DRAINAGE AFFECTS TREE GROWTH AND C AND N DYNAMICS IN A MINEROTROPHIC PEATLAND

Woo-Jung Choi, Scott X. Chang, and Jagtar S. Bhatti

1Department of Biosystems and Agricultural Engineering, Institute of Agricultural Science and Technology, Chonnam National University, Gwangju 500-757 Korea
2Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2E3 Canada
3Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta T6H 3S5 Canada

Abstract. The lowering of the water table resulting from peatland drainage may dramatically alter C and N cycling in peatland ecosystems, which contain one-third of the total terrestrial C pool. In this study, tree annual ring width and C (δ13C) and N (δ15N) isotope ratios in soil and plant tissues (tree foliage, growth rings, and understory foliage) in a black spruce–tamarack (Picea mariana–Larix laricina) mixed-wood forest were examined to study the effects of drainage on tree growth and C and N dynamics in a minerotrophic peatland in west-central Alberta, Canada. Drainage increased the δ15N of soil NH₄⁺ from a range of +0.6‰ to +2.9‰ to a range of +4.6‰ to +7.0‰ most likely through increased nitrification following enhanced mineralization. Plant uptake of 15N-enriched NH₄⁺ in the drained treatment resulted in higher plant δ15N (+0.8‰ to +1.8‰ in the drained plots and −3.9‰ to −5.4‰ in the undrained plots), and deposition of litterfall N enriched with 15N increased the δ13C of total soil N in the surface layer in the drained (+2.9‰) as compared with that in the undrained plots (+0.6‰). The effect of drainage on foliar δ13C was species-specific, i.e., only tamarack showed a considerably less negative foliar δ13C in the drained (−28.1‰) than in the undrained plots (−29.1‰), indicating improved water use efficiency (WUE) by drainage. Tree ring area increments were significantly increased following drainage, and δ15C and δ15N in tree growth rings of both species showed responses to drainage retrospectively. Tree-ring δ13C data suggested that drainage improved WUE of both species, with a greater and more prolonged response in tamarack than in black spruce. Our results indicate that drainage caused the studied minerotrophic peatland to become a more open ecosystem in terms of C and N cycling and loss. The effects of forested peatland drainage or drying on C and N balances deserve further research in order to better understand their roles in future global change.

Key words: black spruce; δ13C; Larix laricina; δ15N; N loss; peatland drainage; photosynthetic capacity; Picea mariana; stomatal conductance; tamarack; tree ring.

INTRODUCTION

Peatlands occupy 500 × 10⁶ ha or 3.8% of the global land surface (Paavilainen and Päivänen 1995) and are estimated to store 455 Pg (Pg = 10¹⁵ g) of C, approximately one-third of the total terrestrial C pool (Gorham 1995). As climate change may disturb peatland ecosystems through changes in precipitation and temperature regimes, there are increasing concerns regarding the potential for peatlands to release the stored C when the biophysical conditions change (such as lowering of the water table as a result of climate change), which thus may provide a positive feedback to anthropogenic increases in greenhouse gas emissions (Wieder 2001). In addition to changes that occur naturally in peatland ecosystems, large areas of forested peatland have been drained for various purposes, particularly in Alberta, eastern Canada, and northern Europe. This is done primarily to increase forest productivity or to create land for agricultural production, because tree growth is most likely restricted by high water table levels under natural peatland conditions (e.g., Mugasha et al. 1993, Westman and Laiho 2003). Drainage of forested peatlands has been considered to be a viable silvicultural tool to increase stand productivity by improving tree growth conditions such as rooting depth and volume (Lieffers and Rothwell 1987), rooting zone aeration (Mugasha et al. 1993), soil temperature (van Cleve et al. 1990), and nutrient availability (Lieffers and Macdonald 1990, Westman and Laiho 2003). In this context, as drainage can affect rooting zone conditions in various ways, evaluation of measures or indices that integrate such complicated effects may provide a better understanding of the responses (particularly in terms of C and N dynamics) of forested peatland ecosystems to drainage retrospectively.

The stable C isotope ratio (δ13C/δ12C, expressed as δ13C) of tree components has served as a useful tool for examining ecosystem responses to environmental changes as altered water use efficiency, the ratio of net
photosynthesis to transpiration, is directly related to discrimination against $^{13}$C during photosynthesis (Farquhar et al. 1989). Many studies have shown that changed water and nutrient availabilities affect plant $^{13}$C through effects on stomatal conductance or photosynthetic capacity (e.g., Farquhar et al. 1989, Korol et al. 1999, Choi et al. 2005a). Therefore, it is expected that changed rooting zone conditions following drainage may be accompanied by altered $^{13}$C signatures in plant tissues, revealing drainage effects on gas exchanges of plants in the drained peatland. However, as far as we know, such examination has not been conducted on peatland ecosystems, although many studies have shown that drainage improved rooting zone conditions as discussed above.

Drainage of peatlands has been shown to alter soil N dynamics by improving conditions (e.g., aeration) for microbial activities. For example, drainage has been shown to increase N mineralization (Updegraff et al. 1995) and subsequent nitrification, which increases N loss potential through leaching or denitrification of NO$_3^-$ (Regina et al. 1996). These findings suggest that in combination with $^{13}$C, stable N isotope ratio ($^{15}$N/$^{14}$N, expressed as $^{15}$N) of plant and soil samples can be used as an isotopic indication of changed soil N dynamics after drainage. It has been well documented that $^{15}$N patterns in soil and plant samples reflect the openness of an ecosystem against N loss. Nitrogen loss leads to $^{15}$N enrichment of the remaining N in the soil due to N isotopic fractionation during N transformations (such as NH$_3$ volatilization, nitrification, and denitrification) involved with N loss (Högberg and Johannisson 1993, Chang and Handley 2000, Robinson 2001, Choi et al. 2005a). Therefore, it is expected that peatland drainage would increase $^{15}$N of soil and plant samples, reflecting increased N loss potential. However, our literature search did not find any published study that investigated the effects of peatland drainage on soil and plant $^{15}$N patterns.

