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

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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. In this study, tree annual ring width and C ($\delta^{13}C$) and N ($\delta^{15}N$) 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 $\delta^{15}N$ of soil NH_4^+ 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 ^{15}N-enriched NH_4^+ in the drained treatment resulted in higher plant $\delta^{15}N$ (+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 ^{15}N increased the $\delta^{15}N$ 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 $\delta^{13}C$ was species-specific, i.e., only tamarack showed a considerably less negative foliar $\delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ in tree growth rings of both species showed responses to drainage retrospectively. Tree-ring $\delta^{13}C$ 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; ^{13}C; Larix laricina; *^{15}N; N loss; peatland drainage; photosynthetic capacity;* Picea mariana; *stomatal conductance; tamarack; tree ring.*

INTRODUCTION

Peatlands occupy 500×10^6 ha or 3.8% of the global land surface (Paavilainen and Päivänen 1995) and are estimated to store 455 Pg (Pg = 10^{15} 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 ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) 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

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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 $\delta^{13}C$ through effects on stomatal conductance or photosynthetic capacity (e.g., Farquhar et al. 1989, Korol et al. 1999, Choi et al. 2005*a*). Therefore, it is expected that changed rooting zone conditions following drainage may be accompanied by altered $\delta^{13}C$ 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 $\delta^{13}C$, stable N isotope ratio ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) 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 $\delta^{15}N$ 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. 2005*a*). Therefore, it is expected that peatland drainage would increase $\delta^{15}N$ 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 $\delta^{15}N$ patterns.

Comparing $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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 warnstorfii*, *S. angustifolium*, *Ptilium crista-castrensis*, *Tomenthypnum nitens*, *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 $\delta^{13}C$ and $\delta^{15}N$ 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 × 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

$$\delta(\%) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \qquad (1)$$

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 ± 0.1‰ for $\delta^{13}C$ and +3.4 ± 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‰ and 0.1‰ 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, Königswinter, Germany). The liberated NH_3 was collected in 0.005 mol/L H_2SO_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 H_2SO_4 solution containing NH_4^+ was evaporated to dryness at 65°C in an oven after adjustment of the solution to pH 3 using 0.05 mol/L H_2SO_4 and analyzed for $\delta^{15}N$ (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 $\delta^{15}N$ of SON was calculated using the isotope mass balance equation (Karamanos and Rennie 1981, Choi and Chang 2005):

$$\begin{aligned}\delta^{15}\mathrm{N}_{\mathrm{SON}} = [(\delta^{15}\mathrm{N}_{\mathrm{SON+NH_4+NO_3}} \times C_{\mathrm{SON+NH_4+NO_3}}) \\ -(\delta^{15}\mathrm{N}_{\mathrm{NH_4}} \times \delta^{15}\mathrm{N}_{\mathrm{NH_4}}) \\ -(\delta^{15}\mathrm{N}_{\mathrm{NO_3}} \times \delta^{15}\mathrm{N}_{\mathrm{NO_3}})]/C_{\mathrm{SON}}\end{aligned} \qquad (2)$$

where $C_{\mathrm{SON+NH_4+NO_3}}$ is total extractable N concentration; C_{SON} is concentration of soluble organic N; $C_{\mathrm{NH_4}}$and $C_{\mathrm{NO_3}}$ are concentrations of NH_4^+ and NO_3^-, respectively; and $\delta^{15}\mathrm{N}_{\mathrm{SON+NH_4+NO_3}}$, $\delta^{15}\mathrm{N}_{\mathrm{SON}}$, $\delta^{15}\mathrm{N}_{\mathrm{NH_4}}$, and $\delta^{15}\mathrm{N}_{\mathrm{NO_3}}$ 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 $\delta^{13}C$ of atmospheric CO_2 on plant $\delta^{13}C$, C isotope discrimination (Δ), which reflects differences in $\delta^{13}C$ between source (atmospheric CO_2) and product (plant C) and thus is independent of $\delta^{13}C$ of atmospheric CO_2, was calculated using the following equation (Farquhar et al. 1989):

$$\Delta = (\delta^{13}C_{\mathrm{air}} - \delta^{13}C_{\mathrm{plant}})/(1 + \delta^{13}C_{\mathrm{plant}}/1000) \qquad (3)$$

where $\delta^{13}C_{\mathrm{plant}}$ and $\delta^{13}C_{\mathrm{air}}$ are the C isotope ratios (as thousandths) of plant and atmospheric CO_2, respectively. The $\delta^{13}C_{\mathrm{air}}$ were obtained using the regression equation developed by Feng (1998). According to the equation of Feng (1998), $\delta^{13}C_{\mathrm{air}}$ decreased from −7.4‰ in 1976 to −8.2‰ in 2003. Eq. 3 indicates that a more negative $\delta^{13}C_{\mathrm{plant}}$ results in a greater Δ.

