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ORIGINAL ARTICLE

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Abstract

The inorganic nitrogen (N) cycle and its dynamics in the soil were observed in the ecosystem at the Spasskaya Pad experimental forest near Yakutsk in northeastern Siberia in order to estimate the N availability for the larch (*Larix cajanderi* Mayr.) The soil pool of bulk N in the forest accounted for up to 866 g N m^{-2} (0–50 cm), whereas up to 1.7% (14.6 g N m^{-2}) was potassium chloride (KCl)-extractable inorganic N. Ammonium was a dominant form of inorganic N. The size of the soil inorganic N pool fluctuated seasonally. It was small in the beginning of the summer and increased rapidly once the cumulative degree day of the soil temperature at 20 cm reached more than 300 (°C days), indicating that active N mineralization began at some point from the middle of July to the beginning of August. This soil pool of inorganic N that had accumulated at the end of the previous summer was consumed by the beginning of the next summer through microbial immobilization, which may have begun in September. Recycling of N in the soil was important because the input of inorganic N by deposition was very small (48 mg N m^{-2} year^{-1}). A tracer ^{15}N experiment showed that larch did not uptake organic N in the form of amino acid (alanine); rather, it used ammonium and nitrate as N sources. The amount of available N for plants was assessed as water-extractable inorganic N in the soil solution that was transported to the rooting area by mass flow driven by plant transpiration, and it accounted for 1.9×10^3 (1.2×10^3 for trees) mg N m^{-2} during the growing season^{-1} (0–50 cm of the mineral soil layer in June, July, and August). Microorganisms in the soil are also expected to be competing for this available N. Our results show that despite a large amount of inorganic N production, N availability for plants is low as the soil pool of inorganic N is built up at the same rate as larch senescence.

Key words: boreal forest, taiga, nitrogen cycle, organic nitrogen uptake, soil nitrogen pool.

1. INTRODUCTION

One of the hottest topics at present is the increase in the concentration of greenhouse gases in the atmosphere, which contribute to global warming (Solomon *et al.* 2007). There is evidence that boreal forests act as a global carbon (C) sink (Schulze *et al.* 1999; Dolman *et al.* 2004). Russian Siberia covers 13 million km², which is almost 10% of the total land

mass of the Earth. Russian forests are a global sink accounting for 0.13 Pg C per year (Goodale *et al.* 2002). This means that the amount of sequestrated carbon dioxide (CO_2) in the Siberian taiga is rather significant, and its changes could affect the C cycle on a global scale.

It is known that the availability of nitrogen (N) is one of the important limiting factors for plants in the northern hemisphere (Aerts *et al.* 1999; Vitousek *et al.* 2002). Therefore, understanding the dynamics of N is fundamental to knowing the effects of global climate change on C cycles in boreal forests. N exists in several forms in soil pools, and the major component is expected to be organic matter. Inorganic N is formed by the microbial processes of decomposition of organic matter in the soil (mineralization). Generally, the rates of mineralization and nitrification depend on several factors, including soil temperature, moisture conditions, and the availability of labile organic matter (Cassman and Munns 1980; Nadelhoffer *et al.* 1991; Sierra 1997). Leaching and denitrification processes are negligible or not significant in our study area, located on the permafrost (Shugalei and Vedrova 2004, Koide *et al.* 2010).

N availability for plants is a complex question that has a long history in research. Several large-scale studies have been conducted in boreal and tundra areas in Europe and North America. These reports showed that N availability in northern ecosystems is generally very limited (Schulze *et al.* 1994; Bauer *et al.* 2000), and proposed various hypotheses to fill the gap between soil N availability and plant demand (Kielland 1994; Harrison *et al.* 2000; Lisuzzo *et al.* 2008; Koyama and Kielland 2011). Direct uptake of organic N in the form of amino acids was found to be an important source of N for some deciduous and conifer plants, although the uptake rate varied greatly among species (Jones *et al.* 2005). The soil inorganic N pool is known to regulate N availability for plants (Schulze *et al.* 1999); however, there are several competitors such as bacteria and fungi, and the proportion readily used by plants needs to be determined further. It is also believed that global warming may increase the fluxes of C and N cycling (Nadelhoffer *et al.* 1991; Borner *et al.* 2008; Chapin *et al.* 2009), whereas the mechanisms and possible effects of such changes on plant N availability are still not clear.

