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Title

Carbon isotope discrimination by *Picea glauca* and *Populus tremuloides* is related to the topographic depth to water index and rainfall

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Abstract

Carbon isotope ratio ($\delta^{13}\text{C}$) has been used as an indicator of water stress since plants discriminate less against ^{13}C when under stress. The depth-to-water (DTW) topographic index provides an estimation of soil moisture based on topographic position and other characteristics of a site. To evaluate whether DTW and carbon isotope discrimination were related and to determine if these relationships are influenced by climate we sampled three time periods, which differed in the amount of annual precipitation (MAP), from tree cores collected from 42 trembling aspen and 43 white spruce trees growing along DTW gradients at two locations in central Alberta, Canada. Increasing MAP led to lower $\delta^{13}\text{C}$, indicating less drought stress as water availability increases, while $\delta^{13}\text{C}$ increased with DTW up to a threshold value, after which the relationship levelled off suggesting that higher DTW values represent stress inducing soil conditions. DTW and MAP were then combined into models (aspen $R^2 = 0.72$, spruce $R^2 = 0.44$) that could be used to delineate drought prone areas during periods of low MAP. Tree height and diameter were also related with DTW suggesting a functional relationship between an index capturing soil properties and tree size. Our results demonstrate the potential to use the DTW index as a measure of site conditions and to predict stand level responses.

Keywords: depth to water, topographic index, carbon isotope ratio, water stress, soil properties.

Introduction

Water stress in woody plants is recorded in the carbon isotope ratio of their leaves and wood. Discrimination against the heavier stable isotope of carbon (i.e., ^{13}C) can occur during the diffusion of atmospheric CO_2 through stomata and at the site of carbon fixation by RuBisCO (Berry 1988). The strength of discrimination is measured by the $^{13}\text{C}/^{12}\text{C}$ ratio of tree tissues relative to the isotopic composition of Pee Dee Belemnite material and is denoted $\delta_{\text{sample}}^{13}\text{C}$ (Farquhar et al. 1982). A more informative definition of $\delta^{13}\text{C}$ is

$$\delta^{13}\text{C} = \delta_{\text{air}}^{13} - a - (b - a) c_i/c_a,$$

where δ_{air}^{13} represents the carbon isotope ratio of the air surrounding the leaf, c_a and c_i are the CO_2 concentrations of the atmosphere and leaf intercellular spaces (Francey and Farquhar 1982). The constant a is the diffusivity of CO_2 in air with a value of 4.4‰, and b is the isotope fractionation of RuBisCO considered to be approximately 30‰. With δ_{air}^{13} equal to about -8‰, the value of $\delta^{13}\text{C}$ is controlled by the c_i/c_a ratio representing photosynthesis rate and stomatal conductance. Therefore, $\delta^{13}\text{C}$ reflects the effects of environmental factors on the c_i/c_a ratio (Francey and Farquhar 1982). Environmental conditions limiting assimilation rates (e.g., low light intensities) will increase c_i/c_a and reduce $\delta^{13}\text{C}$, whereas factors reducing stomatal conductance (e.g., water stress, strong vapour pressure deficits) will lower c_i/c_a and increase $\delta^{13}\text{C}$ (Farquhar et al. 1989). Topography that creates xeric conditions (e.g., ridges, steep slopes) was consistently associated with high $\delta^{13}\text{C}$ in leaves of temperate deciduous trees (Garten and Taylor 1992), however small topographic features (e.g., gullies) did not influence wood $\delta^{13}\text{C}$ in *Sequoia sempervirens* (D. Don) (Roden et al. 2011). In contrast to leaves, wood $\delta^{13}\text{C}$ has the

52 advantage of integrating the large spatial variation of leaf $\delta^{13}\text{C}$ within a crown (Leavitt and Long
53 1986; Waring and Silvester 1994), as well as capturing environmental conditions over multiple
54 seasons.