Intrinsic water use efficiency ($\mathrm{WUE_i}$) 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 $\mathrm{WUE_i}$, defined as the ratio of net C assimilation rate (A, in micromoles of CO_2 per square meter per second) to stomatal conductance (g_w, millimoles of H_2O 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 $\mathrm{WUE_i}$ was calculated using the following equation:

$$\mathrm{WUE_i} = A/g_{\mathrm{w}} = (C_{\mathrm{a}} - C_{\mathrm{i}})/1.6 \qquad (4)$$

where C_a and C_i are atmospheric and intercellular CO_2 concentrations, respectively, and 1.6 is the ratio of diffusivities of water vapor and CO_2 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 $\delta^{13}C_{\mathrm{air}}$ 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):

$$\Delta = a + (b - a)C_{\mathrm{i}}/C_{\mathrm{a}} \qquad (5)$$

where a and b are discriminations against ^{13}C during CO_2 diffusion through stomata (normally 4.4‰) and during CO_2 fixation (normally 27‰), respectively. This equation indicates that an increase in C_i/C_a either by increased stomatal conductance (CO_2 supply) or by decreased carboxylation (CO_2 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, $\delta^{13}C$, N concentration, and $\delta^{15}N$ of tree rings formed between 1976 and 1987 were compared for each species (BS-D vs.

Table 1. The δ^{13}C, δ^{15}N, 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.

Depth (cm)	δ^{13}C (‰)	N (g/kg)	δ^{15}N (‰)	C/N ratio
Undrained				
0–10	−27.9 (0.1)^{a}	10.9 (0.4)^{b}	+0.6 (0.2)^{b}	48.5 (2.6)^{b}
10–20	−27.0 (0.1)^{a}	17.9 (0.9)^{b}	+2.5 (0.3)^{b}	27.2 (1.7)^{b}
20–30	−26.8 (0.1)^{a}	24.7 (2.4)^{b}	+2.4 (0.2)^{b}	21.6 (2.4)^{b}
Drained				
0–10	−27.3 (0.3)^{a}	21.3 (3.3)^{a}	+2.9 (0.5)^{a}	25.1 (3.5)^{a}
10–20	−26.8 (0.1)^{a}	26.8 (2.2)^{a}	+4.1 (0.2)^{a}	19.5 (1.2)^{a}
20–30	−26.8 (0.2)^{a}	27.2 (0.6)^{a}	+3.7 (0.1)^{a}	19.1 (0.2)^{a}

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 $\alpha = 0.05$ when compared at the same soil depth for undrained vs. drained peatland plots.

BS-UD and T-D vs. T-UD) with a *t* test. In this test, the differences in those parameters between the drained and undrained treatments were compared for each of the three time periods (1975–1979, 1980–1983, and 1984–1987) independently. For tree-ring samples, the significance of observed trends in time or age was tested by an autoregressive error model of time series analysis using year as an independent variable. An α value of 0.05 was chosen to indicate statistical significance.

Results

Soil δ^{13}C and δ^{15}N

The δ^{13}C of total soil C in the same depth was not affected by peatland drainage (Table 1). However, drainage significantly increased the concentrations and δ^{15}N 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 (NH_4^+ plus NO_3^-) 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 NH_4^+ concentrations was not consistent among the soil depths studied; however, NO_3^- concentrations were consistently higher in the drained than in the undrained plots. The δ^{15}N of NH_4^+ and NO_3^- were significantly affected by drainage: drainage increased δ^{15}N of NH_4^+ but decreased δ^{15}N of NO_3^-. In contrast, SON concentrations and the corresponding δ^{15}N were quite variable and were not affected by the drainage treatment.

Tree and understory foliar δ^{13}C and δ^{15}N

Foliar δ^{13}C values were significantly ($P < 0.001$) different among the species, i.e., black spruce showed less negative foliar δ^{13}C values as compared with tamarack or Labrador tea (Table 3). Drainage resulted in a less negative foliar δ^{13}C 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 δ^{15}N 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.

Table 2. Concentrations of NH_4^+, NO_3^-, and soluble organic N (SON) and their δ^{15}N values in three soil depths as affected by peatland drainage.

