Trees (2007) 21:479–490
DOI 10.1007/s00468-007-0142-2

ORIGINAL PAPER

Temporal variation of $\delta^{13}C$ of larch leaves from a montane boreal forest in Mongolia

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Received: 20 August 2006 / Revised: 22 January 2007 / Accepted: 25 April 2007 / Published online: 12 June 2007
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Abstract This paper reports the temporal variation (2002–2004) in foliar $\delta^{13}C$ values, which are indicative of long-term integrated photosynthetic and water use characteristics, of Siberian larch (*Larix sibirica* Ledeb.) trees in a montane forest at Mongonmorit, NE Mongolia. At the stand, the $\delta^{13}C$ value for understory shaded leaves was more negative by 2‰ on average than that for sunlit leaves sampled concurrently from open and sun-exposed environments in a forest gap. The $\delta^{13}C$ value of both sunlit and shaded leaves showed pronounced intra- but relatively small inter-seasonal variations. The $\delta^{13}C$ value was more positive for juvenile than mature leaves. We conjecture that juvenile leaves may derive carbon reserves in woody tissues (e.g., stems). Regardless of leaf habitats, the $\delta^{13}C$ value was also affected by insect herbivores occurred in mid summer of 2003, being more negative in newly emerging leaves from the twigs after defoliation than in non-defoliated mature leaves. This pattern seems to contrast with that for the juvenile leaves in the early growing season. We surmise that the newly emerging leaves used stored organic carbon that was depleted due to fractionation during remobilization and translocation for leaf regrowth. There was also intra- and inter-seasonal variation in the foliar N concentrations and C:N ratios. A good positive (negative) correlation between the foliar $\delta^{13}C$ values and N concentrations (C:N ratios) was also observed for both sunlit and shaded leaves, suggesting that the relationship between water and nitrogen use is a crucial factor affecting the plant carbon–water relationship in this mid latitude forest with a cold semiarid climate. Our isotopic data demonstrate that the larches in NE Mongolia exhibits relatively higher water use efficiency with a distinct within-season variability.

Keywords *Larix sibirica* · $\delta^{13}C$ · Foliar nitrogen · Water use efficiency · Insect herbivore · Cold semiarid ecosystem

Communicated by H. Rennenberg.

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Introduction

The larch, also known as the *Larix*, a genus of Pinaceae, is composed of ten species (Farjon 1990). They are deciduous conifers, can grow 15–50 m tall, and prefer habitats with well-drained and well-lit conditions (Gower and Richards 1990). Larches are widely distributed in the cold temperate and boreal forests at high altitudes in the Northern Hemisphere (Farjon 1990). In the boreal (taiga) forests of Siberia and Mongolia, Siberian larch (*Larix sibirica* Ledeb.) is

among the dominant plants (Hilbig 1995; Schulze et al. 1995).

Stable isotopic technique is very useful in exploring ecosystem processes (Ehleringer et al. 2002). Plants discriminate against ^{13}C during photosynthesis, leading to more negative isotopic composition in plant tissue than in the atmosphere (Farquhar et al. 1989a; Ehleringer et al. 2002). The isotope discrimination occurs as a result of the higher stomatal diffusion of atmospheric $^{12}CO_2$ to the chloroplasts than $^{13}CO_2$ and the preferential enzymatic carboxylation of Rubisco for $^{12}CO_2$ over $^{13}CO_2$ (Farquhar et al. 1989a). Since carbon isotope discrimination is highly correlated with water use by plants, the carbon isotopic composition ($\delta^{13}C$) of plant tissue is often used as a surrogate for evaluating plant water use efficiency (WUE) (Farquhar et al. 1989b).

Previous isotopic studies have demonstrated that larches (*Larix* spp.) use water less efficiently than sympatric evergreen conifers (Gower and Richards 1990; Marshall and Zhang 1994; Kloeppel et al. 1998). Kloeppel et al. (1998) found that the difference in WUE of deciduous larches and co-occurring evergreen conifers disappears at elevations higher than 3,000 m. They also found that larches have higher leaf nitrogen concentrations and photosynthetic capacity in comparison to co-occurring evergreen conifers. Their study is focused on the spatial investigation into the water relations of the *Larix* from 20 locations in the Northern Hemisphere, not on the temporal dynamics of the water use by larches. On the other hand, the correspondence between WUE and $\delta^{13}C$ of larches is highly dependent on ecotypes or population differences (Marshall and Zhang 1994; Zhang and Marshall 1994; Zhang et al. 1994).

In Mongolia, larch dominated taiga forests occur mainly in the northern mountain areas (Hilbig 1995). Since they belong to the southern margin of the immense Siberian taiga forest and are adjacent to the extensive Asian steppe, the Mongolian taiga forests are expected to be highly sensitive to the influences from environmental changes and anthropogenic activities (Chuluunbaatar 2002). On the other hand, they provide considerable ecological service for biodiversity conservation, regional climate regulation as well as sustainable development in the country (Batjargal and Enkhbat 1998). However, ecosystem functional processes for the Mongolian taiga forests are very poorly understood to date. Previous research suggests an increasing trend of annual mean temperature and summer precipitation in NE Mongolia as evidenced by meteorological records (Dagvadorj and Mijiddorj 1996) and dendrochronological data (Pederson et al. 2001). Rising temperatures and increased precipitation may be favorable to carbon fixation by taiga forests, leading probably to improved water use efficiency (Saurer et al. 2004). A recent investigation into a *Larix sibirica* forest in NE Mongolia have shown that this larch forest functions as a sink for the atmospheric CO_2, and temperature is one of the most important abiotic variables in controlling the sink strength (Li et al. 2005). During the growing season, larch trees primarily use water from the top 30 cm of the soil after the rainfall events. However, they can also use water at deeper soil layers when topsoil water becomes scarce, as evidenced by the ^{18}O signatures of plant and soil water (Li et al. 2006). This indirectly suggests that water is not the limiting resource for the Mongolian larch forest (Li et al. 2006). It is consistent with the result based on the ^{13}C investigation into the larches by Kloeppel et al. (1998). However, the relationship between tree growth and water use has not only intra- but also inter-seasonal variations with respect to water availability and temperature. An analysis of leaf ^{13}C signatures in larch trees may provide such information since the $\delta^{13}C$ values of plant tissue are a time-integrated measure of plant responses to temporal changes in the environment over the course of the tissue formation (Farquhar et al. 1989a).

