

Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting

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Abstract

We compared the change in microclimate and tree water relations between a boreal mixedwood, variable retention (VR), partially harvested stand and an adjacent, unharvested control stand. A nearly three-fold increase in potential evapotranspiration (ET_p) at the crown level in the VR site was approximately proportional to a 2.8-fold increase in wind speed (u), along with subsidiary increases in net radiation (Q^*) and vapour pressure deficit (D) after harvesting. Soil volumetric moisture content (θ_v) also increased, while there were negligible changes in air temperature (T_a) and relative humidity (RH) after partial harvesting. Whole-tree sap flow response to cutting was measured in white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*) with thermal-dissipation sap flow sensors. After partial harvesting, transpiration per unit leaf area (Q_l) in all three species began earlier in the morning and extended later in the day in VR trees than control trees. Mean maximum sap flow rates per leaf area (Q_{l-max}) during mid-day for *P. glauca* in the VR site were about 2.5 times greater than in the control trees, while *B. papyrifera* Q_{l-max} was approximately 1.6 times higher in the VR site. For *P. balsamifera*, however, Q_{l-max} was only marginally greater in the VR site than in the control. This suggests stomatal closure by the *P. balsamifera* and *B. papyrifera* residual trees likely occurred to prevent excessive xylem cavitation. Xylem pressure potential (Ψ_x) measurements of twigs also indicated water stress in both *P. balsamifera* and *B. papyrifera* in the VR stand, but not for *P. glauca*. However, similarity of sapwood hydraulic conductivity (K_w) between the two sites, for all three species, showed that xylem cavitation of the main stems was insignificant following VR harvesting. Decoupling coefficients (Ω) indicated that all three species were more coupled to the atmosphere in the VR site than in the control. Species differences in susceptibility to atmospheric moisture-stress induced cavitation, combined with differences in stress-coping mechanisms and physiology, appeared to influence the response in transpiration to increased ET_p following VR harvesting. Species susceptibility to atmospheric moisture-stress due to increased ET_p following partial harvesting can be ranked as: *P. balsamifera* > *B. papyrifera* > *P. glauca*.

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1. Introduction

Variable retention (VR) and other partial-cut silvicultural treatments are being practiced over large parts of the world to address a broad array of forest management objectives (North et al., 1996; Progar et al., 1999; Zenner, 2000; Sullivan et al., 2001). These

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practices leave single or small groups of trees in cutover areas. It is often assumed that residual trees will benefit from reduced competition and more open conditions (Wang et al., 1995; Liu et al., 2003). There are however, many examples where residual trees have not responded positively to these partial cutting treatments. There may be decreases in growth rates or higher rates of mortality for some years following VR harvesting (Roy et al., 2001; Bebber et al., 2005).

Apart from problems of increased probability of windthrow, VR may abruptly expose residual trees to altered microclimate, including increased fluctuations in wind speed (u), air temperature (T_a), relative humidity (RH), vapour pressure deficit (D) and net radiation (Q^*) (Cadenasso et al., 1997; Man and Lieffers, 1999; Proe et al., 2001), producing greater evaporative demand in harvested areas (Zheng et al., 2000). While interactions can be complex, generally, evaporative demand is positively associated with T_a , D , u and Q^* ; is negatively associated with RH.

The transpiration response of trees to greater evaporative demand has been shown to exhibit non-linear (asymptotic) relationships with individual components driving atmospheric moisture demand, such as increasing D or Q^* (Martin et al., 1997; Hogg et al., 2000; Ewers et al., 2002), or even a decline in transpiration at high D (Pataki et al., 2000). Both of these responses have been attributed to partial closure of stomata to maintain xylem pressure potential (Ψ_x) above a specific threshold, beyond which xylem dysfunction will occur (Hogg and Hurdle, 1997; Bond and Kavanagh, 1999). The narrowing of stomatal openings reduces stomatal conductance (g_s), and thus is associated with significant declines in photosynthetic rates (Dang et al., 1997; Hogg et al., 2000). If prolonged, this may result in depletion of carbohydrate reserves, defensive compounds, and a loss of total leaf area (Waring, 1987).

During prolonged periods of high atmospheric evaporative demand, some cavitation-induced embolism may be unavoidable in certain species, resulting in decreased water transport to foliage (Jones and Sutherland, 1991; Sperry and Pockman, 1993; Nardini and Salleo, 2000). Xylem dysfunction leads to increased tension in the remaining conduits (Tyree and Sperry, 1988), risking a runaway cycle of embolism (Tyree and Ewers, 1991). Trees may approach this unstable embolism cycle, leading to catastrophic xylem dysfunction, after as little as 5–20% loss of sapwood hydraulic conductivity (K_ψ) (Tyree and Sperry, 1988). Trees experiencing such stress may suffer branch and root die-back, further limiting net carbon assimilation (Roy et al., 2001). A decline in photosynthesis will limit

tree growth, which may increase the probability of whole-tree mortality (Kobe and Coates, 1997). Therefore, we hypothesize that VR may produce microclimatic conditions that result in physiological stress, declining vigour and accelerated mortality of residual trees. To our knowledge, there have been no previous studies demonstrating the physiological response of various species of residual trees to the microclimatic change that occurs after VR harvesting.

This study examined the microclimate immediately after VR harvesting, and investigated the differential species responses in whole-tree water use to this change. The objective was to describe and compare tree sap flow and transpiration responses to microclimate change associated with VR for balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.), the typical retention species in boreal mixedwood stands. We hypothesized that after partial harvesting: (1) microclimate at the crown level would have lower RH and increased T_a , D , u and Q^* ; (2) transpiration rates per unit leaf area (Q_l), mean daily maximum transpiration (Q_{l-max}) and mean total daily water use (Q_d) per tree would increase; (3) that the hardwoods, *P. balsamifera* and *B. papyrifera*, would have larger differences in Q_l and Q_d between VR trees and control trees, compared to *P. glauca*, because of their greater capability for water transport to their crowns (xylem hydraulic conductivity).

2. Methods

2.1. Site description

The study area was 40 km southwest of Drayton Valley, Alberta (53°13'N, 114°59'W), in the Lower Foothills Natural Subregion (approximately 900 m elevation). The two study sites were approximately 300 m apart, within the e2 low-bush cranberry ecosite (Beckingham et al., 1996). Topography was rolling with gentle slopes. Both stands were mixedwoods, consisting of *Populus tremuloides* (38.5%), *B. papyrifera* (28.1%), *P. balsamifera* (19.5%) and *P. glauca* (13.9%). Prior to VR harvesting the overstorey stand density was 1947.0 ± 289.4 trees ha⁻¹, mean basal area was 50.2 ± 9.6 m² ha⁻¹, mean height was 15.8 ± 1.7 m and the mean diameter-at-breast-height (DBH) was 16.9 ± 2.6 cm. The sites had a mesic moisture regime and a medium nutrient regime on a Grey Luvisol with a silty-clay texture developed over morainal till. The mean daily temperature is 2.3 °C (−4.6 to 9.1 °C). The mean daily summer (June to August) temperature is 13.8 °C (7.1–20.5 °C). The peak of summer photoper-

iod is approximately 17 h d^{-1} . The mean annual precipitation is 535 mm, with $\sim 77\%$ falling as rain. The June–August precipitation is 260 mm.

2.2. Experimental design

The study design was approached similar to a “paired basin” watershed experiment (before/after, control/treatment) allowing more powerful control to detect changes in microclimate than other sampling designs. The two sites had similar tree age, species composition, soil type, nutrient regime, moisture regime, slope and aspect. One site was to be harvested, with approximately 10% retention (VR site), and a second area was to remain as a closed canopy forest (control). The control was 100 m from the cut edge, while the site studied in the variable retention (VR) area was 100 m from the forest edge. In both the control and VR site, three co-dominant (CD) trees from each species were selected within a 30 m radius to accommodate the instrumentation. Only healthy trees, showing no sign of damage or disease were sampled. Measurements of tree height, DBH (1.3 m) and live crown ratio were collected from each sample tree (Table 1).

The tree harvest was done by a feller buncher on 9 July 2003. During harvest, machines stayed at least 7 m from sample trees and skidders remained 15 m from the trees. This eliminated bole damage, and minimized soil compaction and root damage to the sample trees.

