Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting

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Summary   Variable retention harvesting (VRH) has been proposed as a silvicultural practice to maintain biodiversity and ecosystem integrity. No previous study has examined tree carbon isotope discrimination to provide insights into water stress that could lead to dieback and mortality of trees following VRH. We measured and compared the carbon isotope ratios ($\delta^{13}C$) in stem wood of trembling aspen (*Populus tremuloides* Michx.) before and after VRH. Eight trees were sampled from isolated residual, edge and control (interior of unharvested stand) positions from each of seven plots in three regions (Calling Lake and Drayton Valley, Alberta and Lac Duparquet, Québec). After VRH, the general trend in mean $\delta^{13}C$ was residual > edge > control trees. Although this trend is indicative of water stress in residual trees, it also suggests that edge trees received some sheltering effect, reducing their stress compared with that of residuals. A strong inverse relationship was found between the $\delta^{13}C$ values and the mean annual precipitation in each region. The trend in mean $\delta^{13}C$ signature was Calling Lake > Drayton Valley > Lac Duparquet trees. These results suggest that residual or edge trees in drier regions are more likely to suffer water stress following VRH. We also observed a trend of greater $\delta^{13}C$ in stout trees compared with slender trees, both before and after VRH. The evidence of greater water stress in stout trees likely occurred because of a positive relationship between stem diameter and crown volume per basal area. Our results provide evidence that water stress could be the driving mechanism leading to dieback and mortality of residual trees shortly after VRH. Additionally, the results from edge trees indicate that leaving hardwood residuals in larger patches or more sheltered landscape positions could reduce the water stress to which these trees are subjected, thereby reducing dieback and mortality.

Keywords: atmospheric water stress, dieback, mortality, Populus tremuloides, regional differences, slenderness coefficient.

Introduction

Variable retention harvesting (VRH) leaves living trees, dispersed or in patches, within the boundaries of the harvested forest area to sustain ecosystem functions and biological diversity at the stand level. Although VRH is a common harvest prescription, neither the underlying ecological assumptions nor the outcomes of this silvicultural practice have been tested thoroughly. Recent observations of VRH cutblocks indicate that there may be a considerable increase in water stress and mortality among residual trees shortly after harvest, which could compromise the desired objectives of maintaining biodiversity and ecosystem integrity (K. Bladon, unpublished data). However, there are circumstances where residual trees remain healthy and persist, probably because of reduced competition for resources. The physiological response of trees to the abrupt change in microclimate following harvesting is likely a critical determinant in their survival and success.

Retained trees are often exposed to increased fluctuations in wind speed, air temperature, relative humidity, vapor pressure deficit and net radiation (Man and Lieffers 1999, Proe et al. 2001), but the main driver producing greater potential evapotranspiration at the canopy level is wind speed (Bladon et al. 2006). These stresses could eventually lead to the death of intolerant species. It is hypothesized that the increased evaporative demand to which residual trees are subjected could cause partial or complete cavitation of the xylem (Jones and Sutherland 1991, Sperry and Pockman 1993). This would limit the ability of the tree to deliver water to the leaves. Inadequate water supply to the foliage would ultimately reduce photosynthesis, leading to branch die-back and, potentially, tree mortality (Kobe and Coates 1997, Roy et al. 2001). Most often, tree response to increased evaporative demand is partial closure of stomata, which maintains shoot water potential above the threshold at which xylem dysfunction occurs (Tyree and Sperry 1988, Hogg and Hurdle 1997, Dang et al. 1997, Hogg et al. 2000). However, the reduction in stomatal aperture also causes a decrease in carbon fixation, which limits tree

growth and increases the probability of tree mortality (Kobe and Coates 1997, Sperry 2000).