Up until now, there is no field data available to describe temporal changes in the $\delta^{13}C$ value of Mongolian larch forest. Therefore, this study was designed to explore whether there is inter- and intra-seasonal variation in foliar $\delta^{13}C$ values of the *Larix sibirica* forest in NE Mongolia. To this end, we measured the $\delta^{13}C$ values of different carbon pools from the forest, including sunlit and shaded leaves of larch trees, larch leaf litter, bulk aboveground litter, and soil organic matter. We made following comparisons: (1) the within- and between-year variation in the leaf $\delta^{13}C$ value of larch trees; (2) the within-canopy variation in the $\delta^{13}C$ value from different carbon pools; and (3) the differences between sunlit versus shaded leaves with respect to leaf development. We also discussed the $\delta^{13}C$ values of newly emerging leaves from twigs after insect herbivores (defoliation effect).

Materials and methods

Site information

The study was conducted within a montane larch forest stand in the Tov province of Mongolia (lat. 48°21.112′N, long. 108°39.260′E, 1630 m a.s.l.). The site was located on a gently southwest facing slope and was used for studies of eco-hydrological processes of the forest (Li et al. 2005). The study area belongs to a cold semiarid continental climate with the mean annual precipitation of 296 mm and the mean annual temperature of –2.7°C (10-year period between 1993 and 2002), reported by the nearest Mongonmorit Weather Station, about 25 km south-west of the study site. The soil is a spodosol (seasonal cryosol). The

vegetation was dominated by Siberian larch (*Larix sibirica* Ledeb.), which mixed with scattered or patchy white birch (*Betula platyphylla* Sukach.) in some places. The mean stand height was about 20 m. The projected leaf area index (LAI) of overstory canopy (larch) was 2.7. The understory was dense and formed a distinct layer of grasses and scattered shrubs, with the maximum LAI of 1.7. The background micrometeorological conditions including air temperature and precipitation were monitored by a 30 m iron tower at the site (Li et al. 2005). Precipitation during the leaf-out period at the tower site was not available and instead precipitation observed at the Mongonmorit Weather Station was used. Additional details about the study site are presented elsewhere (Li et al. 2005, 2006).

Sample collection and processing

Ten individual larch trees with breast height diameter greater than 10 cm were randomly selected and tagged in the forest stand in September 2002 for collecting leaf samples. These trees had ground reachable branches. Among them, five trees (one was logged down in summer of 2004) located within about 50 m close to the tower, were used for collecting shaded leaves. The other five trees, located in an open high light area (gap) about 150 m away from the tower, were used for collecting fully sunlit leaves from exposed south-facing branches, a surrogate for the overstory canopy sunlit larch leaves because they were not easily accessed. The gap was formed by forest fire and subsequent logging in the past. Both sunlit and shaded leaf cohorts were collected from several branches on each tagged tree at around 2–3 m height above the ground. The leaf samples were collected on seven occasions (26 September 2002, 11 June 19 July 19 August and 29 September 2003, and 27 May and 29 July 2004). Because of the international outbreak of severe acute respiratory syndrome (SARS), we were unable to collect samples during the leaf outburst period in May 2003. On 11 June 2003, previous year leaf litterfall (sunlit plus shaded leaves), and bulk aboveground litterfall (including old and new leaf fall of overstory trees and understory grasses and shrubs, and small woody debris) were also collected from the forest floor. On 30 September 2003, leaf samples from three understory plants: sedges (*Carex spp.*), fireweed (*Chamaenerion angustifolium* L.), and shrubby cinquefoil (*Potentilla fruticosa* L.) were collected. Leaves were collected from a couple of individuals of each plant and then combined into one samples.

The Siberian silk moth or larch caterpillar (*Dendrolimus sibiricus* Tschetverikov) feeds on the leaves of larch trees, and is the major pest affecting larch growth. A pest outbreak occurred in July 2003, causing defoliation on most trees scatteredly distributed at the transitional area between forest and adjacent steppe. One of our five tagged larches in the forest stand for sunlit leaf collection was severely defoliated by the larch caterpillar, leading to almost no intact leaves being retained on the tree. This tree was thus not included in computing the mean $\delta^{13}C$ values in August and September of 2003. On our August field trip, however, we found that new leaves emerged from insect-defoliated trees. Thus, we collected newly emerging leaf samples from above two tagged trees in August and September of 2003 in order to find the foliar $\delta^{13}C$ variation after the pest outbreak. On 19 August and 30 September 2003, both old and newly emerging sunlit leaf samples were also taken from the same branch (tagged) on one of the scattered larch trees at the forest-steppe transitional area. The branch-tagged larch on the transitional area was partially defoliated.

Three sets (replicas) of soil profile samples (5–6 m apart) were collected in June 2003 from five depths (0–2, 2–5, 5–10, 10–20, and 20–30 cm), close to the tower. To reduce spatial heterogeneity, the soil at each depth for one set of samples was collected from three to five cores (holes, about 0.5–1.0 m apart) using a soil corer (6 cm in diameter). After collection, the core samples were mixed, and passed through a 2-mm sieve on the spot to exclude live plant materials and un-decomposed litter.