2.3. Micrometeorological measurements

Climate stations were established before harvest at the centre of both the control and treatment sites. All meteorological variables were continuously measured at a height of 12.1 m (mid-crown position) for a period of 26 days (13 June–8 July) prior to the treatment (pre-harvest). The purpose of the pre-harvest measurements was to establish the pre-disturbance relation of the two

sites to each other. Micrometeorological measurements continued for 32 days post-harvest (9–31 July and 13–21 August).

Air temperature (T_a) and relative humidity (RH) were measured with a Vaisala Temperature/Humidity Probe (HMP35C, Campbell Scientific, Logan, UT, USA) protected by a multi-plate radiation shield. The data were used to calculate ambient vapour pressure (e_a ; Pa), saturation vapour pressure (e_s ; Pa) and vapour pressure deficit (D ; Pa). Short wave radiation was measured with a Li-Cor 200SZ pyranometer sensor (Li-Cor, Lincoln, NE, USA), while net radiation (Q^* ; W m^{-2}) data were collected with a net radiometer (NR-Lite and REBS Q-6, Campbell Scientific). An R.M. Young anemometer (Wind Monitor, 05103-10, Campbell Scientific) was used to determine wind speed (u ; m s^{-1}) and wind direction. Two water content reflectometers (CS615, Campbell Scientific) were positioned in opposite directions, 15 m from the centrally located micrometeorological tower, and installed vertically in the upper 30 cm of soil at each site to provide volumetric water content (θ_v). Precipitation was measured with a universal precipitation gage (5-780, Belfort Instrument). Meteorological variables were sampled every 5-s and averaged after 15-min using a CR10X control system (Campbell Scientific). The array was powered with a solar panel mounted on the tower with power storage in a 12 V deep-cycle battery. All micrometeorological sensors were calibrated in the laboratory prior to installation in the field.

2.4. Potential evapotranspiration

Micrometeorological data were used with the Penman combination equation (Van Bavel, 1966) to provide the potential evapotranspiration (ET_p ; m s^{-1}) from each site:

$$\text{ET}_p = \frac{\Delta Q^* + \rho_a c_a u D}{\rho_w \lambda_v (\Delta + \gamma)} \quad (1)$$

Table 1

Mean sample tree characteristics by species (Bw: *Betula papyrifera*; Pb: *Populus balsamifera*; Sw: *Picea glauca*) and standard errors of the mean from the control (CT) and variable retention (VR) sites ($n = 3$)

Species-site	DBH (cm)	TH (m)	A_L (m^2)	A_s (cm^2)	Age (years)	LCR
Bw-CT	14.6 ± 0.7	12.7 ± 0.56	25.6 ± 6.1	105.7 ± 20.5	48.0 ± 2.9	63.3 ± 1.7
Pb-CT	19.6 ± 1.5	16.3 ± 0.58	30.0 ± 4.9	163.4 ± 21.7	50.0 ± 2.8	55.0 ± 8.7
Sw-CT	18.7 ± 3.2	16.3 ± 2.3	27.6 ± 2.7	86.8 ± 7.5	45.8 ± 4.9	88.3 ± 1.7
Bw-VR	14.6 ± 1.8	12.7 ± 1.4	23.8 ± 6.0	95.1 ± 21.3	47.1 ± 1.7	66.7 ± 4.4
Pb-VR	16.7 ± 0.1	15.2 ± 0.3	18.7 ± 2.8	100.9 ± 15.4	51.7 ± 3.9	35.0 ± 5.8
Sw-VR	16.0 ± 1.8	14.6 ± 1.5	33.8 ± 9.9	121.6 ± 32.8	30.8 ± 0.9	91.7 ± 1.7

DBH: diameter at breast height; TH: total height; A_L : leaf area; A_s : sapwood area; LCR: Live crown ratio.

Table 2

Estimates of model parameters and standard errors of the mean ($s_{\bar{y}}$) for the non-linear model ($y = a(1 - \exp(-kx))$) used to fit curves to the relationships between species transpiration rates per unit leaf area (Q_l) and the micrometeorological variables

Species	Treatment	Independent variable	a	$s_{\bar{a}}$	k	$s_{\bar{k}}$	R^2
Bw	CT	D	1.39E-08	1.08E-09	8.54E-04	1.42E-04	0.536
		Q^*	1.41E-08	1.17E-04	3.22E-03	1.21E-03	0.524
		u	1.18E-08	6.20E-10	7.87E+00	1.29E+00	0.434
		ET _P	1.20E-08	4.92E-10	6.13E+01	1.53E+01	0.525
	VR	D	3.28E-08	4.86E-09	3.97E-04	8.60E-05	0.695
		Q^*	2.75E-08	3.17E-09	2.44E-03	1.12E-03	0.674
		u	3.76E-08	1.13E-08	6.16E-01	2.47E-01	0.692
		ET _P	2.54E-08	1.88E-09	9.67E+00	5.37E+00	0.728
Pb	CT	D	2.86E-08	2.43E-09	5.64E-04	5.54E-04	0.740
		Q^*	2.52E-08	2.04E-09	2.76E-03	1.06E-03	0.716
		u	2.02E-08	1.02E-09	7.11E+00	1.04E+00	0.535
		ET _P	2.10E-08	7.32E-10	5.10E+01	1.06E+01	0.703
	VR	D	3.70E-08	5.07E-09	4.06E-04	8.20E-05	0.737
		Q^*	2.77E-08	2.33E-09	3.07E-03	9.27E-04	0.723
		u	4.64E-08	1.41E-08	5.63E-01	2.22E-01	0.655
		ET _P	2.85E-08	1.57E-09	1.02E+01	2.99E+00	0.837
Sw	CT	D	7.85E-09	1.46E-09	4.54E-04	1.32E-04	0.511
		Q^*	1.81E-08	1.38E-08	5.82E-04	9.68E-04	0.657
		u	5.70E-09	5.40E-10	4.67E+00	9.79E-01	0.473
		ET _P	5.62E-09	3.44E-10	3.78E+01	9.28E+00	0.589
	VR	D	1.71E-08	2.11E-09	5.09E-04	1.01E-04	0.660
		Q^*	1.59E-08	1.26E-09	2.78E-03	8.11E-04	0.791
		u	2.67E-08	8.56E-09	5.19E-01	2.12E-01	0.696
		ET _P	1.49E-08	8.66E-10	1.08E+01	3.13E+00	0.799

The dependent variables in the model were *Betula papyrifera* (Bw), *Populus balsamifera* (Pb) and *Picea glauca* (Sw) Q_l from the control (CT) and variable retention (VR) sites. The independent variables in the model were vapour pressure deficit (D), net radiation (Q^*), wind speed (u) and potential evapotranspiration (ET_P).

where Δ is the slope of the saturation vapour pressure versus temperature curve at the air temperature (Pa K^{-1}), Q^* the net radiation ($\text{J m}^{-2} \text{s}^{-1}$), ρ_a the density of air (kg m^{-3}), c_a the heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$), u the wind speed (m s^{-1}), D the vapour pressure deficit (Pa), ρ_w the density of water (kg m^{-3}), λ_v the latent heat of vaporization (J kg^{-1}), and γ is the psychrometric constant (Pa K^{-1}).

2.5. Sap flux measurements

Two constant-heat sap flow sensors constructed after Granier (1985, 1987) were installed at 1.3 m on opposite sides of the stem, facing east and west, in each of the sample trees. For each sensor, two holes were drilled into sapwood with a vertical spacing of 10 cm. Each hole was drilled to a depth of 2.0–2.5 cm to ensure that the sensor was in contact with functional xylem. The mean sapwood depths of the sample trees (*B. papyrifera* = 1.9 cm, *P. balsamifera* = 2.9 cm and

P. glauca = 2.8 cm), indicated that the probes used (2 cm length) likely would have closely approximated the actual sap flux. If necessary for suitable installation, a chisel was used to remove a thin layer of the outer bark. A small amount (~ 0.5 mL) of hydrogen peroxide (30 mg mL^{-1} solution) was injected into each hole to destroy bacteria transmitted from the drill bit. Reflective foil was used to insulate the temperature field around the sensors, limiting the effects of solar radiation and convective heat loss.