In C_3 plants, photosynthetic activity is linked to discrimination against CO_2 containing ^{13}C by the carboxylating enzyme Rubisco (Farquhar et al. 1982). When stomata are open, allowing rapid uptake of atmospheric CO_2 by leaves, ^{12}C is preferentially fixed (O'Leary 1981). Alternatively, when stomata close and resistance to CO_2 diffusion increases, proportionally more ^{13}C is incorporated into photosynthate, increasing the $\delta^{13}C$ ($^{13}C/^{12}C$ fraction) of plant material (Farquhar et al. 1989, McNulty and Swank 1995). Recent studies have taken advantage of ^{13}C fractionation to make inferences about tree stress relative to microclimatic variability. Differences in $\delta^{13}C$ have previously been explained by changes in soil water availability (Korol et al. 1999, Fessenden and Ehleringer 2003), humidity (Madhaven et al. 1991), temperature (Leavitt and Long 1986, Panek and Waring 1995), vapor pressure deficit (Francey and Farquhar 1982, Panek and Waring 1997, Bowling et al. 2002) and precipitation (MacFarlane and Adams 1998). However, we are unaware of any previous attempts to analyze the effects of VRH, and the associated microclimatic change, on the $\delta^{13}C$ of residual trees.

Trembling aspen (*Populus tremuloides* Michx.), a species regularly retained after VRH, is both ecologically and commercially the most important deciduous tree species in the North American boreal forest (Hogg et al. 2002). However, aspen mortality rate in VRH plots was recently observed to be nearly 4-fold greater (6.1% year^{-1}) than the natural mortality rate (Bladon et al. unpublished). If residual aspen trees suffer from water stress following VRH, a $\delta^{13}C$ signature should be detectable in stem growth rings. Less discrimination against ^{13}C in residual trees would provide new evidence about the mechanisms related to crown dieback and mortality of these trees. The objective of this study was to quantify the $\delta^{13}C$ of stem wood in trembling aspen trees in isolated residual (IR), edge (*E*) and interior control (*C*) positions. We hypothesized that discrimination against ^{13}C would be ranked as $C > E > IR$ trees. Edge trees should be subjected to less stress than IR trees because of the greater shelter from wind. Second, because cut trees were skidded to the center of the block, the *E* trees likely experienced less damage to roots than the IR trees. To explore

if VRH subjects residual trees to greater stress in more xeric regions, we analyzed the differences in $\delta^{13}C$ across a continental precipitation gradient. We anticipated that trees in the drier regions would have greater $\delta^{13}C$ and experience greater water stress than trees from regions with higher precipitation. Finally, we hypothesized that slender trees have greater $\delta^{13}C$ than stout trees following VR, because of the greater potential for xylem damage in slender trees caused by increased wind exposure and bending (Fredericksen et al. 1994, Liu et al. 2003).

Materials and methods

Research occurred near Calling Lake (55° 15′ N, 113° 10′ W) and Drayton Valley (53° 13′ N, 114° 59′ W), Alberta, and at the Lac Duparquet Research and Teaching Forest (FERLD) in northwestern Québec (48° 46′ N, 79° 26′ W), which represent three distinct climatic regions (Table 1). All research plots were in boreal mixed-wood forest, with various mixtures of trembling aspen, white birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), balsam fir (*Abies balsamea* L.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.).

In spring 2004, mature aspen trees were sampled from seven VRH areas (4 years old) and adjacent, unharvested forests in each region. Before harvest, both the designated unharvested control stands and the harvested areas were stocked with about 1600–2100 trees ha^{-1}. Xylem samples were collected in each plot from eight isolated residual trees, eight edge trees and eight interior trees, for a total of 504 trees (168 per region). At each location, four trees with high slenderness coefficients (SC > 90; SC = height/diameter at breast height (dbh)) and four trees with a low SC (< 90) were sampled. Isolated residuals included single trees, or those in small patches of trees (< 10 trees), left standing in the harvested area (minimum of four tree lengths from the edge of the harvested area). Edge trees were selected randomly from the south-facing edge of the harvested area. Control trees were selected at a distance of about 50 m from the edge of the contiguous forest adjacent to the harvested area to minimize edge influences. All selected trees

Table 1. Regional characteristics of the three boreal mixedwood sites sampled for $\delta^{13}C$ analysis. Micrometeorological characteristics are the mean daytime (0500–2100 h) values obtained during the growing seasons (May–September) over the measurement period (1997–2003). Abbreviations: T_a = air temperature; RH = relative humidity; and D = vapor pressure deficit.

