) using a Tektronix Inc. 1502C cable tester (Tektronix Inc., Beaverton, OR, USA) employing vertically-oriented TDR probes (0–20 cm; 0–60 cm) from June 6–August 29 2017 and May 12–August 29 2018.

Soil moisture transects were installed in the reference, PC, and SC stands. Two, 100 m long transects approximately 30 m apart were installed in the reference stand, where each transect included 10 measurement locations spaced 10 m apart. Four, 50 m long transects approximately 30 m apart were installed in the PC stand, where each transect included 5 measurement locations spaced 10 m apart. Two, 210 m long transects approximately 30 m apart were installed in the SC stand spanning across the harvested and reserve strips, where each transect included 42 measurement locations spaced 5 m apart. At each measurement location, two 25 cm long (3.2 mm diameter) stainless steel rods and two 65 cm rods were inserted 20 cm and 60 cm below ground in the leaf litter and mineral soil.

Soil cores (0–20 cm, 8 cm diameter) were collected at 11 locations in the reference, SC, and PC stands on June 2018 to confirm the TDR calibration equation. Deeper cores were not

collected due to large cobbles preventing volumetric sampling of a soil core. Volumetric soil water content was consistent between the TDR method and the volumetric soil cores ($R^2 = 0.89$, $n = 11$) within the 0–20 cm layer.

TDR sampling locations within 10 m of the sap flow sensor-instrumented trees were used for calculation of mean θ for each stand ($n = 4$ for the reference stand, $n = 5$ for the PC stand, and $n = 22$ for SC stand). The TDR measurement locations within the SC stand were averaged into four different groups to reflect instrumented tree positions described in section 2.2.2 (SC as a whole, Strip N, Strip S, and Strip mid). Average θ for the harvested strips (both north and south of the reserve strip) was estimated by averaging four TDR locations on each side of the strip.

Mean, hourly volumetric soil moisture (θ ; $\text{cm}^3 \text{H}_2\text{O cm}^{-3}$ soil) and temperature ($^{\circ}\text{C}$) for the reference, PC, and SC stands were measured every 20 min and averaged over the hour using Decagon 5TM soil moisture and temperature probes (Hoskin Scientific, BC, Canada) from June 6–August 29 2017 and May 12–August 29 2018. 5TM sensors were installed in a soil pit (approximately 20 m from the sap flow instrumented tree transects) horizontally at depths of 5 cm, 20 cm, and 60 cm in each of the reference, PC, and SC stands in June 2017. All sensors were connected to an Em50 Decagon datalogger (Decagon Devices, Pullman, WA, USA).

Soil matric potential (Ψ ; kPa) was measured using soil matric potential sensors (MPS-1, Decagon Devices, Pullman, WA, USA). Each MPS-1 sensor was inserted into wet-native soil to generate a sealed contact with the ceramic plate. The MPS-1 sensors were installed at 10 cm in the mineral soil at each sap flow tree location: reference ($n = 6$), PC ($n = 5$), and SC ($n = 11$). Trees that were within two meters of each other were allocated the same MPS-1. All MPS-1 sensors were connected to an Em50 Decagon datalogger (Decagon Devices, Pullman, WA, USA) and recorded every 20 minutes and averaged daily in reference, PC, SC, and at different positions within the reserve strip (Strip N, Strip S, and Strip mid). Averages of Ψ mirrored the sap flow averaging: reference ($n = 6$), PC ($n = 5$), SC ($n = 11$), Strip N ($n = 4$), Strip S ($n = 4$), and Strip mid ($n = 4$).

Soil particle size analysis was measured on soil samples from 0–20 cm and 20–60 cm in the reference, SC, and PC stands using the Bouyoucos hydrometer method (Carter and Gregorich 2008), and used to estimate percent (mass) of sand ($50 \mu\text{m} - 2 \text{mm}$ diameter), silt ($2 - 50 \mu\text{m}$) and clay ($< 2 \mu\text{m}$ diameter).

3.2.5 Atmospheric and edaphic indices

Two separate indices were used to examine the combined effects and the relative influence of harvest associated changes in above- and below-ground controls on transpiration after PC and SC harvests.

3.2.5.1 Hydrometeorologic Dryness Index (HDI)

The hydrometeorologic dryness index (HDI; $\text{mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$) was used to evaluate the overall effects of both the atmospheric and edaphic drivers in the reference, PC, and SC stands (Martin et al. 2017) (Equation 3-2):

$$\text{HDI} = \frac{D}{\theta} \quad [3-2]$$

Where hourly D (mb) was measured at each meteorological station in the SC, PC, and reference stands, and θ is the mean, hourly volumetric water content ($\text{cm}^3 \text{H}_2\text{O cm}^{-3} \text{soil}$) in each stand. Under dry conditions, θ decreases and D increases, thereby increasing the HDI, whereas under moist conditions, D decreases and θ increases, thereby decreasing HDI. HDI_{crit} ($57.2 \text{ mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$) was considered a critical threshold value of the HDI where radial growth in four conifers (Douglas fir, Ponderosa pine, western larch (*Larix occidentalis*), and Engelmann spruce) across a variety of moisture regimes has been shown to decline above this value (Martin et al. 2017). In the reference, SC, and PC stands, the days that met the condition $\text{HDI} < \text{HDI}_{\text{crit}}$ were summed up and reported as days of potential radial growth.

3.2.5.2 Relationships between stomatal conductance, vapour pressure deficit, and soil wetness

The relationships between stomatal conductance with D and θ were also used to explore the relative role of harvest associated changes in above- and below-ground controls regulating transpiration following PC and SC harvests after Novick et al. (2016). Stomatal conductance (g_s ; mm s^{-1}) was estimated from measured transpiration per leaf area Q_L ($\text{L m}^{-2} \text{h}^{-1}$) (Chapter 2) and a

simplified version of the Penman-Monteith equation (Martínez-Vilalta et al. 2003; Kozłowski 1968; Jarvis and Stewart 1979) (Equation 3-3).

$$g_s = \frac{\gamma \lambda Q_L}{\rho_a c_a D} \quad [3-3]$$

Where λ is the latent heat of vapourization (MJ kg^{-1}), ρ_a is the density of air (1.225 kg m^{-3}), c_a is the heat capacity of air ($1.0 \cdot 10^{-3} \text{ MJ kg}^{-1} \text{ K}^{-1}$), and γ is the psychrometric constant ($0.056 \text{ kPa } ^\circ\text{C}^{-1}$) (Martínez-Vilalta et al. 2003; Monteith 1965; Reid et al. 2006). Similar to the approach used by Novick et al. (2016), the coupling of Q_L to D was evaluated by exploring variation in the relationship between D and g_s at different levels (percentiles) of soil wetness (Equation 3-4):

$$g_s = g_{s\text{ref}} [1 - m \cdot \ln D] \quad [3-4]$$

Mean hourly measurements/estimates of g_s , D , and θ were used for the analysis where relationships between D and g_s for PC, SC, and reference stands were evaluated across four levels of increasing θ (0–25, 25–50, 50–75, and 75–100 percentiles) for 2018. The soil moisture percentiles were representative of the distribution of shallow soil moisture rather than the absolute values in the reference, PC, and SC stands, where the SC stand demonstrated an elevated range of soil moisture compared to the other stands (Figure 3-9). The sensitivity of g_s to D or θ is described by the reference stomatal conductance ($g_{s\text{ref}}$; mm s^{-1}) and the slope of the relationship with D (m ; kPa^{-1}) (Novick et al. 2016; Oren et al. 1999) (Equation 3-4). Reference stomatal conductance is the stomatal conductance when $D = 1 \text{ kPa}$. The parameter m (kPa^{-1}) “describes the sensitivity of surface conductance to D ” (Novick et al. 2016; Oren et al. 1999). Both parameters $g_{s\text{ref}}$ and m were determined from Equation 3-4 within each θ percentile category (quartile) by a linear regression of g_s versus $\ln D$ (Novick et al. 2016; Oren et al. 1999). The parameters derived from Equation 3-4 were then used to assess whether θ or D likely limited g_s in SC, PC, and reference stands.

3.2.6 Data analysis

Repeated measures ANOVA was used to evaluate differences in seasonal microclimate variables (T_a , RH, D, μ , Q^*), their combined effect on atmospheric moisture demand (E_o), soil moisture content (θ), and soil water potential (Ψ) between the reference, PC, and SC (harvested and reserve) stands. Linear mixed models were evaluated with day as the random component and a correlation structure (AR 1) for temporally auto-correlated data (Pinheiro et al. 2018). Welch's ANOVA was used if data met the assumption of normality but not homogenous variance. The Kruskal-Wallis test was used if data did not meet the assumption of normality but had homogenous variance. Otherwise least square means were used to evaluate differences in microclimate variables, E_o , θ , and Ψ between all study treatments.

Variation in transpiration as a function of atmospheric (E_o) and edaphic (θ) drivers, independent of harvesting, were evaluated. Daily transpiration, E_o , and θ in 2017 and 2018 were used in linear, mixed models with tree as the random component. Standardized coefficients of the model were extracted to determine the relative importance of explanatory variables to whole tree transpiration. Standardized coefficients are helpful when variables have different scales of measurement because they allow for comparability across variables by standardizing according to common characteristics – means and standard deviations (Kim and Ferree 1981). All analyses were implemented in R (R Core Team 2018), with significance reported relative to $\alpha = 0.05$.

3.3 Results

3.3.1 Microclimate conditions

Relationships between Q^* and Q during 2018 used to gap fill missing 2017 records for Q^* were $Q^* = 0.8027 Q - 56.952$ ($R^2 = 0.75$) for the reference stand, $Q^* = 0.8334 Q - 64.453$ ($R^2 = 0.99$) for the SC stand, and $Q^* = 0.6621 Q - 57.383$ ($R^2 = 0.92$) for the PC stand. All regressions were applied to the measured Q in 2017 to infer Q^* for 2017.

2017 and 2018 growing season averages of T_a ($^{\circ}\text{C}$), D (mb), RH (%), μ (m s^{-1}), Q^* (W m^{-2}), and daily E_o (mm d^{-1}) are presented in Table 3-1. While T_a , D, and RH did not vary significantly between harvest and reference stands ($p > 0.05$) minor (non-significant) differences

in mean D (3 % and 7 % greater in the SC stand and PC stand compared to the reference stand, respectively) and RH (2 % and 3 % less in the SC stand and the PC stand compared to the reference stand, respectively) were weakly evident. In contrast, μ was elevated by 50 % in the SC reserve strip, by 228 % in the SC harvested strip, and by 333 % in the PC stand compared to the reference ($p < 0.05$). Similarly, Q^* was elevated by 15 % in the SC reserve strip but was 6 % and 2 % lower in the SC harvested strip and PC stand compared to the reference ($p < 0.05$).

3.3.2 Combined atmospheric controls (E_o)

Daily atmospheric demand for moisture (E_o ; mm d^{-1}) ranged from 0.2–7.4 mm d^{-1} across both growing seasons in the SC, PC, and reference stands (Figure 3-1). Mean E_o was greater in SC and PC stands compared to the reference stand throughout the growing season. The 2017 average daily E_o in the reference stand was 4.5 mm d^{-1} , compared to 4.7 mm d^{-1} , and 4.9 mm d^{-1} for SC and PC, respectively. In 2018, the reference was 4.0 mm d^{-1} , SC was 4.3 mm d^{-1} , and PC was 4.3 mm d^{-1} (Table 3-1). With respect to total E_o , all three sites were significantly different in 2017, whereas SC and PC were only marginally significantly different from reference in 2018 (Figure 3-2). Total growing season E_o ranged from 405–490 mm for the reference, SC, and PC stands. Early season (May 19–July 15) cumulative E_o ranged from 246–307 mm and the late season (July 16–August 29) ranged from 159–208 mm. In the SC stand total E_o was 6 % and 7 % greater, while in the PC stand total E_o was greater by 9 % and 8 % compared to the reference stand for 2017 and 2018, respectively.