The upper probe was heated constantly with a 0.2 W direct current, producing a maximum temperature difference of 8–10 °C under zero flow conditions. The temperature differences, monitored with thermocouples, were related to the mass flow of water from the empirical calculation (Granier, 1987):

$$v_s = 119 \times 10^{-6} \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231} \quad (2)$$

where v_s (m s^{-1}) is the mean sap velocity on a sapwood area basis along a radius, ΔT_M the temperature difference when sap flow is assumed to equal 0 (night values), and ΔT is the temperature difference between the two probes. As sap flow increases, progressively more heat is moved away from the upper probe, decreasing ΔT . A thermocouple multiplexer (AM25T, Campbell Scientific) was used to connect sensors to the data logger, where probe signals were scanned every 15-s and 15-min means were recorded. The rate of sap flow (Q , $\text{m}^3 \text{s}^{-1}$) was then calculated as

$$Q = v_s A_s \quad (3)$$

where A_s (m^2) is the cross-sectional sapwood area. This was determined for each tree from 1 cm disks cut at breast height (1.3 m) from frozen samples harvested at the end of the study. The sapwood-heartwood boundary was marked as samples thawed. Samples were scanned and A_s was calculated with imaging software (Sigma Scan 3.0, Jandel Scientific, San Rafael, CA, USA). The total Q for each tree was determined from the mean of the two probes in each tree.

Transpiration rate per unit leaf area (Q_l ; $\text{m}^3 \text{H}_2\text{O m}^{-2} A_L \text{s}^{-1}$) was calculated for each stem as follows (Ewers and Oren, 2000):

$$Q_l = \frac{Q}{A_L} \quad (4)$$

where A_L (m^2) is the total leaf area for each tree (Table 1). We collected all leaves from each tree and oven-dried (65°C for 72 h) in the laboratory. Leaves were then hand sorted to eliminate debris. The remaining leaves and petioles were weighed to determine the total dry biomass per plant (m_d ; kg). The A_L for each tree was then calculated by

$$A_L = m_d \text{SLA} \quad (5)$$

where SLA is the specific leaf area (i.e. one-sided leaf area per unit leaf dry mass; $\text{m}^2 \text{kg}^{-1}$) from the sub-sample. Leaf sub-samples from the deciduous (approximately 100 leaves per tree) and coniferous trees (approximately 50 twigs with needles) were collected to capture the variability in leaf size and weight throughout the entire crown. Deciduous tree sub-sample leaf area was calculated using the average of three measurements of all sub-sample leaves to reduce the potential error from a LI-3100 Area Meter (Li-Cor). Leaf areas of coniferous sub-samples were determined using a scanner and imaging software (Sigma Scan 3.0, Jandel Scientific).

2.6. Coupling calculations

The dimensionless decoupling coefficient ($0 \leq \Omega \leq 1$), where those trees that are aerodynamically well coupled to the atmosphere have Ω near zero, was calculated for each tree species as (Jarvis and McNaughton, 1986):

$$\Omega = \frac{1 + \varepsilon}{1 + \varepsilon + g_a/g_c} \quad (6)$$

where ε is Δ/γ , g_a the aerodynamic conductance and g_c is the canopy conductance. Canopy conductance (m s^{-1}) was estimated as

$$g_c = \frac{\gamma \lambda_v Q_l}{\rho_a C_p D} \quad (7)$$

where C_p is the specific heat of dry air at constant pressure ($\text{J kg}^{-1} \text{K}^{-1}$). Aerodynamic conductance (m s^{-1}) was calculated as

$$g_a = \left[\frac{u}{u_*^2} \right]^{-1} \quad (8)$$

where u_* is the friction velocity (m s^{-1}).

2.7. Sapwood hydraulic characteristics

At the end of the field experiment, trees were destructively sampled. Stem sections 100 cm long and centred on breast height (1.3 m) were cut, double-wrapped in polyethylene bags (0.15 mm thick), iced and transported to the laboratory. The sections were kept water saturated and refrigerated (4°C) in a dark room for up to two weeks, until hydraulic conductivity was measured (Sperry et al., 1988; Mencuccini et al., 1997).

Stem samples (15–20 cm long), centred on the breast height position, were cut with a band saw. Cut surfaces were smoothed with a sharp, low-angle (30°) block plane, eliminating resinous exudates and sawdust from the surface (Mencuccini et al., 1997). Each stem segment was installed in an apparatus that used a hanging water column to generate a constant pressure head ($\Delta\Psi$) of 17.45 kPa across the sample, which was insufficient pressure to flush embolisms. Filtered ($0.2 \mu\text{m}$), degassed water was perfused through each sample in the natural direction of flow. Outflow water temperature was recorded to correct for variations in viscosity. An electronic balance and computer recorded outflow for 15 min following 5 min of stable flow.

Sapwood hydraulic properties were quantified as discussed in Reid et al. (2005). Hydraulic conductivity (K_ψ , $\text{m}^2 \text{Pa}^{-1} \text{s}^{-1}$), as described by Darcy's law, was

calculated using

$$K_{\psi} = \frac{QL}{A_s \Delta\Psi} \quad (9)$$

where Q is the flow or volumetric discharge per unit time ($\text{m}^3 \text{s}^{-1}$) through the stem section with a sapwood area (A_s) and length (L). $\Delta\Psi$ is the water potential difference driving flow, expressed using pressure units (Pa). An estimate of the capacity of the stem segment to conduct water was calculated from

$$Q_h = K_{\psi} A_s \quad (10)$$

where Q_h ($\text{m}^4 \text{Pa}^{-1} \text{s}^{-1}$) is the hydraulic capacity, which expresses volumetric flow ($\text{m}^3 \text{s}^{-1}$) per unit of hydraulic gradient (Pa m^{-1}). This value provides a description of regulated flow through stems as the combined effects of hydraulic conductivity and conducting sapwood area under a unit hydraulic gradient. To quantify the relationship between the water conducting properties of xylem and leaf area, leaf specific hydraulic capacity (Q_L , $\text{m}^2 \text{Pa}^{-1} \text{s}^{-1}$) was defined as

$$Q_L = \frac{Q_h}{A_L} \quad (11)$$

where A_L is the leaf area distal to the stem segment measured.

2.8. Xylem pressure potential measurements

On a warm, clear day in July 2005, sites were revisited to measure xylem pressure potential (Ψ_x) with a pressure chamber instrument (Model 600, PMS Instruments, Corvallis, OR, USA). Soil moisture was recharged by recent rains. Pressure chamber readings were taken at mid-day (1225–1625 MDT), when water stress would be greatest. Sample twigs were collected from mid-canopy from trees that appeared healthy, with no signs of leaf senescence or branch dieback. We alternated between the control and VR site until six trees from each species at each site had been sampled.

2.9. Data analyses

Correlations of micrometeorological variables pre-harvest (13 June–8 July) and post-harvest (9–31 July and 13–21 August) were compared between control and VR sites. Differences in slopes and intercepts were tested using t -tests in a method analogous to that of testing for differences between two population means (Zar, 1999). Two-tailed t -tests were also used to compare Ψ_x between the control and VR site for each of the species (PROC TTEST). Relationships between

Q_L and D , Q^* , u and ET_P for all three species, in both the VR and control sites, were produced using hourly averages (0900–1500 MDT) from the entire post-harvest period. Days with precipitation were eliminated from the data set. The non-linear function $y = a(1 - \exp(-kx))$ was used to fit curves to the relationships between individual species $Q_L(y)$ and each of the micrometeorological variables (x) (PROC NLIN). Model parameters are presented in Table 2. An overall test for coincidental regressions was used to test whether the slopes and intercepts were identical (Zar, 1999). Function parameters (k = slope and a = asymptote) were analysed using PROC GLM and post hoc mean separation tests (Tukey's) to determine where they were different between species and treatments. Adjusted R^2 values for all equations were calculated as $1 - (\text{error sum of squares}/\text{corrected total sum of squares})$ (Cornell and Berger, 1987). All statistical analyses were performed using the SAS statistical package (Version 9.1, SAS Institute Inc., Cary, NC), with $\alpha = 0.05$ as the threshold for statistical significance.

3. Results

3.1. Micrometeorology

Pre-harvest mean air temperature (T_a) was 13.9°C in both the control and VR sites. The post-harvest measurement period was warm, with mean T_a of 18.0°C in both sites. The observed post-harvest T_a in the VR site was only 0.17°C (1.02%) lower than the predicted values determined from the pre-harvest calibration period. While there was a slight difference in T_a between the two sites from the pre-harvest to the post-harvest period, there was no difference in the slopes ($t = 0.97$; $P > 0.30$) or intercepts ($t = -0.49$; $P > 0.50$) of the bivariate plot of the control versus VR site before and after treatment (Fig. 1A).