Characteristic	Calling Lake, AB	Drayton Valley, AB	Lac Duparquet, QC
Site location (latitude and longitude)	55°30′ N, 113°40′ W	53°13′ N, 114°59′ W	48°30′ N, 79°22′ W
Elevation (m)	550–650	900–1000	250–300
Dominant soils	Luvisolic	Luvisolic	Luvisolic
Parent material	Glaciolacustrine	Morainal till	Glaciolacustrine
T_a (°C)	14.1	12.7	14.2
RH (%)	57.9	59.5	64.6
D (kPa)	0.819	0.739	0.702
Precipitation (mm)	382	527	809

were older than 30 years to avoid confounding treatment effects on $\delta^{13}C$ with any effect of tree age (Francey and Farquhar 1982). We selected trees of similar size, shape and growth conditions to ensure an accurate relationship between $\delta^{13}C$ and microclimate (Panek and Waring 1995). Trees displaying signs of disease, insect defoliation or bole damage from harvesting equipment were excluded. Measurements were recorded for height, dbh, crown class, height to live crown (htlc), crown radius, and SC for each tree. We assumed tree crowns were parabloids, and estimated crown volume (V; m^3) as:

$$V = \frac{\pi d_b^2 L}{12} \qquad (1)$$

where d_b is the diameter (m) of the crown at its base and L is the crown length (m).

Xylem samples (~5 × 5 cm) were collected at 1.3 m height with a hammer and a chisel. To ensure samples included pre- and postharvest annual rings, at least 15 annual rings were collected. In the laboratory, 3 years of preharvest annual rings and 3 years of postharvest annual rings were excised from each sample. Samples from four trees in the same position (IR, E or C), slenderness class (slender or stout) and time period (before and after VRH) were pooled (Leavitt and Long 1984). Pooled samples were oven-dried at 65 °C for 72 h and ground with a Wiley mill (40 mesh) before holocellulose extraction for stable carbon isotope analysis by a modified version of the "Jayme-Wise" method (Leavitt and Danzer 1993). Isolated holocellulose was ground with a ball grinder and analyzed with a mass spectrometer for the $^{13}C/^{12}C$ ratio. Carbon isotope ratios ($\delta^{13}C$) with respect to the PeeDee Belemnite (PDB) carbonate standard were calculated as:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{PDB}} - 1 \right) 1000 \qquad (2)$$

where $\delta^{13}C$ is expressed in per mill (‰) units. During holocellulose extraction, samples were soaked in bleach solution for 1 h, centrifuged and weighed to determine the lignin content.

Foliar nitrogen analysis

We measured the foliar nitrogen concentration ([N]) of two slender and two stout IR trees in each of the seven stands in the Drayton Valley study area as an indicator of photosynthetic capacity (Livingston et al. 1998). Foliage was collected with a shotgun in summer 2005 from relatively exposed, south-facing branches located in the middle or upper third of the crown. Samples were dried at 65 °C for 72 h, ground with a Wiley mill (40 mesh) and evaluated with an auto-analyzer.

Statistical analysis

Differences in $\delta^{13}C$ values between the three regions and between the C, E and IR trees both before and after VRH were tested as a randomized block, split-split plot design. Region (Calling Lake, Drayton Valley and Lac Duparquet), slender-

ness class (slender and stout) and tree position (C, E and IR) were the fixed main plot effects, and time (before and after VR) was the fixed subplot effect. Analysis of variance (ANOVA) with a Tukey multiple comparisons test was used to analyze this design. A paired two-tailed t test was used to compare foliar [N] between slender and stout trees.