There have been many reports from European and North American boreal ecosystems. However, only a few studies have been conducted in Siberia, where the larch, a deciduous conifer, dominates the area. The majority of these works have been reported in Russian; therefore, up to now, these studies have not been available to most scientists outside Russia. Based on accessible information, the available inorganic N was likely to be a limiting factor for plant growth in central (Tokuchi *et al.* 2010) and northeastern parts of Siberia (Schulze *et al.* 1995). In addition, the amount of N in the soil pools, the plant N (Matsuura and Hirobe 2010), the soil inorganic N, and the decomposition rate (Shugalei and Vedrova 2004) in central Siberia, have been observed.

The Siberian taiga consists of larch forests that include several species. The dominant species in the eastern part of the Siberian taiga is *Larix cajanderi* Mayr (Pozdnyakov 1975). Previous studies performed in northeastern Siberia demonstrated the importance of water and temperature for plant growth (Maximov *et al.* 2010). The permafrost system was shown to be important because it provides a source of water for the larch trees (Sugimoto *et al.* 2002). In addition, the seasonal dynamics of soil respiration have also been observed (Kononov 2006). Only one report has been published on the N cycle in the forest at the study site (Koide *et al.* 2010), and no study on N dynamics has yet been performed.

This study is a pioneering study of N dynamics in this area. Therefore, the main objectives of the current research are to monitor the seasonal fluctuation of soil N availability in the taiga forest ecosystem in northeastern Siberia, to estimate N demand of the tree stands, and to identify the factors that regulate N availability.

2. STUDY SITE AND METHODS

2.1. Study site

Observations were conducted at the Spasskaya Pad experimental forest (62.15°N, 129.37°E, 220 m above sea level) of the Institute for Biological Problems of Cryolithozone, Siberian Branch of the Russian Academy of Sciences, which is located on the first terrace (left bank) of the Lena river, about 25 km northwest of Yakutsk, Russia, in a continuous permafrost area. The soil type is classified as Gelisols according to the USDA. The period of observation of soil N was mostly from 2005 to 2011 and intensive observation was conducted during the period from 2009 to 2011. The climate in the study area is sharply continental, with monthly mean temperatures ranging from +19°C in July to –40°C in January. The annual mean precipitation in the study area is quite low, i.e., on average 238 mm (from 1971 to 2000), of which two-thirds occurs in the summer. The active layer depth (defined as the soil layer that thaws during the warm period) is usually 1.2–1.4 m. Soil thaw starts from the surface layer at the end of April, and the thaw depth increases until October, whereas the surface soil layer starts to freeze in September and the soil stays frozen for seven months of the year.

Larix cajanderii Mayr is the dominant species at the study site, and *Betula platyphylla* Sukaczev is found in a gap. The forest floor is covered by various plant species: *Vaccinium vitis-idaea* L., *Pyrola rotundifolia* L., *Ledum palustre* L., and *Arctostaphylos uva-ursi* (L.) Spreng are typically found. The growing season is short: It begins with leaf unfolding (from mid-May to the beginning of June), when the surface layer of the soil thaws, and it ends with senescence at the end of August or the beginning of September; litterfall takes place in the middle of September.

The plot (20 × 20 m) for samplings and installation of observation materials was established in a non-disturbed area of a larch forest that is located about 100 m northeast of the observation tower where meteorological and hydrological observations have been conducted. The forest floor is covered with a thin layer of litter and an organic layer (A_0), typically 8 cm thick; a mineral soil layer lies underneath. Mineral soil is typically sandy loam or sandy clay loam and is rich in carbonates. Total (inorganic and organic) C content sharply decreases with depth. It is about 2–3%, with the C/N ratio of the soil at 22, at the border with an organic layer, and it increases to 34 at a depth of 50 cm. The plant roots are mainly distributed down to 20 cm in mineral soil layer and rarely found below 50 cm.

2.2. Observation and analyses

2.2.1. Soil moisture and temperature and meteorological conditions

Volumetric soil water content was manually observed at the study site using time domain reflectometry (Moisture Point, Environmental Sensors Inc.). The soil temperature was measured using a thermometer with a data-logger (Tidbit, Onset, USA). Automatic measurements of soil moisture and temperature in the larch forest were initiated by GAME-Siberia [GEWEX (The Global Energy and Water Cycle Experiment) Asian Monsoon Experiment] (Ohta *et al.* 2008), and continued by JAMSTEC (Japan Agency for Marine-Earth Science and Technology). The soil moisture-water equivalent was calculated with the same method by Sugimoto *et al.* (2003) using both manual and automatic measurement data. Air temperature and precipitation data were obtained through an NCDC NOAA (National Climatic Data Center, National Oceanic and Atmospheric Administration) summary-of-the-day web database.