55 The increasing availability of remotely-sensed accurate digital elevation models (DEM)
56 allows the collection of valuable up-to-date information about the topography of large forested
57 areas with relatively low costs (Moore et al. 1991). Simple topographic indices such as slope,
58 aspect or profile curvature have been used to predict soil pH and texture (Moore et al. 1993),
59 which are also related to landscape position (Brubaker et al. 1993), whereas Allen et al. (1991)
60 combined topographic position, potential solar radiation and aspect into a topographic moisture
61 index to predict species composition. The most widely used complex terrain index is the
62 topographic wetness index (TWI), defined as the logarithm of the ratio of upslope area to local
63 slope (Beven and Kirkby 1979). TWI has been used to map the extent of water-saturated areas
64 (Burt and Butcher 1985; Guntner et al. 2004) or predict detailed soil properties (e.g., thickness,
65 pH and C:N ratio of the organic horizon) in the Swedish boreal forest (Seibert et al. 2007). These
66 and other authors indicate that different algorithms must be used in different landscapes or for
67 different applications. A flow routing algorithm which accumulates water (e.g., D8, D ∞) was
68 recommended to delineate flow channels (Sorensen et al. 2006; Tarboton 1997), whereas more
69 distributed flow algorithms (e.g., MD ∞ , FD8) are better suited for mapping of broad features
70 such as species composition (Kopecky and Cizkova 2010).

71 The depth-to-water (DTW) index integrates the horizontal and vertical distance from a
72 given point in the landscape to the nearest flow channel. The latter is defined by the choice of a
73 flow initiation area (Murphy et al. 2007). The DTW index was found to be superior to TWI in
74 mapping of wet areas in the boreal forest since TWI is strongly dependent on the upslope area,

while local downslope topography is a major determinant of soil moisture conditions (Murphy et al. 2009). Changing the flow initiation area affects the extent of the flow channel network, adapting the DTW index to various landscape configurations and geologies, and temporal changes in soil moisture (e.g., wet or dry years). DTW calculated at a large flow initiation area (i.e., >8 ha) performed better on terrain with strong topography and high hydraulic conductivity while a smaller threshold area (i.e., 1 ha) was suggested for an area with low topography and poor drainage (Ågren et al. 2014). Field observations in the boreal forest of Alberta indicated that flow channels delineated at a flow initiation area of 4 ha correspond to streams with permanent or intermittent flow representing soil conditions late in the season (White et al. 2012). Further, a companion study showed that DTW is related to the depth to mottles in the soil and to drainage regime, which allowed us to develop a model of soil moisture based on DTW and other topographic indices (Oltean et al. 2016). Further testing of the DTW index is needed to evaluate its capabilities and limitations in areas with contrasting topography.

Depth-to-water rasters are available for extensive areas in Alberta and New Brunswick where DTW was shown to perform better than TWI (Murphy et al. 2009; Murphy et al. 2011). Thus, a deeper understanding of the ecological significance of DTW values, as well as its potential applications and limitations to the use of this index are needed. The objectives of the present study were (1) to evaluate the relationship between DTW and $\delta^{13}\text{C}$, (2) to explore a gradient of flow initiation area thresholds in contrasting terrains, and (3) to assess the association between DTW and tree size (i.e., height and diameter). We expected that DTW would be related with $\delta^{13}\text{C}$ and tree size but will present a threshold after which its influence diminishes, and that optimal flow initiation area would depend on terrain morphology.

Materials and methods

Study sites

We selected a trembling aspen (*Populus tremuloides* Michx.) stand located 30 km south of Grande Prairie in the Boreal Mixedwoods ecoregion of Alberta, and a white spruce (*Picea glauca* (Moench) Voss) stand situated 16 km west of Whitecourt on the eastern side of the Foothills ecoregion (Fig. 1). The aspen site occurred on fine-textured deposits of glacial origin forming a typical flat terrain (i.e., slope of 2.5%), whereas coarser material carried from the Canadian Rockies and deposited in the Foothills area (MacCormack et al. 2015) formed steeper slopes (i.e., 10.9%) at the spruce site. Consequently, these two sites provided suitable conditions to evaluate the DTW index in terrains with contrasting geology and topography. The climate at these two locations is dominated by long cold winters and warm summers, with Grande Prairie having a lower mean annual temperature (i.e., 2.2 °C) and receiving less annual precipitation (i.e., 445.1 mm) than the site near Whitecourt (i.e., 2.9°C and 544.4 mm; Table 1). These differences in topography and climate between the two areas can change water availability in the soil, thus affecting the carbon isotope ratio of trees growing on these sites. Both stands were 23 years old at the time of sampling; the aspen stand had regenerated from root suckers after harvest in the winter of 1990 – 91, but it was sampled early in the spring of 2014 before bud break, whereas the spruce stand had been planted in May 1993 with 1 year old stock and was sampled in late-summer of 2014.