Results

We observed a difference in overall mean $\delta^{13}C$ between C, E and IR trees in all regions combined after VRH ($P < 0.0001$), but not before the treatment ($P = 0.48$). Mean $\delta^{13}C$ in the three years before the harvest was –25.76 ± 0.11‰ in the C trees, –25.63 ± 0.11‰ in the E trees and –25.68 ± 0.11‰ in the IR trees. In the 3 years after VRH, the general pattern of $\delta^{13}C$ was IR (–24.78 ± 0.11‰) > E (–25.31 ± 0.12‰) > C (–25.71 ± 0.12‰).

In each region, variation in carbon isotope discrimination owing to tree position was also evident (Calling Lake, $P = 0.03$; Drayton Valley, $P < 0.01$; Lac Duparquet, $P < 0.001$; Figure 1). This difference was not present before VRH in any region (Calling Lake, $P = 0.58$; Drayton Valley, $P = 0.96$; Lac Duparquet, $P = 0.65$). The interaction of time and position was also significant in all regions ($P < 0.001$), indicating that a change in carbon isotope discrimination occurred between C,
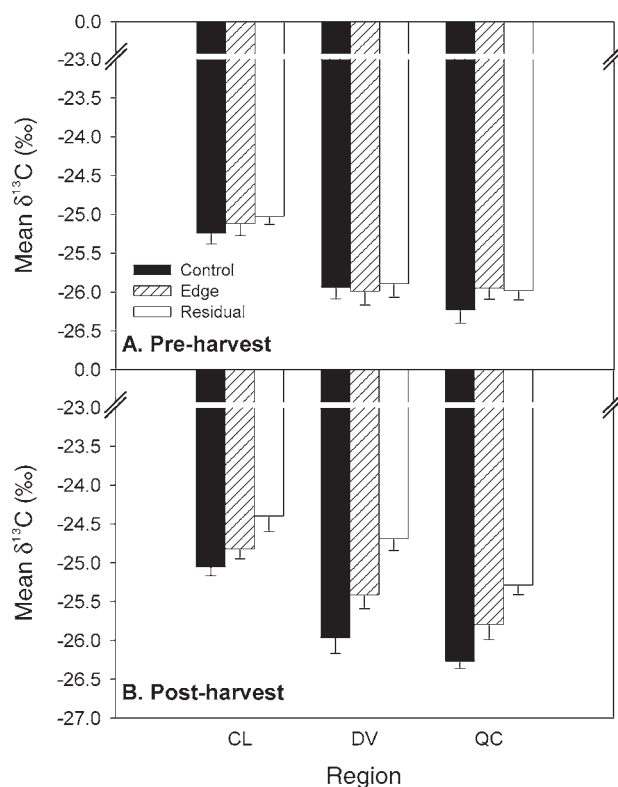

Figure 1. Comparison of mean stable carbon isotopic composition ($\delta^{13}C$) of control, edge and isolated residual *Populus tremuloides* trees in Calling Lake (CL) and Drayton Valley (DV), Alberta and Lac Duparquet, Québec (QC) both (A) pre- and (B) post-variable retention harvesting.

E and IR after VRH.

The general regional pattern of $\delta^{13}C$ was Calling Lake > Drayton Valley > Lac Duparquet (Figure 1), which was the inverse of the regional precipitation gradient (Calling Lake < Drayton Valley < Lac Duparquet; Table 1). The increase in $\delta^{13}C$ with decreasing precipitation was consistent for all three tree positions before and after VRH (Figure 2). Carbon isotope ratios before VRH were –25.13 ± 0.08‰ in Calling Lake, –25.94 ± 0.10‰ in Drayton Valley and –26.05 ± 0.08‰ in Lac Duparquet. After VRH, the mean $\delta^{13}C$ increased in all regions (Calling Lake = –24.76 ± 0.10‰; Drayton Valley = –25.35 ± 0.14‰; Lac Duparquet = –25.78 ± 0.11‰). Regionally, these differences in carbon isotope discrimination were significant both before ($P < 0.0001$) and after ($P < 0.0001$) harvest.