Mean relative humidity (RH) declined 9%, from 0.66 to 0.60, in the control site from the pre- to post-harvest period, while decreasing 14%, from 0.76 to 0.65, in the VR site. The bivariate plot of RH of the control versus VR site (Fig. 1B) showed a slightly lower intercept and greater slope, or drier atmosphere, in both sites post-harvest. The slopes ($P < 0.001$) and intercepts ($P < 0.001$) were significantly different. However, the actual difference between the observed and predicted RH in the VR site, post-harvest was only 1.84 (3.57%).

Mean vapour pressure deficit (D) in the control site increased 44% from the pre-harvest ($\bar{X} = 707.4 \text{ Pa}$) to the post-harvest measurement period ($\bar{X} = 1023.3 \text{ Pa}$). Similarly, in the VR site, mean D increased 53% from

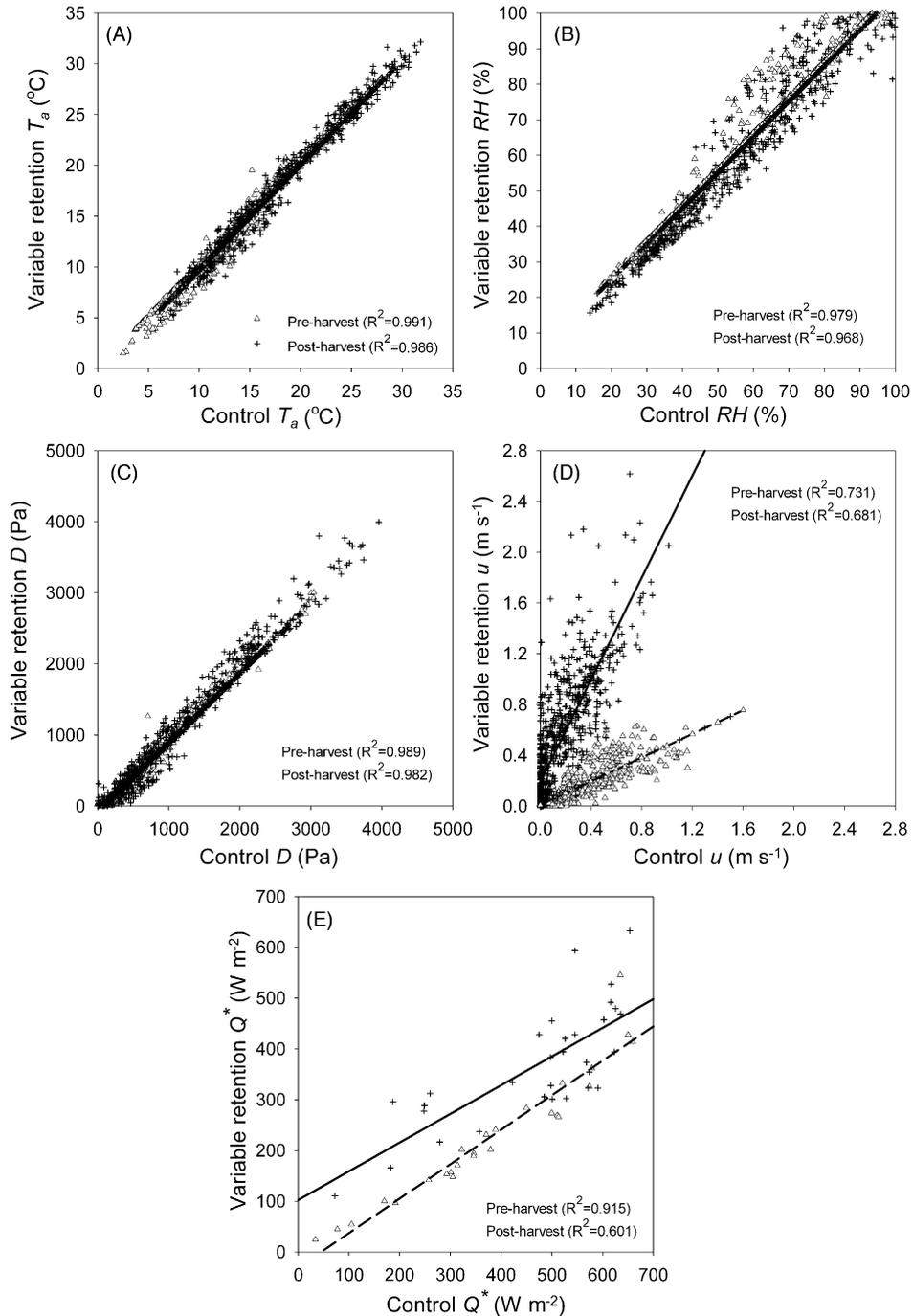


Fig. 1. Relationships between control and variable retention site micrometeorological variables, pre-harvest (triangles) and post-harvest (crosses), for (A) air temperature (T_a ; pre-harvest $y = 1.0484x - 0.7031$; post-harvest $y = 1.0425x - 0.7687$), (B) relative humidity (RH; pre-harvest $y = 1.007x + 0.0576$; post-harvest $y = 1.0219x + 0.0302$), (C) vapour pressure deficit (D ; pre-harvest $y = 0.9926x - 0.0844$; post-harvest $y = 1.0067x - 0.0802$), (D) wind speed (u ; pre-harvest $y = 0.4668x + 0.0074$; post-harvest $y = 2.0119x + 0.1872$) and (E) mean mid-day (1100 – 1445 MDT) net radiation (Q^* ; pre-harvest $y = 0.679x - 30.881$; post-harvest $y = 0.5654x + 102.3$). Best fit lines not shown for clarity.

the pre-harvest ($\bar{X} = 617.7$ Pa) to the post-harvest period ($\bar{X} = 950.1$ Pa). The slopes ($P < 0.001$) and intercepts ($P < 0.001$) of the plot of D between the control and VR site were different from the pre- to post-harvest period (Fig. 1C). However, the observed post-harvest D in the VR site was only 18.8 Pa (2.69%) different from the predicted values.

Wind speed (u) in the VR site increased several fold after harvesting. The mean u observed prior to harvest in the control site was 0.25 m s^{-1} (0–1.40 m s^{-1}) and in the VR site was 0.13 m s^{-1} (0–0.67 m s^{-1}). The post-harvest mean u declined to 0.14 m s^{-1} (0–1.01 m s^{-1}) in the control site, while increasing in the VR site to 0.50 m s^{-1} (0–3.57 m s^{-1}). This equates to a mean decrease in u of 44% in the control site and a 284% increase in the VR site after harvesting. Both the slope and intercept of the bivariate plot of u of the control versus VR site shifted upwards (Fig. 1D), reflecting the large increase in u in the VR site post-harvest (slopes: $P < 0.001$; intercepts: $P < 0.001$). The actual difference between the observed and predicted u in the VR site, post-harvest was 0.28 m s^{-1} (339.6%).

Both the pre- and post-harvest periods had mostly sunny days. Before the harvest mean net radiation (Q^*) during the mid-day (1100–1445 MDT), when peak daily Q_1 was observed, was 363.9 W m^{-2} (33.7–659.5 W m^{-2}) in the control and 224.9 W m^{-2} (24.0–545.1 W m^{-2}) in the VR site. The post-harvest mean mid-day Q^* was 469.6 W m^{-2} (72.2–653.9 W m^{-2}) in the control and 367.8 W m^{-2} (110.3–632.7 W m^{-2}) in the VR site. This represents a mean increase in Q^* of

29% in the control and 63% in the VR site. There was a significant difference in the pre- and post-harvest slopes ($P < 0.001$) and intercepts ($P < 0.001$) of the bivariate plots of Q^* between the control and VR site (Fig. 1E). The observed post-harvest Q^* in the VR site was 79.9 W m^{-2} (52.5%) greater than the predicted values determined from the pre-harvest calibration period.

Prior to harvest, volumetric soil moisture (θ_v) in the control and VR sites tracked each other through precipitation events (Fig. 2). The control site had higher θ_v ($\bar{X} = 0.359$) compared to the VR site ($\bar{X} = 0.335$) prior to harvest. After harvest, the VR site θ_v ($\bar{X} = 0.402$) rose above the control ($\bar{X} = 0.332$). In days following precipitation, θ_v declined more rapidly in the control site than the VR site. Total precipitation pre-harvest was normal with 72.8 mm, but was well below average during the post-harvest period with just 43.4 mm of precipitation. The full range of θ_v values in both the control and VR site were within the typical range of plant available water or gravitational water values for a silty-clay soil (Dingman, 2002).