Comparing $^{13}$C and $^{15}$N patterns between undrained and drained forested peatlands would provide insights into C and N dynamics and how they are affected by changed biophysical conditions in peatland ecosystems. Because C stocks in forest ecosystems are largely affected by interactions between climate, soil moisture condition, soil temperature, and nutrient (mainly N) availabilities, examination of C and N dynamics will improve our understanding as to whether drained forested peatlands may act as a C sink or source under predicted future climates that will continue to change (Moore et al. 1998, Bhatti et al. 2002).

In this study, we investigated the variations of radial growth and $^{13}$C and $^{15}$N signatures in tree rings, tree and understory foliage, and soil in a black spruce–tamarack (Picea mariana–Larix laricina) mixed-wood forested minerotrophic peatland to study C and N isotopic responses of peatland ecosystems to drainage. We hypothesized that C and N dynamics in peatlands that are altered by drainage could be inferred from $^{13}$C and $^{15}$N signatures left in plant and soil samples.

**Materials and Methods**

**Study Site**

This study was conducted on the Wolf Creek Peatland Drainage Project site (53°26′ N, 116°01′ W) located in central Alberta, Canada. The characteristics of the site are documented elsewhere (Mugasha et al. 1993, 1999). Briefly, the Wolf Creek study area is classified as a minerotrophic peatland or intermediate fen. The soil is a Terric Fibric Mesisol (Soil Classification Working Group 1998), which is characterized by 122 ± 10 cm of peat over mineral soil. Before drainage, the mean stand density of overstory vegetation, tamarack, and black spruce, ranged from 1740 to 2240 stems/ha (basal area 3.6 to ~4.5 m$^2$/ha). The understory consisted primarily of shrubs (Betula pumila, Salix pedicellaris, Kalmia polifolia, and Ledum groenlandicum), herbs (Carex spp.), and mosses (Sphagnum warnstorffii, S. angustifolium, Ptilium crista-castrensis, Tomethypnum nitiens, Pleurozium schreberi, and Hylocomium splendens).

The drainage ditches were excavated in fall 1987 with parallel ditches 40 m apart and 90 cm deep from the peat surface. The undrained plots were set up at least 75 m away from the nearest drainage ditch. To compare the differences caused by drainage, we selected three paired (drained vs. undrained) plots (each plot 20 × 20 m in size) along the perimeter of the drained peatland to minimize potential differences between the paired plots in stand density, tree size, and tree and understory species composition prior to the drainage treatment being applied (Mugasha et al. 1999). The pairs are at least 200 m apart from one another. The layout of experimental plots resulted in a randomized block design with three replications. Before 1987, the mean water table in these plots was 20 cm below the surface and after drainage it was lowered to 72 cm between 1988 and 1996 (Hillman 1997). In the undrained plots, the mean depth to water table increased to 24 cm during the post-drainage period (1988–1996). After drainage, the depth to water table in the drained area was significantly greater than in the control. Water tables frequently reached their lowest levels in October. During a dry spell in July–August 1990 and 1995, water table levels dropped below 1 m. A detailed description of the effects of drainage on groundwater table levels at Wolf Creek is provided in Hillman (1997).

Because tree rings formed between 1976 (12 years before the drainage treatment was applied) and 2003 (when trees were destructively sampled) were analyzed for $^{13}$C and $^{15}$N in our study, we report climate data for the same period. The mean annual air temperature and precipitation at the Edson weather station (53°35′ N, 116°28′ W, 35 km northwest of the study site) are 2.4°C and 529 mm, respectively. During the last 28 years, total precipitation in the active tree growing
season (May to September) ranged between 196.7 and 624.2 mm, showing a decreasing pattern with time ($r^2 = 0.34$, $P = 0.002$), whereas mean monthly temperature during the same period ranged between 10.9° and 12.7°C and did not show any systematic pattern of change.

**Soil and plant sampling**

Soil and plant samples were collected from the study site in September 2003. In each plot, three trees each of the tamarack and black spruce species were randomly selected that roughly represented the tree diameter range, and disks were collected at breast height (3 plots x 3 trees = 9 disks for each species and for each treatment). After collecting tree disks, foliage samples were collected from the branches in the upper one-third of the crown and composited for each plot ($n = 3$ for each treatment). Tamarack is a deciduous conifer and only one age class foliar sample could be collected, while only the current-year foliar samples were collected from the black spruce trees, although many different age class foliar samples could be collected from this species. Composite soil samples were collected to a depth of 30 cm in 10-cm intervals at five randomly selected points in each plot ($n = 3$ for each treatment). Labrador tea (*Ledum groenlandicum*), a dominant understory species in both the drained and undrained plots, was also collected at the five points where soil samples were collected for each plot ($n = 3$ for each treatment).

**Plant sample analyses**

The tree ring disks were sanded to make the growth rings visible and were then scanned. Digital images prepared using Adobe Photoshop 5.5 were then used to measure ring width using DendroScan, a computer program developed by Varem-Sanders and Campbell (1996). The diameter inside the bark of each tree was calculated as two times the summation of the annual ring width. Tree age was determined by ring counting. The age of trees ranged from 29 to 99 and 28 to 95 years old for black spruce in the drained (BS-D) and undrained plots (BS-UD) and from 39 to 57 and 49 to 95 years old for tamarack in the drained (T-D) and undrained plots (T-UD), respectively. Annual basal area increment was calculated assuming that tree rings are concentric circles and was used as an indicator of tree growth to minimize age-related growth trends.