Despite small differences in tree age among regions, differences in precipitation and regional $\delta^{13}C$ discrimination were strongly correlated with differences in tree size among regions. Regionally, the trend in tree height and dbh was Lac Duparquet > Drayton Valley > Calling Lake (Table 2). Additionally, trees in Lac Duparquet supported more crown volume than trees in Drayton Valley (2.3 times more) and Calling Lake (2.8 times more). We found no differences in SC between the regions. There was minimal difference in tree heights between slender and stout trees in each region; however, the mean dbh was typically much smaller for slender trees in all three regions. Stout trees generally supported 2.1- to 2.7-fold more crown volume than slender trees.

We observed a general pattern of less discrimination against ^{13}C by stout trees than by slender trees, both before and after VRH. Overall, $\delta^{13}C$ of slender trees increased from –25.78 ± 0.08‰ (preharvest) to –25.43 ± 0.10‰ (postharvest). Stout trees had a slightly greater increase in $\delta^{13}C$, from –25.54 ± 0.10‰ (preharvest) to –25.10 ± 0.11‰ (postharvest). The mean increase in $\delta^{13}C$ in Drayton Valley was 1.28‰ for stout trees and 1.13‰ for slender trees (Figure 3). In Calling Lake, the increase in $\delta^{13}C$ was most noticeable in the stout IR trees, with a mean increase of 0.89‰, whereas slender trees increased only 0.36‰ after VRH (Figure 3). In the Lac Duparquet IR trees, we observed a mean increase in $\delta^{13}C$ of 0.86‰ in slender trees and 0.63‰ in stout trees (Figure 3). In both Calling Lake and Drayton Valley, the difference in $\delta^{13}C$ between slender and stout trees was not significant preharvest

($P = 0.76$ and 0.15, respectively), but was significant in the 3 years after VRH ($P = 0.05$). There was no difference in carbon discrimination between slender and stout isolated residual

Table 2. *Populus tremuloides* sample tree mean characteristics and standard error from the three boreal mixedwood regions used for $\delta^{13}C$ analysis. Abbreviations: CL, Calling Lake, AB; DV, Drayton Valley, AB; QC, Lac Duparquet, QC; dbh, diameter at breast height; and htlc, height to live crown.

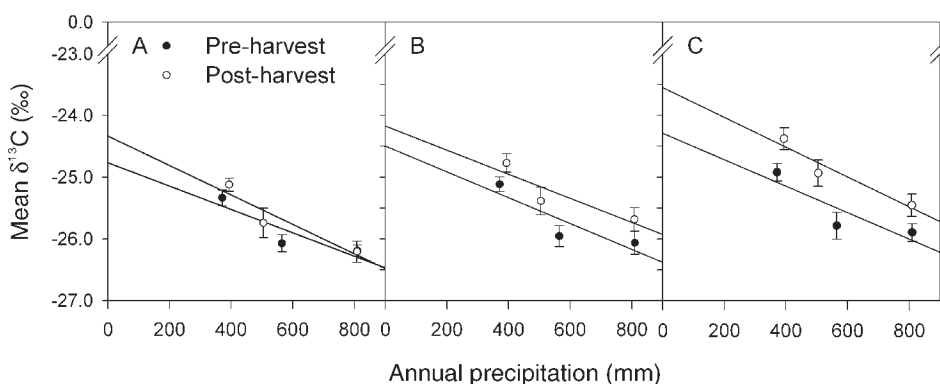| Characteristic	CL	DV	QC
Age (years)	58.0 ± 2.0	72.2 ± 3.7	67.5 ± 1.00
Height (m)			
Mean	20.6 ± 0.22	22.4 ± 0.29	26.2 ± 0.29
Slender	20.8 ± 0.33	22.1 ± 0.45	25.5 ± 0.47
Stout	20.5 ± 0.28	22.7 ± 0.35	26.4 ± 0.35
dbh (cm)			
Mean	24.9 ± 0.45	27.3 ± 0.64	33.8 ± 0.71
Slender	21.1 ± 0.32	22.0 ± 0.50	24.7 ± 0.66
Stout	28.7 ± 0.59	32.5 ± 0.86	37.0 ± 0.70
htlc (m)			
Mean	12.5 ± 0.20	13.7 ± 0.29	15.3 ± 0.41
Slender	12.0 ± 0.26	13.3 ± 0.39	14.7 ± 0.49
Stout	13.0 ± 0.30	14.0 ± 0.44	17.0 ± 0.69
Crown length (m)			
Mean	8.2 ± 0.18	8.7 ± 0.19	10.9 ± 0.36
Slender	7.8 ± 0.27	7.6 ± 0.25	8.6 ± 0.66
Stout	8.5 ± 0.24	9.4 ± 0.27	11.7 ± 0.41
Crown radius (m)			
Mean	2.1 ± 0.044	2.2 ± 0.059	3.1 ± 0.083
Slender	1.8 ± 0.043	1.8 ± 0.059	2.3 ± 0.15
Stout	2.5 ± 0.13	2.6 ± 0.095	3.4 ± 0.090
Crown volume (m^3)			
Mean	45.4 ± 3.1	55.2 ± 5.0	128.6 ± 8.8
Slender	28.9 ± 2.4	31.4 ± 2.9	57.8 ± 8.0
Stout	61.9 ± 5.0	79.0 ± 8.9	154.0 ± 10.6
Slenderness coefficient			
Mean	85.8 ± 1.2	86.6 ± 1.4	81.3 ± 1.5
Slender	99.1 ± 1.2	101.0 ± 1.1	93.3 ± 2.7
Stout	72.7 ± 0.96	73.4 ± 1.6	69.1 ± 1.8