	NH_4^+		NO_3^-		$NH_4^+ + NO_3^-$		SON	
Depth (cm)	N (mg/kg)	δ^{15}N (‰)	N (mg/kg)	δ^{15}N (‰)	N (mg/kg)	δ^{15}N (‰)	N (mg/kg)	δ^{15}N (‰)
Undrained								
0–10	59.8 (9.8)^{b}	+0.6 (1.3)^{b}	22.0 (2.8)^{b}	+2.4 (0.2)^{b}	81.8 (12.4)^{b}	+1.2 (0.9)^{b}	159.5 (61.8)^{a}	+3.4 (0.9)^{a}
10–20	69.4 (13.0)^{b}	+2.9 (0.5)^{b}	13.4 (1.6)^{b}	+1.1 (0.6)^{b}	82.8 (12.2)^{b}	+2.7 (0.3)^{b}	39.1 (12.5)^{a}	+3.8 (0.6)^{a}
20–30	28.2 (1.6)^{a}	+2.8 (0.5)^{b}	15.2 (0.9)^{b}	+2.7 (0.6)^{a}	43.5 (2.2)^{b}	+2.7 (0.5)^{a}	9.5 (6.1)^{a}	+3.6 (4.4)^{a}
Drained								
0–10	146.2 (29.2)^{a}	+5.9 (0.3)^{a}	77.6 (24.7)^{a}	−3.4 (1.1)^{a}	223.8 (15.6)^{a}	+2.8 (0.5)^{a}	143.5 (53.5)^{a}	+3.7 (1.1)^{a}
10–20	38.1 (6.1)^{a}	+7.0 (0.7)^{a}	119.3 (12.7)^{a}	−1.5 (0.1)^{a}	157.4 (13.8)^{a}	+0.5 (0.3)^{a}	25.9 (4.6)^{a}	+0.3 (3.8)^{a}
20–30	23.2 (1.1)^{a}	+4.6 (0.4)^{a}	68.1 (5.4)^{a}	+2.3 (1.5)^{a}	91.3 (5.1)^{a}	+2.9 (1.2)^{a}	51.9 (23.7)^{a}	+2.0 (3.3)^{a}

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 $\alpha = 0.05$ when compared at the same soil depth for undrained vs. drained peatland plots.

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

Species	δ^{13}C (‰)	N (g/kg)	δ^{15}N (‰)	C/N ratio
Undrained				
Black spruce	−26.8 (0.2)^{c}	10.4 (0.3)^{a}	−5.4 (0.1)^{a}	56.0 (1.6)^{e}
Tamarack	−29.1 (0.2)^{a}	20.7 (0.2)^{d}	−4.7 (0.1)^{a}	28.0 (2.5)^{b}
Labrador tea	−28.0 (0.1)^{b}	16.6 (0.3)^{c}	−3.9 (0.3)^{a}	34.5 (0.5)^{c}
Drained				
Black spruce	−26.4 (0.4)^{c}	13.5 (0.1)^{b}	+1.8 (0.3)^{b}	43.3 (0.7)^{d}
Tamarack	−28.1 (0.2)^{b}	33.1 (0.6)^{e}	+1.6 (1.1)^{b}	17.3 (0.4)^{a}
Labrador tea	−28.4 (0.2)^{ab}	21.2 (0.2)^{d}	+0.8 (0.8)^{b}	29.1 (0.2)^{b}

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.

δ^{13}C and Δ in tree rings and WUE_i

The δ^{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 δ^{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 δ^{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 Δ of black spruce ranged between 17.6‰ and 18.0‰ and the Δ 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 Δ; for tree rings formed between 1988 and 1991, the calculated Δ was 17.3‰ for black spruce and 17.5‰ for tamarack in the drained plots. Thereafter, the Δ increased gradually as δ^{13}C gradually decreased with time.

In the undrained plots, WUE_i of both species increased with time from 85.8 to 91.8 μmol/mol for black spruce ($r^2 = 0.73$, $P < 0.05$) and from 78.5 to 83.6 μmol/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 μmol/mol and for tamarack from 80.7 to 90.9 μmol/mol between the periods of 1984–1987 (before drainage) and 1988–1991 (after drainage), while in the undrained plots WUE_i changed for black spruce from 87.8 to 89.5 μmol/mol and for tamarack from 79.4 to 79.5 μmol/mol during the same interval. Overall, under the same drainage condition (drained or undrained) tamarack had significantly more negative δ^{13}C values, greater Δ, and lower WUE_i than black spruce (Fig. 2).