Wood samples in four-year growth ring bands during the 1976–2003 period were taken from each disk, resulting in seven tree ring samples including samples from before (1976–1979, 1980–1983, and 1984–1987) and after drainage (1988–1991, 1992–1995, 1996–1999, and 2000–2003). Such pooling was done due to very small annual rings and the high cost of analysis. Wood samples from each growth ring band of each tree were analyzed and the mean value of the three trees in each plot was used for further data analysis. Tree and Labrador tea foliar samples were oven-dried at 60°C, and a subsample of soil was air-dried. The samples were ground with a ball mill (Retsch, Haan, Germany) to a fine powder and analyzed for $\delta^{13}$C, $\delta^{15}$N, and N concentration using a continuous-flow stable isotope ratio mass spectrometer (Delta plus Advantage, Thermo Finnigan, Bremen, Germany). In this study, isotope compositions of whole-plant tissue samples were investigated for the following reasons. First, for C isotope analysis, Loader et al. (2003) compared whole-tissue, cellulose, and lignin samples and showed that whole tissue retains the strongest C isotope signal for environmental conditions. Similarly, Korol et al. (1999) and Warren et al. (2001) also found similar $\delta^{13}$C patterns between whole tissue and cellulose samples. Secondly, N isotope variation among specific N-bearing compounds in tree rings is not well understood, and the low N concentration of tree rings precluded extraction of specific N compounds (Poulson et al. 1995). The whole tissue was used for $\delta^{15}$N analysis also because there is no N in cellulose.

Carbon and N isotope compositions were calculated as

\[
\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where $R$ is the ratio of $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N, and the standards are the Pee Dee Belemnite (PDB) standard for C and atmospheric N$_2$ for N. The precision and reproducibility of the measurements of $\delta^{13}$C and $\delta^{15}$N checked with an internal reference material, corn tissue ($-12.3 \pm 0.1\%$ for $\delta^{13}$C and $+3.4 \pm 0.1\%$ for $\delta^{15}$N), calibrated against National Institute of Standards and Technology Standard Reference Materials (NIST SRM) 8542 (sucrose, $-10.5\%$) for $\delta^{13}$C and against International Atomic Energy Agency nitrogen stable isotope standard number 2 (IAEA-N2) (ammonium sulfate, $+20.3\%$) for $\delta^{15}$N, were better than 0.2% for $\delta^{13}$C and 0.3% and 0.2% for $\delta^{15}$N, respectively. For tree ring samples of which N concentrations are too low to be analyzed for both $\delta^{13}$C and $\delta^{15}$N simultaneously using peak jumping, the $^{15}$N abundance was analyzed again by optimizing the mass spectrometer for $\delta^{15}$N alone. In this case, up to 10 mg of wood samples were used depending on the N concentration to meet a minimum N amount to improve the reproducibility of the $\delta^{15}$N analysis. Repeated measurements of tree ring samples resulted in a precision better than 0.2% for both $\delta^{13}$C and $\delta^{15}$N.

**Soil sample analyses**

To determine N concentration and $\delta^{15}$N of NH$_4^+$, NO$_3^-$, and soluble organic N (SON), fresh soil samples were extracted with 2 mol/L KCl at a 1:10 ratio. A portion of the extract was steam-distilled with MgO to determine NH$_4^+$ concentrations; thereafter the sample in the flask was distilled again after addition of Devarda’s alloy to determine NO$_3^-$ concentrations on a steam distillation system (Vapodest 20, C. Gerhardt, Königs-winter, Germany). The liberated NH$_3$ was collected in 0.005 mol/L H$_2$SO$_4$ solution (Keeney and Nelson 1982).
To prevent isotopic cross-contamination between samples, 25 mL of reagent-grade ethanol was added to distillation flasks and steam-distilled for 3 min between sample distillations (Hauck 1982). Nitrogen concentrations were determined by titration with 0.01 mol/L NaOH using an automatic potentiometric titrator (719s Titrino, Metrohm, Herisau, Switzerland). The concentration of total N in the 2 mol/L KCl extracts was determined by the Kjeldahl digestion and distillation method (Bremner 1996), and SON concentration was determined by subtracting mineral N from the total extractable N concentrations.

The H2SO4 solution containing NH4+ was evaporated to dryness at 65°C in an oven after adjustment of the solution to pH 3 using 0.05 mol/L H2SO4 and analyzed for δ15N (Hauck 1982, Feast and Dennis 1996) using the stable isotope mass spectrometer described above. The precision and reproducibility of the analytical procedure checked with reference materials, IAEA-N2 (ammonium sulfate, +20.3‰) and IAEA-N3 (potassium nitrate, +4.6‰), were better than 0.3 and 0.2‰, respectively. The δ15N of SON was calculated using the isotope mass balance equation (Karamanos and Rennie 1981, Choi and Chang 2005):

\[
\delta^{15}N_{SON} = [(\delta^{15}N_{SON+NH_4+NO_3} \times C_{SON+NH_4+NO_3}) - (\delta^{15}N_{NH_3} \times \delta^{15}N_{NH_3}) - (\delta^{15}N_{NO_3} \times \delta^{15}N_{NO_3})] / C_{SON}
\]

where \(C_{SON+NH_4+NO_3}\) is total extractable N concentration; \(C_{SON}\) is concentration of soluble organic N; \(C_{NH_3}\) and \(C_{NO_3}\) are concentrations of \(NH_4^+\) and \(NO_3^-\), respectively; and \(\delta^{15}N_{SON+NH_4+NO_3}\), \(\delta^{15}N_{SON}\), \(\delta^{15}N_{NH_3}\), and \(\delta^{15}N_{NO_3}\) are their corresponding \(\delta^{15}N\) values.