3.3.3 Relationship of transpiration with E_o

The relationships between mean, hourly transpiration (Q_L ; $\text{L m}^{-2} \text{h}^{-1}$) and atmospheric moisture demand (E_o , mm h^{-1}) varied strongly between the early and late season (same dates as section 2.3.2) in the reference, PC, and SC stands (Figure 3-3 and Table 3-2). Transpiration increased strongly with E_o early in the growing season while Q_L was far less sensitive to variation in E_o during the latter part of the growing season in all stands for both 2017 and 2018 (Figure 3-3). However, early season increases in Q_L with E_o were greater in both PC and SC stands compared to the reference stand. Among harvest treatments, transpiration was most

strongly elevated in the PC stand compared to the SC stand and the reference stand. Differences in relationships between Q_L and E_o among harvested and reference stands were notably weaker late in the growing season in both 2017 and 2018. In contrast, late season Q_L in the SC stand was greater than the PC stand which was greater than the reference stand in both 2017 and 2018.

Similar patterns in the relationships between mean hourly transpiration (Q_L ; $L\ m^{-2}\ h^{-1}$) and atmospheric moisture demand (E_o ; $mm\ h^{-1}$) during the early and late season (same dates as section 2.3.2) were evident across different positions within the reserve strip of the SC stand (Strip N, Strip S, and Strip mid; Figure 3-4 and Table 3-3). The increase in early season Q_L to E_o in the Strip N position was greater than Strip S which was greater than Strip mid in 2017, in contrast to 2018 when Strip mid was greater than Strip N which was greater than Strip S. Late season Q_L was also less sensitive to variation in E_o , however trees in the N position showed greater Q_L and greater sensitivity to variation in E_o than Strip S and Strip mid during both years (Figure 3-4).

The standardized coefficients extracted from the mixed model showed that the variation of transpiration was most significantly influenced during the early season by atmospheric controls (E_o , standard coefficient = 0.48) compared to -0.031 as the standard coefficient for below ground soil moisture controls (0–20 cm depth layers).

3.3.4 Edaphic conditions

Soil textural class was similar between the reference, SC, and PC stands. The texture of the top 0–20 cm samples was loam in the SC stand and sandy loam in the reference and PC stands. The texture of the 20–60 cm samples was loam in the SC stand and sandy clay loam in the reference and PC stands (Table 3-4). The average thickness of the LFH layer for the 0–20 cm and 0–60 cm TDR measurement locations were 4.4 ± 0.8 cm and 5.3 ± 1.0 cm, respectively for the reference stand, 5.9 ± 0.9 cm and 6.5 ± 0.9 cm for the SC stand, and 3.4 ± 0.9 cm and 4.2 ± 1.2 cm for the PC stand (data not shown).

Surface soil moisture (0–20 cm) differed strongly across stands where TDR-measured θ (0–20 cm) was consistently greatest in SC compared to the reference stand, while θ in the reference stand was marginally greater than PC (Figure 3-5). For all three treatments, TDR-measured θ (0–20 cm) ranged from 0.1–0.4 $cm^3\ cm^{-3}$ with a general decline towards August 29.

Surface soil moisture in SC was 67 % and 35 % greater, whereas PC was 13 % and 6 % less than the reference stand in 2017 and 2018, respectively. Soil moisture in SC, PC, and reference stands were all significantly different from each other throughout 2017 whereas in 2018, soil moisture in only the SC stand was significantly greater than both PC and reference stands. Similarly, surface θ (0–20 cm) in the northern portion of the reserve strip (Strip N) was consistently greater than both Strip S and Strip mid (Figure 3-6). Soil moisture in Strip N was 21 % and 35 % greater than Strip mid in 2017 and 2018, respectively ($p < 0.05$). Soil moisture in Strip S was 8 % less ($p < 0.05$) in 2017 but was similar to Strip mid in 2018. Soil moisture in Strip N was 17 % and 18 % greater than Strip S in 2017 and 2018, respectively ($p < 0.05$). Soil moisture varied significantly across (Strip N, Strip S, and Strip mid) throughout 2017 whereas in 2018, only Strip N differed from Strip S and Strip mid.

Strip harvesting had a large effect on surface soil moisture through the growing season (Table 3-5). Mean θ in the top 20 cm of harvested strips was significantly greater than in the reserve strips where the harvested strips on the southern side (more exposed to direct radiation, see Figure 2-1) of the reserve strips had 36 % greater moisture and the harvested strip on the more shaded northern side had 61 % greater moisture than the un-harvested reserve strip ($p < 0.05$, Table 3-5). Across the harvested strip a gradient of surface soil moisture developed (from the northern shaded side to the direct radiation, southern side). The gradient of soil moisture changed within the growing season where during the early season the gradient was approximately 15 % higher on the northern side, however with the onset of the drier season the gradient increased from 28 % to 35 % higher on the northern side compared to the southern side in late July to mid-August, respectively.

Growing season averaged TDR-measured θ in the deeper 20–60 cm soil layers of the PC stand was greater than the SC stand which was greater than the reference stand for both 2017 and 2018 (Table 3-6). For all three treatments, deeper θ (20–60 cm) ranged from 0.2–0.4 cm³ H₂O cm⁻³ soil with a general decline towards August 29. Soil moisture of deeper soils in PC were 33 % and 50 % greater, while θ in SC was similar to the reference stand in 2017 and 2018, respectively (Table 3-6). Similarly, mean growing season deeper θ (20–60 cm) in differing positions in the reserve strip was greatest in Strip mid compared to Strip S and Strip N for both 2017 and 2018 (Table 3-6). Deeper θ in Strip N was 18 % and 23 % less, while Strip S was 5 % and 9 % less than deep soil moisture in Strip mid during 2017 and 2018, respectively.

Consistent with spatial and temporal patterns in soil moisture, mean daily soil matric potential (Ψ ; kPa) showed strong seasonal variation across the growing season in all stands (Figure 3-7 and 3-8). Variability between the matric potential sensors was moderate ($\sim 30\%$), therefore while absolute values were interpreted with caution, relative differences across the season provided insights into spatial and temporal patterns. Mean soil Ψ was consistently greatest in the SC harvested stand and lowest in the PC harvested stand and was significantly different among all treatments ($p < 0.05$) for both 2017 and 2018. For all three treatments, mean daily Ψ ranged from 0 to -350 kPa and showed a gradual decline to August 29 (Figure 3-7). Mean growing season Ψ in the SC stand was 28 % and 7 % greater, while mean Ψ in the PC stand was 41 % and 65 % less compared to the reference stand in 2017 and 2018, respectively (Table 3-1). Similarly in the reserve strip, mean daily Ψ in the Strip mid position was constantly greater than in Strip N which was greater than Strip S for both 2017 and 2018. Mean daily Ψ ranged from 0 to -300 kPa (Figure 3-8) with Strip mid being significantly different from Strip N and Strip S in 2017 and all reserve positions were significantly different in 2018. Mean growing season Ψ in Strip N was 66 % and 16 % less, while Ψ in Strip S was 61 % and 36 % less than in Strip mid during 2017 and 2018, respectively.

3.3.5 Relationship of transpiration and edaphic controls

Relationships between mean daily Q_L ($L\ m^{-2}\ d^{-1}$) and mean daily surface (0–20 cm) θ ($cm^3\ H_2O\ cm^{-3}$ soil) across the growing season illustrated highly variable sensitivity (regression slopes) of Q_L to variation in θ across reference, PC, and SC stands (Figure 3-9 and Table 3-7). Slopes of the regression between Q_L and θ during the early growing season in 2017 were 4.83 and 3.17 for PC and reference stands compared to 0.24 for SC, while late season regressions were more similar among stands (3.87 for PC, 4.81 for reference, and 2.50 for SC). In 2018, no coherent relationship between Q_L and θ was evident during the early growing season, while during the late season the slopes of these relationships were 2.85 for PC, 3.13 for reference, and 3.43 for SC.

While no generally consistent pattern in the relationships between Q_L and θ were observed during the early season, these relationships indicated a greater degree of sensitivity of Q_L to variation in θ later in the growing season of both years. This was confirmed by the

standardized coefficients from the mixed model that showed that the variation in transpiration as a function of θ was the dominant control over transpiration during the late season with a standardized coefficient of 0.51 compared to 0.24 for the above ground driver (E_o) during the same period.

3.3.6 Combined influence of atmospheric and edaphic controls on transpiration

The hydrometeorologic dryness index (HDI) ($\text{mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$) for the 0–20 cm and the 20–60 cm soil layer was estimated and compared with daily transpiration (Q_L) in the reference, SC, and PC stands for the 2017 and 2018 growing season in Figure 3-10 and Figure 3-11. For HDI, the mean and range of this index is less important than other key parameters such as the a) initial cross-over date (date when low early season HDI exceeds transpiration rates (Q_L) during drier, late growing season periods) and b) when HDI indicates favorable conditions for radial tree growth ($\text{HDI} < \text{HDI}_{\text{crit}} 57.2 \text{mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$) (Martin et al. 2017).

HDI and Q_L for both shallow (0–20 cm) and deeper (20–60 cm) soil layers co-varied throughout the two growing seasons in 2017 and 2018 with the shallow layer demonstrating more variation in the HDI index. During the early growing season, when conditions were non-moisture limiting, Q_L remained high with a corresponding low HDI. However, later in the season when environmental conditions became drier in all stands, HDI increased with a corresponding decline in Q_L . Within each stand, similar patterns of increasing late season HDI corresponding to declining Q_L as moisture limitations developed were evident during both years, however the timing of this pattern varied among stands. The cross-over date is representative of a change from wetter to drier conditions indicated by a rising HDI with a declining Q_L likely reflecting stomatal restrictions to conserve water. HDI based on shallow soil moisture storage (0–20 cm) exceeded Q_L in the reference stand on Julian day 203 and 210 in 2017 and 2018, respectively (Table 3-8), whereas this occurred in the SC stand 5 days and 10 days later in 2017 and 2018, respectively. This suggests that SC was less moisture limited than the reference stand in both years. Cross-over dates in the PC stand occurred within a day of the reference stand. Cross-over dates for HDI and Q_L based on soil moisture of deeper soil layers (20–60 cm) depth did not seem to differ in 2017. However in 2018, the cross-over date in the SC and PC stand occurred 10 and 8

days later than the reference stand, respectively, suggesting residual trees in both harvested stands were less moisture limited than the reference stand in 2018.

Similarly, HDI in the shallow (0–20 cm) soil layer was less than HDI_{crit} (indicating favourable conditions for radial tree growth) for an average of 36 days in the reference stand, 51 days in the SC stand, and 36 days in the PC stand (Table 3-9). The SC stand had 40 % greater number of days when HDI was below HDI_{crit} and the PC stand had the same number of days that $HDI < HDI_{crit}$ compared to the reference stand. In the deeper (20–60 cm) soil layer HDI was less than HDI_{crit} for an average of 51 days in the reference stand, 49 days in the SC stand and 66 days in the PC stand (Table 3-9). The SC stand had a 4 % fewer days when HDI was below HDI_{crit} compared to the reference stand; in contrast to the PC stand which had 29 % greater number of days below this threshold compared to the reference stand. HDI of both shallow and deeper soil layers indicated more favourable conditions for radial growth in the harvested stands compared to the reference stand.