Sample collection and preparation

We used existing DEM and DTW rasters for the two sites to select locations that covered a wide range of topographic conditions and DTW values (Fig. 1). We navigated to each point

and then selected a dominant tree, for which we measured the diameter at breast height (dbh), total height, height to live crown, crown radii on the northern and western directions, and made notes about the conditions in which the trees were growing (e.g., edge tree, open grown). A total of 42 trembling aspen and 43 white spruce trees were selected and their locations recorded with a Trimble GeoExplorer 6000 series GeoXT handheld device (Trimble, Los Altos, California) with GNSS capabilities ensuring sub-meter accuracy for 78% of the aspen and 87% of the spruce tree positions. The crown measurements were used to calculate the volume, projected and surface area of the crowns, which were assumed to be paraboloids for the aspen and conical for the spruce trees.

From each tree we collected two cores from the north and south facing side of the stem as recommended by Leavitt and Long (1984). The cores were cleaned and carefully divided into three periods selected based on the annual precipitation relative to the 30-year (1981 – 2010) normals. In order to have a reasonable amount of wood to analyse for carbon isotopes, we identified two to four years that received either more or less rainfall relative to the climate normals, without fixing the number of years. For the aspen site we selected the 1999 – 2003 and 2008 – 2010 as dry and 2004 – 2007 as wet periods, while the periods 2002 – 2003 and 2008 – 2009 were dry and 2011 – 2012 was relatively wet at the spruce site (Fig. 2). The 2004 – 2007 period at the aspen site included one dry season but we did not remove it because its effect was mitigated by the large amount of precipitation in the following year. For each period and species, the sections from the north and south core were both placed in a vial and dried in an oven at 70 °C for 48 hours. The dried wood samples were finely ground with a Retsch MM 200 ball grinder (Retsch, Dusseldorf, Germany) to ensure sample homogeneity, and then analyzed for their isotopic composition using a mass spectrometer at the Natural Resources Analytical Laboratory

(University of Alberta, Edmonton, AB). We used wood for our isotopic analyses since Walia et al. (2010) found that the $\delta^{13}\text{C}$ of whole wood remains constant even if the ratio of lignin to holocellulose changes.

The Depth-to-Water index

The depth-to-water index is defined as the cumulative slope along the least cost path from any cell in the landscape to the nearest flow channel (Murphy et al. 2007). The measurement unit for DTW is meters and is calculated as

$$DTW = \left[\sum \frac{dz_i}{dx_i} a \right] x_c (m),$$

where dz_i and dx_i are the vertical and horizontal distance between two cells, a is a constant equal to 1 if the path is parallel to the cell edge or $\sqrt{2}$ if the cells are connected across the diagonal, and x_c is the size of the raster cell (i.e., 1 m). Thus, a cell farther from the channel or at a higher elevation will receive a large DTW value indicating the weak hydrological connection between that cell and its source of water (Murphy et al. 2009). DTW was calculated using a digital elevation model derived from an airborne LiDAR (Light Detection and Ranging) point cloud with 0.5 to 3 points per square meter and vertical accuracy of 30 cm. False depressions and other artifacts that artificially obstruct water flow were removed from the 1 m resolution DEM, and flow direction based on the slope to the neighbouring cells was determined for each cell. Flow accumulation (FA) area, defined as the upslope area draining to each cell, was calculated using the highly convergent D8 flow routing algorithm which directs flow to the adjacent cell with the steepest slope (O'Callaghan and Mark 1984). The flow direction and FA rasters were used to determine the cells delineating the flow channels, which receive a DTW value of 0 m. Flow initiation areas of 0.5, 1, 2, 4, 8, 12 and 16 ha were used as starting points for the flow channels,

with a new DTW raster being calculated for each threshold.

Statistical analysis

To address the first two objectives we used $\delta^{13}\text{C}$ as the dependent variable and modeled it as a function of DTW, FA and slope averaged over a circular plot centered on the tree and with a radius of 3 m. Preliminary analyses did not show differences between radii of 1, 3, 5, 7.5 and 10 m, thus the selected radius was consistent with the accuracy of the tree locations. Since the conditions in which tree crowns develop has strong effects on carbon isotope discrimination (Leavitt 1993), we first tested the $\delta^{13}\text{C}$ difference between trees growing in a closed canopy and those that were in open conditions or at stand edge. Values of $\delta^{13}\text{C}$ in trees exposed to more radiation and stronger vapour pressure deficits were significantly higher for both aspen ($-26.08 > -26.36$, $P = 0.0468$) and spruce ($-25.47 > -26.15$, $P < 0.0001$), thus the open-grown and stand edge trees were removed prior to any analyses of $\delta^{13}\text{C}$ data. This reduced our sample sizes to 30 aspen and 26 spruce trees.