Throughout the measurement period before the harvest, potential evapotranspiration (ET_P) traces in the control site were slightly greater than observed in the VR site (Fig. 3A). Immediately following harvest, this trend was reversed, with ET_P values in the VR site exceeding the control site (Fig. 3B). While control ET_P values decreased minimally, the values in the VR site were doubled and often tripled following the harvest. A mean daily sum of 15 min. ET_P values showed a 9% decline in the control site from 2.05 mm d^{-1} (pre-

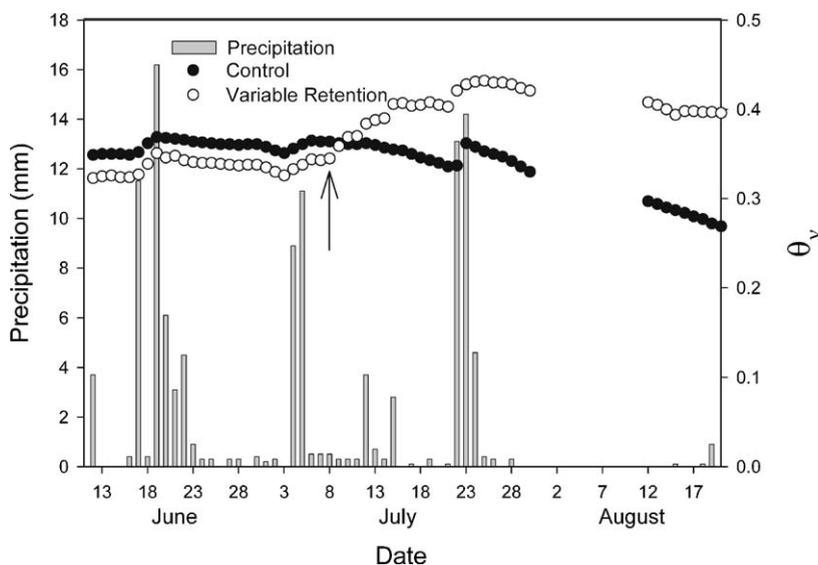


Fig. 2. Mean daily volumetric soil moisture content (θ_v) and precipitation (mm) in the control and variable retention sites for each day pre- and post-harvest (13 June–31 July and 13–21 August 2003). The arrow indicates the time of partial harvest (9 July 2003).

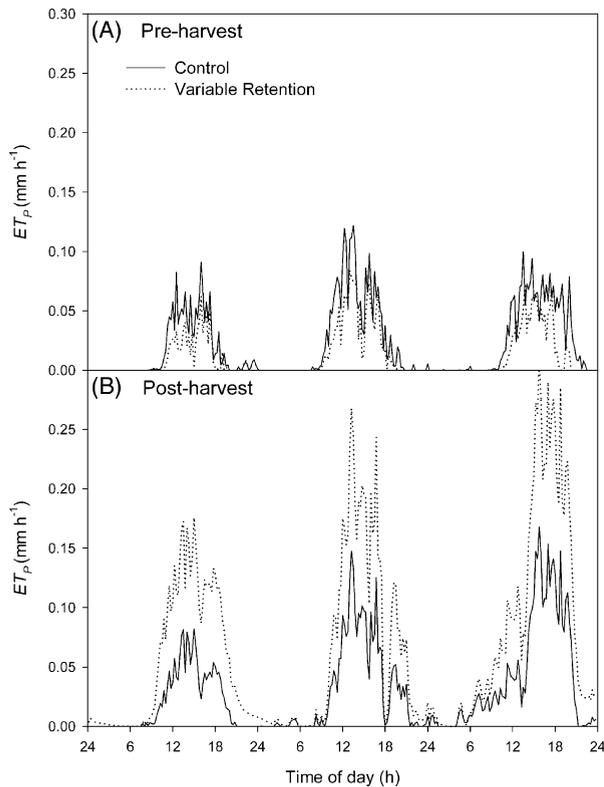


Fig. 3. Typical 3-day pattern of potential evapotranspiration (ET_p) in the control and variable retention sites, determined from the Penman combination equation for free-water evaporation. (A) Pre-harvest (6–8 July 2003) and (B) post-harvest (15–17 July 2003).

harvest) to 1.86 mm d^{-1} (post-harvest). Conversely, there was a 290% increase mean daily ET_p in the VR site from 1.27 mm d^{-1} (pre-harvest) to 4.95 mm d^{-1} (post-harvest). In the control site the average number of hours per day when ET_p was greater than 0 increased from 14.4 h d^{-1} (pre-harvest) to 14.6 h d^{-1} (post-

harvest), compared to the increase from 13.8 h d^{-1} (pre-harvest) to 17.5 h d^{-1} (post-harvest) in the VR site.

3.2. Transpiration rates

Post-harvest daily patterns of transpiration rates per unit leaf area per tree (Q_l) illustrate that transpiration in *P. glauca* was generally lowest among the species (Fig. 4A–C). *P. glauca* also showed the greatest differences between the control and VR sites; mid-day Q_l was two-times greater in VR site trees compared to the control site. Alternatively, *B. papyrifera* had higher Q_l than *P. glauca*, but showed moderate differences between sites, with Q_l in the VR site 1.25–1.5 times greater than in the control site. *P. balsamifera* generally showed similar Q_l as *B. papyrifera* post-harvest; however, there were only marginal differences in the diurnal patterns of Q_l in the control and VR site (Fig. 4C). The timing of water use also appears to be different between the control and VR site, with Q_l beginning earlier in the day and extending later into the evening and even into the pre-dawn hours in the VR site.

The $Q_{l\text{-max}}$ was about 2.5-times greater in *P. glauca* trees in the VR site than in the control during the post-harvest period (Fig. 5A). Similarly, *B. papyrifera* trees in the VR site had a $Q_{l\text{-max}}$ approximately 1.6-times greater than in the control site. *P. balsamifera* trees $Q_{l\text{-max}}$ was only marginally different between the two sites. Variation in total daily transpiration (Q_d) among species and treatments showed a similar pattern as $Q_{l\text{-max}}$. *P. glauca* trees showed the greatest difference in Q_d per tree, with VR site trees utilizing approximately 3.2-times more water per day than control trees (Fig. 5B). Total daily transpiration for *B. papyrifera* was about 1.6-times greater in the VR site than in the control

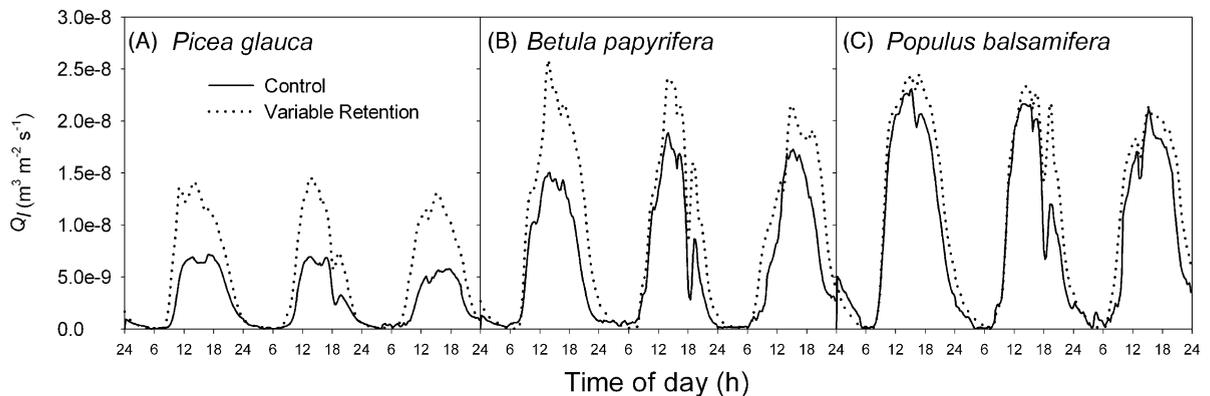


Fig. 4. Typical pattern of mean transpiration rate per unit leaf area per tree (Q_l) on 3 clear days following partial harvest. (A) *Picea glauca*, (B) *Betula papyrifera* and (C) *Populus balsamifera* from the control (solid line) and variable retention (dashed line) sites (15–17 July 2003).