**Calculation of C isotope discrimination and intrinsic water use efficiency**

For tree ring samples, to eliminate the effects of annual changes in δ13C of atmospheric CO2 on plant δ13C, C isotope discrimination (Δ), which reflects differences in δ13C between source (atmospheric CO2) and product (plant C) and thus is independent of δ13C of atmospheric CO2, was calculated using the following equation (Farquhar et al. 1989):

\[
\Delta = (\delta^{13}C_{air} - \delta^{13}C_{plant}) / (1 + \delta^{13}C_{plant} / 1000)
\]

where \(\delta^{13}C_{plant}\) and \(\delta^{13}C_{air}\) are the C isotope ratios (as thousandths) of plant and atmospheric CO2, respectively. The \(\delta^{13}C_{air}\) were obtained using the regression equation developed by Feng (1998). According to the equation of Feng (1998), \(\delta^{13}C_{air}\) decreased from −7.4‰ in 1976 to −8.2‰ in 2003. Eq. 3 indicates that a more negative \(\delta^{13}C_{plant}\) results in a greater Δ.

Intrinsic water use efficiency (WUEi) was also calculated to compare intrinsic physiological responses of trees to drainage and how the responses differ between species and time of tissue formation. The WUEi, defined as the ratio of net C assimilation rate (\(A\), in micromoles of CO2 per square meter per second) to stomatal conductance (\(g_s\), millimoles of H2O per square meter per second), is less susceptible to instantaneous environmental conditions such as temperature and humidity and thus is believed to be more closely associated with physiological properties of plants than WUE, which quantifies the amount of C assimilated per unit leaf area per unit time per unit cost of water (Farquhar et al. 1989). The WUEi was calculated using the following equation:

\[
WUE_i = A / g_w = (C_a - C_i) / 1.6
\]

where \(C_a\) and \(C_i\) are atmospheric and intercellular CO2 concentrations, respectively, and 1.6 is the ratio of diffusivities of water vapor and CO2 in air. The \(C_a\) values were estimated using another equation developed by Feng (1998); the value increased from 333.0 to 362.3 μmol/mol from 1976 to 2003. The historical \(\delta^{13}C_{air}\) and \(C_a\) data are also available from McCarroll and Loader (2004) and monthly changes in \(C_a\) can also be obtained from the Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, USA. These values are comparable to one another. The \(C_i\) values were calculated using the relationship between Δ and \(C_i/C_a\) as follows (Farquhar et al. 1989):

\[
\Delta = a + (b - a)C_i / C_a
\]

where \(a\) and \(b\) are discriminations against \(^{13}C\) during CO2 diffusion through stomata (normally 4.4‰) and during CO2 fixation (normally 27‰), respectively. This equation indicates that an increase in \(C_i/C_a\) either by increased stomatal conductance (CO2 supply) or by decreased carboxylation (CO2 consumption) results in a greater Δ, leading to a more negative \(\delta^{13}C\) (Eq. 3) and vice versa.

**Statistical analysis**

All statistical analyses were performed with the SPSS 11.5 package (SPSS, Chicago, Illinois, USA). For soil, understory foliage, and tree foliage samples, ANOVA was performed to examine the drainage effect (and the species effect for plant samples) using the general linear models (GLM) procedure. Prior to ANOVA, data were tested for homogeneity of variance and normality of distribution; none of those assumptions were violated. Where ANOVA showed significant effects, means were separated by the least significant difference (LSD) test. In all statistical analyses on tree ring samples, the mean values of the three trees of each species per plot were used. Comparison of the tree ring data before (1984–1987 tree rings) and after (1988–1991 tree rings) drainage was conducted with a paired t test to examine the effect of drainage on each species. To test whether the tree growth conditions of the plots were similar before the implementation of the drainage treatment, ring area, δ13C, N concentration, and δ15N of tree rings formed between 1976 and 1987 were compared for each species (BS-D vs.
The δ13C, δ15N, N concentrations, and C/N ratios of total soil as affected by peatland drainage in three soil depths at the Wolf Creek Peatland Drainage Project site, central Alberta, Canada.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>δ13C (%)</th>
<th>N (g/kg)</th>
<th>δ15N (%)</th>
<th>C/N ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undrained</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>−27.9 (0.1)a</td>
<td>10.9 (0.4)b</td>
<td>+0.6 (0.2)b</td>
<td>48.5 (2.6)b</td>
</tr>
<tr>
<td>10–20</td>
<td>−27.0 (0.1)b</td>
<td>17.9 (0.9)b</td>
<td>+2.5 (0.3)b</td>
<td>27.2 (1.7)b</td>
</tr>
<tr>
<td>20–30</td>
<td>−26.8 (0.1)b</td>
<td>24.7 (2.4)b</td>
<td>+2.4 (0.2)b</td>
<td>21.6 (2.4)b</td>
</tr>
<tr>
<td>Drained</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>−27.3 (0.3)a</td>
<td>21.3 (3.3)a</td>
<td>+2.9 (0.5)a</td>
<td>25.1 (3.5)a</td>
</tr>
<tr>
<td>10–20</td>
<td>−26.8 (0.1)b</td>
<td>26.8 (2.2)a</td>
<td>+4.1 (0.2)a</td>
<td>19.5 (1.2)a</td>
</tr>
<tr>
<td>20–30</td>
<td>−26.8 (0.2)b</td>
<td>27.2 (0.6)a</td>
<td>+3.7 (0.1)a</td>
<td>19.1 (0.2)a</td>
</tr>
</tbody>
</table>

Notes: Values in parentheses are standard errors of the means (n = 3). Values in the same column followed by different superscript letters are significantly different at α = 0.05 when compared at the same soil depth for undrained vs. drained peatland plots.