We began our analysis with a linear mixed-effects model between $\delta^{13}\text{C}$ and mean annual precipitation (MAP) for each time period with random effects for the intercept, which induces a compound symmetry correlation structure for the $\delta^{13}\text{C}$ measurements made on the same tree. Likelihood ratio tests, recommended to select the optimal structure for the random effects (Pinheiro and Bates 2000), indicated that a random effect for the slope was not needed. Since each tree was allowed to have a different intercept, the conditional modes of the random effects represented the variation of $\delta^{13}\text{C}$ between tree locations. Therefore, the null hypothesis of no relationship between $\delta^{13}\text{C}$ and the topographic indices (i.e., DTW, FA slope) was tested using the conditional modes. Moreover, this approach allowed us to combine the three $\delta^{13}\text{C}$ values per

tree into a single number. The relation between $\delta^{13}\text{C}$ and DTW, calculated at the seven flow initiation areas, was modeled with an asymptotic function of the form

$$(Eq. 1) \quad y(x) = a + (b - a)\exp[-\exp(c)x],$$

where a is the asymptote as $x \rightarrow \infty$ and b is the value of y at $x = 0$. The expression $\exp(c)$ is the rate parameter and is used in this form to ensure that the model approaches an asymptote. This curve becomes a flat line when $\exp(c) = 0$, indicating no relationship between the two variables. A significance test for the estimate of c cannot be devised since $\exp(0) = 1$ and $\exp(c) \rightarrow 0$ as c becomes more negative ($\exp(-2) = 0.14$). Instead, we used the coefficient of determination (i.e., R^2) to compare among the different flow initiation areas while providing the estimate of c for the relevant models to judge significance. We selected this asymptotic function based on an expected functional relationship between $\delta^{13}\text{C}$ and DTW (i.e., $\delta^{13}\text{C}$ is not influenced by large DTW values), which was supported by empirical evidence. Simple linear regression was used to test the association between the conditional modes of the random effects and FA and slope.

Once the strongest predictor was selected, we introduced it as a covariate in the initial mixed model which included only MAP. In this updated model formulation, the random effect for the intercept was removed since that variability was now explained by the topographic index (Pinheiro and Bates 1995). Autocorrelation between the three $\delta^{13}\text{C}$ measurements made on the same tree was accounted for with a general correlation structure found most suitable using likelihood ratio tests (Pinheiro and Bates 2000). This correlation model is more parameter expensive but our short time series (i.e., 3 periods) introduced only two extra parameters over a first order autoregressive model suggested by Monserud and Marshall (2001) while allowing for greater flexibility. Furthermore, their study focused on a time-series analysis of $\delta^{13}\text{C}$ much longer than ours (i.e., 90 years) which made an autoregressive model necessary. Residual plots

and the Shapiro-Wilk normality test were used to assess model fit and the validity of the assumptions imposed on the models. Equation 1 was also used to model the relationship between tree size and the topographic indices but a correlation structure or random effects were not necessary since the data did not present a hierarchical structure with multiple measurements on the same individual. We applied the same modeling approach to both aspen and spruce. The parameters of the mixed-effects models were estimated using the method of maximum likelihood implemented in the nlme library v. 3.1-120 (Pinheiro et al. 2015) within the R environment for statistical modeling v. 3.2.0 (R Core Team 2015).

Results

Annual precipitation and $\delta^{13}\text{C}$

Carbon isotope ratio was negatively related to mean annual precipitation for both aspen and spruce (Fig. 3). The linear mixed-effects model fit for each species had the form

$$(\text{Eq. 2}) \quad \delta^{13}\text{C}_{i,t} = (\beta_0 + b_i) + \beta_1 \text{MAP} + \varepsilon_{i,t},$$

where $\delta^{13}\text{C}$ was the carbon isotope ratio for tree i at period t , β_0 and β_1 were the intercept and slope, respectively. The slope was fixed but b_i represented the deviations of the intercept among trees, considered to be independent and identically distributed (i.i.d.) as $b_i \sim N(0, \sigma_b^2)$. The errors were also considered i.i.d. as $\varepsilon_{i,t} \sim N(0, \sigma^2)$. The variation between trees (σ_b^2) was larger than the unexplained variability (σ^2) in the case of both species (Fig. 3). Aspen had $\sigma_b = 0.48$ and $\sigma = 0.37$ while spruce had $\sigma_b = 0.58$ and $\sigma = 0.52$. The mean $\delta^{13}\text{C}$ value for aspen (-26.36) was lower than that of spruce (-26.15), but this difference diminished as annual precipitation decreased due to the more negative slope for aspen ($\beta_1 = -0.0047$, $P < 0.0001$) than for spruce ($\beta_1 = -0.0016$, P

= 0.0008). The intercept varied about 2‰ between trees, from −27.14 to −25.18 for aspen and from −26.85 to −24.95 for spruce.