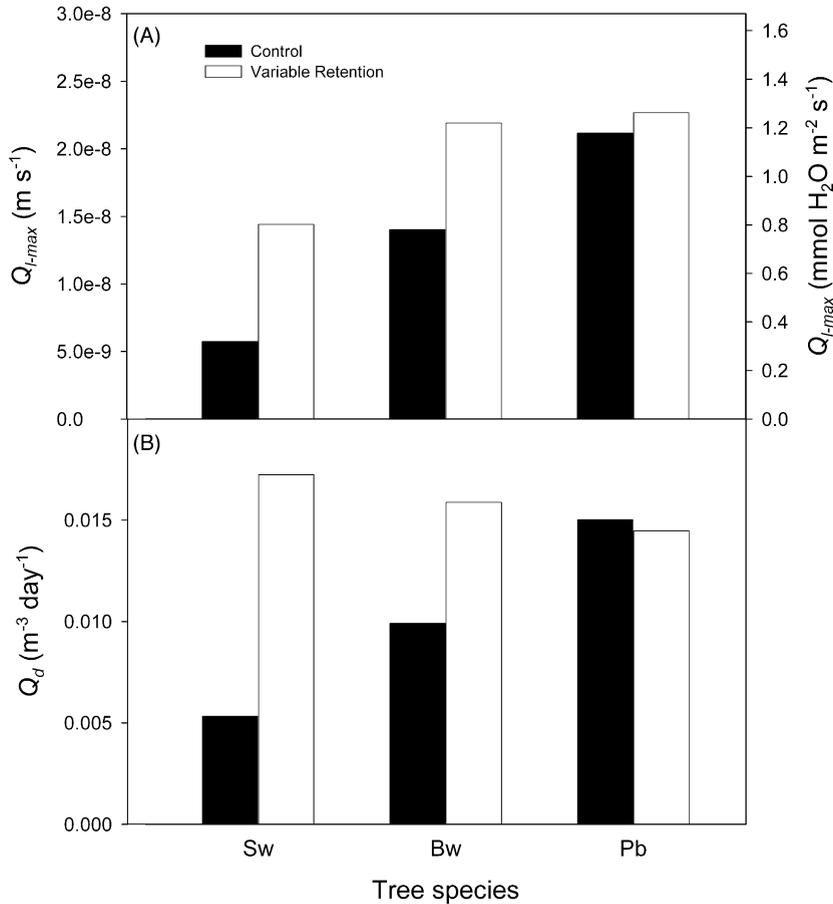


Fig. 5. (A) Mean daily maximum transpiration rate per unit leaf area ($Q_{l,max}$) and (B) mean daily water use (Q_d) per tree of *Picea glauca* (Sw), *Betula papyrifera* (Bw) and *Populus balsamifera* (Pb) from the control and variable retention sites for the entire post-harvest period (9–31 July and 13–21 August 2003; $n = 3$).

throughout the post-harvest measurement period, while only a marginal difference in Q_d was evident for *P. balsamifera* trees. The maximum Q_d values occurred on days which were characterized by high T_a , D and Q^* , low RH and above average mid-day u .

Differential responses among species to individual microclimate variables were also evident between the VR and control sites. Asymptotic relationships between daytime Q_1 and D , Q^* , u and ET_P were observed for all three species in both sites (Fig. 6). All species had increased Q_1 with D but, *P. glauca* was least responsive and *P. balsamifera* was most responsive to changes in D in both sites. Additionally, there were strong differences between the VR and control sites in the relationship between Q_1 and D for *P. glauca* ($P < 0.0001$), while weaker, yet significant differences (particularly at low D) were observed in *B. papyrifera* ($P < 0.0001$) between the two sites. No differences in the relationships were evident for *P. balsamifera* ($P = 0.39$)

between VR and control sites. We observed similar general patterns for Q_1 in relation to Q^* in both sites (i.e. *P. glauca* < *B. papyrifera* < *P. balsamifera*) but, the relationships between Q_1 and Q^* were significantly different ($P < 0.0001$) between the VR and control site for all three species (Fig. 6). The pattern of Q_1 across the range of u values among species was generally similar to the response to D and Q^* (i.e. *P. glauca* < *B. papyrifera* < *P. balsamifera*). However, at low wind speeds, Q_1 of all three species appeared to be greater in the control trees compared to the VR trees. Furthermore, at the higher u observed in the VR site, *P. glauca* Q_1 continued to rise at a similar rate as observed in the control site ($P = 0.12$). Conversely, *P. balsamifera* Q_1 increased at a much lower rate in the VR site with increased u ($P < 0.0001$). Despite the greater u in the VR site, the highest Q_1 values observed in the VR trees rarely exceeded those observed in the control site for this species. The response of *B. papyrifera* to increased

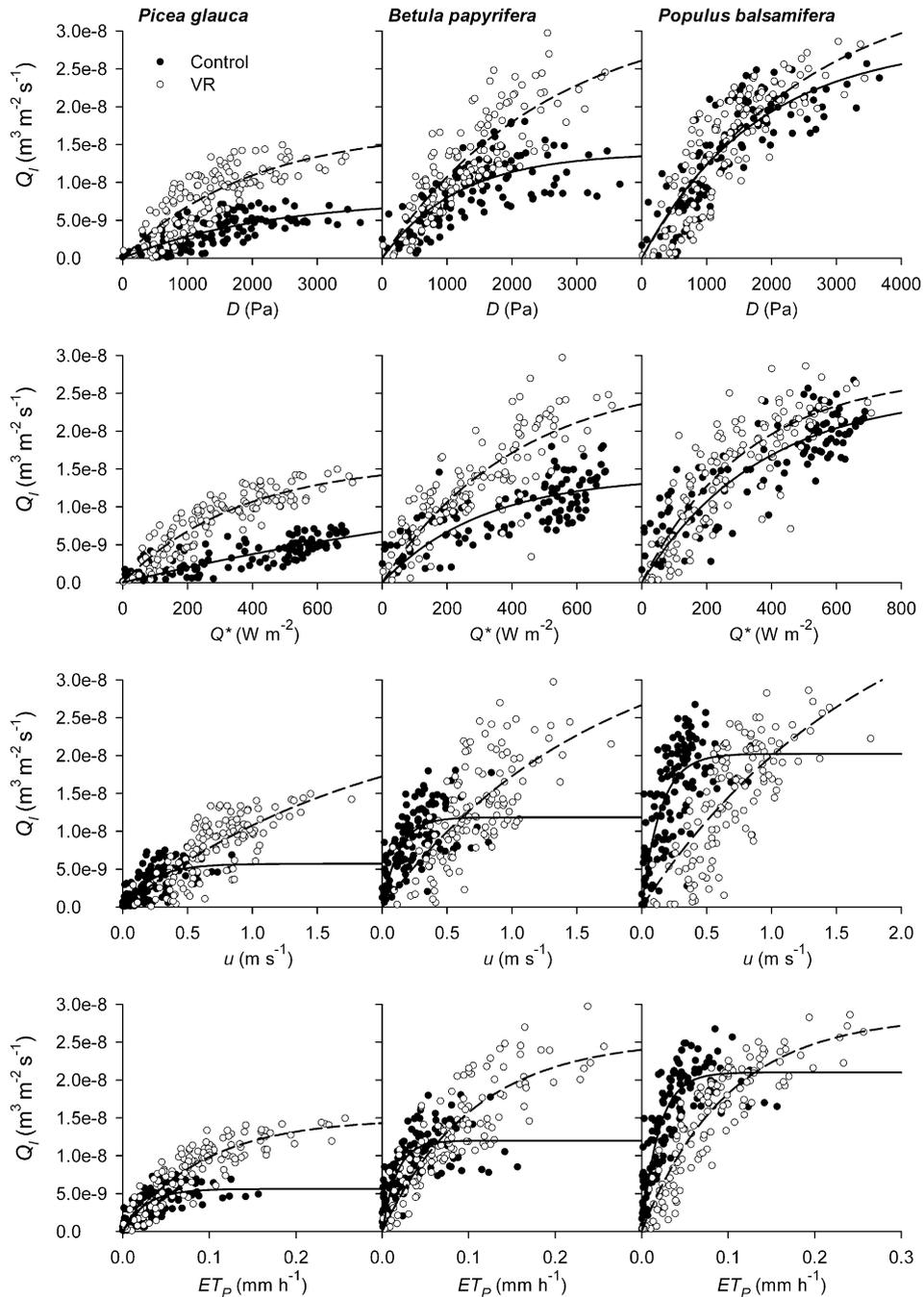


Fig. 6. Response curves of transpiration rates per unit leaf area (Q_l) to vapour pressure deficit (D), net radiation (Q^*), wind speed (u) and potential evapotranspiration (ET_p) for *Picea glauca*, *Betula papyrifera* and *Populus balsamifera* from the control and variable retention sites (0900–1500 MDT; 9 July–21 August 2003).

u in the VR site was intermediate to the other two species. Transpiration increased with greater u , but at a slightly slower rate than in the control site ($P < 0.001$). The combined effect of these three microclimatic variables is reflected in potential evapotranspiration.