Figure 2. Comparison of mean annual precipitation (mm) from Calling Lake and Drayton Valley, Alberta and Lac Duparquet, Québec to the mean stable carbon isotopic composition ($\delta^{13}C$) of (A) control pre- (●; $r^2 = 0.80$) and postharvest (○; $r^2 = 0.89$), (B) edge pre- (●; $r^2 = 0.78$) and postharvest (○; $r^2 = 0.80$) and (C) isolated residual pre- (●; $r^2 = 0.78$) and postharvest (○; $r^2 = 0.92$) *Populus tremuloides* trees before and after variable retention harvesting.
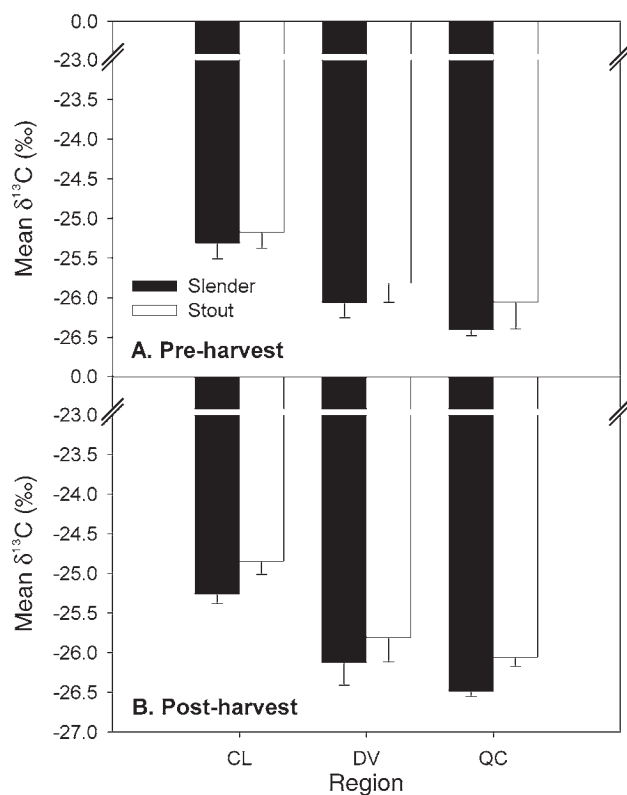
Figure 3. Mean stable carbon isotopic composition ($\delta^{13}C$) of slender and stout isolated residual *Populus tremuloides* trees (A) pre- and (B) post-variable retention harvesting in Calling Lake (CL) and Drayton Valley (DV), Alberta and Lac Duparquet, Québec (QC).

trees in Lac Duparquet, either before ($P = 0.72$) or after VHR ($P = 0.35$).