2.2.2. Inorganic N in throughfall

For determining the amount of N deposited via throughfall (wet and dry), samples were collected from 29 May 2009 to 27 August 2009, from 5 June 2010 to 1 August 2010, from 25 May 2011 to 29 July 2011, and from 15

October 2011 to 28 February 2012. During summer observations, sampling containers were placed under the canopy in the forest so that dry particulate matter and rainwater were collected together (n = 9). Throughfall samples were collected after a major rainfall and weighed. An aliquot was transferred to a 50-mL plastic tube and kept frozen at –18°C until analysis. To observe the amount of N deposited during the winter, a sampling tube (diameter 0.1 m) was used to collect samples at various depths of snow cover under the canopy (*n* = 3). Snow samples were liquefied and stored as described above.

2.2.3. Soil inorganic and amino acid N pools

Soil sampling was done for the organic layer, and at depths of 5, 15, and 50 cm for the mineral layer. To calculate the amount of N per unit area, the soil densities from previous observations were assumed. For the organic layer, a value of 0.30 g cm^{-3} was used; as for the mineral layer, values of 1.34, 1.45 and 1.65 g cm^{-3} were used for depths of 0–10, 10–30, and 30–50 cm, respectively.

Bulk N concentration in the soil pool was determined using samples taken between 4 and 8 August 1999, and on 11 August 2004, 10 August 2005, and 15 August 2006. Soil samples were collected in the forest, oven-dried at 60°C, and separated from debris. The soils were finely ground in a ceramic bowl and analyzed for bulk N.

For studying the soil inorganic N pool, soil samples were collected from June to August in 2005, 2009, 2010, and 2011. Fresh soil samples were sieved (2 mm mesh), and N was immediately extracted using a 2 M potassium chloride (KCl) solution or ion exchange water [soil:solvent ratio was 4:40 (w/v)] on a reciprocating shaker (1 h), then filtrated with a prewashed cellulose filter. Extracts were frozen and maintained at –18°C until analysis. 10 g of each sample was oven dried at 105°C and used for dry weight estimation.

Total free amino acids were extracted from samples collected on 15 June, 1 July, and 21 July 2011 using ion exchange water [soil:solvent ratio was 4:40 (w/v)]. The samples were filtered using a 0.45-µm syringe filter and were then frozen.

2.2.4. Ion exchange resins

The ion exchange resin bags method has been used frequently *in situ* to evaluate nutrient availability in various types of forests (Giblin *et al.* 1994). Binkley and Matson (1983) have suggested that the ion exchange resin bags method gives a comprehensive picture of the soil status of plant-available nutrients, especially because membranes resemble the structure of a plant root. The ion-

exchange resin bags method was reported to overcome the disadvantage of chemical extractions accounting for the kinetics of nutrient release and transport (Curtin *et al.* 1987; Abrams and Jarrell 1992) and mobilizing nutrient forms that are truly available for plants (Skogley and Dobermann 1996). Using this method, the relative amounts of inorganic N percolating through the soil profile with the soil solution can be determined; this is especially informative in a permafrost area with a dry climate, where water moves vertically upward and downward seasonally.

Ammonium and nitrate percolating in the soil solution were collected using ion-exchange resin plates. A mixture of cation and anion exchange resins (5 g each) was packed in a plate (5 cm diameter, 1 cm thick). Three plates were installed at depths of 5 and 15 cm in the observation plot during the following periods: 13 August 2005 to 6 August 2006, 7 August 2006 to 7 July 2007, 6 June 2009 to 21 August 2009, 22 August 2009 to 17 August 2010, and 18 August 2010 to 25 July 2011. After recovering the plates from the soil, they were oven dried at 40°C and kept in plastic bags until analysis. For the analysis, extraction of ions from resins was done using 2 N hydrochloric acid (HCl).