The general pattern of species sensitivity and differences in Q_l between VR and control sites for ET_p was most similar to the patterns observed in the response to wind speed. In *P. glauca*, Q_l was similar in the VR and control sites at low ET_p . However, the increase in Q_l

with high ET_P was greater in the VR site compared to the control site for this species ($P < 0.0001$). In contrast, at low evaporative demand, *P. balsamifera* transpiration was notably lower and the rate of increase in Q_1 with ET_P was not as steep in the VR site as in the control site ($P < 0.0001$). At high evaporative demand, the increase in *P. balsamifera* in the VR site was limited compared to the other two species. For *B. papyrifera*, the overall response in Q_1 to ET_P was similar in both sites ($P = 0.26$), and intermediate between the responses observed in *P. glauca* and *P. balsamifera*.

Mean separations tests of the non-linear function parameters for the relationships between transpiration and the micrometeorological variables indicated that the asymptotes (a) were different between all species and between the control and VR sites (Table 2). However, tests of slopes (k) showed no differences between any of the three species, but still showed differences between the two sites.

3.3. Decoupling coefficients

The mean decoupling coefficients (Ω) in the control site indicated that *P. glauca* was the most well coupled species to the atmosphere ($\Omega = 0.16$), followed by *B. papyrifera* ($\Omega = 0.36$), and *P. balsamifera* ($\Omega = 0.40$). Although the decoupling coefficients of all species were lowered in the VR sites (indicating greater atmospheric coupling), *P. glauca* experienced the lowest relative change in atmospheric coupling ($\Omega = 0.11$; 33% increase), followed by *B. papyrifera* ($\Omega = 0.19$; 47% increase) and *P. balsamifera* ($\Omega = 0.18$; 55% increase).

3.4. Hydraulic characteristics

Main stem K_ψ , Q_h and Q_L was generally greater in the VR site than the control site for all three species. None of the differences were statistically significant for any of the species. However, there were consistent differences between the species in their ability to transport water to their leaves. For all of the hydraulic characteristics we found *B. papyrifera* > *P. balsamifera* > *P. glauca* in both the control and VR site. The small sample size ($n = 3$) may have contributed to the lack of significant difference in hydraulic characteristics between VR and control trees.

3.5. Xylem pressure potential

Variable retention harvesting resulted in significantly lower midday Ψ_x in the VR trees than in the control trees for all three species (Fig. 7). The mean Ψ_x were

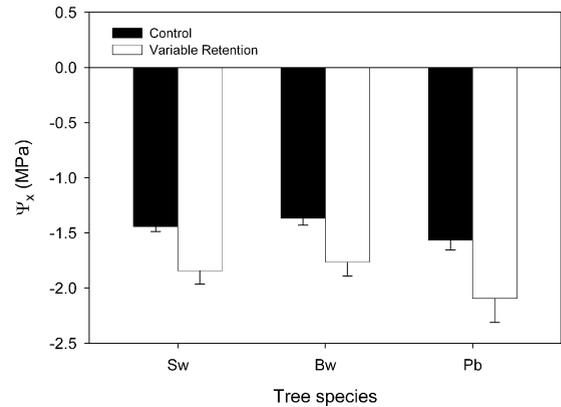


Fig. 7. Mean xylem pressure potentials (Ψ_x) of *Picea glauca* (Sw), *Betula papyrifera* (Bw) and *Populus balsamifera* (Pb) from the control and variable retention sites (8 July 2005; $n = 6$).

significantly more negative in the VR trees than in the control trees for *B. papyrifera* ($P = 0.02$), *P. balsamifera* ($P = 0.04$), and *P. glauca* ($P = 0.01$).

4. Discussion

4.1. Micrometeorology

Variable retention (VR) harvesting produced a nearly three-fold increase in potential evapotranspiration (ET_P) immediately following harvesting. The most dramatic change in meteorological variables contributing to the increase in evaporative demand was the large increase in wind speed (u) at crown level in the VR site. Rudnicki et al. (2003) observed similar magnitudes of u increases (three-times) at the canopy level following thinning of lodgepole pine stands. Generally, as u increases, leaf boundary layer resistance decreases, directly influencing transpiration rates and leaf temperature (Daudet et al., 1999; Wullschlegler et al., 2000). Depending on how well coupled a plant is with the atmosphere, increased flow of air over a leaf should increase turbulence, boundary layer conductance and, hence increase transpiration rates (Van Gardingen and Grace, 1991; Hollinger et al., 1994).

The 63% increase in mid-day net radiation (Q^*) in the VR site also contributed to the near tripling of ET_P . Exposure of residual trees to increased radiant energy could partially explain the increased transpiration rates per unit leaf area (Q_1) and more negative xylem pressure potentials (Ψ_x) measured in all three species in the VR site. Increases in Q^* , and its influence on leaf temperature, has been observed to increase stomatal conductance (g_s) and Q_1 in many species (Wullschlegler et al., 2000; Pataki and Oren, 2003). While leaf

temperatures were not measured, we speculate that during very calm conditions leaf temperature likely increased as more of the crowns were fully exposed to solar radiation. This may have had a greater influence on transpiration rates of *P. glauca* compared to the deciduous species because of the long, dense crowns of the conifers.

Contrary to our hypotheses, we did not observe large decreases in relative humidity (RH) or increases in air temperature (T_a) and vapour pressure deficit (D) at the crown level in the VR site. While the change in these variables following harvesting may have been statistically significant because of a very large sample size (>2500 measurements), the actual differences appear to be physiologically negligible. In contrast, others have demonstrated that at positions near ground level (~0.2 m) harvested stands had lower RH and higher T_a and D than control sites (Barg and Edmonds, 1999; Man and Lieffers, 1999; Zheng et al., 2000). The discrepancy between these results and our findings is likely related to strong differences in advection and lapse conditions for water vapour and sensible heat at mid-canopy (12 m) of our sites, producing very similar humidity and temperature conditions between control and VR sites (Oke, 1987).

We also observed considerable increases in volumetric soil moisture (θ_v) in the partial cutover, despite below average precipitation during the post-harvest period. Decreased total transpiration and rainfall interception following harvesting is probably responsible for increased θ_v in the VR site, similar to other studies (Childs and Flint, 1987; Kranabetter and Coates, 2004). Thus, any differences in Q_1 observed in our study were unlikely to be related to θ_v . Also, given the fine soil texture at our sites, it is likely that xylem dysfunction would produce a greater limitation to plant flux than rhizosphere conductance (Sperry et al., 1998).