Soil samples were oven-dried at 105°C for three days in the lab while plant samples were air-dried in the field and then oven-dried in the lab at 65°C for three days. Coarse grinding was done for the soil samples with a mortar and pestle. Leaf samples were frozen using liquid nitrogen and then ground by hand to a fine powder with the mortar and pestle. Both the soil and plant samples were sifted with the 425 μm mesh sieve, and then sealed in glass vials prior to isotope analyses. In order to remove inorganic carbonate carbon, soil samples were treated with 1 N HCl at 25°C for one to three days and then rinsed with distilled water. Subsamples (about 2 mg for leaf samples, and 2–15 mg for soil samples depending on depths) were placed in tin capsules (Universal tin container, Thermoquest Italia SPA, Rodano, Milan, Italy). They were prepared for determination of carbon isotopic composition ($\delta^{13}C$), mass-based carbon (C) concentration, and mass-based nitrogen (N) concentration (N_{mass}) using an isotope ratio mass spectrometer (Finnigan MAT delta S, Bremen, Germany) coupled with an elemental analyzer (Carlo Erba EA1108 elemental analyzer, Fisons Instruments, Danvers, MA, USA) at the Center for Ecological Research, Kyoto University, Japan. Precision of individual measurement on the spectrometer was ±0.15‰ for $\delta^{13}C$.

Isotopic and elemental analyses

The $\delta^{13}C$ value was calculated as the molar ratio of the carbon isotopic composition of the sample (R_{sample}) to that

of the Pee Dee Belemnite (PDB) carbonate standard ($R_{standard}$), and expressed in parts per thousand (‰):

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1,000 \quad (1)$$

A positive (negative) $\delta^{13}C$ value indicates the enrichment (depletion) of the heavy isotope relative to the light one according to a known standard.

Leaf carbon isotopic discrimination (Δ_{leaf}, in ‰) can be described as (Farquhar et al. 1989a):

$$\Delta_{leaf} = \frac{\delta_{atm} - \delta_{leaf}}{1 + \delta_{leaf}/1000}, \quad (2)$$

where δ_{atm} is the isotopic composition of the atmosphere (typically –8‰), and δ_{leaf} is that of the leaves. There exists the relationship between isotope discrimination and intercellular CO_2 of leaves of C_3 plants (Farquhar et al. 1982, 1989a):

$$\Delta_{leaf} = a + (b - a)\frac{c_i}{c_a}, \quad (3)$$

where a is the discrimination caused by CO_2 diffusion in air (4.4‰), b is the net discrimination associated with enzymatic carboxylation processes (mainly discrimination by Rubisco, approximately 27‰), c_i is the intercellular CO_2 concentration, and c_a is the atmospheric CO_2 concentration.

The relationship between instantaneous water use efficiency (WUE) and Δ_{leaf} can be illustrated by (Farquhar et al. 1982, 1989b):

$$WUE = \frac{A}{E} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6\upsilon}, \quad (4)$$

where A is the assimilation rate, E is the transpiration rate, υ is the water vapor concentration difference outside and inside the leaf, and 1.6 is the ratio of diffusion coefficients of water vapor and CO_2 molecules in air. Equations 3 and 4 show that WUE and Δ_{leaf} are correlated to each other, and both are a linear function of c_i/c_a. WUE is positively related to $\delta^{13}C$ and negatively related to Δ_{leaf} as implied from Eqs. 3 and 4.

Statistical analyses

Within- and across-year differences between two groups were compared using the t test when the sample size was the same and the Mann–Whitney U-test when the sample size was not equal (Sokal and Rohlf 1995). Linear regression and Pearson product–moment correlation analyses were conducted between the studied variables. The linear regressions were conducted with average values.

Results

Temporal variations of $\delta^{13}C$, N concentration and C:N ratio of larch leaves

The intra- and inter-seasonal trends of the $\delta^{13}C$ were quite similar for both sunlit and shaded leaves (Fig. 1a). Sunlit leaves exhibited consistently higher (2.0‰ on average) $\delta^{13}C$ values than shaded leaves throughout the measurement period ($n = 6$, $P < 0.05$). The $\delta^{13}C$ values decreased from June through September in 2003 with an intra-seasonal variation of 2.8‰ (ranging between –25.8 and –23.0‰) for sunlit leaves and 1.9‰ for shaded leaves (ranging between –27.1 and –25.2‰), respectively. Both

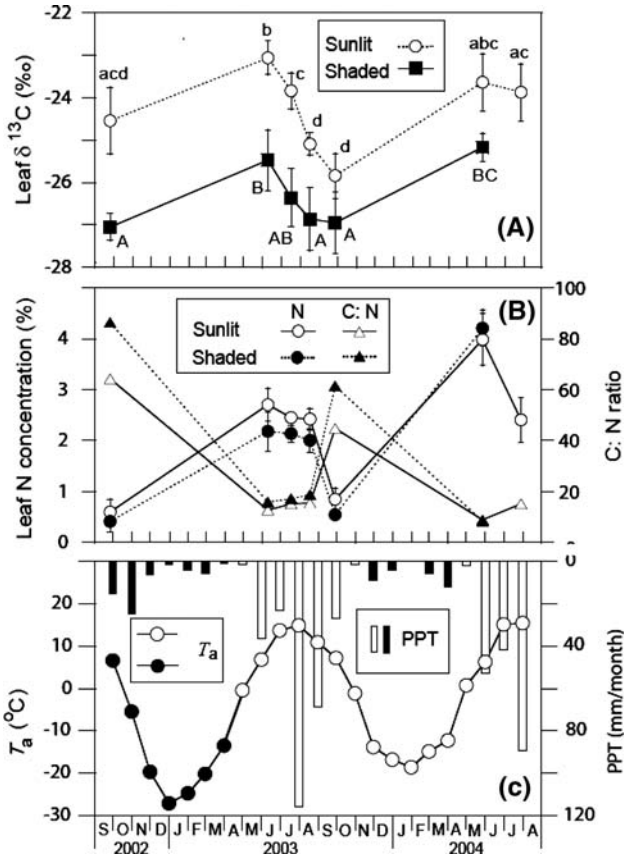

Fig. 1 The temporal courses of (**a**) the mean $\delta^{13}C$ values (**b**) mass-based N concentration (N_{mass}) and C:N ratio of larch leaves, and (**c**) air temperature and precipitation in a Siberian larch forest in NE Mongolia. *Vertical bars* represent ±1 SD of the mean (n = 4–5). *Lowercase* (*uppercase*) letters beside the means in (**a**) indicate statistical differences among the means for sunlit (*shaded*) leaves at the level of $\alpha = 0.05$. *Solid symbols* in (**c**) denote that the data are from the Mongonmorit Weather Station

sunlit and shaded leaves had significantly higher $\delta^{13}C$ values in June than in other months (Fig. 1a, $P < 0.05$). By examining the foliar $\delta^{13}C$ values of the same month in different years, we found that there was no significant across-year difference (e.g., September 2002 vs. September 2003 for both sunlit and shaded leaves, and July 2003 vs. July 2004 for sunlit leaves) (Fig. 1a, $P > 0.05$).