2.2.5.   Production of inorganic N

Production of inorganic N was observed using the *in situ* incubation method. Observation of the mineral soil layer was conducted from 21 August 2009 to 17 August 2010 and from 18 August 2010 to 21 July 2011 at depths of 5, 15, and 50 cm (for each depth, $n = 12$). The method was described (Nadelhoffer *et al.* 1984) with the modification suggested in Tokuchi *et al.* (2010). Briefly, soil was placed in 30-mL loosely capped bottles to keep the plant roots out and at the same time to allow the exchange of water and gases. To obtain the initial condition, the same soil was used for extraction of inorganic N with 2 M KCl. Bottles filled with soil were returned to the original position in the soil. After about 1 year of incubation, the bottles were recovered and then inorganic N was extracted using 2 M KCl.

2.2.6.   Ammonium, nitrate and amino acid tracer experiment

^{15}N-ammonium and nitrate tracer labeling experiments were carried out to determine the preferred form of inorganic N. An experimental plot (15 m × 15 m) was established in the larch forest site 200 m southwest of the tower site. A total of 18 trees with an average total height of about 1.5 m were used for the experiment. Nine trees were treated with ammonium sulfate $(^{15}NH_4^+)_2SO_4$ (min.

60 at% of ^{15}N) and another nine trees with sodium nitrate $Na^{15}NO_3$ (min. 60 at% of ^{15}N), which were dissolved in ion exchange water. One hundred milliliters of a tracer containing 0.02 M-N was applied under the organic layer around the main root of each tree. Labeling was done on 28 May 2009. On Day 26, branches were sampled from the middle part of the labeled trees, and oven dried at 60°C; the needles were then separated. Needle samples were milled for analyzing C and N content and isotope ratios.

Tracer experiments with dual labels, $^{13}C^{15}N$-alanin and ^{15}N-ammonium, were conducted to detect the possibility of organic and inorganic N uptake by the larch trees. Since the ratio of $^{13}C:^{15}N$ of alanine was 3:1, if this alanine was assimilated directly, the increase of heavy isotopes in the labeled trees would follow the same proportion. Experiments were held twice: from 30 June to 2 July, and from 27 to 29 July 2011. For each experiment nine larch seedlings (about 40 cm total height) were chosen at the tracer experimental plot: Three were used as the control, three for the ^{15}N-ammonium treatment and three for the $^{13}C^{15}N$-alanine treatment. Control trees were watered with 100 mL of ion exchange water and did not receive any nutrition. Amino acid treated trees received 100 mL of 0.018 M of ^{13}C-^{15}N-alanine (min. 99.9 at% of ^{13}C and ^{15}N) and 0.010 M of non-labeled ammonium sulfate solution, whereas ammonium labeled trees received 100 mL 0.010 M of ^{15}N-ammonium sulfate (min. 60 at% of ^{15}N) and 0.018 M of non-labeled alanine. Needles were collected from each tree at intervals of 1, 2, 4, 8, 12, 24, and 48 h.

2.2.7.   Laboratory analyses

Ammonium and nitrate concentrations in the throughfall and soil extracts were analyzed using a continuous flow spectrophotometer autoanalyzer (Bran & Luebbe, Norderstedt, Germany). Amino acid content in soil extract was assessed using ninhydrin (Moore 1968) with a modified method by Lipson and Monson (1998) with alanine as the standard. The ammonium interference effect was subtracted using ammonium concentration data. Bulk C and N content and isotopic ratios were assessed using an elemental analyzer (Flash EA, Thermo Scientific, Billerica, MA) coupled with an isotope ratio mass-spectrometer (Delta V, Thermo Scientific). Results are expressed in delta notation ($\delta^{13}C$ or $\delta^{15}N$):

$$\delta = (R_{sample}/R_{standard} - 1) \times 1000 \, (\text{‰}) \qquad (1)$$

where R_{sample} and $R_{standard}$ denote the isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample and the standard, and the standard is PDB (Pee Dee Belemnite) for ^{13}C or

atmospheric N_2 for ^{15}N. Precision for analyses of amino acid standards was ≤ 0.1‰ for $\delta^{13}C$ and ≤ 0.3‰ for $\delta^{15}N$.