N concentrations and δ^{15}N in tree rings

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

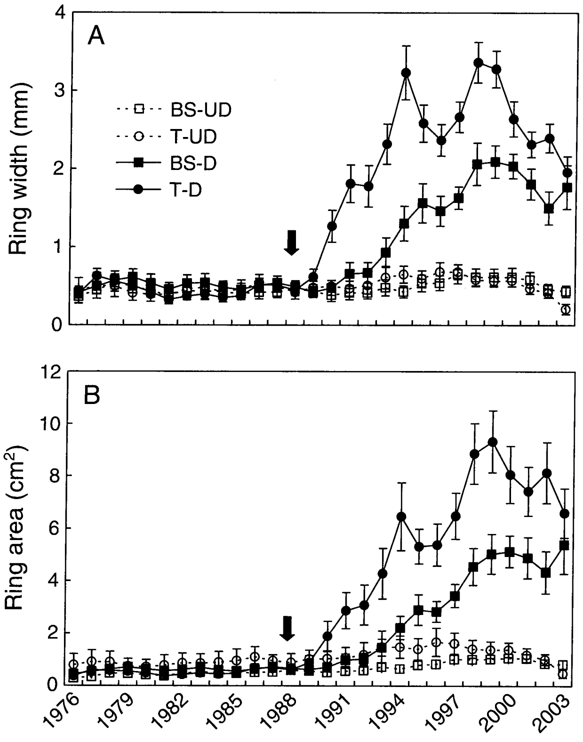

FIG. 1. Changes in (A) growth ring width and (B) growth ring area in black spruce and tamarack between 1976 and 2003 at the Wolf Creek Peatland Drainage Project site located in central Alberta, Canada. The drainage treatment was implemented in the fall of 1987, as indicated by the arrow. Vertical bars are standard errors of the means ($n = 3$). BS-UD, T-UD, BS-D, and T-D are black spruce in undrained plots, tamarack in undrained plots, black spruce in drained plots, and tamarack in drained plots, respectively.

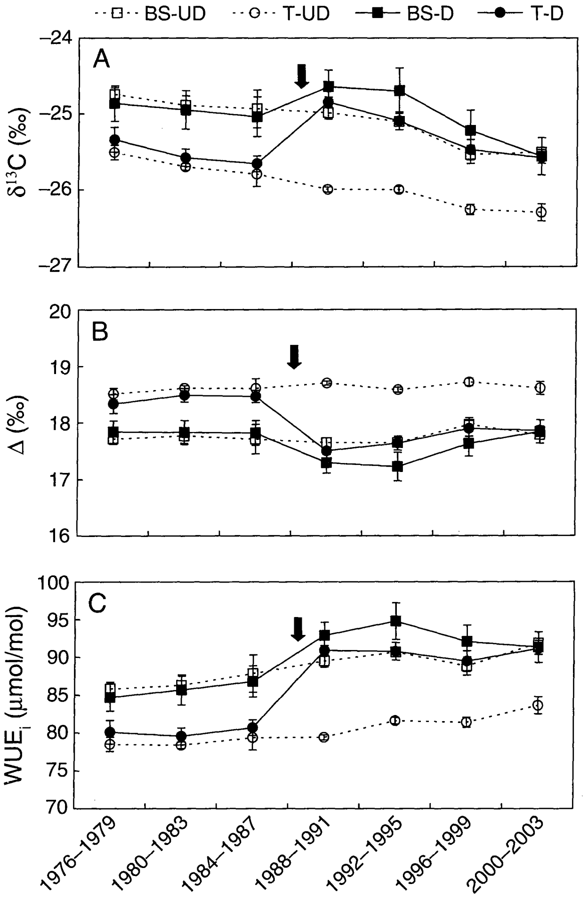

FIG. 2. Changes in (A) carbon isotope ratio, (B) carbon isotope discrimination, and (C) intrinsic water use efficiency in four-year tree ring bands in black spruce and tamarack between 1976 and 2003. Carbon isotope discrimination, Δ (in ‰), reflects differences in δ^{13}C between atmospheric CO_2 and plant C, as defined by Eq. 3.The drainage treatment was implemented in the fall of 1987, as indicated by the arrow. Vertical bars are standard errors of the means ($n = 3$). BS-UD, T-UD, BS-D, and T-D are black spruce in undrained plots, tamarack in undrained plots, black spruce in drained plots, and tamarack in drained plots, respectively.