The depth-to-water index and $\delta^{13}\text{C}$

The conditional modes (b_i) of the random effects for the intercept in Eq. 2 were related to DTW (Fig. 4) based on a flow initiation area of 1 ha for aspen ($R^2 = 0.42$) and 16 ha for spruce ($R^2 = 0.16$). The corresponding estimates of the rate parameter in Eq. 1 were $\exp(2.297) = 9.944$ for aspen and $\exp(-2.193) = 0.112$ in the case of spruce. Increasing or decreasing flow initiation area at the aspen site resulted in a gradual decline in the strength of the relationship, with threshold areas of 8, 12 and 16 ha providing similar results ($R^2 = 0.107$, Table 2). In the case of spruce, the coefficients of determination remained below those for aspen while following a pattern of gradual increase with larger flow initiation areas, reaching a plateau at catchment areas of 12 and 16 ha (Table 2). Flow accumulation and local slope were not significantly related with the conditional modes (b_i) of the random effects ($P > 0.2500$), yielding weak relationships ($R^2 < 0.047$) for both species.

The strongest predictor from Table 2 (boldfaced values) was incorporated into Eq. 2 to obtain a model that combines climate and topography to explain variation in $\delta^{13}\text{C}$, for each species (Fig. 5). The two models thus obtained can be expressed as

$$\text{(Eq. 3)} \quad \delta^{13}\text{C}_{i,t} = \beta_1 + (\beta_2 - \beta_1) \exp(-\exp(\beta_3)\text{DTW}) + \beta_4\text{MAP} + \varepsilon_{i,t},$$

where $\delta^{13}\text{C}$ was the carbon isotope ratio for tree i at period t , β_1 was the asymptote, β_2 the value of $\delta^{13}\text{C}$ at DTW of 0 m, $\exp(\beta_3)$ the rate parameter, and β_4 the slope parameter for mean annual precipitation. The errors were considered to be i.i.d. as $\varepsilon_{i,t} \sim N(0, \sigma^2)$, with a general correlation structure for the within-tree residuals. The parameter estimates indicate that aspen experienced

greater $\delta^{13}\text{C}$ values than spruce at very large or 0 m DTW and no annual precipitation (β_1 and β_2 in Table 3). However, $\delta^{13}\text{C}$ was lower for aspen than spruce at average and high levels of precipitation since the slope of MAP was more negative for aspen than spruce (β_4 in Table 3). The relationship between $\delta^{13}\text{C}$ and DTW was steeper for aspen, while a gradual change in $\delta^{13}\text{C}$ with DTW was observed in the case of spruce (β_3 in Table 3). The plateau was reached at DTW around 0.4 m for aspen and 7 – 8 m for spruce, but these values cannot be directly compared since different flow initiation areas were used to calculate DTW for each species (Fig. 5). Since these two models were fit using the method of maximum likelihood, we calculated a generalized coefficient of determination ($\bar{R}_{\text{LR}}^2$) using the likelihood ratio of the candidate model with the null model (Cox and Snell 1989; Nagelkerke 1991). The $\delta^{13}\text{C}$ model for aspen yielded a $\bar{R}_{\text{LR}}^2$ value of 0.72, whereas the model for spruce had a lower $\bar{R}_{\text{LR}}^2$ of 0.44. The residual plots showed a lack of systematic bias, while the Shapiro-Wilk test indicated that the normality assumption was met for both models (Fig. 5).

Tree size and the depth-to-water index

Tree height was more strongly related with DTW than diameter at breast height for both aspen and spruce (Eq. 1, Table 2). Height and diameter of spruce showed stronger relationships with DTW (i.e., R^2 of 0.56 and 0.41, respectively) than was the case for aspen (i.e., R^2 of 0.27 and 0.16, respectively). Similarly to $\delta^{13}\text{C}$, flow initiation areas of 1 ha for aspen and 16 ha for spruce provided the strongest relationship for height of both species (Table 2). Although diameter of aspen was more strongly related with DTW calculated at 2 ha (Table 2), because the difference was small, we used the model with DTW calculated at 1 ha. Aspen were taller than spruce, with a narrower range of heights from low DTW ($b = 10.4$ m) to high DTW conditions (a