The relationships between the 2018 normalized stomatal conductance ($g_s g_{sref}^{-1}$; $mm\ s^{-1}\ mm^{-1}\ s$) and D (kPa) showed considerable variation of stomatal sensitivity to D across the variable soil moisture regimes (4 soil moisture quartiles) in the reference, SC, and PC stands (Figure 3-12). Under conditions where g_s is less sensitive to variation in soil moisture, relationships between $g_s g_{sref}^{-1}$ and D would show little variation in intercepts. In contrast, where g_s is more sensitive to variation in atmospheric drought, variation in regression slopes indicates greater sensitivity to D. Trees from all stands in this study showed considerable variation in both intercepts and slopes indicating a moderate to high degree of stomatal sensitivity to variation in both atmospheric and soil drought (Table 3-10). At the driest, lower quartile of soil moisture, trees in all stands showed little sensitivity (slope parameter m) in $g_s g_{sref}^{-1}$ to variation in D (Figure 3-12), whereas under moister conditions (upper soil moisture quartile), $g_s g_{sref}^{-1}$ was more sensitive (greater slope or parameter m) to variation in D (particularly in the PC and SC stands). However, the greatest differences were evident across stand types and the sensitivity of $g_s g_{sref}^{-1}$ to soil drought (intercepts). For example, $g_s g_{sref}^{-1}$ in the reference stand was reduced from approximately 1.79 to 0.59 (~ 67 %) when soil moisture was reduced to median values (50th percentile) and by a similar percentage (~ 67 %) in the PC stand. In contrast, $g_s g_{sref}^{-1}$ was reduced by a much lower proportion (~ 37 %) in the SC stand, indicating lower sensitivity to soil drought relative to the reference stand.

3.4 Discussion

Results of this study showed that spatial patterns of surface soil moisture and atmospheric moisture demand increased transpiration rates of residual lodgepole pine after harvesting with both distributed single tree PC, and spatially discrete SC harvesting strategies. The differential patterns of transpiration in the harvested and un-harvested stands mirrored the spatial distribution of altered post-harvest soil moisture and atmospheric moisture demand. Residual trees in all harvested and un-harvested sites were generally more influenced by atmospheric moisture demand earlier in the season when soil moisture was greater, but soil moisture was the main driver of tree water relations during the drier, late season.

3.4.1 Atmospheric demand and transpiration

Daily atmospheric moisture demand (E_o ; mm d^{-1}) was elevated in the strip-shelterwood (SC) and partial-cut (PC) stands compared to the reference stand throughout the season (Figure 3-1; 3-2). Differences in mean daily and total E_o between harvested and reference stands were consistent with similar effects on post-harvest changes in atmospheric demand for moisture reported by previous studies on partial cutting (Marenholtz et al. 2010; Bladon et al. 2006; Reid et al. 2006). Total E_o was greatest in the PC stand followed by the SC stand which were both greater than in the reference stand for both growing seasons. Wind speed and net radiation were the main factors driving this E_o response, where wind speeds increased by two–four fold in the harvested sites compared to the reference stand and net radiation decreased in the harvested sites, likely due to an increase in outgoing radiation. However, in this study the increase in E_o ($< 10\%$) in the harvested stands was less than the increases in E_o reported in Bladon et al. (2006) (290%) and Marenholtz et al. (2010) (37%). Differences in both harvest intensity and height of the anemometers were likely factors in explaining the discrepancy in E_o increases among studies, where Bladon et al. (2006) and Marenholtz et al. (2010) reported on changes in microclimate after 90% and 74% tree removal, respectively, compared to an average harvest intensity of 34% in this study. Similarly, anemometers were situated lower (12 m and 2 m above ground, respectively) compared to the 14 m in this study.

Hourly transpiration (Q_L , $L\ m^{-2}\ h^{-1}$) as a function of hourly atmospheric moisture demand (E_o , $mm\ h^{-1}$) under clear-sky conditions (both early and late season) displayed an asymptotic relationship during the morning to early afternoon hours (7:00–14:00) (Figure 3-3). The reduction in both mid-day and late growing season Q_L likely reflected stomatal closure to limit the loss of hydraulic conductivity and cavitation during high mid-day atmospheric moisture demand and with the decline in soil moisture availability during the late season (Brix 1978; Lopushinsky and Klock 1974; Reid et al. 2006). However, despite high evaporative demand during the drier, late season, trees in both PC and SC stands were able to maintain greater transpiration rates compared to those in reference stands, illustrating the importance of even small increases in soil moisture in harvested sites during this period. In the SC stands, greater soil moisture during dry periods in Strip N were also associated with notably greater transpiration of trees in this position (Figure 3-4).

3.4.2 Soil moisture availability and transpiration

Shallow soil moisture θ (0–20 cm) was greater in the harvested sites due to the combined increases in throughfall of spring/summer rain that would occur after canopy removal and reduced total transpiration losses. Soil moisture (0–50 cm) has been observed to increase (4–30 %) after harvest due to reduced interception and increased infiltration (Lagergren et al. 2008; Bladon et al. 2006). In this study, shallow soil moisture (0–20 cm) increased by 50 % in the SC stand and decreased by 10 % in the PC stand compared to the reference stand while deeper soil moisture (20–60 cm) increased by 50 % in the PC stand and remained the same in the SC stand compared to the reference stand. The spatial pattern of moisture within the entire 0–60 cm TDR-measured profile likely governed the transpiration response of the residual stand. Other studies on soil moisture after thinning reported that during times of periodic drought, a small increase in soil moisture can benefit the stand greatly (Saxton and Rawls 2006; Lagergren et al. 2008). In this study, the key role of moisture was apparent in all stands during the 2017 and 2018 drought years. Both growing seasons during this study had < 50 % summer precipitation compared to the 10 year average and the PC and reference stands approached wilting point conditions (sandy loam to loam ($\theta \sim 11\ %$)) by late July in 2017 and 2018 (Saxton and Rawls 2006). The important role of soil moisture was further evident in the SC stand (specifically the northern side of the

strip). The alternating pattern in the SC stand of harvested and un-harvested strips delayed snowmelt due to shading, resulting in 18 % greater soil moisture and soil matric potential on the northern side compared to the southern side of the reserve strip. This moisture gradient was likely a crucial factor in the elevated transpiration response of trees in the Strip N position which likely reflected greater roots access to moisture through to the late, drier season.

3.4.3 Drivers of transpiration – atmospheric or edaphic?

Seasonal patterns of water use illustrated that both atmospheric moisture demand and soil moisture are the primary above- and below-ground controls over transpiration in lodgepole pine.

Both PC and SC harvest strategies produced strong variation in these drivers across the wetter and drier part of the growing season compared to the reference stand. The HDI reported in this study were within the range of HDI reported in Martin et al. (2017). HDI based on shallow (0–20 cm) soils in the SC stand remained low throughout the season indicating less moisture limitations compared to the reference and the PC stand. Similarly, the SC stand also displayed the greatest number of days with favourable radial growing conditions in both years where shallow $HDI < HDI_{crit}$ ($57.2 \text{ mb cm}^{-3} \text{ H}_2\text{O cm}^3 \text{ soil}$) and had a delayed initial cross-over date for both shallow and deep soil layers, indicating less moisture limitation in that stand. HDI based on deeper (20–60 cm) soils in the PC stand remained low throughout the season indicating less moisture limitations compared to the reference and the SC stand. Similarly, the PC stand displayed the greatest number of days with favourable radial growing conditions in both years where deeper $HDI < HDI_{crit}$ and had a delayed initial cross-over date for the deep soil layers in 2018 indicating less moisture limitation. The greater soil moisture availability both in the top 20 cm and the 20–60 cm soil layers in the harvested sites were likely key factors in the increased transpiration rates after harvesting in the PC and the SC stands.

The greater number of days with favourable radial growing conditions ($HDI < HDI_{crit}$) in the harvested stands compared to the un-harvested stand is an important finding. The alternative harvests were established in mature lodgepole pine stands where pre-harvest conditions likely had limited or stagnant growth and high competition for water and nutrients. Increasing the number of days with favourable radial growing conditions would be a benefit to the growth of the forest stand for future harvesting operations.

An analysis from Novick et al. (2016) was used as a second method to determine the primary driver (above-ground (D) or below-ground (θ)) that governed transpiration in the reference, SC, and PC stands. Exploring the sensitivity of g_s to D or θ across PC and SC harvesting strategies has not (in my knowledge) been previously documented. Previous studies have assessed the sensitivity of g_s to D or θ over a wide range of xeric to mesic biomes and/or species (Novick et al. 2016; Novick et al. 2019). However, this study assessed the same species but explored whether the influence of the above- or below-ground controls changed with harvest. Trees from all stands showed considerable variation in both the intercepts and slopes of the relationship between $g_s g_{sref}^{-1}$ and D. The intercept will decrease as the influence of soil conductance to stomatal conductance increases or also in response to the regulation of leaf water potential during periods of hydrologic stress (isohydric response) (Novick et al. 2016). Patterns of the relationships observed in this study were consistent with xeric type biomes with a dryness index (annual E_o precipitation⁻¹) of around five reported in Novick et al. (2016), while this study had a dryness index of 0.67 (10 year average of annual potential evapotranspiration is 589 mm and annual precipitation is 876 mm). This discrepancy is a result of the study location. The dryness index incorporates annual potential evapotranspiration and precipitation therefore in a snow-dominated forested watershed, such as the southern Rockies, evapotranspiration will be minimal with below zero temperatures when the precipitation is primarily tied up in snowpack.

The slopes of the relationship between $g_s g_{sref}^{-1}$ with D or θ were moderately similar among stands, however the decline in intercepts illustrates the transpiration responses to harvest effects on θ , where the SC stand in particular was not as sensitive to the onset of soil drought as the other two stands. Greater soil moisture in the SC stand was likely aided by greater θ in the adjacent harvested strips which likely contributed to elevated stomatal conductance in the SC stand compared to the other harvested and un-harvested stands with declining late season soil moisture.

Within each stand, the slope of the relationship between $g_s g_{sref}^{-1}$ and D in each soil moisture percentile provided an indication of the seasonal influence of each driver (D or θ) governing transpiration. Early season transpiration was governed by the atmospheric controls (D) when soil moisture was not limiting (Figure 3-12; greatest slope at highest soil moisture percentile). In contrast, the slope of the relationship between $g_s g_{sref}^{-1}$ and D at the lowest soil moisture percentile (0-25; late season moisture) was minimal likely because of stomatal closure

and little, if any sensitivity to atmospheric control. This idea of soil moisture primarily governing late season with atmospheric moisture demand exerting greater control in the early season is supported both by the relationships between transpiration (Q_L) and θ in Figure 3-9 and is consistent with suggestions from previous harvesting studies (Lagergren et al. 2008; Simonin et al. 2007).

Determining a concrete driver that influences transpiration can be difficult in a natural setting, let alone determining one between an un-harvested to harvested mature stand. Some studies have found that transpiration increases linearly with D but only to a certain point (0.8- 1 kPa) (MacKay et al. 2012) where other studies have concluded soil moisture is the limiting factor (Donner and Running 1986). While, it has been well-documented that water is the most important limiting resource for tree growth (Granier and Breda 1996; Wullschleger, S.D. and Hanson 2006), results of this study suggest that soil water availability appears as the main driver governing transpiration in the harvested and un-harvested stands while atmospheric moisture demand has a moderate impact but only during times of greater soil moisture conditions.

3.5 Conclusion

The atmospheric moisture demand increased and spatial patterns of surface soil moisture (0–20 cm) developed after two alternative harvest (PC and SC) strategies were employed in mature, moderately dense lodgepole pine. Elevated atmospheric moisture demand in the harvest stands was a product of higher wind speeds and modified radiation regimes. Surface soil moisture (θ) was the greatest in the SC stand particularly on the northern edge of the reserve strip, whereas the PC stand produced the greatest θ in the 20–60 cm depth. These spatial patterns were indicative of decreased interception and delay in snowmelt. The differential patterns of transpiration in the harvested and un-harvested stands mirrored the spatial distribution of soil moisture and atmospheric moisture demand. Timing was key in determining which above- or below-ground driver governed transpiration. Residual trees in all harvested and un-harvested sites were generally more influenced by the atmospheric moisture demand earlier in the season when soil moisture was non-limiting, but soil moisture was the main driver during the drier, late season.

Table and Figures

Table 3-1. Mean (\pm standard error) growing season micrometeorological conditions for 2017 and 2018 in reference, strip-shelterwood (SC), and partial-cut (PC) stands. Treatments with the same letter are not significantly different at $\alpha = 0.05$. E_o not estimated in SC (harvested).