Table 2. Concentrations of NH4+, NO3−, and soluble organic N (SON) and their δ15N values in three soil depths as affected by peatland drainage.

<table>
<thead>
<tr>
<th>NH4+</th>
<th>NO3−</th>
<th>NH4+ + NO3−</th>
<th>SON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (cm)</td>
<td>N (mg/kg)</td>
<td>δ15N (%)</td>
<td>N (mg/kg)</td>
</tr>
<tr>
<td>Undrained</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>59.8 (9.8)b</td>
<td>+0.6 (1.3)b</td>
<td>22.0 (2.8)b</td>
</tr>
<tr>
<td>10–20</td>
<td>69.4 (13.0)b</td>
<td>+2.9 (0.5)c</td>
<td>13.4 (1.6)c</td>
</tr>
<tr>
<td>20–30</td>
<td>28.2 (1.6)b</td>
<td>+2.8 (0.5)c</td>
<td>15.2 (0.9)b</td>
</tr>
<tr>
<td>Drained</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–10</td>
<td>146.2 (29.2)c</td>
<td>+5.9 (0.3)a</td>
<td>77.6 (24.7)c</td>
</tr>
<tr>
<td>10–20</td>
<td>38.1 (6.1)a</td>
<td>+7.0 (0.7)c</td>
<td>119.3 (12.7)c</td>
</tr>
<tr>
<td>20–30</td>
<td>23.2 (1.1)c</td>
<td>+4.6 (0.4)c</td>
<td>68.1 (5.4)c</td>
</tr>
</tbody>
</table>

Notes: Values in parentheses are standard errors of the means (n = 3). Values in the same column followed by different superscript letters are significantly different at α = 0.05 when compared at the same soil depth for undrained vs. drained peatland plots.

**RESULTS**

**Soil δ13C and δ15N**

The δ13C of total soil C in the same depth was not affected by peatland drainage (Table 1). However, drainage significantly increased the concentrations and δ15N of total soil N in all three soil depths examined. The increased N concentrations resulted in lower C/N ratios in the drained plots. Concentrations of mineral N (NH4+ plus NO3−) also increased by more than two-fold for all three depths as a result of drainage, and such effects were most dramatic for the top 10 cm soil layer (Table 2). The effect of drainage on NH4+ concentrations was not consistent among the soil depths studied; however, NO3− concentrations were consistently higher in the drained than in the undrained plots. The δ15N of NH4+ and NO3− were significantly affected by drainage: drainage increased δ15N of NH4+ but decreased δ15N of NO3−. In contrast, SON concentrations and the corresponding δ15N were quite variable and were not affected by the drainage treatment.

**Tree and understory foliar δ13C and δ15N**

Foliar δ13C values were significantly (P < 0.001) different among the species, i.e., black spruce showed less negative foliar δ13C values as compared with tamarack or Labrador tea (Table 3). Drainage resulted in a less negative foliar δ13C for tamarack but not for the other species. Nitrogen concentrations were also significantly (P < 0.001) different among the species: tamarack > Labrador tea > black spruce. Irrespective of plant species, drainage significantly increased foliar N concentrations, and the drainage effect was most remarkable for tamarack. An increase in N concentration resulted in a lower C/N ratio in plant tissues (Table 3). Foliar δ15N values were significantly increased (P < 0.001) by drainage from −5.4 to +1.8‰ for black spruce, from −4.7 to +1.6‰ for tamarack, and from −3.9 to +0.8‰ for Labrador tea.

**Tree radial growth**

Diameters of the sampled trees ranged between 63.4 mm and 99.6 mm for BS-D, 40.6 mm and 94.6 mm for BS-UD, 63.3 mm and 157.9 mm for T-D, and 41.5 mm and 135.4 mm for T-UD. Annual increments of ring width and area did not differ between species or treatment plots until 1987, when ditches were constructed in the drained plots; thereafter, ring width and area of both species were significantly (P < 0.001) increased by drainage (Fig. 1). Radial growth response to drainage was greater in tamarack than in black spruce; i.e., the ratio of annual ring area increment of each species in the drained to that in the undrained plots averaged 3.4 ± 0.4 (mean ± SE) for black spruce and 4.6 ± 0.7 for tamarack between 1988 and 2003.
The $d_{13}C$ in tree rings from the undrained plots decreased linearly from $-25.5$ to $-26.3\%$ for tamarack ($r^2 = 0.99$, $P < 0.001$) and from $-24.7$ to $-25.5\%$ for black spruce ($r^2 = 0.76$, $P < 0.05$) during the 28 years between 1976 and 2003 (Fig. 2A). Before the drainage treatment was applied, the $d_{13}C$ of each species did not differ between drained and undrained plots. However, the drainage treatment implemented in 1987 immediately resulted in a significantly less negative $d_{13}C$ ($-24.6\%$ for black spruce and $-24.8\%$ for tamarack) of tree rings formed between 1988 and 1991, and thereafter it followed a decreasing pattern as in the undrained plots.

In the undrained plots, the $D$ of black spruce ranged between $17.6\%$ and $18.0\%$ and the $D$ of tamarack ranged between $18.5\%$ and $18.7\%$ and did not change with time throughout the studied period (Fig. 2B). Drainage resulted in a significant decrease in $D$; for tree rings formed between 1988 and 1991, the calculated $D$ was $17.3\%$ for black spruce and $17.4\%$ for tamarack in the drained plots. Thereafter, the $D$ increased gradually as $d_{13}C$ gradually decreased with time.