In comparison with their intra- and inter-seasonal trends of the $\delta^{13}C$, sunlit and shaded leaves showed a similar temporal variation pattern for mass-based N concentration (N_{mass}), but an opposite pattern for C:N ratios (Fig. 1b). Higher values of N_{mass} consistently corresponded to lower C:N ratios for both sunlit and shaded leaves. Although not statistically significant ($P > 0.05$), in most occasions, N_{mass} was higher in sunlit than shaded leaves whereas C:N ratios were slightly lower in the sunlit than shaded leaves. N_{mass} had a large intra- and inter-seasonal (ranging between 0.4 and 4.2%) variation for both sunlit and shaded leaves. Alike, the C:N ratios varied substantially from 8.3 to 86.4 during the sampling period. During the 2003 growing season, for both sunlit and shaded leaves, N_{mass} decreased slightly throughout summer from June to August and precipitously from August to September, and thus it was significantly lower in September than in other months (Fig. 1b, $P < 0.05$). A comparison of N_{mass} in larch leaves between August and September displays that a large proportion of N (approximately 65% for sunlit leaves and 73% for shaded leaves, respectively) was allocated to other plant tissues (e.g., the bark of stems or roots) in response to leaf senescence. The C:N ratios were relatively stable (only slightly increasing with time) in the early growing season, but a considerable increase occurred in the later growing season. Contrary to the within-season variation of N_{mass}, the C:N ratios were significantly higher in September than in other months (Fig. 1b, $P < 0.05$).

At the site, the growing season (roughly from May through September, Li et al. 2005) is in phase of the rainy season. Precipitation during the growing season was 230 mm in 2002 (measured at the Mongonmorit Weather Station), 271 mm in 2003, and 256 mm in 2004, respectively (shown partially in Fig. 1c). The rainy season is also in phase of the warmer season as indicated by air temperature (Fig. 1c).

Correlation between $\delta^{13}C$ values and N concentration in larch leaves

For both sunlit and shaded leaves, the mean $\delta^{13}C$ values were highly correlated with their respective mean N_{mass} or mean C:N ratios. The Pearson product–moment correlation coefficient (r) between $\delta^{13}C$ values and N_{mass} was 0.654 for sunlit leaves, and 0.855 for shaded leaves, respectively. The r between $\delta^{13}C$ values and C:N ratios was –0.562 for sunlit leaves, and –0.717 for shaded leaves, respectively. For both sunlit and shaded leaves, the regression analyses suggest that the $\delta^{13}C$ values increased with an increase of N_{mass} (Fig. 2a), and decreased with an increase of C:N ratio (Fig. 2b). The slope of $\delta^{13}C$ against N_{mass} plot indicates that a 1% increase of N_{mass} will yield a decrease of the $\delta^{13}C$ value by 0.54‰ for sunlit leaves, and by 0.50‰ for shaded leaves, respectively. Similarly, the slope of the $\delta^{13}C$ versus C:N ratio regression shows that an increase of the C:N ratio by 10 will yield a decrease of the $\delta^{13}C$ value by 0.26‰ for sunlit leaves, and by 0.18‰ for shaded leaves, respectively.

Vertical $\delta^{13}C$ stratification within the forest stand

The mean $\delta^{13}C$ values of soil organic matter (SOM) showed an increasing trend with depth from –26.8 ± 0.4

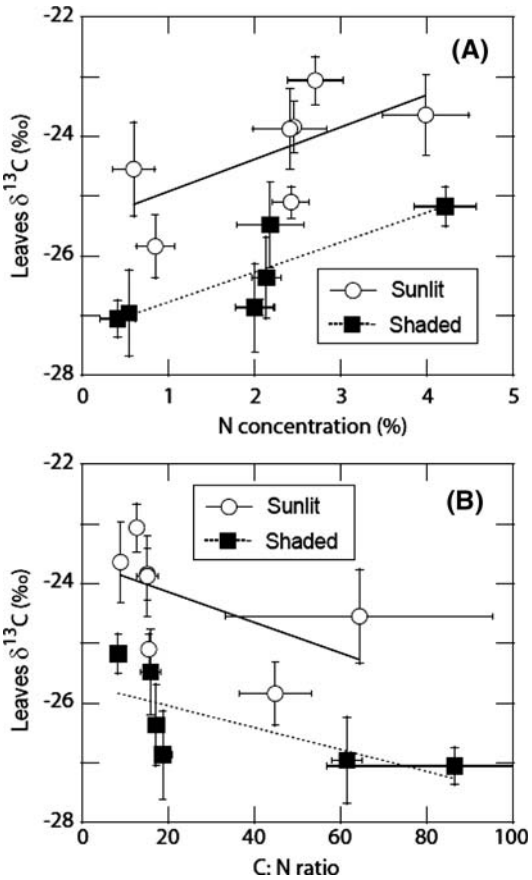

Fig. 2 Relationships (**a**) between foliar $\delta^{13}C$ values and mass-based N concentration (N_{mass}), and (**b**) between foliar $\delta^{13}C$ values and C:N ratios of the larch trees in a Siberian larch forest in NE Mongolia. The linear regression was fitted to the data: **a** $y = 0.539x–25.46$ for sunlit leaves ($n = 7$, adjusted $R^2 = 0.314$, $F = 3.74$, and $P = 0.111$ for the slope), and $y = 0.501x–27.27$ for shaded leaves ($n = 6$, adjusted $R^2 = 0.664$, $F = 10.9$, and $P = 0.030$ for the slope); **b** $y = –0.026x–23.63$ for sunlit leaves ($n = 7$, adjusted $R^2 = 0.179$, $F = 2.31$, and $P = 0.189$ for the slope), and $y = –0.018x–25.68$ for *shaded leaves* ($n = 6$, adjusted $R^2 = 0.392$, $F = 4.22$, and $P = 0.109$ for the slope)