= 12.4 m), whereas spruce trees varied from 4.3 m at low DTW to 8.9 m at large DTW. Tree height became independent of DTW when DTW values exceeded 0.9 m for aspen and 11 m for spruce (Fig. 6). Diameter of aspen trees was smaller than that of the spruce trees, and quickly increased with DTW from 8.1 cm to 9.9 cm at $DTW > 0.4$ m. In the case of spruce, diameter increased more gradually from 8.9 cm at low DTW to 16.6 cm at $DTW > 25$ m. Tree height was estimated more tightly with standard error of about 1 m, whereas diameter estimates had a standard error of up to 2.5 cm in the case of spruce. Flow accumulation was not associated with height or diameter of either species, whereas slope was positively related with height of the spruce trees with a slope of 0.05 ($P = 0.0196$).

Discussion

Topography and precipitation

The model described by Eq. 3 incorporates both a topographic index and a climate variable to explain variation in carbon isotope ratio of trembling aspen and white spruce. As expected, the largest $\delta^{13}\text{C}$ values are found in areas with high DTW and periods with low annual precipitation (Fig. 5). Leavitt and Long (1986) suggest that a high resolution topographic index that reflects site conditions could account for about 2 and 3% of the variation in $\delta^{13}\text{C}$ between trees. The relationship between $\delta^{13}\text{C}$ and DTW is positive up to certain thresholds after which it levels off (Fig. 4). An effect of topography on $\delta^{13}\text{C}$ was also found by Garten and Taylor (1992), who reported that foliar $\delta^{13}\text{C}$ was higher for deciduous trees growing on drier areas (i.e., ridges and slopes) than for those from wetter conditions (i.e., riparian). Similarly, more positive $\delta^{13}\text{C}$ values were reported for leaves of broadleaved species growing on ridges than for those found in the valley (Hanba et al. 2000).

The relationship between $\delta^{13}\text{C}$ and DTW was not very strong (i.e., R^2 of 0.42 for aspen and 0.16 for spruce) since $\delta^{13}\text{C}$ enrichment can be influenced by a range of environmental factors as well as genotypic variation between trees. Weak relationships with DTW may also occur because the DTW index does not completely or accurately integrate all site conditions influencing availability of soil moisture, stomatal conductance and carbon fixation. Photosynthesis is dependent on the amount of radiation intercepted by the leaf, thus increasing light availability can lead to higher carbon demand which can also result in larger $\delta^{13}\text{C}$ values (Sohn et al. 2013; Warren et al. 2001). Larger $\delta^{13}\text{C}$ values were also reported for mature aspen trees that had been left standing after variable retention harvesting as a result of sudden exposure to full sunlight, which led to higher evaporative demand and water stress (Bladon et al. 2007). An effect of shading was found in our dataset, but we removed trees receiving more radiation (i.e., edge and open grown trees) since they had higher $\delta^{13}\text{C}$ values than the trees growing in closed canopy stands. Furthermore, mineral nutrition can have strong influences on carbon assimilation and $\delta^{13}\text{C}$ (Francey and Farquhar 1982), as shown for $\delta^{13}\text{C}$ in wood of *Tsuga heterophylla* (Raf.) Sarg. (Walia et al. 2010). A proportion of the unexplained variation in $\delta^{13}\text{C}$ might also be the result of inherited differences between trees, as indicated by a study that found high heritability of $\delta^{13}\text{C}$ (i.e., 0.54 compared to 0.39 for height) in *Picea mariana* (Mill.) BSP (Johnsen et al. 1999).

Although topography influences water movement, several other studies have reported that topography was not related with $\delta^{13}\text{C}$. Topographic position did not have an effect on $\delta^{13}\text{C}$ in tree rings of *Sequoia sempervirens* D. Don growing in an area with homogeneous terrain morphology (Roden et al. 2011), while the effect of topography on $\delta^{13}\text{C}$ was masked by the ability of *Pinus ponderosa* Dougl. ex Laws. trees to access deep water sources and reduce water

stress (Adams et al. 2014). Thus, topographic effects on $\delta^{13}\text{C}$ might be inhibited by redistribution of water taken up from deep soil layers or adjacent wet areas through tree roots and root grafts (Burgess et al. 1998). Water redistribution among trees in clonal aspen stands (Brown et al. 2014) may also reduce the magnitude as well as the occurrence of drought stress.