In the undrained plots, WUE$_i$ of both species increased with time from 85.8 to 91.8 l mol/mol for black spruce ($r^2 = 0.73$, $P < 0.05$) and from 78.5 to 83.6 l mol/mol for tamarack ($r^2 = 0.94$, $P < 0.01$) between 1976 and 2003 (Fig. 2C). Drainage enhanced this increasing pattern; i.e., drainage increased WUE$_i$ for black spruce from 86.8 to 92.9 l mol/mol and for tamarack from 80.7 to 90.9 l mol/mol during the same interval. Overall, under the same drainage condition (drained or undrained) tamarack had significantly more negative $d_{13}C$ values, greater $D$, and lower WUE$_i$ than black spruce (Fig. 2).

Overall, black spruce had higher N concentrations in tree rings than tamarack, with no significant temporal variations of N concentrations within tree rings detected for each species (Fig. 3A). Considering that the increased radial growth after drainage can cause a dilution effect, we compared a weighted N concentration that was calculated by multiplying the N concentration with ring area (Fig. 3B). The weighted N concentration, which is related to the amount of N assimilated during each four-year growth interval, significantly ($P < 0.001$) increased after drainage. In contrast to the N concentration pattern, tamarack had higher weighted N concentrations than black spruce in the undrained plots.

### Table 3. Tree and understory foliar carbon and nitrogen isotope ratios, N concentrations, and C/N ratios as affected by peatland drainage.

<table>
<thead>
<tr>
<th>Species</th>
<th>$d_{13}C$ ($%$)</th>
<th>N (g/kg)</th>
<th>$d_{15}N$ ($%$)</th>
<th>C/N ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Undrained</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce</td>
<td>$-26.8 (0.2)^a$</td>
<td>10.4 (0.3)$^a$</td>
<td>$-5.4 (0.1)^a$</td>
<td>56.0 (1.6)$^a$</td>
</tr>
<tr>
<td>Tamarack</td>
<td>$-29.1 (0.2)^a$</td>
<td>20.7 (0.2)$^a$</td>
<td>$-4.7 (0.1)^a$</td>
<td>28.0 (2.5)$^b$</td>
</tr>
<tr>
<td>Labrador tea</td>
<td>$-28.0 (0.1)^a$</td>
<td>16.6 (0.3)$^a$</td>
<td>$-3.9 (0.3)^a$</td>
<td>34.5 (0.5)$^a$</td>
</tr>
<tr>
<td><strong>Drained</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce</td>
<td>$-26.4 (0.4)^a$</td>
<td>13.5 (0.1)$^b$</td>
<td>$+1.8 (0.3)^b$</td>
<td>43.3 (0.7)$^a$</td>
</tr>
<tr>
<td>Tamarack</td>
<td>$-28.1 (0.2)^b$</td>
<td>33.1 (0.6)$^b$</td>
<td>$+1.6 (1.1)^b$</td>
<td>17.3 (0.4)$^a$</td>
</tr>
<tr>
<td>Labrador tea</td>
<td>$-28.4 (0.2)^b$</td>
<td>21.2 (0.2)$^b$</td>
<td>$+0.8 (0.8)^b$</td>
<td>29.1 (0.2)$^b$</td>
</tr>
</tbody>
</table>

Notes: Values in parentheses are standard errors of the means ($n = 3$). Values in the same column followed by different superscript letters are significantly different at $\alpha = 0.05$, regardless of species.
concentrations than black spruce for each specific four-year growth ring band, reflecting tamarack’s better radial growth response to drainage than black spruce (Fig. 1).

The $\delta^{15}$N in tree rings formed during the same period was not different between the drained and undrained plots for both species studied. However, temporal variation in $\delta^{15}$N of annual rings showed a different pattern between the drained and undrained plots. In the undrained plots, while not statistically significant, $\delta^{15}$N in tree rings showed a decreasing tendency over the last 28 years; $\delta^{15}$N of black spruce decreased from $-2.8\%$o to $-3.9\%$o ($r^2 = 0.47$, $P = 0.013$) and that of tamarack decreased from $-2.4\%$o to $-4.4\%$o ($r^2 = 0.61$, $P = 0.11$; Fig. 3C). The $\delta^{15}$N values in tree rings formed between 1988 and 1991 (right after the drainage treatment was applied) were not different from those formed between 1984 and 1987, before drainage. However, in the drained plots, the $\delta^{15}$N values significantly increased from $-3.9\%$o to $-2.9\%$o for black spruce and from $-4.4\%$o to $-3.3\%$o for tamarack between the periods of 1988–1991 and 1992–1995, contrasting the pattern observed in the undrained plots during the same growth interval.

**DISCUSSION**

**Effects of drainage on soil and plant N concentrations and $\delta^{15}$N**

The data support our hypothesis that rhizosphere conditions changed by drainage may leave a specific $\delta^{15}$N signature in soil and plant samples. Improved rhizosphere conditions (e.g., aeration) in the drained peatland plots can directly affect plant growth and nutrient uptake (Lieffers and Macdonald 1990, Westman and Laiho 2003). In our study, drainage increased concentrations than black spruce for each specific four-year growth ring band, reflecting tamarack’s better radial growth response to drainage than black spruce (Fig. 1).
N mineralization and N availability as indicated by the higher mineral N concentrations in the soil (Table 2), which led to higher foliar N concentrations of plant species in the drained plots (Table 3). Increased N concentrations and growth rates (measured as growth ring width or area; e.g., Fig. 1) also indicate that plant N uptake was greater in the drained plots. In addition to improved aeration for microbial activity, improved substrate quality (e.g., lower C/N ratios; Table 1) may also have enhanced the decomposition of organic matter (Tian et al. 1995), leading to increased nutrient availability in the soil. Increased total soil N concentrations in the drained over those in the undrained plots throughout the depths examined (Table 1) reflected the changed quality, such as N concentration and C/N ratio, of organic matter input (through litterfall) from the tree and understory (Table 3).