SD‰ at 0–2 cm to –24.8 ± 0.4 SD ‰ at 20–30 cm, but this increase was not statistically significant beneath the depth of 2 cm ($P > 0.05$) (Fig. 3a). The mean $\delta^{13}C$ values of fresh leaf litter fallen in the previous year were significantly greater than those of bulk aboveground litter ($P = 0.0043$), indicating a strong isotopic influence from understory shrubs and grasses, which had more negative $\delta^{13}C$ values than larch trees. For example, the mean $\delta^{13}C$ value of mature leaves (–28.8 ± 0.5 SD‰) of three understory species sampled in September of 2003 was 1.8‰ lower than that (–27.0 ± 0.7 SD‰) of the understory shaded larch leaves, and 3.0‰ lower than that (–25.8 ± 0.5 SD ‰) of the sunlit larch leaves ($P < 0.01$). The 0–2 cm SOM had a mean $\delta^{13}C$ value very similar to the average (–26.9 ± 0.3 SD ‰) of the bulk aboveground litter ($P = 0.734$), indicating their close correlation. Juvenile larch leaves collected in mid June 2003 showed significantly higher $\delta^{13}C$ values than the bulk aboveground litter and the 0–2 cm SOM ($P < 0.05$). For example, relative to the 0–2 cm SOM, sunlit juvenile larch leaves were enriched with ^{13}C by approximately 3.8‰ at the stand (Fig. 3a). Assuming the bulk aboveground litter was simply composed of leaf fall from overstory larches and understory grasses and shrubs in the end of growing season (late September), an estimate with a simple two-end number model suggests that approximately 63% of the bulk aboveground litter was from overstory larches, and the remaining 37% was from the understory plant species.

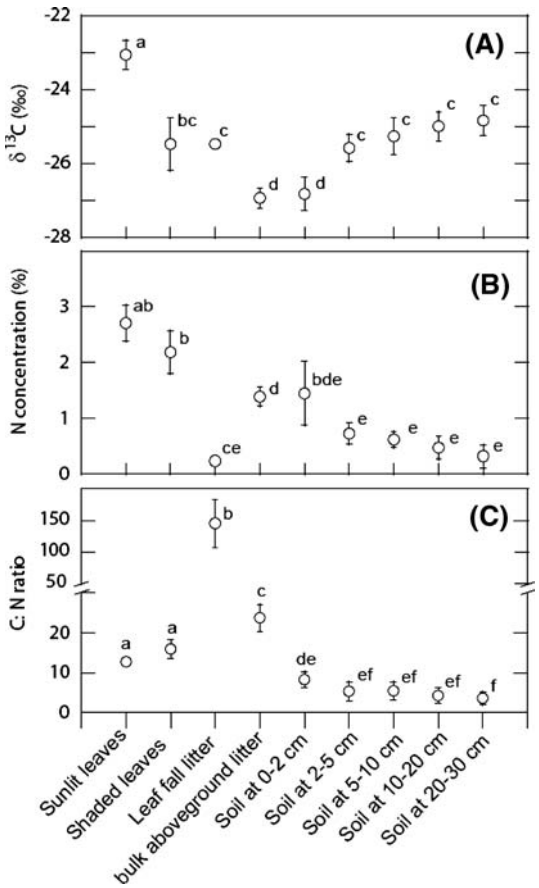

Fig. 3 The $\delta^{13}C$ values (**a**), mass-based N concentration (N_{mass}) (**b**), and C:N ratios (**c**) of larch leaves, larch leaf litter, bulk aboveground litter, and soil organic matter in 11 June 2003 for a Siberian larch forest in NE Mongolia. *Vertical bars* represent ±1 SD of the mean ($n = 3$–5). *Different lowercase letters* above the means represent significant differences among the group means at the level of $\alpha = 0.05$

Larch leaf litter fallen in the previous year had much lower N_{mass} than juvenile leaves of the current year ($P < 0.05$), but was not significantly different from the sunlit or shaded leaves collected in late September ($P = 0.074$) (Fig. 3b). Juvenile larch leaves had significantly higher N_{mass} than litter and SOM. There was a decreasing trend of N_{mass} with increasing soil depth although not statistically significant (Fig. 3b).

At the site, litterfall, especially the leaf litter of larch fallen in the previous year, had significantly higher C:N ratios than juvenile larch leaves and SOM ($P < 0.05$) (Fig. 3C). The change in C:N ratio with soil depth was relatively minor, and only the C:N ratios in the 0–2 cm layer were significantly ($P < 0.05$) greater than those in 20–30 cm soil layer (Fig. 3c). As expected, the C:N ratios in any plant tissue were significantly higher than those in the SOM.

Effect of insect herbivores

Both in the forest gap and in the transitional area, the newly emerging larch leaves had more negative $\delta^{13}C$ values than the leaves that were attacked by insects (Table 1). The differences in the $\delta^{13}C$ values between these two types of leaves were more pronounced in the transitional area (2.5–4.0‰) than in the forest gap (1.9–2.2‰) (Table 1). The lowest $\delta^{13}C$ value (–28.7‰) was observed in late September of 2003 in newly emerging leaves of scattered larch trees in the transitional area, about 4‰ lower than mature leaves on the same branch that were not defoliated by the insect (Table 1).

Interestingly, N_{mass} of newly emerging leaves after defoliation appeared to vary little as compared to those that were not affected by the insect herbivores (Table 1).