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 δ^{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 δ^{15}N of annual rings showed a different pattern between the drained and undrained plots. In the undrained plots, while not statistically significant, δ^{15}N in tree rings showed a decreasing tendency over the last 28 years; δ^{15}N of black spruce decreased from −2.8‰ to −3.9‰ ($r^2 = 0.47$, $P = 0.013$) and that of tamarack decreased from −2.4‰ to −4.4‰ ($r^2 = 0.61$, $P = 0.11$; Fig. 3C). The δ^{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 δ^{15}N values significantly increased from −3.9‰ to −2.9‰ for black spruce and from −4.4‰ to −3.3‰ 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 δ^{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

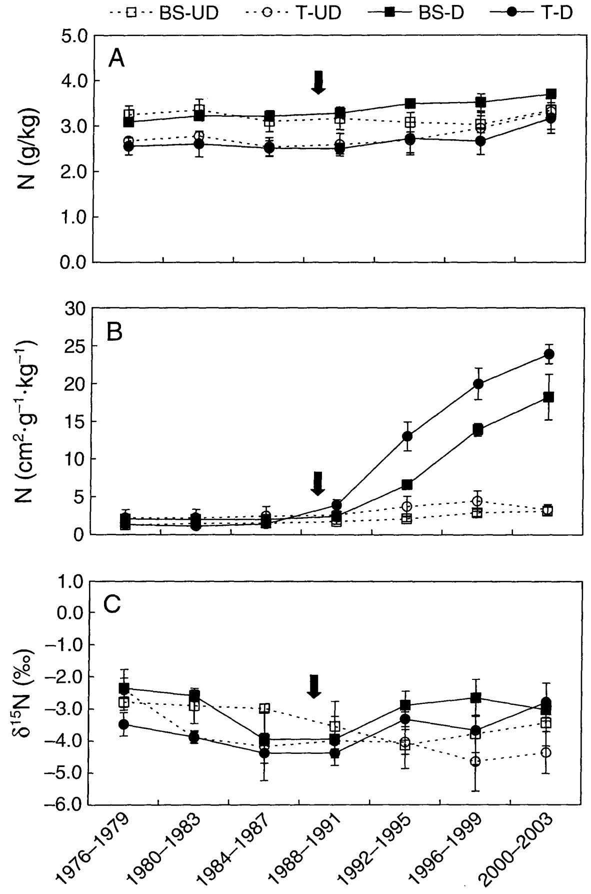

FIG. 3. Changes in (A) nitrogen concentration, (B) nitrogen concentration weighted by growth ring area, and (C) nitrogen isotope ratio in four-year tree ring bands in black spruce and tamarack between 1976 and 2003. The drainage treatment was implemented in the fall of 1987 as indicated by the arrow. Vertical bars are standard errors of the means ($n = 3$). BS-UD, T-UD, BS-D, and T-D are black spruce in undrained plots, tamarack in undrained plots, black spruce in drained plots, and tamarack in drained plots, respectively.

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 ^{15}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. 2005*a*). 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. (2005*a*), 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 N availability after drainage. Higher foliar N concentrations can increase photosynthetic enzyme activities responsible for CO_2 assimilation without causing a substantial change in stomatal conductance (Liu and Dickmann 1996, Korol et al. 1999, Livingston et al. 1999, Meinzer et al. 2004, Choi et al. 2005*a*).

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 $\delta^{13}C$, N concentrations, and $\delta^{15}N$ 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 retrospectively by examining $\delta^{13}C$ signals stored in tree rings. In the undrained plots, the decreasing pattern of $\delta^{13}C$ in tree rings with time can primarily be attributed to the increasing atmospheric CO_2 concentration via increased emission of anthropogenic CO_2 depleted in ^{13}C (Bert et al. 1997, Feng 1998, Choi et al. 2005*b*), as the Δ values were virtually unchanged throughout the period examined (Fig. 2B). In agreement with a general assumption that WUE increases under increasing atmospheric CO_2 concentration due to increases in carboxylation rate and decreases in stomatal conductance (Ehleringer and Cerling 1995, Bert et al. 1997, Choi et al. 2005*b*), WUE_i calculated in our study showed an increasing pattern, with some temporal variations in the drained plots (Fig. 2C).

In combination with improved tree growth (Fig. 1), changes in Δ and WUE_i (Fig. 2B, C) in tree rings formed between 1988 and 1991 clearly show drainage effects on gas exchange of both species. According to Eqs. 4 and 5, drainage can decrease Δ (or increase WUE_i) either by decreasing stomatal conductance or by increasing photosynthetic capacity, as both result in a lower C_i (Farquhar et al. 1989). Considering the improved radial growth of trees following drainage, however, an increase in photosynthetic capacity rather than a decrease in stomatal conductance was the most likely cause of the changed Δ and WUE_i after drainage (Islam et al. 2003). This is also supported by higher N concentrations in foliage (Table 3) and in tree rings weighted by ring area (Fig. 3B), as plants tend to decrease discrimination against ^{13}C under high nutrient (particularly N) availability (Korol et al. 1999, Livingston et al. 1999, Choi et al. 2005*a*). However, this explanation does not preclude the contribution of decreased stomatal conductance to greater WUE_i. In the future, the oxygen isotope ratio ($\delta^{18}O$) technique needs to be explored to evaluate whether stomatal limitations of gas exchange exist as $\delta^{18}O$ in plant tissues reflects evaporation, which is largely dependent on stomatal conductance. In addition to stomatal effects, plant tissue $\delta^{18}O$ is also susceptible to many other factors, such as the $\delta^{18}O$ of source water and isotopic fractionation during lignin synthesis (McCarroll and Loader 2004), as well as humidity and temperature.