The negative relationship between $\delta^{13}\text{C}$ and mean annual precipitation suggests that trees experienced less stress during periods of higher precipitation (Fig. 3). A strong influence of precipitation as well as air temperature on the seasonal pattern of $\delta^{13}\text{C}$ was found in semi-arid ecosystems with an aspen component in Utah (Buchmann et al. 1997). A similar effect of water availability was found for 50 tree species growing along a rainfall gradient in northern Australia (Schulze et al. 1998). Our analysis used time periods corresponding to wet-dry episodes and does not allow us to explore the seasonality of the isotopic signal and the climate factors controlling stomatal conductance. The DTW topographic index could be used to delineate the most and least drought prone areas during years with low amounts of precipitation, and could also help explain the spatial variability in drought related mortality in the boreal forest (Hogg et al. 2008).

Optimal flow initiation area

Flow initiation area controls the extent of the flow channel network used to calculate the DTW raster. Using a small flow initiation area extends flow channels farther into the headwaters of the watershed creating an extensive network of flow channels, which results in generally lower DTW values. On the other hand, only major channels are identified when large flow initiation areas are used. Our results show that selection of optimal flow initiation area depends on topography of the study area. The relatively flat (i.e., slope of 2.5%) topography of the Grande Prairie site was better captured with a smaller flow initiation area (i.e., 1 ha), whereas the

Whitecourt site with a more pronounced topography (i.e., 10.9% slope) was more strongly represented by larger flow initiation areas (i.e., 12 or 16 ha). These findings are consistent with a study from Sweden that also emphasized the importance of substrate permeability, since it controls drainage rate of water (Ågren et al. 2014).

Tree size and topography

Tree height varied more widely at the spruce site since the northern part of that area (i.e., shown in dark blue in Fig. 1) was covered by a bog where trees were shorter. Tree height was more strongly related to DTW than diameter since diameter increment is affected by stand structure to a greater extent than elongation of the terminal shoot (Oliver and Larson 1996). The stronger relationship between height and DTW in spruce might be explained by the stronger topographic gradients at the Whitecourt site, exerting a greater influence on soil attributes. The relationship between tree size and DTW followed a similar pattern to that found for $\delta^{13}\text{C}$, suggesting that tree size does not increase with DTW after a certain DTW value. Other authors reported weak to no relationships between tree size and other topographic indices which may result from the coarse resolution (i.e., 30 – 35 m) DEM used to calculate TWI (Byun et al. 2013; Ehara et al. 2009). Conceptually, height of both species should reach a maximum value at intermediate levels of DTW, and decline with either increasing or decreasing DTW (Wang and Klinka 1996). Testing DTW with a wider range of tree ages and sizes could provide further information on the pattern and nature of the relationship.

Conclusions

This study presents a model that uses information at two scales, small-scale through a

topographic index and large-scale through a climate variable, to explain variation in carbon isotope discrimination as a measure of tree physiological activity. More importantly, our results validate the DTW index as a tool that can provide information about the status of individual trees, particularly the effects of water availability in the soil. Results also highlight the importance of choosing flow initiation areas that are appropriate to local site characteristics to permit accurate representation of site properties through the DTW index. Tree height can be measured from LiDAR point clouds or estimated using empirical models, but the model presented here implies a functional relationship of tree height with a terrain attribute that captures site conditions controlling tree growth. This opens the way for future studies that can evaluate the potential to use the DTW index as predictor of stand-level properties, especially site productivity with possible linkages to forecasting impacts of drought induced by climate change.

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Table 1. Geographic location, topography and climate at the two study sites where trembling aspen and white spruce trees were sampled for carbon isotope analyses. DBH – diameter at breast height, MAT – mean annual temperature, MAP – mean annual precipitation.

	Grande Prairie	Whitecourt
Species	trembling aspen	white spruce
Number of trees	42	43
Height (m)	11.5	8.2
Height range (m)	8.8 – 14.2	4.7 – 10.3
Diameter (cm)	9.5	13.7
DBH range (cm)	6.8 – 12.4	6.5 – 19.5
Latitude (° N)	54.9099	54.1198
Longitude (° W)	118.9251	115.9269
Elevation (m)	711.8	839.7
Slope (%)	2.5	10.9
MAT* (°C)	2.2	2.9
MAP* (mm/yr)	445.1	544.4
Weather Canada station	Grande Prairie A	Whitecourt A

* extracted from "1981–2010 Canadian Climate Normals available online at <http://climate.weather.gc.ca> accessed on August 27, 2014

Table 2. Coefficients of determination (R^2) shown for the regression models between the topographic indices and the conditional modes (b_i) of the random effects in Eq. 2, height, and diameter of the trembling aspen and white spruce trees. The asymptotic function in Eq. 1 was used for the models with the depth-to-water index as predictor, and simple linear regression for flow accumulation (FA) and slope.