Discussion

Temporal variation and leaf development

Both sunlit and shaded leaves from *Larix sibirica* growing in the montane area in NE Mongolia showed a large degree of variation (up to 2‰) in $\delta^{13}C$ values within the growing season, being higher in early than later growing season

Table 1 Effect of insect herbivores on the $\delta^{13}C$ values, N concentration (N_{mass}) and C:N ratios of sunlit larch leaves from an open area in the forest stand (a forest gap, elevation 1,630 m) and the transitional area from the forest to steppe (elevation 1,560 m)

Site	Date	$\delta^{13}C$ (‰)	N_{mass} (%)	C:N	*N*
Forest gap	Aug. 19, 03	–25.1 ± 0.3	2.4 ± 0.2	15.5 ± 1.0	4
	Aug. 19, 03	–27.0[a]	2.3	15.3	1
	Sept. 29, 03	–25.8 ± 0.5	0.8 ± 0.2	44.8 ± 8.4	4
	Sept. 29, 03	–28.0[a]	0.9	29.9	1
Transitional area	Aug. 19, 03	–23.9	3.1	12.3	1
	Aug. 19, 03	–26.4 [a]	2.6	14.0	1
	Sept. 30, 03	–24.7	1.0	35.0	1
	Sept. 30, 03	–28.7[a]	0.9	39.5	1

Values are mean ± 1 SD

[a] Newly emerging leaves from the twigs after insect herbivores

(Fig. 1a). This variability should integrate and represent substantial within-season eco-physiological variations considering the pronounced seasonality of temperature and precipitation at the site.

We found that there was no significant difference in the mean $\delta^{13}C$ values for both sunlit and shaded leaves when comparing the isotopic data of the same month in different years. This suggests that environmental influences on carbon isotope discrimination are less variable between years than seasonally during the measurement period. Similar inter-annual correlations are also reported for Mediterranean oaks (*Quercus pubescences* and *Quercus ilex*) in southern France (Damesin et al. 1998), and for western hemlock (*Tsuga heterophylla*) in the Pacific Northwest of the USA (Fessenden and Ehleringer 2002).

The $\delta^{13}C$ values (Table 1) of mature sunlit leaves lie in the upper half of the range (–25.4 to –29.5‰) of the $\delta^{13}C$ variation for mature sunlit foliage from eight larch species growing at 20 locations in the Northern hemisphere (Kloeppel et al. 1998). They are even more positive than those from the same species growing in the habitats of lower elevations (less than 200 m) in Russia and Iceland (Kloeppel et al. 1998). However, the larches in NE Mongolia exhibit a considerably low N_{mass} (less than 1%) in the end of the growing season in comparison to those larches in other natural habitats, which have relatively higher N_{mass} (ranging between 1.4 and 2.7%) (Kloeppel et al. 1998). This suggests that before senescence induced leaf yellowing in the end of the growing season, most N in larch leaves has been allocated to the bark of stems or roots as a reserve (Chapin et al. 1990). Higher N_{mass} in the newly emerging leaves at the beginning of the second growing season is due to remobilization or reallocation of this N reserve for an internal cycling purpose (Chapin et al. 1990; Millard 1996).

Mature larch leaves (either sunlit or shaded) showed greater carbon isotope discrimination capacity, as indicated by more negative $\delta^{13}C$ values in every instance, than juvenile leaves (Fig. 1). Numerous studies have previously reported similar differences between juvenile and mature leaves for other forests (e.g., Terwilliger 1997; Damesin et al. 1998; Terwilliger et al. 2001; Ometto et al. 2002; Holtum and Winter 2005). However, the causes are still a matter of debate (e.g., Le Roux-Swarthout et al. 2001). Stems and roots usually have $\delta^{13}C$ values 2–5‰ higher than leaves (Leavitt and Long 1986; Medina et al. 1986; Damesin and Lelarge 2003). If juvenile leaves used the more ^{13}C-enriched carbon stored in the stems during leaf expansion, then their $\delta^{13}C$ values would be consequently more positive (Brendel et al. 2003). With progress of the growing season, the decrease of foliar $\delta^{13}C$ values is associated with a change in the relative proportion and activity of in vitro phosphoenolpyruvate carboxylase (PEPC) and ribulose bisphosphate carboxylase–oxygenase (Rubisco) in leaves (Terwilliger et al. 2001). Furthermore, a change in the relative fractions of structural (non-mobile) and non-structural (mobile and with a rapid turnover) carbohydrates with various $\delta^{13}C$ values in the leaves is an influential factor in driving the variability of the bulk foliar $\delta^{13}C$ values (Brendel 2001; Damesin and Lelarge 2003; Hobbie and Werner 2004). Therefore, at a given time, the $\delta^{13}C$ values of the bulk current year foliage are a consequence of the balance between these two contrasting carbon pools, respectively products of two effects: current photosynthetic fractionation (Farquhar et al. 1989a) and post-photosynthetic fractionation (Yoneyama et al. 1997; Pate and Arthur 1998; Hobbie and Werner 2004; Badeck et al. 2005). There may exist a shift of dominance from heterotrophic (imported from reserves) to autotrophic (own photosynthetic) carbon during leaf growth (Le Roux-Swarthout et al. 2001; Damesin and Lelarge 2003; Hobbie and Werner 2004). With leaf growth, an increased fraction of structural compounds (such as lipids and lignin) with low $\delta^{13}C$ values may lead to a decrease in the foliar $\delta^{13}C$

values (DeNiro and Epstein 1977; Benner et al. 1987; Hobbie and Werner 2004). Additionally, N_{mass} in larch leaves decreased with the season (Fig. 1b). Therefore, the decrease in the $\delta^{13}C$ values with leaf growth might be partly due to within-season decrease in N_{mass} because N deficiency often results in a reduction in foliar $\delta^{13}C$ values (Raven and Farquhar 1990; Livingston et al. 1999).