With respect to the temporal variation of $\delta^{13}C$ in tree rings, the so-called tree size (or age) effect, a pattern of decreasing Δ (increasing $\delta^{13}C$) with tree development (Francey and Farquhar 1982) should be considered. Such effects are often considered to be related to water stress (stomatal limitation) caused by decreased hydraulic conductance (Fessenden and Ehleringer 2002, McDowell et al. 2002) or by increased foliage biomass or leaf area index (Munger et al. 2003) with increasing tree growth. In our study, however, there was no tree size effect in the undrained plots as indicated by the virtually same Δ values throughout the period examined. Hietz et al. (2005) suggested that the tree size effect is not always discernible. In the drained plots, however, it is more difficult to determine from our data whether there was tree size effect or not, and we cannot rule out the potential effect of tree size to the decreased Δ after drainage.

The differences in tree ring $\delta^{13}C$, Δ, and WUE_i 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 $\delta^{13}C$ and Δ data. For example, a significantly lower $\delta^{13}C$ 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). In spite of the initial effect of drainage on tree ring $\delta^{13}C$, Δ, and WUE_i 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 $\delta^{13}C$ data; black spruce had virtually the same $\delta^{13}C$ between the drained and undrained plots, while tamarack had a higher $\delta^{13}C$ 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 $\delta^{13}C$ signature in tamarack may be a sensitive and long-term surrogate for measuring changed environmental conditions in peatlands.

While statistically not significant, the $\delta^{15}N$ 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 $\delta^{15}N$ in tree rings of hemlock (*Tsuga canadensis*) over time to the increasing deposition of ^{15}N-depleted N compounds, and Peñuelas and Estiarte (1997) hypothesized that decreased N loss and increased N fixation and mineralization rates might explain the $\delta^{15}N$ 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 $\delta^{15}N$ variations across tree rings is not a straightforward matter. In our study, drainage tended ($P > 0.05$) to increase $\delta^{15}N$ in tree rings (Fig. 3C) similar to drainage effects on foliar $\delta^{15}N$ (Table 3). Such tendency suggests that drainage slowed or reversed the decreasing $\delta^{15}N$ pattern through supplying NH_4^+-N enriched with ^{15}N resulting from enhanced nitrification (Tables 1 and 2). However, before using $\delta^{15}N$ 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. 2005*b*) have suggested that the removal of the extractive N fraction in wood samples could remove the "noise" from the isotopic "signal" that reflects $\delta^{15}N$ 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_i 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 $\delta^{15}N$ variations in plant and soil samples. Specifically, drainage enhanced N mineralization and nitrification as indicated by higher NH_4^+ and NO_3^- concentrations, a higher $\delta^{15}N$ of NH_4^+, and a lower $\delta^{15}N$ of NO_3^- in the drained than in the undrained plots. The uptake of NH_4^+ enriched with ^{15}N by plants and the subsequent deposition of tree and understory litter was assumed to lead to increased $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ patterns reflected the processes that were altered by peatland drainage and the $\delta^{13}C$ and $\delta^{15}N$ techniques are useful tools for investigating the impact of environmental changes on C and N cycling in forested peatland ecosystems.

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LITERATURE CITED

Bert, D., S. W. Leavitt, and J. L. Dupouey. 1997. Variations of wood $\delta^{13}C$ and water-use efficiency of *Abies alba* during the last century. Ecology 78:1588–1596.

Bhatti, J. S., M. J. Apps, and H. Jiang. 2002. Influence of nutrients, disturbances and site conditions on carbon stocks along a boreal forest transect in central Canada. Plant and Soil 242:1–14.

Bremner, J. M. 1996. Nitrogen—total. Pages 1085–1121 *in* D. L. Sparks, editor. Methods of soil analysis. Part 3. Chemical methods. Soil Science Society of America, Madison, Wisconsin, USA.