The higher \( \delta^{15}N \) of plant and total soil N in the drained than in the undrained plots (Tables 1 and 3) reflected different soil N dynamics, including mineralization, nitrification, and N loss. It has been frequently reported that ecosystems having a higher N loss potential tend to be enriched with \( ^{15}N \), because N loss leads to \( ^{14}N \) enrichment of the remaining N due to N isotopic fractionation associated with N transformations and loss (Högberg and Johannisson 1993, Chang and Handley 2000, Robinson 2001, Choi et al. 2005a). Among the N transformation processes, nitrification is considered to play a key role in increasing soil \( \delta^{15}N \), as denitrification and preferential leaching of NO\(_3^-\) that may be produced through incomplete nitrification are the main pathways of N loss resulting in \( ^{15}N \) enrichment of the remaining NO\(_3^-\) (Mariotti et al. 1981, Choi and Ro 2003). Despite higher plant N uptake as we discussed earlier, mineral N (NH\(_4^+\) plus NO\(_3^-\)) concentrations were higher in the drained than in the undrained plots (Table 2), suggesting again that N mineralization rates were much greater in the drained plots. Similarly, the higher NO\(_3^-\) concentrations in the drained plots (Table 2) reflected increased nitrification rates under better soil aeration. The consistently higher \( \delta^{15}N \) of NH\(_4^+\) than that of NO\(_3^-\) in all depths in the drained plots clearly indicates the presence of significant nitrification that enriched NH\(_4^+\) (the substrate) with \( ^{15}N \) and produced NO\(_3^-\) (the product) depleted in \( ^{15}N \) (Mariotti et al. 1981, Choi and Ro 2003). Input of tree and understory litter with a higher \( \delta^{15}N \) (Table 3) seemed to have subsequently resulted in \( ^{15}N \) enrichment of the total soil N in the drained over that in the undrained plots, particularly in the surface soil layer (Table 1) as the difference in \( \delta^{15}N \) of total soil N between the drained and undrained plots was 2.3\% for the 0–10 cm depth but decreased to 1.3\% for the 20–30 cm depth.

The \( ^{15}N \) enrichment of NO\(_3^-\) by N loss, however, is clearly not supported by our data due to the complexity of N transformations involved with NO\(_3^-\). For example, \( \delta^{15}N \) of NO\(_3^-\) is susceptible to both NO\(_3^-\)-producing (nitrification) and -removing processes (e.g., denitrification or preferential leaching of the NO\(_3^-\) produced through incomplete nitrification), which can result in \( ^{15}N \) depletion or enrichment in NO\(_3^-\), respectively (Mariotti et al. 1981, Choi and Ro 2003). In our study, a lower \( \delta^{15}N \) of NO\(_3^-\) than NH\(_4^+\) in the drained plots suggests that \( \delta^{15}N \) of NO\(_3^-\) tends to be more affected by nitrification rather than by denitrification or leaching in the drained peatland that we studied. Overall, the pattern of \( \delta^{15}N \) of NH\(_4^+\) rather than NO\(_3^-\) or SON was consistent with \( \delta^{15}N \) differences in plant and total soil N pools between the drained and undrained plots (Table 2), suggesting that trees rely more on NH\(_4^+\) than NO\(_3^-\) in the studied peatland ecosystem. This result is consistent with Choi et al. (2005a), who reported that \( \delta^{15}N \) of NH\(_4^+\) rather than NO\(_3^-\) was correlated with foliar \( \delta^{15}N \) of loblolly pine due primarily to conifer preference for NH\(_4^+\) over NO\(_3^-\) and suggested that \( \delta^{15}N \) of NH\(_4^+\) has value in predicting foliar \( \delta^{15}N \) of conifers. Hence, our data indicate that \( \delta^{15}N \) of NH\(_4^+\) rather than other soil labile N pools serves as a reliable indication of the changed soil N dynamics, particularly nitrification, and that such isotopic information explains \( \delta^{15}N \) patterns in plant and soil samples in the drained and undrained plots.

### Effects of drainage on \( \delta^{13}C \) of foliar samples

Drainage effects on gas exchange of tree species have rarely been reported, while the effects of the reverse treatment (flooding or water saturation) have been extensively studied (e.g., Liu and Dickmann 1996, Islam et al. 2003, Islam and Macdonald 2004). In our study, a more negative \( \delta^{13}C \) (a greater discrimination) in tamarack in the undrained than in the drained plots (Table 3) indicates an improvement of WUE after drainage. This \( \delta^{13}C \) pattern suggests that drainage tended to increase CO\(_2\) assimilation (non-stomatal regulation) to a great extent as compared to changes in stomatal conductance (stomatal regulation), allowing greater gain of C with less loss of water. Such \( \delta^{13}C \) patterns could be ascribed to the improved capacity of foliage for CO\(_2\) assimilation resulting from increased soil aeration, improved growth conditions following drainage. The apparently greater foliar \( \delta^{13}C \) response (increase in WUE) of tamarack (Table 3) likely reflected its greater ability than black spruce to take advantage of improved growth conditions following drainage. The growth of tamarack has been shown to respond more dramatically to drainage than that of black spruce (Macdonald and Yin 1999). This is generally ascribed to an inherently faster growth rate (Strong and La Roi 1983), a greater ability to take up N (Macdonald and Lieffers 1990), and a deeper and greater root system (Lieffers and Rothwell 1987) of tamarack than black.
spruce. A greater and faster response to drainage in growth ring width or growth ring area of tamarack than that of black spruce that we observed in this study (Fig. 1) is consistent with the literature.