Sunlit versus shaded leaf habitats

Throughout the measurement period, significant differences in mean $\delta^{13}C$ values between sunlit and shaded larch leaves were detected (Fig. 1a). Sunlit leaves had $\delta^{13}C$ values that were 2.0‰ on average more positive than shaded leaves, indicating that the sunlit leaves discriminate against ^{13}C lower than shaded leaves. As shown in Eq. 3, leaf carbon isotopic discrimination (Δ_{leaf}) is positively related to the ratio of intercellular to atmospheric CO_2 concentration (c_i/c_a). Therefore, lower Δ_{leaf} (or more positive $\delta^{13}C$) values corresponded to lower c_i/c_a ratios. A decrease in the c_i/c_a ratio should be caused by either a decrease in the stomatal conductance (g) or an increase in the photosynthetic capacity (A), two contrasting but correlated factors (Farquhar et al. 1989b). At the site, the growing season is in phase of the rainy season, and thus the effect of stomatal closure due to shortage of water supply is relatively small (Li et al. 2005, 2006). Therefore, we believe that the major reason for more positive mean $\delta^{13}C$ values in sunlit than shaded leaves is probably due to higher photosynthetic capacity, or a higher ratio of g to A, under strong light intensity conditions, which leads to lower c_i/c_a ratios (Farquhar et al. 1989a). In contrast, the lower $\delta^{13}C$ values in shaded leaves are likely to be associated with both the reduction in atmospheric vapor pressure deficit (high air humidity within the canopy) and the limited photosynthesis (higher discrimination against ^{13}C) caused by decreased within-canopy light intensity (Francey et al. 1985, 1989a; Ehleringer et al. 1986; Le Roux et al. 2001). Also, understory shaded leaves might partially photosynthesize isotopically lighter CO_2 (depleted in ^{13}C) produced from soil and plant respiration (recycling of respired CO_2), and thus become isotopically lighter than sunlit leaves (Vogel 1978; van der Merwe and Medina 1989; Sternberg et al. 1989). However, the ^{13}C signals from respiratory CO_2 is likely to contribute very little to the isotopic signatures of understory shaded leaves, considering that the forest stand is located on a mountain slope where turbulent mixing is usually strong during daytime photosynthesizing hours. It is reported that N stressed seedlings of white spruce (*Picea glauca*) exhibit lower $\delta^{13}C$ values than fertilized seedlings (Livingston et al. 1999). At our site, N_{mass} was relatively lower in shaded than in sunlit leaves (Fig. 1b). Thus, this discrepancy in N_{mass} is probably a contributor to the general trend of more positive $\delta^{13}C$ values in sunlit than shaded leaves (Fig. 1a). Other studies have also reported a decrease in Δ_{leaf} in forest gaps (France 1996; West et al. 2001) or in cleared forest areas (van der Merwe and Medina 1989).

Water use efficiency and nutrient use efficiency

Our results show that the mean ^{13}C values and N_{mass} for both sunlit and shaded leaves were positively correlated (Fig. 2a), implying that larches use water more efficiently under conditions of higher N_{mass}. The pattern based on temporal investigation into the $\delta^{13}C$–N_{mass} correlation of Siberian larch in NE Mongolia contrasts with that for larches growing in other places, in which the foliar $\delta^{13}C$ values are not markedly corelated with their respective N concentrations (Kloeppel et al. 1998). There exist positive (Raven and Farquhar 1990; Körner et al. 1991; Sparks and Ehleringer 1997; Livingston et al. 1998), negative (DeLucia and Schlesinger 1991; Welker et al. 2003), or no (Damesin et al. 1997; Patterson et al. 1997; Kloeppel et al. 1998) correlations between foliar $\delta^{13}C$ values and N concentration. The $\delta^{13}C$–N_{mass} correlation is also depending on canopy position that links with photosynthetic capacity as reflected in the N_{mass} (Prasolova et al. 2001). Duursma and Marshall (2006) found that $\delta^{13}C$ was strongly correlated with leaf area based N concentration, but weakly correlated with leaf mass based N concentration. Nitrogen is directly responsible for producing leaf chlorophyll needed for photosynthesis (Field and Mooney 1986), and thus leaf N is a reliable indicator of photosynthetic capacity (Duursma et al. 2005). Since the relationships between photosynthesis, nitrogen content and stomatal conductance vary with species, with time, and with canopy position, and are bio-physiologically complicated (Field et al. 1983; Field and Mooney 1986), the mechanisms underlying the $\delta^{13}C$–N_{mass} correlation remain unclear. It has been reported that lower WUE under lower N_{mass} is likely associated with increased photosynthetic capacity due to an increase in the internal conductance to CO_2 diffusion from intercellular air spaces to the site of carbon fixation or decreased c_i/c_a ratios (Patterson et al. 1997; Sparks and Ehleringer 1997; Livingston et al. 1998).

At the site, the mean $\delta^{13}C$ value was found to be negatively correlated with the C:N ratio, an index of nitrogen use efficiency (NUE) of plants (Chapin and van Cleve 1990) (Fig. 2b). Similar results are reported for five co-occurring California evergreens (Field et al. 1983), American elm (*Ulmus americana*) (Reich et al. 1989), and two spruce species (*Picea glauca* and *Picea mariana*) (Patterson et al. 1997; Livingston et al. 1999). A higher WUE in response to a lower NUE is biologically meaningful because a strong control of leaf N over A is exerted

through an optimal allocation of N in the plants to maximize carbon assimilation (Field 1983; Hirose and Werger 1987). Since larches generally have higher N concentration than co-occurring evergreen conifers (Schulze et al. 1995), the former exhibit higher light use efficiency than the latter (Gower et al. 1999).