Chang, S. X., and L. L. Handley. 2000. Site history affects soil and plant ^{15}N natural abundances ($\delta^{15}N$) in forests of northern Vancouver Island, British Columbia. Functional Ecology 14:273–280.

Choi, W. J., and S. X. Chang. 2005. Nitrogen dynamics in co-composted drilling wastes: effects of compost quality and ^{15}N fertilization. Soil Biology and Biochemistry 37:2297–2305.

Choi, W. J., S. X. Chang, H. L. Allen, D. L. Kelting, and H. M. Ro. 2005*a*. Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. Forest Ecology and Management 213:90–101.

Choi, W. J., S. M. Lee, S. X. Chang, and H. M. Ro. 2005*b*. Variations of $\delta^{13}C$ and $\delta^{15}N$ in *Pinus densiflora* tree-rings and their relationship to environmental changes in eastern Korea. Water, Air, and Soil Pollution 164:173–187.

Choi, W. J., and H. M. Ro. 2003. Differences in isotopic fractionation of nitrogen in water-saturated and unsaturated soils. Soil Biology and Biochemistry 35:483–486.

Ehleringer, J. R., and T. E. Cerling. 1995. Atmospheric CO_2 and the ratio of intercellular to ambient CO_2 concentrations in plants. Tree Physiology 15:105–111.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40: 503–537.

Feast, N. A., and P. E. Dennis. 1996. A comparison of methods for nitrogen isotope analysis of groundwater. Chemical Geology 129:167–171.

Feng, X. 1998. Long-term c_i/c_a response of trees in western North America to atmospheric CO_2 concentration derived from carbon isotope chronologies. Oecologia 117:19–25.

Fessenden, J. E., and J. R. Ehleringer. 2002. Age-related variations in $\delta^{13}C$ of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. Tree Physiology 22:159–167.

Francey, R. J., and G. D. Farquhar. 1982. An explanation of $^{13}C/^{12}C$ variations in tree rings. Nature 297:28–31.

Gorham, E. 1995. The biogeochemistry of northern peatlands and its possible response to global warming. Pages 169–187 *in* G. M. Woodwell and F. T. Mackenzie, editors. Biotic feedbacks in the global climatic system. Oxford University Press, Oxford, UK.

Hart, S. C., and A. T. Classen. 2003. Potential for assessing long-term dynamics in soil nitrogen availability from variations in $\delta^{15}N$ of tree rings. Isotopes in Environmental and Health Studies 39:15–28.

Hauck, R. D. 1982. Nitrogen-isotope ratio analysis. Pages 735–779 *in* A. L. Page, editor. Methods of soil analysis. Part 2. Chemical and microbiological properties. Soil Science Society of America, Madison, Wisconsin, USA.

Hietz, P., W. Wanek, and O. Dünisch. 2005. Long-term trends in cellulose $\delta^{13}C$ and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. Tree Physiology 25:745–752.

Hillman, G. R. 1997. Effects of engineered drainage on water tables and peat subsidence in an Alberta treed fen. Pages 253–272 *in* C. C. Trettin, M. F. Jurgensen, D. F. Grigal, M. R. Gale, and J. K. Jeglum, editors. Northern forested wetlands: ecology and management. CRC Lewis, Boca Raton, Florida, USA.

Högberg, P., and C. Johannisson. 1993. ^{15}N abundance of forests is correlated with losses of nitrogen. Plant and Soil 157:147–150.

Islam, M. A., and S. E. Macdonald. 2004. Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. Trees—Structure and Function 18:35–42.

Islam, M. A., S. E. Macdonald, and J. J. Zwiazek. 2003. Responses of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) to flooding and ethylene. Tree Physiology 23: 545–552.

Karamanos, R. E., and D. A. Rennie. 1981. The isotope composition of residual fertilizer nitrogen in soil columns. Soil Science Society of America Journal 45:316–321.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Pages 643–698 *in* A. L. Page, editor. Methods of soil analysis. Part 2. Chemical and microbiological properties. Soil Science Society of America, Madison, Wisconsin, USA.

Korol, R. L., M. U. F. Kirschbaum, G. D. Farquhar, and M. Jeffereys. 1999. Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. Tree Physiology 19:551–562.

Lieffers, V. J., and S. E. Macdonald. 1990. Growth and foliar nutrient status of black spruce and tamarack in relation to depth of water table in some Alberta peatlands. Canadian Journal of Forest Research 20:805–809.

Lieffers, V. J., and R. L. Rothwell. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Canadian Journal of Botany 65:817–821.

Liu, Z., and D. I. Dickmann. 1996. Effects of water and nitrogen interaction on net photosynthesis, stomatal conductance, and water-use efficiency in two hybrid poplar clones. Physiologia Plantarum 97:507–512.