**Effects of drainage on δ^{13}C, N concentrations, and δ^{15}N in tree rings**

Our data suggest that drainage-induced changes in tree physiological characteristics (such as stomatal conductance, carboxylation, or both) associated with photosynthesis can be detected retroactively by examining δ^{13}C signals stored in tree rings. In the undrained plots, the decreasing pattern of δ^{13}C in tree rings with time can primarily be attributed to the increasing atmospheric CO2 concentration via increased ring band was most likely due to tamarack’s greater ability to maintain a higher stomatal conductance when they were grown under the same conditions (Islam and Macdonald 2004). In spite of the initial effect of drainage on tree ring δ^{13}C, Δ, and WUEi between black spruce and tamarack (Fig. 3) seemed to reflect again differences in their ability to adapt to different peatland conditions, consistent with the foliar δ^{13}C and Δ data. For example, a significantly lower δ^{13}C in tamarack than in black spruce in the same growth ring band was most likely due to tamarack’s greater ability to maintain a higher stomatal conductance when they were grown under the same conditions (Islam and Macdonald 2004).

The differences in tree ring δ^{13}C, Δ, and WUEi for both species, the magnitude of the differences of these values between the drained and undrained treatments for black spruce decreased with time and disappeared in the tree rings formed immediately prior to sampling, whereas tamarack consistently maintained such differences throughout the period examined (Fig. 2). This result is consistent with the foliar δ^{13}C data; black spruce had virtually the same δ^{13}C between the drained and undrained plots, while tamarack had a higher δ^{13}C in the drained plots at the sampling time (Table 3). Even though the response of tree ring C isotope discrimination to drainage diminished in black spruce 16 years after the treatments was applied, ring growth enhancement persisted, reflecting the effect of greater leaf area per tree (because of bigger trees) on individual tree growth in the drained plots. Hence, the δ^{13}C signature in tamarack may be a sensitive and long-term surrogate for measuring changed environmental conditions in peatlands.

While statistically not significant, the δ^{15}N in tree rings of both species in undrained plots tended to decrease with time, consistent with the observations of Poulson et al. (1995) and Peñuelas and Estiarte (1997). Poulson et al. (1995) attributed the decreasing pattern of δ^{15}N in tree rings of hemlock (Tsuga canadensis) over time to the increasing deposition of 15N-depleted N compounds, and Peñuelas and Estiarte (1997) hypothesized that decreased N loss and increased N fixation and mineralization rates might explain the δ^{15}N patterns in tree rings they observed. However, as N may move across tree rings accompanied with N isotopic fractionation (Shepard and Thompson 2000, Hart and Classen...
2003), the interpretation of \( ^{15}N \) variations across tree rings is not a straightforward matter. In our study, drainage tended \((P > 0.05)\) to increase \( ^{15}N \) in tree rings (Fig. 3C) similar to drainage effects on foliar \( ^{15}N \) (Table 3). Such tendency suggests that drainage slowed or reversed the decreasing \( ^{15}N \) pattern through supplying \( \text{NH}_4^+ \)-N enriched with \( ^{15}N \) resulting from enhanced nitrification (Tables 1 and 2). However, before using \( ^{15}N \) of tree rings as an indicator of environmental conditions, more research on isotopic fractionation during inter-ring translocation of N needs to be conducted. A few studies (Shepard and Thompson 2000, Hart and Classen 2003, Choi et al. 2005b) have suggested that the removal of the extractive N fraction in wood samples could remove the “noise” from the isotopic “signal” that reflects \( ^{15}N \) of N assimilated by trees.

In summary, we found that drainage improved radial growth (C gain) of trees, while increasing soil C and N mineralization rates (or C and N losses) of the minerotrophic forested peatland ecosystem. The tree ring growth, N content, and WUE, data suggested that increased radial growth by drainage was due to increased C fixation resulting from N-induced increases in photosynthetic capacity and from an overall increase in leaf area, rather than changes in stomatal conductance. The above effect was consistently more apparent for tamarack, which is better adapted to peatland conditions as compared with black spruce. For black spruce, drainage effects on gas exchange were not detected in current-year tree foliage and growth rings formed immediately prior to sampling. Changed N cycling could be inferred from \( ^{15}N \) variations in plant and soil samples. Specifically, drainage enhanced N mineralization and nitrification as indicated by higher \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) concentrations, a higher \( ^{15}N \) of \( \text{NH}_4^+ \), and a lower \( ^{15}N \) of \( \text{NO}_3^- \) in the drained than in the undrained plots. The uptake of \( \text{NH}_4^+ \) enriched with \( ^{15}N \) by plants and the subsequent deposition of tree and understory litter was assumed to lead to increased \( ^{15}N \) of soil total N in the drained plots, particularly in the 0–10 cm layer. Our data clearly suggest that tamarack would respond to peatland drainage more strongly than black spruce in improved WUE and growth; therefore tamarack-dominated stands should be the choice of peatland sites for drainage if such management practices are desirable for increasing forest productivity. Our study showed that soil and plant \( ^{13}C \) and \( ^{15}N \) patterns reflected the processes that were altered by peatland drainage and the \( ^{13}C \) and \( ^{15}N \) techniques are useful tools for investigating the impact of environmental changes on C and N cycling in forested peatland ecosystems.

Acknowledgments

We thank the Killam and the Alberta Ingenuity postdoctoral fellowships for their support to the senior author. The research was also supported by an NSERC Discovery grant and a Canadian Foundation for Innovation (CFI) grant to S. X. Chang and federal government grants to J. S. Bhattacharjee, Kaixia Zhan assisted in tree ring analysis. Clive Figureado performed stable isotope analysis. Three anonymous reviewers provided helpful comments that improved the manuscript. We also thank Dr. Eun-Sik Park of the Department of Information Statistics, Chonnam National University, Korea, for the advice on time series analysis.

Literature Cited