4.2. Tree response

Contrary to our expectation, that all species would respond to greater ET_P in the VR site with increased water use, maximum transpiration per unit leaf area (Q_{1-max}) and total daily water use (Q_d) for *P. balsamifera* trees in the VR site was only marginally greater than in the control trees. Relative to *B. papyrifera* and *P. glauca*, the *P. balsamifera* trees had high Q_{1-max} and low mean xylem pressure potential (Ψ_x) in the control site. Additionally, the saturation of Q_1 at high D and Q^* (Fig. 6) by this species in the control site suggests stomatal closure to maintain Ψ_x above the critical point of xylem cavitation. These findings provide evidence

that *P. balsamifera*, with its high level of Q_1 saturation, may normally function with minimal safety margin against catastrophic xylem dysfunction (Tyree et al., 1994), compared to the low level for saturation of *P. glauca*. It must also be remembered, however, that apparent differences in the way that Q_1 responded to D between the control and VR sites (Fig. 6) was related to other values such as u or Q^* , which actually varied between the two sites. While mid-day Ψ_x for *P. balsamifera* in our study was as low as -2.1 MPa, xylem pressure potentials of -1.5 MPa in *P. balsamifera* and other cottonwoods have been observed to result in as much as 50% loss of hydraulic conductivity from cavitation (Sperry et al., 1994). Thus, *P. balsamifera* trees in the VR site likely responded to the abrupt increases in u and ET_P with further stomatal closure in order to limit Q_1 and Q_{1-max} and to prevent runaway cavitation (Schulte et al., 1987; Hinckley et al., 1994; Rood et al., 2003). However, response curves for this species (Fig. 6) show that at low ET_P transpiration in the VR site trees was lower than Q_1 of the control trees, indicating that the VR trees may have suffered some xylem dysfunction. Shortly after the VR harvest, we also noted leaf rolling and leaf wilting in the *P. balsamifera* trees. By the summer of 2005, many of the *P. balsamifera* residuals in the VR site had shed leaves from their upper canopy, and several nearby trees had died. Shedding leaves and small twigs is a common drought response of cottonwood species (Rood et al., 2000), and is considered to be a mechanism to reduce transpirational water loss after xylem cavitation (Zimmermann, 1978). Our laboratory measurements of hydraulic conductivity and other hydraulic characteristics indicate that VR harvesting did not result in significant reductions in the ability of the main stems of *P. balsamifera* to transport water to their leaves. Part of the reason for this lack of significance might be related to the small sample size ($n = 3$). However, xylem dysfunction typically occurs in the most distal and expendable branches (i.e. vulnerability segmentation) rather than the main bole (Tyree and Sperry, 1989; Tyree et al., 1993), so the lack of difference in hydraulic characteristics between the two sites is not surprising. Our observation of upper crown dieback and subsequent development of adventitious branches on the stems of *P. balsamifera* in partial cut areas are consistent with the theory of vulnerability segmentation.

Our data for Q_{1-max} and Q_d indicates that *P. glauca* responded well to the VR harvest. The nearly three-fold increase in Q_{1-max} and Q_d of *P. glauca* in the VR site over the control site trees suggests that this species was able to respond directly to the rise in ET_P with only limited

stomatal closure. *P. glauca* Q_1 was positively related to both D and Q^* , but the response curves show that Q_1 was still able to increase with greater u and ET_P in the VR site (Fig. 6). The substantial increase in Q_{1-max} in the *P. glauca* trees is likely to have contributed to the more negative mid-day Ψ_x values we observed for this species in the VR site. However, there was probably limited risk of cavitation because (1) the sap fluxes were comparatively low and (2) like many coniferous species, *P. glauca* are highly resistant to water stress-induced cavitation (Maherali et al., 2004). The ability of *P. glauca* to increase Q_1 , Q_{1-max} and Q_d in response to increased ET_P could translate into increased carbon fixation and growth, as observed in other conifers following partial harvesting (Bebber et al., 2003).

Betula papyrifera residual trees also had greater Q_1 in response to increased ET_P in the VR site. Similar to *P. glauca*, the Q_1 response curves for *B. papyrifera* (Fig. 6) indicate that trees in the VR site were able to increase Q_1 at high wind speeds. Furthermore, at high D and Q^* , trees in the VR site transpired at higher rates than trees in the control sites. However, there appears to be some limitation on water use by *B. papyrifera* in the VR site. At low evaporative demand, Q_1 in VR site trees rose more slowly than in the control trees, suggesting either stomatal closure or xylem dysfunction. Additionally, the mean Q_{1-max} was only about 1.6-times greater for VR trees than control trees for this species, while ET_P increased nearly three-fold. Like many other deciduous trees, *B. papyrifera* are known to be extremely susceptible to water stress-induced cavitation (Sperry and Sullivan, 1992; Sperry et al., 1994). Thus, some stomatal closure in the VR site trees likely occurred in response to increased u and ET_P in order to prevent Ψ_x values from dropping to levels inducing extensive cavitation. However, the general increase in Q_1 with greater evaporative demand supports the hypothesis that *Betula* stomata are incapable of long-term regulation of Q_1 below levels that induce cavitation (Sperry and Pockman, 1993). The highly negative Ψ_x values measured in *B. papyrifera* trees in the VR site provides additional evidence of water stress sufficient to produce cavitation and embolism. If high ET_P persists for several years after VR, xylem dysfunction in *B. papyrifera* could be cumulative and dieback may appear in subsequent years. It is important to consider that *B. papyrifera* has been reported to have the ability to refill embolized xylem tissue (Sperry et al., 1994). Thus, if refilling is a viable mechanism to help this species cope with atmospheric drought-induced cavitation, then constraining Q_1 through stomatal closure may not be as important for *B. papyrifera* as for *P. balsamifera*.

Refilling of embolized conduits could allow residual *B. papyrifera* trees to delay crown dieback by re-increasing hydraulic conductivity. However, the potential root damage or soil compaction associated with normal harvesting operations (Kozlowski, 1999) could prevent this species from using this mechanism to cope with the stresses associated with large and persistent increases in ET_P in VR harvested stands. Thus, we believe that the inability to control Q_1 in response to high evaporative demand combined with the potential inability to repair xylem dysfunction due to root damage could explain the signs of leaf rolling, wilting, crown dieback and whole-tree mortality of *B. papyrifera* residuals we have observed in partially harvested cutovers throughout the region.

Estimates of the degree of canopy–atmosphere coupling indicated that *P. balsamifera* were the least coupled species ($\Omega = 0.40$), likely because they had the thickest leaf boundary layer of the three species due to their large and smooth leaves. However, we found this species to be highly coupled in the VR site ($\Omega = 0.18$). Our findings in the control site were similar to Hinckley et al. (1994), who found *P.* hybrid trees to be partially decoupled from the atmosphere ($\Omega = 0.66$). As a result of moderate coupling, *P. balsamifera* transpiration would be highly dependent on Q^* and on the factors that influence canopy boundary layer, such as u and canopy roughness, rather than D (Jarvis and McNaughton, 1986). Similarly, *B. papyrifera* was moderately coupled in the control site ($\Omega = 0.36$), and was highly coupled in the VR site ($\Omega = 0.19$). We did not anticipate that *B. papyrifera* would have similar Ω values as *P. balsamifera*; however, the ability of the leaves of both species to swing in the wind likely reduces the boundary layer resistance comparably. Alternatively, *P. glauca* was found to be highly coupled to the atmosphere in both the control ($\Omega = 0.16$) and VR site ($\Omega = 0.11$). Similar to other conifers, *P. glauca* possibly had high atmospheric coupling because of their many, small leaves, aerodynamically rough canopy and large boundary layer conductance (Meinzer, 1993; Martin et al., 1999). While some conifers have been shown to be poorly coupled due to high needle packing of sun shoots (Smith and Carter, 1988), this was likely not the case for our sample trees which were recently exposed from closed canopy conditions. We believe that the large and persistent increase in u , combined with the overall increase in canopy surface roughness and atmospheric turbulence following VR harvesting, greatly increased the canopy–atmosphere coupling in all species. As u increased in the VR site, the leaf boundary layer was likely eroded in all species, increasing aerodynamic conductance (g_a) and

stomatal control of Q_1 (Schuepp, 1993; Martin et al., 1999; Wullschlegel et al., 2000). This suggests that when there are large and persistent increases in u , as in VR cutovers, Q_1 will be primarily driven by the vapour pressure gradient between the leaf surface and the surrounding air, and relatively insensitive to changes in Q^* (Hollinger et al., 1994). This is consistent with suggestions by Wullschlegel et al. (2000) that tree response to changes in u , Q^* and D are highly dynamic and related to forest structure.

Immediately after VR harvesting, we observed increased ET_p and various signs of stress in *P. balsamifera* and *B. papyrifera* residual trees. Long-term stomatal regulation of Q_1 to prevent xylem cavitation is unlikely for both hardwood species. Thus, *P. balsamifera* and *B. papyrifera* residual trees may suffer extensive dieback and mortality, unless they are capable of adapting within a couple years after harvesting. We believe that only those trees with sufficient root or twig xylem conductivity, to meet the greater evaporative demand, will respond favourably to VR harvesting. Additional research is necessary to determine if it is possible to identify trees at the time of harvest that are most likely to adapt well to the abrupt change in microclimate. For *P. glauca*, we feel that, if they are windfirm, most trees should benefit from reduced competition and more open growing conditions after partial harvesting.

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