Livingston, N. J., R. D. Guy, and G. J. Ethier. 1999. The effects of nitrogen stress on the stable carbon isotope composition, productivity and water use efficiency of white spruce (*Picea glauca* (Moench) Voss) seedling. Plant, Cell and Environment 22:281–289.

Loader, N. J., I. Robertson, and D. McCarroll. 2003. Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. Palaeogeography, Palaeoclimatology, Palaeoecology 196:395–407.

Macdonald, S. E., and V. J. Lieffers. 1990. Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. Canadian Journal of Forest Research 20:995–1000.

Macdonald, S. E., and F. Yin. 1999. Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth. Journal of Ecology 87: 404–412.

Mariotti, A., J. C. Germon, P. Hubert, P. Kaiser, R. Letolle, A. Tardieux, and P. Tardieux. 1981. Experimental determination of nitrogen kinetic isotope fractionation: some principles; illustration for the denitrification and nitrification processes. Plant and Soil 62:423–430.

McCarroll, D., and N. J. Loader. 2004. Stable isotopes in tree rings. Quaternary Science Reviews 23:771–801.

McDowell, N. G., N. Phillips, C. Lunch, B. J. Bond, and M. G. Ryan. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiology 22:763–774.

Meinzer, F. C., D. R. Woodruff, and D. C. Shaw. 2004. Integrated response of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. Plant, Cell and Environment 27:937–946.

Moore, T. R., N. T. Roulet, and J. M. Waddington. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. Climate Change 40: 229–245.

Mugasha, A. G., D. J. Pluth, and G. R. Hillman. 1993. Foliar responses of tamarack and black spruce to drainage and fertilization of a minerotrophic peatland. Canadian Journal of Forest Research 23:166–180.

Mugasha, A. G., D. J. Pluth, and S. E. Macdonald. 1999. Effects of fertilization on seasonal patterns of foliar mass and nutrients of tamarack and black spruce on undrained and drained minerotrophic peatland sites. Forest Ecology and Management 116:13–31.

Munger, G. T., R. E. Will, and B. E. Borders. 2003. Effects of competition control and annual nitrogen fertilization on gas exchange of different-aged *Pinus taeda*. Canadian Journal of Forest Research 33:1076–1083.

Paavilainen, E., and J. Päivänen. 1995. Peatland forestry: ecology and principles. Springer Verlag, Berlin, Germany.

Peñuelas, J., and M. Estiarte. 1997. Trends in plant carbon concentration and plant demand for N throughout this century. Oecologia 109:69–73.

Poulson, S. R., C. P. Chamberlain, and A. J. Friedland. 1995. Nitrogen isotope variation of tree rings as a potential indicator of environmental change. Chemical Geology 125: 307–315.

Regina, K., H. Nykänen, J. Silvola, and P. J. Martikainen. 1996. Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity of the peat. Biogeochemistry 35:401–418.

Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends in Ecology and Evolution 16:153–162.

Shepard, P. R., and T. L. Thompson. 2000. Effect of extraction pretreatment on radial variation of nitrogen concentration in tree rings. Journal of Environmental Quality 29:2037–2042.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Publication 1646 (Revised). Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.

Strong, W. L., and G. H. La Roi. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Canadian Journal of Forest Research 13:1164–1173.

Tian, G. B., L. Brussaard, and B. T. Kang. 1995. An index for assessing the quality of plant residues and evaluating their effects on soil and crop in the (sub-) humid tropics. Applied Soil Ecology 2:25–32.

Updegraff, K., J. Pastor, S. D. Bridgeham, and C. A. Johnston. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications 5:151–163.

van Cleve, K., W. C. Oechel, and J. L. Hom. 1990. Response of black spruce (*Picea mariana*) ecosystems to soil temperature modifications in interior Alaska. Canadian Journal of Forest Research 20:1530–1535.

Varem-Sanders, T. M. L., and I. D. Campbell. 1996. DendroScan: a tree-ring width and density measurement system. Northern Forest Research Center Special Report 10. Canadian Forest Research Service, Edmonton, Alberta, Canada.

Warren, C. R., J. F. McGrath, and M. A. Adams. 2001. Water availability and carbon isotope discrimination in conifers. Oecologia 127:476–486.

Westman, C. J., and R. Laiho. 2003. Nutrient dynamics of drained peatland forests. Biogeochemistry 63:269–298.

Wieder, R. K. 2001. Past, present, and future peatland carbon balance: an empirical model based on ^{210}Pb-dated cores. Ecological Applications 11:327–342.