We found no trends in the cellulose to lignin ratio between pre- and postharvest samples ($P = 0.33$) or between the different trees positions ($P = 0.97$). The nutritional analysis showed that foliar nitrogen concentration was $1.71 \pm 0.17\%$ for slender trees and $1.77 \pm 0.15\%$ for stout trees, and this difference was not significant ($P = 0.47$).

Discussion

In the three years after VRH, the abundance of ^{13}C (expressed as $\delta^{13}C$) in the wood of IR trees was consistently greater than in the wood of *E* and *C* trees (Figure 1). Trees on the edge of cutblocks had intermediate discrimination against ^{13}C between IR and *C* trees. Because there was no difference in $\delta^{13}C$ between the trees in the different positions before VRH, this finding indicates that the IR and *E* trees may have suffered from atmospheric water stress after the disturbance.

It is likely that increased potential evapotranspiration at the crown level, which has been observed following VRH (Zheng et al. 2000, Bladon et al. 2006), caused stomatal closure and enhanced $\delta^{13}C$ in the IR and *E* trees. Plant responses to changes in microclimate are often related to stomatal sensitivity, resistance to xylem dysfunction and local site conditions

(Picon et al. 1996, Zhang et al. 1997, Martinez-Vilalta et al. 2004). Furthermore, aspen trees, like other hardwoods, are known to be susceptible to xylem dysfunction (Sperry et al. 1991, Sperry and Sullivan 1992). They possess stomata that are sensitive to changes in evaporative demand, which maintain leaf and stem water potentials above a critical threshold, thereby preventing xylem cavitation (Hogg and Hurdle 1997, Dang et al. 1997, Hogg et al. 2000).

The greater discrimination against ^{13}C by *E* trees than by IR trees indicates that there may be some sheltering effect of the adjacent contiguous forest. The sheltering effect of edges, and potentially of patches, may have resulted in lower temperatures or radiation, or higher relative humidity, than in exposed harvested areas (Chen et al. 1995). However, the largest impact on evaporative demand was likely due to lower canopy-level wind speeds along the edge (Chen et al. 1993, Bladon et al. 2006).

Soil compaction and root damage provide another possible explanation for the difference in $\delta^{13}C$ between *E* and IR trees. It is likely that IR trees were subjected to greater heavy equipment traffic during harvesting operations than *E* trees, resulting in altered soil properties and reduced plant available water (Greacen and Sands 1980, Kozlowski 1999, Gomez et al. 2002). Thus, soil compaction could influence $\delta^{13}C$ by creating greater water stress for IR trees than for *E* trees. Additionally, similar to edge trees, we would expect residual trees aggregated in patches to be subjected to less heavy equipment traffic than IR trees and thus, to experience less water stress.

We found a regional trend in carbon isotope ratios, with the $\delta^{13}C$ in Calling Lake > Drayton Valley > Lac Duparquet, both before and after VRH (Figure 1). Increased mean annual precipitation and relative humidity, and lower mean daily vapor pressure deficit from Calling Lake to Lac Duparquet (Table 1), appeared to be associated with a reduction in regional mean tree water stress and increased site productivity, as reflected in mean tree height, diameter and crown volume (Table 2). This supports the notion that regional hydro-climate governs growing season stress and forest productivity (Grier and Running 1977, Kergoat 1998). These results also indicate that water stress following VRH is potentially a greater concern in more xeric regions, where trees may already be showing signs of atmospheric water stress before harvest, than in moister regions.