2017	reference	SC (reserve)	SC (harvested)	PC	<i>p</i>	ref: SC (reserve): SC(harvested): PC
Ta (°C)	15.0 \pm 0.4	15.0 \pm 0.4	15.0 \pm 0.4	15.0 \pm 0.4	> 0.05	a:a:a:a
D (mb)	9.7 \pm 0.5	9.9 \pm 0.5	9.9 \pm 0.5	10.3 \pm 0.5	> 0.05	a:a:a:a
μ (m s ⁻¹)	0.30 \pm 0.02	0.30 \pm 0.02	0.98 \pm 0.03	1.30 \pm 0.06	< 0.05	a:a:b:c
Q* (W m ⁻²)	132 \pm 5	155 \pm 5	124 \pm 4	129 \pm 4	< 0.05	a:b:a:a
RH (%)	51 \pm 1	50 \pm 2	50 \pm 1	49 \pm 1	> 0.05	a:a:a:a
Ψ (kPa)	-174 \pm 8	-125 \pm 8	-	-246 \pm 12	< 0.05	a:b::-c
E_o (mm d ⁻¹)	4.5 \pm 0.2	4.7 \pm 0.1	-	4.9 \pm 0.1	< 0.05	a:b::-c

2018	reference	SC (reserve)	SC (harvested)	PC	<i>p</i>	ref: SC (reserve): SC(harvested): PC
Ta (°C)	14.0 \pm 0.4	14.2 \pm 0.5	14.8 \pm 0.5	15.0 \pm 0.4	> 0.05	a:a:a:a
D (mb)	8.6 \pm 0.5	8.9 \pm 0.5	8.9 \pm 0.5	9.2 \pm 0.5	> 0.05	a:a:a:a
μ (m s ⁻¹)	0.31 \pm 0.02	0.61 \pm 0.02	0.99 \pm 0.04	1.30 \pm 0.06	< 0.05	a:b:c:d
Q* (W m ⁻²)	121 \pm 5	139 \pm 6	113 \pm 5	118 \pm 4	< 0.05	a:b:a:a
RH (%)	56 \pm 1	54 \pm 2	55 \pm 2	54 \pm 1	> 0.05	a:a:a:a
Ψ (kPa)	-68 \pm 7	-63 \pm 7	-	-112 \pm 9	< 0.05	a:b::-c
E_o (mm d ⁻¹)	4.0 \pm 0.2	4.3 \pm 0.2	-	4.3 \pm 0.1	< 0.05	a:b::-b

Table 3-2. Summary of relationships between hourly Q_L ($L m^{-2} h^{-1}$) and E_o ($mm h^{-1}$) for reference, strip-shelterwood (SC), and partial-cut (PC) during early and late season in 2017, 2018, shown in Figure 3-3.

		2017		2018	
		Early	Late	Early	Late
reference		$y \sim 0.03\sqrt{x} - 0.005$ $R^2 = 0.83$	$y \sim 0.01\sqrt{x} - 0.002$ $R^2 = 0.48$	$y \sim 0.02\sqrt{x} - 0.002$ $R^2 = 0.71$	$y \sim -0.01\sqrt{x} + 0.003$ $R^2 = 0.61$
SC		$y \sim 0.05\sqrt{x} - 0.01$ $R^2 = 0.88$	$y \sim 0.02\sqrt{x} - 0.0004$ $R^2 = 0.74$	$y \sim 0.043\sqrt{x} - 0.01$ $R^2 = 0.78$	$y \sim 0.01\sqrt{x} - 0.002$ $R^2 = 0.56$
PC		$y \sim 0.07\sqrt{x} - 0.02$ $R^2 = 0.87$	$y \sim 0.02\sqrt{x} - 0.003$ $R^2 = 0.47$	$y \sim 0.07\sqrt{x} - 0.03$ $R^2 = 0.69$	$y \sim -0.0004\sqrt{x} + 0.002$ $R^2 = 0.002$

Table 3-3. Summary of relationships between hourly Q_L ($L m^{-2} h^{-1}$) and E_o ($mm h^{-1}$) for Strip mid, Strip S, and Strip N during early and late season in 2017, 2018, shown in Figure 3-4.

		2017		2018	
		Early	Late	Early	Late
Strip mid		$y \sim 0.04\sqrt{x} - 0.01$ $R^2 = 0.87$	$y \sim 0.01\sqrt{x} - 0.0003$ $R^2 = 0.68$	$y \sim 0.05\sqrt{x} - 0.01$ $R^2 = 0.83$	$y \sim 0.01\sqrt{x} - 0.0004$ $R^2 = 0.25$
Strip S		$y \sim 0.05\sqrt{x} - 0.01$ $R^2 = 0.89$	$y \sim 0.01\sqrt{x} - 0.0006$ $R^2 = 0.82$	$y \sim 0.03\sqrt{x} - 0.009$ $R^2 = 0.75$	$y \sim 0.01\sqrt{x} - 0.002$ $R^2 = 0.49$
Strip N		$y \sim 0.06\sqrt{x} - 0.01$ $R^2 = 0.87$	$y \sim 0.02\sqrt{x} - 0.0004$ $R^2 = 0.79$	$y \sim 0.04\sqrt{x} - 0.01$ $R^2 = 0.74$	$y \sim 0.04\sqrt{x} - 0.009$ $R^2 = 0.77$

Table 3-4. Mean soil texture using the Bouyoucos hydrometer method for shallow (0–20 cm) and deeper soil profiles (20–60 cm) in reference, strip-shelterwood (SC), and partial-cut (PC) stands. Soil texture is as follows- Sandy Clay Loam (SCL), Sandy Loam (SL), and Loam (L).

Harvest Treatment	0–20cm				20–60cm			
	Sand (%)	Silt (%)	Clay (%)	Soil Texture	Sand (%)	Silt (%)	Clay (%)	Soil Texture
reference	61	30	9	SL	48	24	28	SCL
PC	50	26	15	SL	59	18	23	SCL
SC	51	34	15	L	52	29	19	L

Table 3-5. Mean (\pm standard error) TDR-measured soil moisture (θ ; $\text{cm}^3 \text{H}_2\text{O cm}^{-3}$ soil) of shallow (0–20 cm) soil layers in reserve and harvested strips during 2017, 2018.

	2017	2018	2017 % Δ from reserve strip	2018 % Δ from reserve strip	<i>p</i> for 2017	<i>p</i> for 2018
Harvested strip (southern edge of reserve)	0.31 \pm 0.05	0.30 \pm 0.04	29 % \uparrow	43 % \uparrow	<0.05	<0.05
Reserve Strip	0.24 \pm 0.04	0.21 \pm 0.04	-	-	-	-
Harvested strip (northern edge of reserve)	0.37 \pm 0.05	0.35 \pm 0.05	54 % \uparrow	67 % \uparrow	<0.05	<0.05

Table 3-6 Mean seasonal TDR-measured soil moisture (θ ; $\text{cm}^3 \text{H}_2\text{O cm}^{-3}$ soil) in deeper soil layers (20–60 cm) during 2017 and 2018. The percent difference is shown relative to reference or Strip mid, respectively.

	2017	2018	% Δ 2017	% Δ 2018	<i>p</i> for 2017	<i>p</i> for 2018
reference	0.21	0.20	-	-	-	-
SC	0.21	0.20	+/- 0 %	+/- 0 %	>0.05	>0.05
PC	0.28	0.30	33 % \uparrow	50 % \uparrow	<0.05	<0.05
Strip mid	0.22	0.22	-	-	-	<0.05
Strip S	0.21	0.20	5 % \downarrow	9 % \downarrow	>0.05	<0.05
Strip N	0.18	0.17	18 % \downarrow	23 % \downarrow	>0.05	<0.05

Table 3-7 Relationships between mean daily Q_L ($L\ m^{-2}\ d^{-1}$) and mean daily TDR-measured θ (0–20 cm) ($cm^3\ H_2O\ cm^{-3}$ soil) during the early and late growing seasons in 2017 and 2018 presented in Figure 3-9.

2017	Early	Late
reference	$y = 3.17x - 0.23$ $R^2 = 0.12\ p < 0.05$	$y = 4.81x - 0.50$ $R^2 = 0.57\ p < 0.05$
SC	$y = 0.24x - 0.17$ $R^2 = 0.007\ p > 0.05$	$y = 2.50x - 0.31$ $R^2 = 0.49\ p < 0.05$
PC	$y = 4.83x - 0.29$ $R^2 = 0.38\ p < 0.05$	$y = 3.87x - 0.25$ $R^2 = 0.63\ p < 0.05$
2018	Early	Late
reference	$y = 0.51x + 0.07$ $R^2 = 0.012\ p > 0.05$	$y = 3.13x - 0.32$ $R^2 = 0.69\ p < 0.05$
SC	$y = -0.01x + 0.23$ $R^2 = 1E-05\ p > 0.05$	$y = 3.43x - 0.38$ $R^2 = 0.75\ p < 0.05$
PC	$y = -0.62x + 0.42$ $R^2 = 0.014\ p > 0.05$	$y = 2.85x - 0.23$ $R^2 = 0.89\ p < 0.05$

Table 3-8. Initial cross-over date (Julian Day) when growing season HDI in the shallow (0–20 cm) and deeper (20–60 cm) soil layer exceeds the transpiration Q_L ($L\ m^{-2}\ d^{-1}$) time series

	Initial cross-over date (0–20 cm)		Initial cross-over date (20–60 cm)	
	2017	2018	2017	2018
reference	203	210	209	211
SC	208	220	207	221
PC	202	211	208	219

Table 3-9. Length of time (days) during the growing season when conditions were favorable for tree radial growth ($HDI < HDI_{crit} 57.2 \text{ mb cm}^{-3} \text{ H}_2\text{O cm}^3 \text{ soil}$) in shallow (0–20 cm) and deeper (20–60 cm) soil layers in reference, SC, and PC stands during 2017 and 2018.

	HDI (0–20 cm)		HDI (20–60 cm)	
	2017	2018	2017	2018
reference	18	54	38	64
SC	33	68	31	67
PC	15	57	52	80

Table 3-10. Slope ($m; \text{kPa}^{-1}$) and normalized stomatal conductance intercept ($g_s g_{sref}^{-1}; \text{mm}^{-1} \text{ s mm s}^{-1}$) for reference, strip-shelterwood (SC), and partial-cut (PC) in 2018 presented in Figure 3-12.

Soil θ percentile	reference		PC		SC	
	slope	intercept	slope	intercept	slope	intercept
75-100	-0.003	1.79	-0.35	1.81	-0.18	1.44
50-75	-0.112	1.49	-0.29	1.45	-0.22	1.29
25-50	-0.074	0.59	-0.08	0.59	-0.22	0.91
0-25	-0.013	0.13	-0.01	0.14	-0.03	0.36

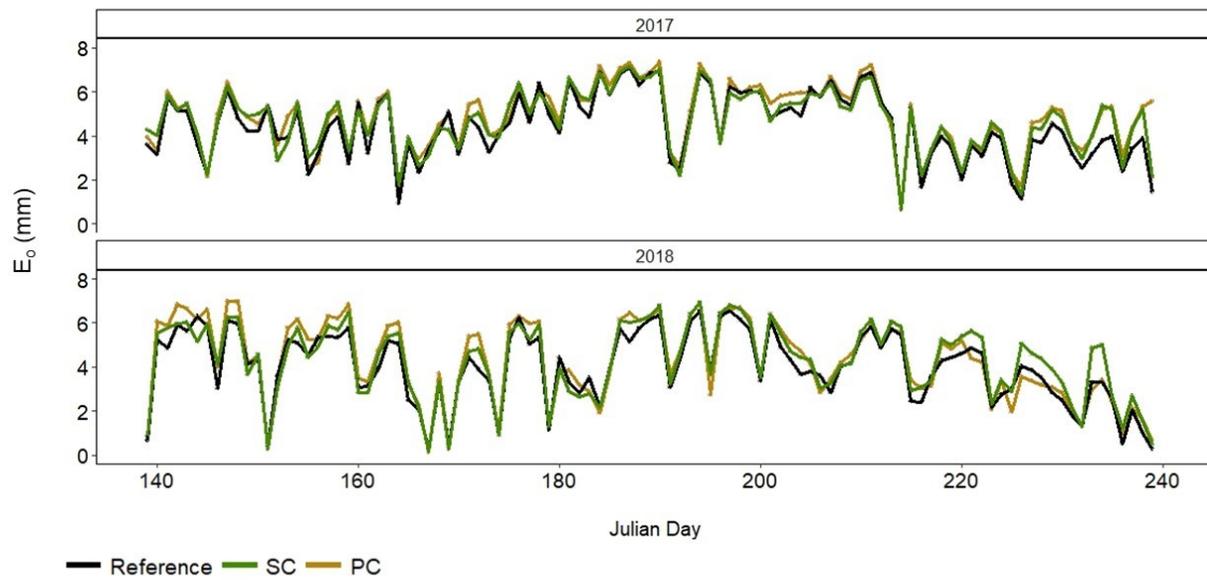


Figure 3-1. Daily atmospheric moisture demand E_o (mm d^{-1}) during 2017 and 2018 in the reference, strip-shelterwood (SC), and partial-cut (PC) stands from May 19–August 29.