	R^2	Flow initiation area used to calculate the depth-to-water index							$\log_{10}(\text{FA})$	Slope
		0.5 ha	1 ha	2 ha	4 ha	8 ha	12 ha	16 ha		
Trembling aspen	$b_i (\delta^{13}\text{C})$	0.176	0.419	0.296	0.143	0.107	0.107	0.107	0.008	0.047
	height	0.148	0.272	0.235	0.187	0.059	0.060	0.060	0.001	0.000
	diameter	0.088	0.119	0.158	0.002	0.016	0.017	0.017	0.000	0.019
White spruce	$b_i (\delta^{13}\text{C})$	0.002	0.028	0.108	0.063	0.139	0.158	0.160	0.035	0.003
	height	0.129	0.277	0.393	0.278	0.362	0.546	0.563	0.018	0.126
	diameter	0.088	0.226	0.161	0.139	0.208	0.410	0.414	0.002	0.046

Table 3. Parameter estimates and 95% confidence intervals (CI) for the models (Eq. 3) of carbon isotope ratio ($\delta^{13}\text{C}$) in wood tissue of trembling aspen and white spruce as a function of depth-to-water (DTW) and mean annual precipitation (MAP). DTW was calculated a flow initiation area of 1 ha for aspen and 16 ha for spruce. The generalized coefficient of determination ($\bar{R}^2_{\text{LR}}$) is shown for both models.

	Parameters in Eq. 3				Residual SD
	β_1 (asymptote)	β_2 ($= y(0,0)$)	β_3 (DTW)	β_4 (MAP)	(σ)
Trembling aspen ($\bar{R}^2_{\text{LR}} = 0.72$)					
Estimated parameter	-23.997	-25.740	2.305	-0.0054	0.505
(95% CI)	(-24.349 – -23.645)	(-27.160 – -24.321)	(1.261 – 3.350)	(-0.0061 – -0.0047)	(0.424 – 0.603)
White spruce ($\bar{R}^2_{\text{LR}} = 0.44$)					
Estimated parameter	-25.265	-26.187	-1.795	-0.0010	0.733
(95% CI)	(-26.236 – -24.295)	(-27.267 – -25.106)	(-5.105 – 1.515)	(-0.0018 – -0.0002)	(0.604 – 0.890)

Location of the two study sites in the Boreal Mixedwoods and Foothills ecoregions of Alberta, Canada, from where trembling aspen and white spruce trees were selected (points). The hillshade images (lower panels) show the contrasting topography between the two sites, which controls the flow channel delineation and depth-to-water (DTW) raster calculation (upper panels). Note that DTW was calculated at a flow initiation area of 1 ha for the aspen site and 16 ha for the spruce site.

Annual precipitation and 30-year (1981-2010) normals (flat line) at the Grande Prairie (aspen) and Whitecourt (spruce) study sites from 1995 to 2013. The selected periods for carbon isotope analysis are shaded in the darker brown color if precipitation was less than normal (i.e., dry) and lighter blue if it exceeded normal values (i.e., wet).

Carbon isotope ratio in woody tissue of trembling aspen and white spruce decreased with mean annual precipitation. The darker green shading shows the 95% confidence band for the linear mixed-effects model in Eq. 2 while the lighter gray shows the 95% confidence envelope including the intercept variance (σ_b^2).

Note the greater variation between trees compared to the residual error.

Fitted asymptotic (Eq. 1) regression between the conditional modes (b_i) of the random effects in Eq. 2, representing the inter-tree variation in carbon isotope ratio, and depth-to-water calculated at a flow initiation area of 1 ha for trembling aspen and 16 ha for white spruce.

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Carbon isotope ratio ($\delta^{13}\text{C}$) in wood tissue of trembling aspen and white spruce modeled as a function of depth-to-water (DTW) and mean annual precipitation (Eq. 3). DTW was calculated at a flow initiation area of 1 ha for aspen and 16 ha for spruce. The residual plots (bottom) and the Shapiro-Wilk test confirm the good fit of the model. Note that the points on the model surface are the fitted values.

Fitted nonlinear regression (Eq. 1) and 95% confidence envelope for tree height and diameter at breast height of trembling aspen and white spruce modeled as a function of depth-to-water, calculated at a flow initiation area of 1 ha for aspen and 16 ha for spruce. Note that the scale of the y-axis is not the same across panels.