However, caution may be necessary in interpreting the link between precipitation and wood $\delta^{13}C$. In a study of *Eucalyptus* species, Schulze et al. (2006) found that specific leaf area or soil water-holding capacity explained a greater proportion of the variability in $\delta^{13}C$ than precipitation. Nevertheless, given the large number of replications and several lines of evidence depicted in Figures 1 and 2, we maintain that it is likely that the stress we identified by the analysis of $\delta^{13}C$ in wood is related to the new stresses imposed by VRH and differences in regional climate.

Contrary to our expectation, we found a general trend of greater $\delta^{13}C$ in stout trees than in slender trees in all regions, both before and after VRH (Figure 3). This finding contrasts with the idea that trees experiencing more bending suffer greater damage to xylem permeability than more rigid trees as

a result of increased windsway following VRH (Frederickson et al. 1994). The stout trees probably suffered greater water stress because they supported 15–19% more crown volume per basal area and likely had a higher water demand per unit leaf area compared with the slender trees (Table 2). Additionally, less dominant trees have been observed to have greater stem hydraulic capacity per unit leaf area, improving their ability to survive short-term water stress compared with dominant trees (Reid et al. 2003). Following VRH, stout E and IR trees had larger increases in $\delta^{13}C$ than slender trees in the same locations (Figure 4), indicating that stout aspen trees, with large crowns, may suffer greater water stress than slender trees following VRH, perhaps because of their inability to transport sufficient water to a greater volume of foliage. However, in a related study, we found no relationship between residual tree mortality and slenderness (Bladon et al. unpublished). Thus, although stout trees could suffer greater short-term water stress following VRH, other factors (e.g., hydraulic characteristics, root structure, soil water availability, nutrient regime) likely determine the post-harvest fate of an individual residual tree.

In conclusion, our results suggest that trees are subjected to increasing water stress after VRH (IR > E > C). Leaving broadleaf residuals in larger patches or more sheltered landscape positions could reduce the atmospheric drought to which these trees are subjected, ultimately reducing dieback and mortality. Our study also showed that VRH-induced water stress could be a more critical problem in drier regions, where trees may already be subject to water stress before the harvest. Finally, we found that, following VRH, trees supporting a larger volume of leaf area per basal area may suffer greater short-term water stress.

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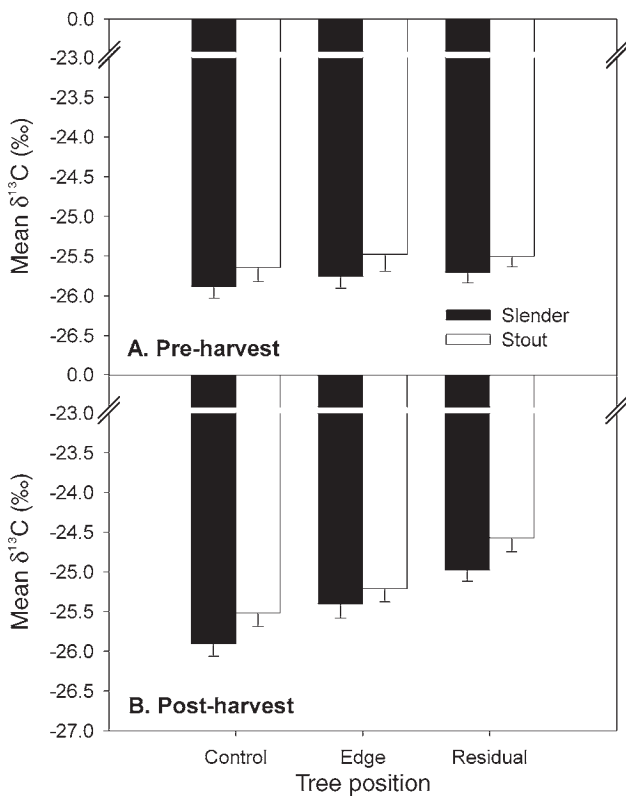

Figure 4. Mean stable carbon isotopic composition ($\delta^{13}C$) of slender and stout *Populus tremuloides* trees from control, edge and isolated residual positions (A) pre- and (B) post-variable retention harvesting in Calling Lake and Drayton Valley, Alberta and Lac Duparquet, Québec.

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