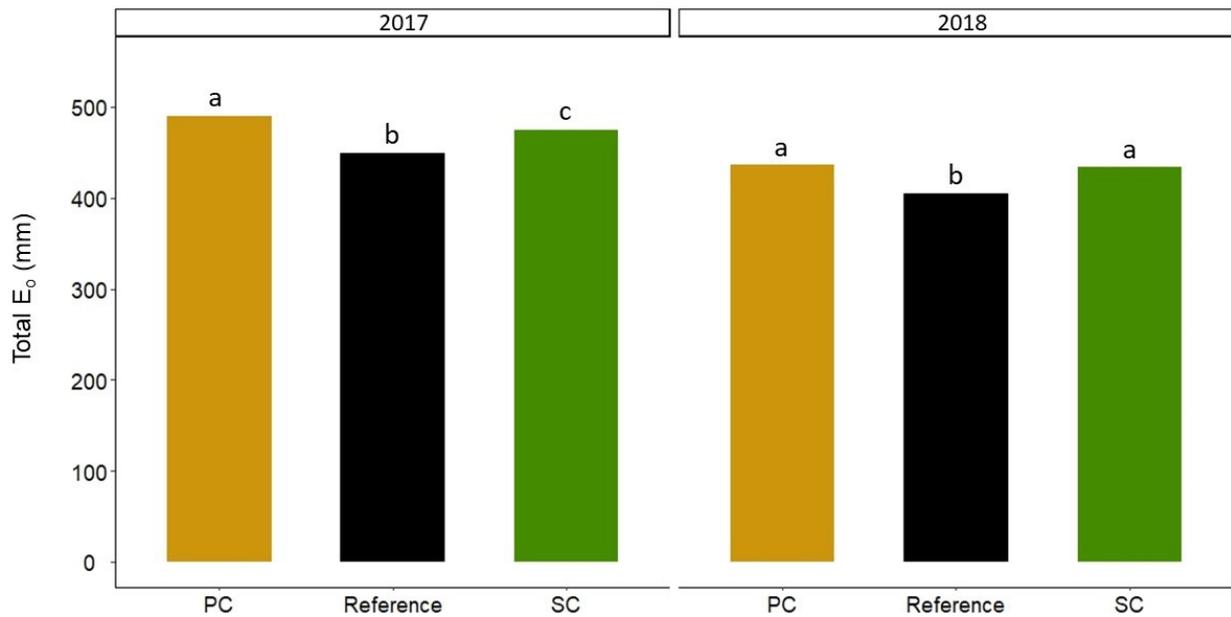


Figure 3-2. Total seasonal atmospheric moisture demand E_o (mm) during 2017 and 2018 in reference, strip-shelterwood (SC), and partial-cut (PC) stands from May 19–August 29. Different letters, within each year, are indicative of significantly different E_o ($p < 0.05$).

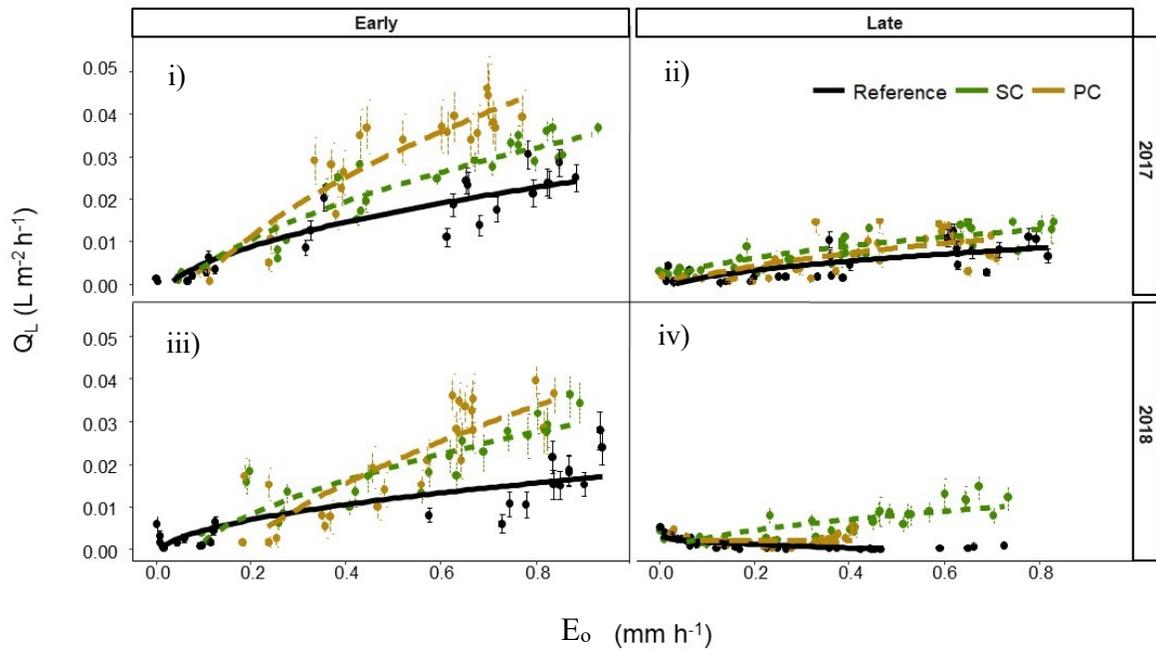


Figure 3-3. Relationship between mean hourly transpiration per leaf area (Q_L ; $L\ m^{-2}\ h^{-1}$) and mean hourly atmospheric moisture demand (E_o ; $mm\ h^{-1}$) in the strip-shelterwood (SC), reference, and partial-cut (PC) stands. The time period spans from 7:00–14:00. i) early season 2017 (June 30–July 3), ii) late season 2017 (August 15–18), iii) early season 2018 (June 24–27), and iv) late season 2018 (August 15–18). Error bars indicate one standard error. Equations are summarized in Table 3-2.

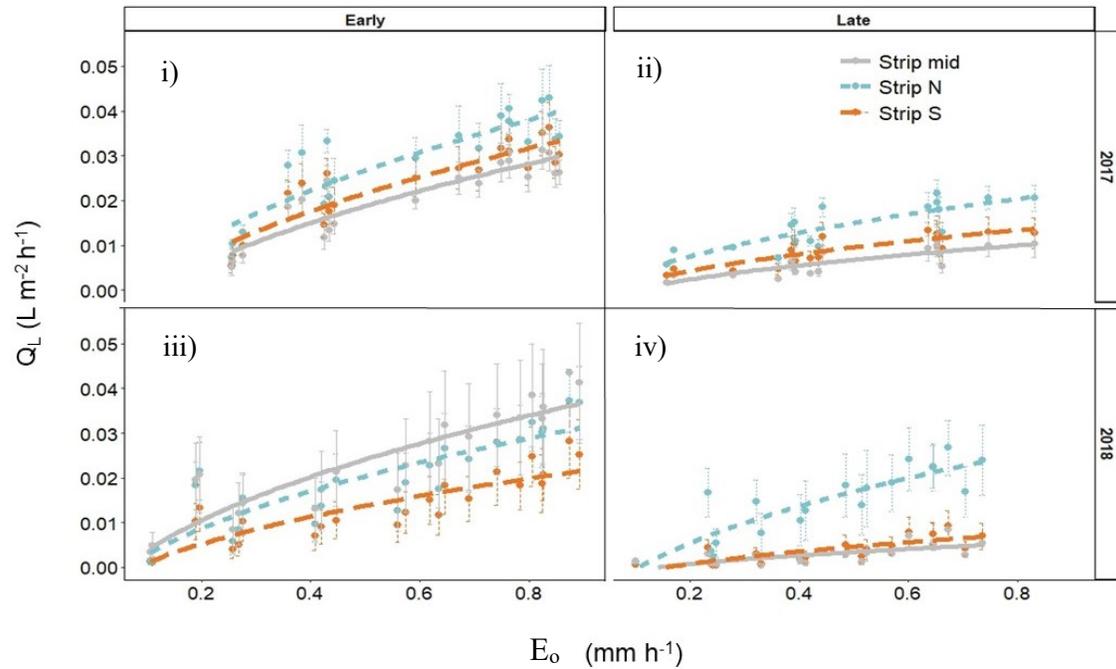


Figure 3-4. Relationship between mean hourly transpiration per leaf area (Q_L ; $L\ m^{-2}\ h^{-1}$) and mean hourly atmospheric moisture demand (E_o ; $mm\ h^{-1}$) in the strip-shelterwood (Strip mid, Strip N, and Strip S) stands. The time period spans from 7:00–14:00. i) early season 2017 (June 30–July 3), ii) late season 2017 (August 15–18), iii) early season 2018 (June 24–27), and iv) late season 2018 (August 15–18). Error bars indicate one standard error. Equations are summarized in Table 3-3.

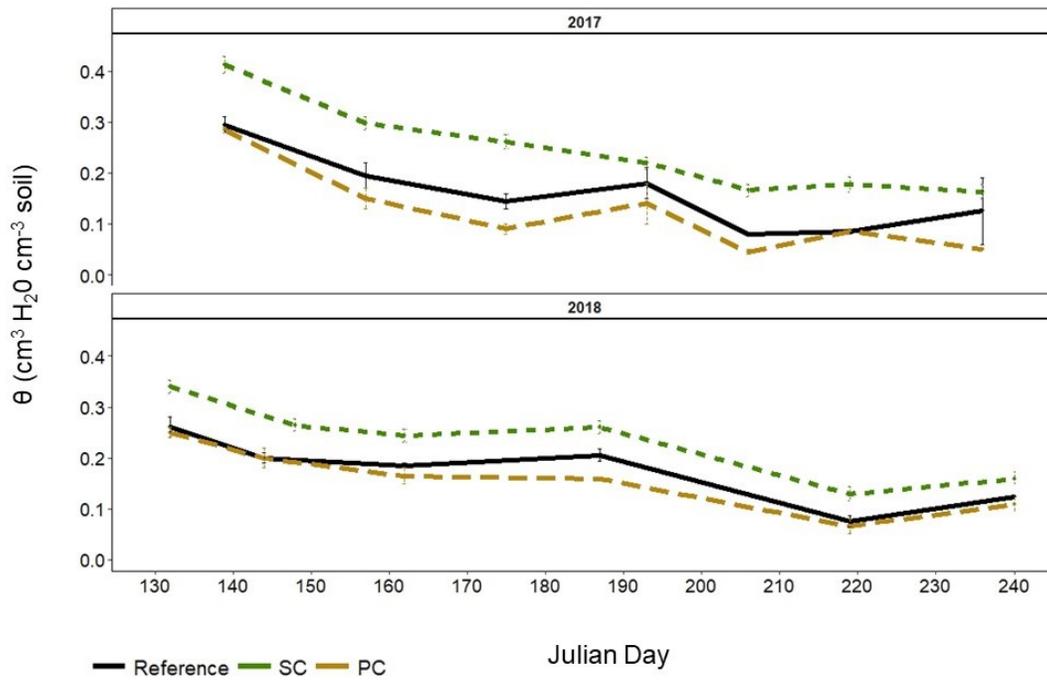


Figure 3-5 Mean TDR-measured volumetric soil moisture (θ ; $\text{cm}^3 \text{H}_2\text{O cm}^{-3} \text{soil}$) in shallow (0–20 cm) soil layers during the 2017 and 2018 growing seasons (Julian Day 139–239; May 19–August 29) in reference, strip-shelterwood (SC), and partial-cut (PC) stands. Error bars represent one standard error.