Soil depth effect

We oberved a small progressive enrichment in ^{13}C (around 2‰) with depth within a 30 cm soil layer (Fig. 3a). The surface soil layer was more depleted in ^{13}C because of direct influence of recent litterfall from overlying plants. Similar patterns have been reported in numerous observations in literature for forest and grassland ecosystems (e.g., Nadelhoffer and Fry 1988; Balesdent et al. 1993; Schwartz et al. 1996; Bunchmann et al. 1997; Boutton et al. 1998). However, there is still controversy as to the causes for the variation of SOM $\delta^{13}C$ values with soil depth. Several hypotheses have been proposed to explain this phenomenon (Ehleringer et al. 2000; Garten et al. 2000). These mainly include: (1) the Suess effect, i.e., a dilution of atmospheric CO_2 by isotopically more depleted CO_2 emitted from fossil fuel combustion and biomass burning over the last two centuries; (2) the carbon mixing of new and old SOM pools with different $\delta^{13}C$ signatures; and (3) the isotope fractionation effect due to preferential decomposition of isotopically more depleted compounds by soil microbes (Ehleringer et al. 2000; Garten et al. 2000). The first two effects or their combination appear to be most important in the progressive enrichment in ^{13}C with soil depth (Ehleringer et al. 2000; but see Garten et al. 2000). In addition, the vertical gradient is also associated with litter quality, which is one of critical factors affecting litter decomposability by microbes (Aerts 1997), and a small vertical gradient of soil $\delta^{13}C$ values is reported to be associated with poorer litter quality (higher C:N ratios) (Garten et al. 2000). At our site, new larch leaf litter is of low quality, as indicated by its very high C:N ratio in the end of the growing season, which may contribute to some extent to a smaller vertical enrichment in ^{13}C with soil depth. However, it is difficult to assess this effect because the litter decomposition is likely to be limited by low temperatures in this cold semiarid forest ecosystem. At broad geographic scales, Garten et al. (2000) argued that climate, especially temperature, is a more important factor affecting SOM decomposition than litter quality, and found a greater gradient in soil $\delta^{13}C$ values with increasing mean annual temperature at six forests in the Southern Appalachian Mountains in USA.

Small vertical gradients in N_{mass} and C:N ratio of SOM were also observed (Fig. 3b, c). Under cold semiarid climate conditions at the site, such factors as seasonality of temperature and soil moisture avalability, microbial acitivity, and litter decomposability in association with soil C and N turnover, vertical mixing and SOM formation are likely responsible for changing N_{mass} and C:N ratios with soil depth.

Nevertheless, the soil depth effects on mean $\delta^{13}C$, N_{mass} and C:N ratio of SOM at our site each appear to be not significant except for the upper very thin soil layer (0–2 cm). This, on the other hand, suggests a close correlation between soil $\delta^{13}C$ values, N_{mass}, and C:N ratios in terms of their respective vertical distributions.

Defoliation effect

Newly emerging sunlit larch leaves from twigs after insect herbivores, which defoliated partially or completely older leaves, had more negative $\delta^{13}C$ values, relative to those that were concurrently sampled but not affected by insect herbivores (Table 1). Contrary to our observation, from a sprouting cutting experiment of *Salix interior* under wet and dry soil-moisture conditions in a controlled environmental chamber, Le Roux-Swarthout et al. (2001) observed that the $\delta^{13}C$ values of newly emerging leaves following defoliation were significantly more positive by 2–4‰ than those for mature leaves. They found that the cause for this discrepancy is depending on soil moisture availability. Under continuous dry-to-dry or wet-to-wet conditions, the discrepancy is principally because the newly emerging leaves use ^{13}C-enriched stem-stored carbon imported during the early stages of leaf growth (Le Roux-Swarthout et al. 2001). By contrast, under the wet–dry or dry–wet shifting conditions, apart from influences from imported carbon, additional biochemical fractionation processes are likely involved (Le Roux-Swarthout et al. 2001). We cannot provide such direct evidence to confirm the observed very negative $\delta^{13}C$ values for newly emerging sunlit larch leaves following the insect herbivores. However, we speculate that this should be associated with leaf development and carbon sources. Nevertheless, it is worthwhile to conduct further studies using the ^{13}C pulse-chase labeling technique (Avice et al. 1996) to explore the physiological processes involved in leaf regrowth after insect herbivores.

Ecological implication

It is now recognized that understanding the biogeochemical processes of high-latitude ecosystems, especially boreal forests, is very important in global change study. This study reports the temporal variation of foliar $\delta^{13}C$ from a montane *Larix siberica* forest in NE Mongolia. Some preliminary information is also provided on close correlation between carbon isotope discrimination and nitrogen

concentration dynamics in the stand. Our results have some ecological implications for an improved understanding of how carbon and water are cycled in this cold semi-arid ecosystem.

In contrast to the previous studies showing that larches (*Larix* spp.) use water less efficiently than sympatric evergreen conifers (Gower and Richards 1990; Kloeppel et al. 1998), our isotopic data suggest that relative to other larch forests across the world, the Mongolian larch forest exhibits a higher WUE with a strong within-season variability. This is likely to be referred as an adaptive strategy for growth and survival of the larch trees in this cold semi-arid environment, especially under the scenario of climate change (Saurer et al. 2004).

Since most factors (c_i/c_a ratio, light intensity, re-utilization of respired CO_2, temperature, water availability and N deficiency) affecting leaf carbon isotope discrimination not only interrelate but also present spatio-temporal variability per se, there are many uncertainties are involved in interpreting the variability in the $\delta^{13}C$ values (Farquhar et al. 1982, 1989a; Ehleringer et al. 2002; Duursma and Marshall 2006). Clearly, the $\delta^{13}C$ values observed in this study can be only a reflection of some facets of the net effect of these interrelated factors in the forest. Further studies are required to accurately estimate the contribution of these influential factors to the variation in the $\delta^{13}C$ values.

Acknowledgments This study has been supported in part by the Japan Science and Technology Agency through a grant under the Core Research for Evolutional Science and Technology (CREST) program funded for the RAISE project. Partial support is from the Global Environment Research Fund of the Ministry of Environment of Japan. S.-G. Li is supported by the ''Hundred Talents'' Program of the Chinese Academy of Sciences, and by Chinese Academy of Sciences International Partnership Project ''Human Activities and Ecosystem Changes'' (CXTD-Z2005–1).

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