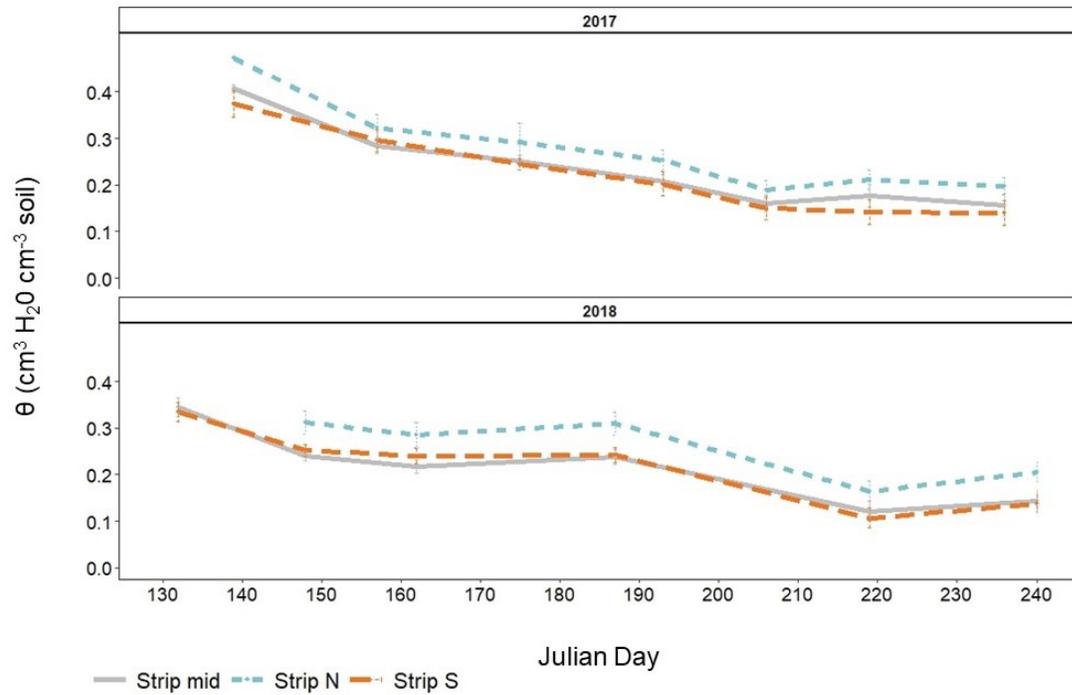


Figure 3-6 Mean TDR-measured volumetric soil moisture (θ ; $\text{cm}^3 \text{H}_2\text{O cm}^{-3} \text{soil}$) in shallow (0–20 cm) soil layers during the 2017 and 2018 growing seasons (Julian Day 139–239; May 19–August 29) in strip-shelterwood (Strip mid, Strip N, and Strip S). Error bars represent one standard error.

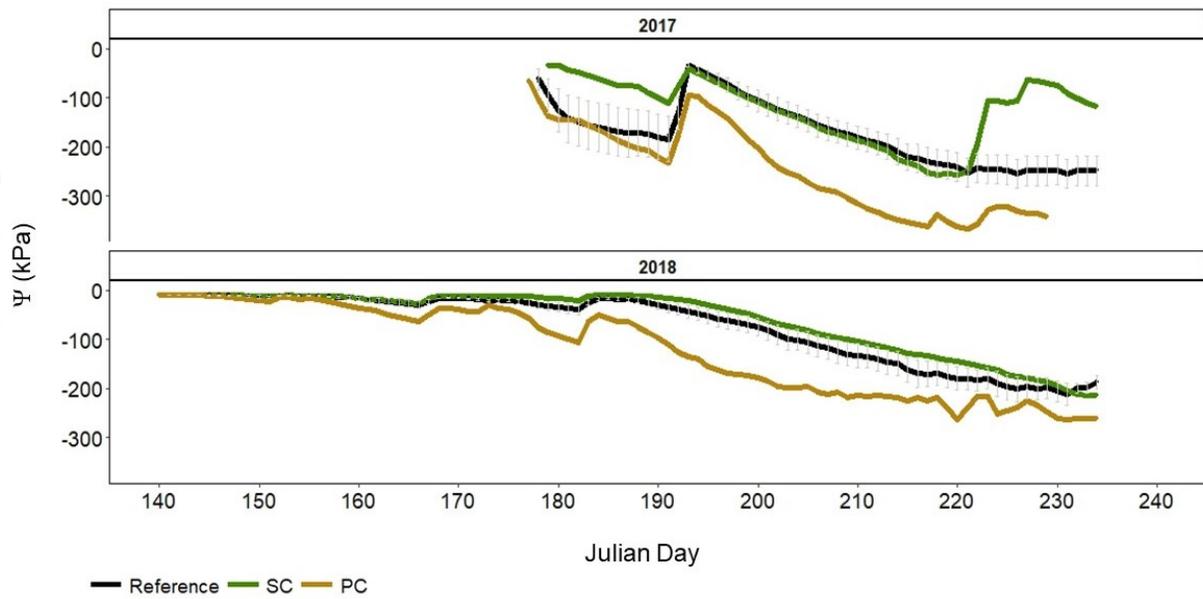


Figure 3-7. Mean daily soil matric potential (Ψ ; kPa) during the 2017 and 2018 growing seasons (Julian Day 139–239; May 19–August 29) in the reference, strip-shelterwood (SC), and partial-cut (PC) stands. Error bars represent one standard error and are only represented for the reference stand for clarity.

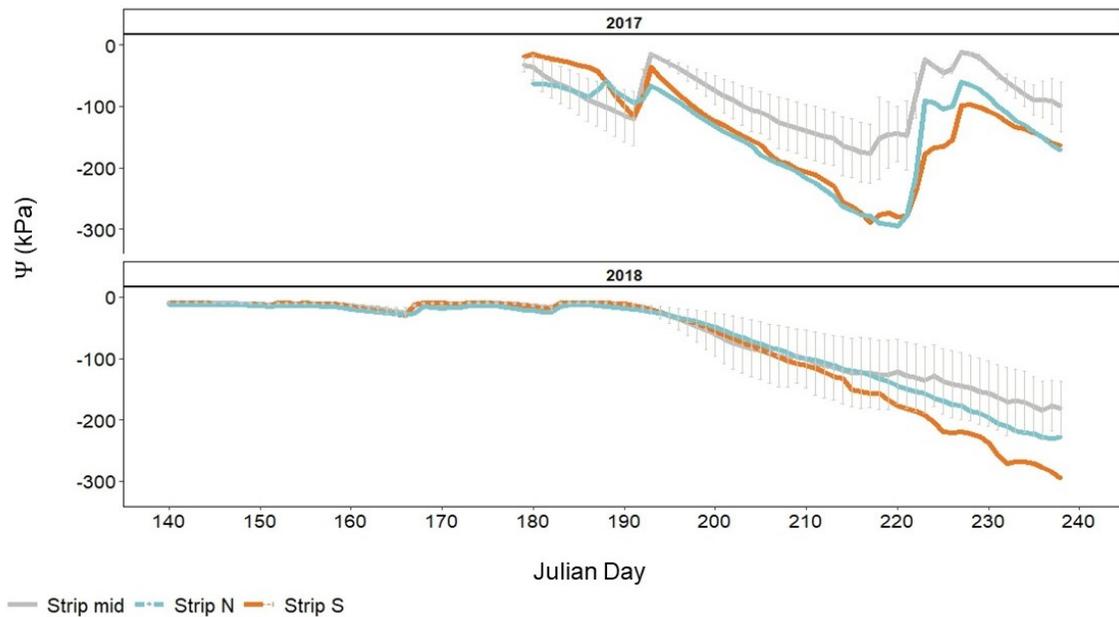


Figure 3-8. Mean daily soil matric potential (Ψ ; kPa) during the 2017 and 2018 growing seasons (Julian Day 139–239; May 19–August 29) in the strip-shelterwood (Strip mid, Strip N, and Strip S). Error bars represent one standard error and are only represented for the Strip mid stand for clarity.

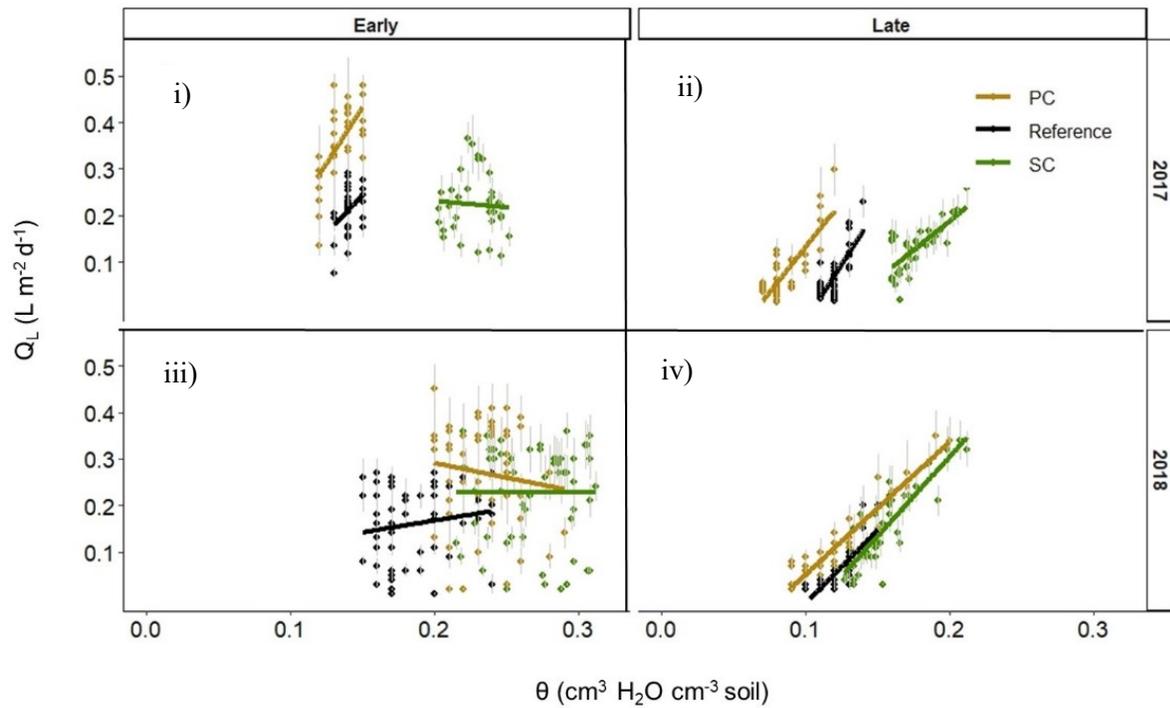


Figure 3-9 relationship between mean daily transpiration (Q_L ; $L\ m^{-2}\ d^{-1}$) and mean TDR-measured daily volumetric soil moisture (0–20 cm) (θ ; $cm^3\ H_2O\ cm^{-3}\ soil$) in reference, strip-shelterwood (SC), and partial-cut (PC) stands. i) early season (June 10–July 15) 2017, ii) late season (July 16–August 29) 2017, iii) early season (May 19–July 15) 2018, and iv) late season (July 16–August 29) 2018. Error bars indicate one standard error. Linear regressions are summarized in Table 3-7.

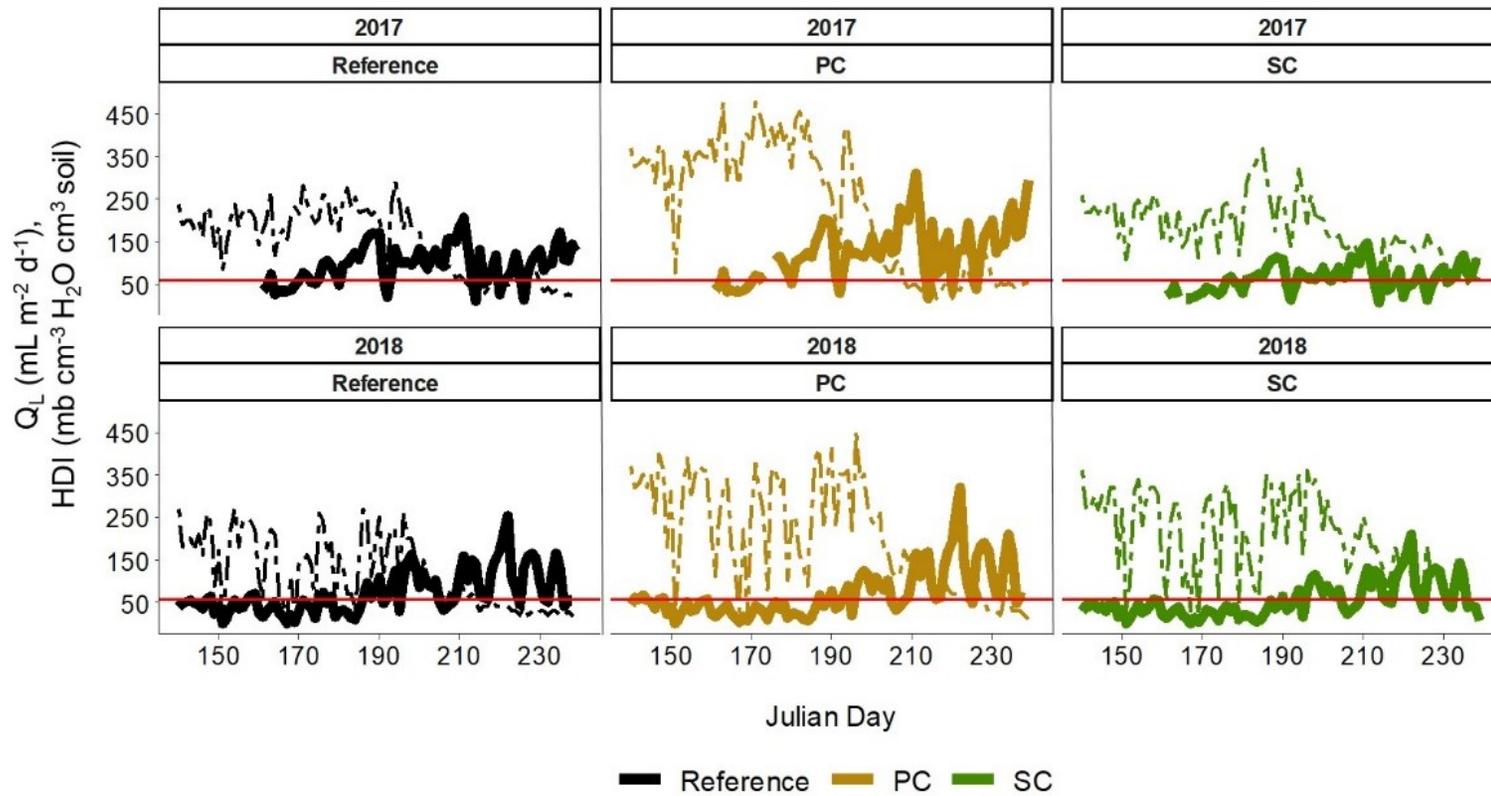


Figure 3-10. Mean daily transpiration per leaf area Q_L ($\text{mL m}^{-2} \text{d}^{-1}$) (hashed line) and hydrometeorologic dryness index (HDI) ($\text{mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$) (solid line) for 0–20 cm soil layers during the 2017 and 2018 growing seasons. The red line indicates HDI_{crit} ($57.2 \text{mb cm}^{-3} \text{H}_2\text{O cm}^3 \text{soil}$).

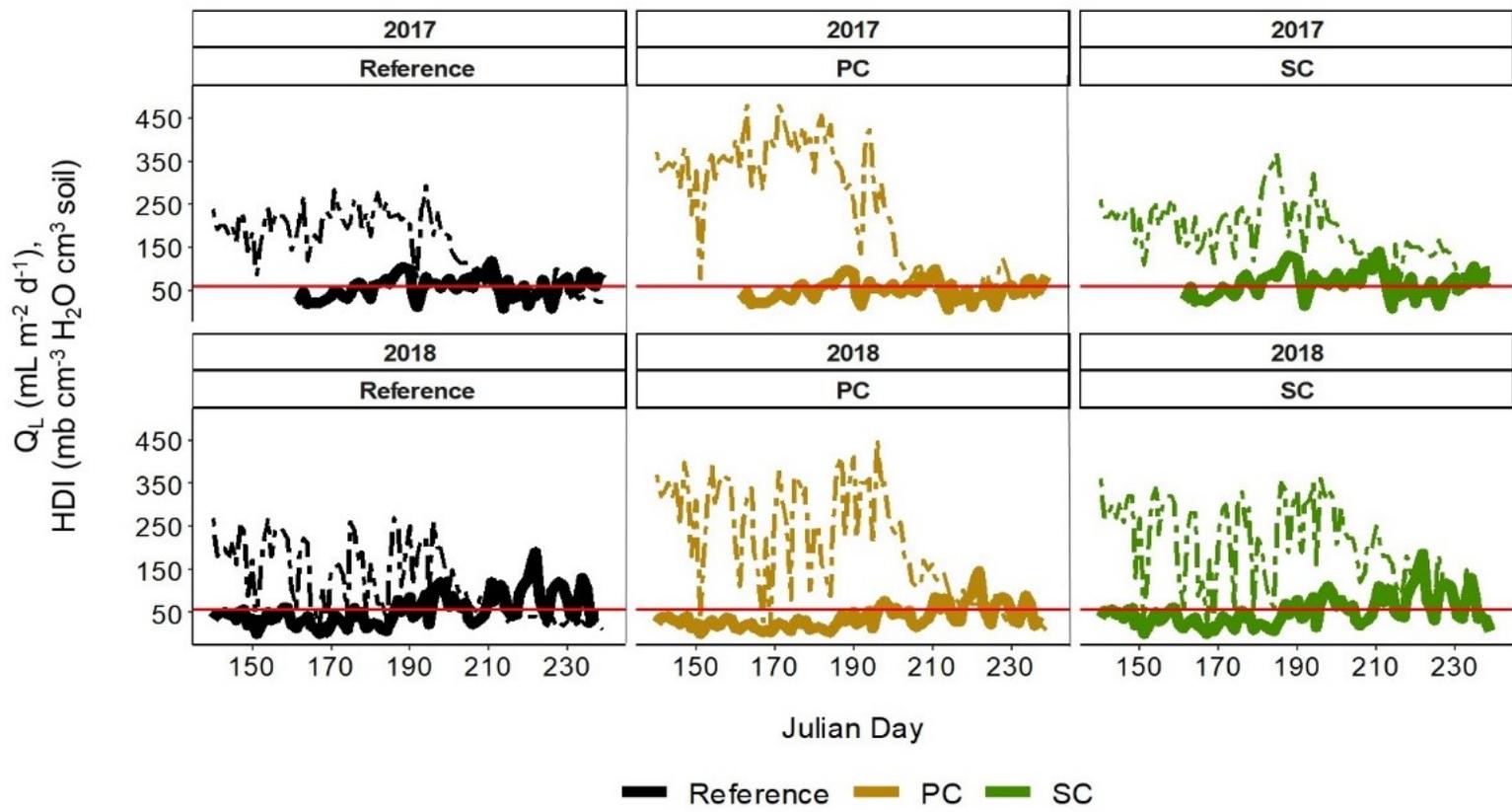


Figure 3-11. Mean daily transpiration per leaf area Q_L ($\text{mL m}^{-2} \text{d}^{-1}$) (hashed line) and hydrometeorologic dryness index (HDI) ($\text{mb cm}^{-3} \text{H}_2\text{O cm}^{-3} \text{soil}$) (solid line) for 20–60 cm soil layers during the 2017 and 2018 growing seasons. The red line indicates HDI_{crit} ($57.2 \text{mb cm}^{-3} \text{H}_2\text{O cm}^{-3} \text{soil}$).

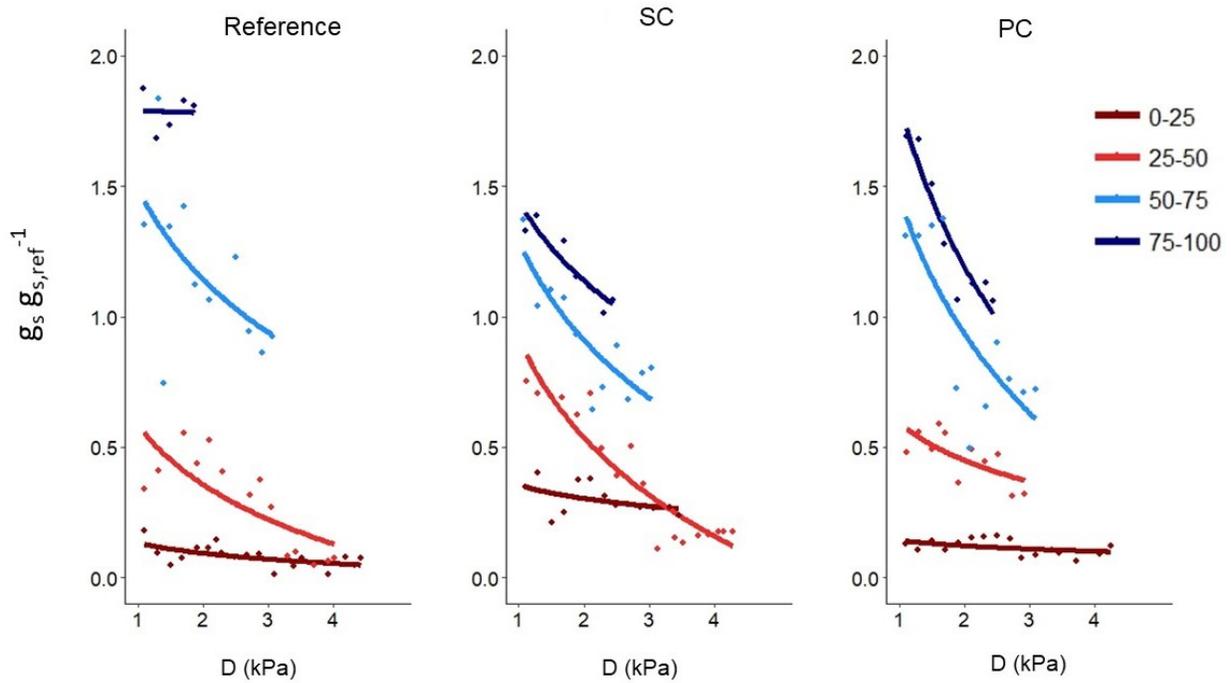


Figure 3-12. 2018 relationship between stomatal conductance normalized by its well-watered reference rate ($g_s / g_{s,ref}^{-1}$; $mm^{-1} s mm s^{-1}$) and compared to the vapour pressure deficit (D ; kPa) for reference, strip-shelterwood (SC), and partial-cut (PC). Soil moisture (0–20 cm) was categorized across four levels of increasing θ (0–25, 25–50, 50–75, and 75–100 percentiles). Dark red (0–25) represents the driest percentile. Dark blue (75–100) represents the wettest percentile. Points represent average ($g_s / g_{s,ref}^{-1}$) within the unique D and soil moisture bins. Lines are best fit of Equation 3-4 and are summarized in Table 3-10.

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Chapter 4: Synthesis and forest management implications

The overall objectives of this research were to 1) explore the change in evaporative fluxes, specifically the transpiration response, of a mature lodgepole pine stand post-harvest after two alternative harvest strategies- partial-cut (PC) and strip-shelterwood (SC); 2) quantify the harvest-induced spatial patterns of above-ground (atmospheric moisture demand) and below-ground (soil moisture) regulating these transpiration responses; and 3) interpret the interaction between the post-harvest transpiration as governed by above and below-ground controls to evaluate their relative influence on transpiration throughout the season.

The first data chapter of this study (Chapter 2) reported on diurnal and seasonal transpiration of lodgepole pine in the SC, PC, and reference stands over two growing seasons 2017–2018. The diurnal and seasonal transpiration in a mature, moderately dense lodgepole pine stand increased in both the distributed single tree PC and spatially discrete SC harvesting strategies compared to the reference stand. Plot scale transpiration rates (both hourly and daily) were greater on the edges of the retention strips (SC harvest), with the northern shaded side of the strip transpiring more than the southern side of the strip. This increase in transpiration was likely caused by a soil moisture legacy, increased sunlight exposure, and less competition for water, nutrients, and light (Williams et al. 1999; Vyse et al. 2006; Sparks et al. 2001). Patterns of seasonal transpiration showed increased transpiration in the PC stand during the early non-moisture limiting season and in the SC stand during the late moisture limiting season compared to the reference stand. The reduction in transpiration rates in the PC stand was in contrast to what was previously documented for partial cutting, where transpiration rates from a partial-cut stand have been reported to have a sustained transpiration rate above the reference/un-cut stand through to the late, dry season (Lagergren et al. 2008). This study highlights that in drought years this may not be the case where stomatal closure may limit water use by the partial-cut stand. In contrast, results also show that during the drier, late growing season, trees in the SC stand may have been able to exploit the greater late season soil moisture produced by the delayed snowmelt from the SC harvest. The alternating strips caused a shading pattern on the north-facing slope delaying snowmelt which was critical for trees during the drier, late growing season in the adjacent strips.

Transpiration was within the range of magnitude reported in other partial-cutting studies from various densities, ages, and species (Bladon et al. 2006; Knight et al. 1981; Reid et al. 2006; Lagergren et al. 2008). However, this study was unique in showing increased water use by mature (> 50 years) stands after SC and PC harvest, which to my knowledge has not been previously studied. Stand age is likely an important factor in mature stands that would typically be harvested in contrast to younger stands that would be expected to have greater hydraulic conductance (lower hydraulic resistance (shorter stands)), and greater xylem permeability (Irvine et al. 2004; Delzon and Loustau 2005), thus greater ability to respond to harvest associated changes in microclimate and soil moisture availability. This in turn, is important in understanding how harvesting operations are likely to affect evaporative fluxes regulating the water balance and hydrologic responses of forested watersheds.

Plot scale transpiration was scaled up to sub-watershed scale to assess the likely effects of harvesting on watershed scale evaporative fluxes that would be expected to regulate post-harvest hydrologic impacts. The increased post-harvest transpiration in the SC and PC stands was estimated to largely, or entirely compensate for the direct reduction in total transpiration associated evaporative losses after forest harvesting. This is a novel finding because management strategies focus on limiting the total or percent harvest area in watersheds (e.g. equivalent clear-cut area [ECA] procedures) to minimize downstream hydrologic impacts (bank stability, water quality) (Winkler et al. 2017). In particular, because this research showed that transpiration of residual trees increased after harvesting, this research suggests that the area harvested may not serve as a good direct proxy for indicators of potential hydrologic change.

This has several important implications for both fundamental watershed hydrology and forest watershed management. Firstly, there is a long history of forest hydrologic research that has focused on exploring the variation in watershed scale effects of forest harvesting on streamflow response that have been observed across varied forest types and hydro-climatic regimes (Bosch and Hewlett 1982; Stednick 1996). While these studies have focused on causal mechanisms explaining the high variation in relationships between water yield and area harvested across forest types and climatic regions, results of this study show that area harvested is not likely a good direct proxy indicator (independent variable) for these hydrologic effects. Similarly, this research also suggests management approaches to limit hydrologic impacts such as ECA, that assume these impacts are linearly proportional to harvested area, may overestimate

potential impacts on total watershed evaporative losses and hydrologic change. Increased transpiration by residual trees near the edges of harvested areas are likely to offset some of those projected effects. Thus, this potential compensatory effect should be incorporated into these procedures to better estimate the likely effects of forest management activities on hydrologic impacts in forested watersheds.

The second data chapter of this study (Chapter 3) reported on the spatial patterns of atmospheric moisture demand and soil moisture after two alternative harvest strategies- PC and SC. The atmospheric moisture demand was elevated (~ 10 %) in both harvested sites due to an increase in wind and radiation regimes. However this elevated atmospheric moisture demand in stands studied here, were not as elevated as previously reported after other partial-cutting studies (Bladon et al. 2006; Marenholtz et al. 2010), which may be partially explained by the difference in harvest intensity and the measurement height for wind speed. However, fewer studies have documented concurrent harvest effects on both microclimate and soil moisture that would collectively regulate potential transpiration responses of residual trees to different forest harvest strategies. The shallow soil moisture was observed to increase by 50 % for the SC stand and in the deeper soil layers by 42 % in the PC stand. Within the SC stand the northern shaded side had 18 % greater moisture than the southern side. These spatial patterns of moisture were a product of increased throughfall, reduced total transpiration losses and a delayed snowmelt due to shading of residual trees. The transpiration response within the harvested and reference stands mirrored the spatial pattern of soil moisture, where the PC stand had the greatest transpiration rate early season and the SC stand had the greatest transpiration during the late season.

Two indices (HDI and the relationship between stomatal conductance and vapour pressure deficit) were used to attempt to disentangle the combined effects of above-ground or below-ground controls to evaluate the primary drivers of transpiration and if this driver was meaningfully changed by the two harvesting strategies. This element of the research is also novel where previous studies have primarily used these indices to explore variation in physiological water use adaptation among species across different forest biomes (Novick et al. 2016). The weight of evidence approach using two independent indices strongly support the general conclusion that atmospheric drivers primarily governed transpiration but only during times of non-limiting soil moisture. Once the soil moisture became more limiting (~ mid-late July for southern Rockies) below-ground drivers played a pivotal role in the transpiration responses. This

highlights the potential importance of implementing forest harvest strategies that can exploit shading and reducing interception to provide more soil moisture throughout the season.

Both partial-cut (PC) and strip-shelterwood (PC) harvesting were implemented in a headwater catchment that has an important role of supplying water from the eastern slopes of the southern Rockies. The role of moisture was a key component in the transpiration response of the lodgepole pine stands. Situated on a north, north-east facing slope with harvest designs that have the potential to affect the radiation pattern (shading) was a key causal mechanism that modified the moisture regime of these stands during the drier, late growing season. The residual SC stand showed the least reduction in transpiration rates out of all stands which was almost entirely explained by harvest effects improving the soil moisture regime for tree growth. The SC harvest, if implemented on a north facing slope, is a suitable candidate for future operation designs as the wind distribution of the snow and the modified radiation through shading make for a suitable environment to grow and provide a delayed snowmelt subsequently supplying moisture thru to the late season.

4.1 Future Research

While this study addressed the short-term (two to three years) transpiration response of a mature, lodgepole stand after two alternative harvesting strategies, it remains unclear if these transpiration responses will continue to be sustained 10 or 20 years into the future. Previous studies on partial-cutting have highlighted the varying transpiration responses within 5 years after harvesting (Reid et al. 2006) and that was comprised of a younger stand which would not reflect stand ages that are more typical of most forest harvesting operations. Future research into assessing the long term (10 or 20 year) transpiration responses after the PC and SC harvest strategies would provide a broader perspective of the suitability of these alternative harvest strategies for consideration in future of forest harvesting designs.

This research also explored the effects of a strip-shelterwood cut that was approximately two tree lengths in harvested strip width. Future research exploring variable shapes of the harvest cuts to evaluate their effectiveness in snowpack capture and delay in melt rate would be an interesting addition. The transpiration response of the residual trees greatly mirrored the spatial distribution of soil moisture. Therefore a modified design with the strips being narrower (one to

one and a half tree lengths) would promote more snowpack retention and subsequent effects on soil moisture regimes which may be potentially important in the future under warming climatic conditions. The alternative harvesting strategies evaluated in this study appear to promote additional soil moisture that may become increasingly important with warming air temperatures and increasing risk of drought.

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Appendix A – Calibration of and quality control of TDP sap flow sensors

Four separate quality control tests were performed prior to sap flow measurement to ensure all TDP-30 sensors were properly functioning and producing similar measurement readings. The first test was to determine the proper resistance was being measured by each TDP-30 instrument. Second test was to determine the coherence in temperature difference (ΔT) among sensors when connected to power before and after installation. The third was to quantify the natural thermal gradient. The fourth test were to determine whether natural temperature gradients were having an effect on the maximum temperature difference (ΔT_m) within tree boles.

The first test was conducted in the lab prior to installation in the field. A multi-meter was used to confirm the factory stated ohm (Ω) provided by the manufacturer (Dynamax, Houston, TX, USA). All sensors were within 0.1 Ω of factory calibration.

The second test was implemented (May 12, 2018) during the early morning hours to determine consistency of measured temperature differences among TDP-30 prior to installation. Sensors were positioned on the north side of each tree bole to minimize direct solar heating so that the ΔT would reflect only variation in temperature under consistent environmental conditions. 10 min mean ΔT was recorded for all trees for one hour which resulted in a mean ΔT of 15.9 ± 0.4 ° C (mean \pm standard error) across all instrumented trees.

The third test was implemented to quantify natural thermal gradients within the tree. Several thermal measuring devices like the TDP assumes natural thermal gradients are negligible in the sapwood area (Do and Rocheteau 2002). If not quantified, these thermal gradients can fluctuate the ΔT_m and subsequently the perceived sap flow velocity v_s (Do and Rocheteau 2002). One solution proposed by (Do and Rocheteau 2002) was to record ΔT continuously with a non-heating system. July 6-8, 2018 the heater voltages were turned off and the temperature difference recorded 10 min timestamps for 24 hours each day. The ΔT among the sensors recorded an amplitude ranging from -0.4 to 0.4 ° C.

The fourth test was continuous heat applied to all sensors installed in the trees. This test was implemented to determine the effect of natural temperature gradients on ΔT . During the day, the influence of natural gradients can be hard to detect due the dynamics of solar radiation and sap flow rate itself (Do and Rocheteau 2002). During the nighttime, the effect of natural gradients is easier to detect with high fluctuations in ΔT_m . Progressive changes in ΔT_m is an

indication of changes in heat dissipation mechanisms due to shrinkage of wood after needle insertion or seasonal wood water content. From June 11- 18, 2018 the sensors measured and recorded 10 min averages of ΔT 24 hours each day. This record gave insight to each sensor's range of ΔT_m from night to night. Over the course of eight days ΔT_m changed 0.05 ° C within one sensor's time series.

The third and fourth test confirmed that natural temperature gradients are no more than 6 % of ΔT at any given time therefore the influence of natural thermal gradients was considered negligible. Furthermore placing the TDP sensor on the north azimuth mitigated large fluctuations of temperature gradients as (Do and Rocheteau 2002) study had concluded.