3. RESULTS

3.1. N budget

3.1.1. *Inorganic N deposition*

The total amounts of N in throughfall or deposition for three summer seasons and one winter season are presented in Table 1. During the summers, ammonium in throughfall varied from 8.6 to 27.2 mg N m^{-2}, respectively, which was larger than that of nitrate (from 0.18 to 8.1 mg N m^{-2}). Nitrite (less than 0.31 mg N m^{-2}) was not significant (not shown). Each observational period presented in Table 1 consists of 1 to 10 individual samplings, although one was a snow sample taken during the winter after the snow cover stabilized. The concentration of inorganic N (the sum of ammonium and nitrate) in throughfall ranged from 0.32 to 139.88 μmol L^{-1}. The amount of water during rain events ranged from 1 to 21 mm. Among the samples collected during the period from 25 May to 29 July 2011, the highest deposition rate of N (35.3 mg N m^{-2}) was observed in the sample taken for 17 to 22 July 2011, which overlapped a state of emergency declared by the local government due to a forest fire. This was probably caused by complete and incomplete combustion of organic matter (Olivier *et al.* 1994; Bouwman *et al.* 1997; Anderson *et al.* 2003; Coheur *et al.* 2009; Polischuk *et al.* 2011).

Winter deposition for the period from 15 October 2011 to 28 February 2012 was observed as deposited N in the snow cover. This snow cover sample accumulated 8.2 mg N m^{-2} of ammonium, 11.0 mg N m^{-2} of nitrate, and 0.07 mg N m^{-2} of nitrite. For each sample, including that from the winter data, a positive correlation between total deposited N and sampling duration ($r = 0.92$) was observed, except for the summer of 2011, when very high deposition was observed as a result of the forest fire described

above. An increase in ammonium deposition during the warm period and an increase in nitrate deposition during the winter are consistent with the observation made in central Yakutia (Makarov 2007).

Since the observation of deposited inorganic N did not cover a full year, the annual deposition was estimated using a daily average total N deposition (131.2 μg N m^{-2} day^{-1}) calculated except for the data from the summer of 2011. Estimated annual total N deposition was 48 mg N m^{-2}year^{-1} (Table 1), which was similar to that reported in Makarov (2007) for central Yakutia (1–40 mg N m^{-2} year^{-1}) and lower than that reported for the Asian part of Russia (50–2.95 × 10^3 mg N m^{-2} year^{-1}) (Polischuk *et al.* 2011). The amount of N deposited annually appeared to be very low compared to that observed in Europe (less than 100 to greater than 7500 mg N m^{-2} year^{-1}) and North America (from 310 to 3200 mg N m^{-2} year^{-1}) (Aber *et al.* 1989; Dise and Wright 1995; Fenn *et al.* 1998; Galloway *et al.* 2004).

3.1.2. *Soil N pool*

Bulk, inorganic, and organic N pools observed in the organic and mineral soil layers are summarized in Table 2, and vertical profiles are presented in the supporting information (Table S1). The amount of bulk N observed in the organic soil layer was 99 × 10^3 and 116 × 10^3 mg N m^{-2}, while the amount in the mineral soil layer was much larger, ranging from 608 × 10^3 to 866 × 10^3 mg N m^{-2}. N content in the soil decreased markedly with depth from the organic layer (0.007–0.008% in dry weight) down to 5 cm of the mineral layer (0.002% in dry weight), after which it exhibited a small variation around 0.001% dry weight (data not shown). Such a distribution is consistent with studies performed in the larch forests in central Siberia (Shugalei and Vedrova 2004).

The amount of KCl-extractable ammonium dominated the soil inorganic N pool irrespective of seasons or year-

Table 1 Observed and estimated total inorganic nitrogen (N) in throughfall and deposition

		Ammonium (mg N m^{-2})	Nitrate (mg N m^{-2})	Total N (mg N m^{-2})	Period (days)
2009	29 May to 27 Aug	8.6	3.2	11.8	91
2010	5 Jun–21 Aug	13.6	0.2	13.8	78
2011	25 May–29 Jul	27.2	8.1	35.3	66
2011–2012	15 Oct–28 Feb	8.2	11.1	19.3	137
Estimated daily average[†]		0.110	0.039	0.131	
Estimated annual average		40.0	14.3	48	365

[†] For estimation of average daily deposition data of 2009, 2010 and 2011–2012 winter were used. Data of 2011 summer was excluded from calculation because forest fire disturbance was expected. The average was calculated based on every observation period daily average (standard deviation ± 24.8).

Table 2 Soil nitrogen (N) pools in the organic layer and mineral soil layer 0 to 50 cm: average with standard deviation (SD) and repeated number of samples (in parentheses) for bulk N, potassium chloride (KCl)-extractable and water-extractable ammonium (g N m^{-2}), nitrate and total free amino acid (mg N m^{-2}).

Data Layer	Bulk N (g N m^{-2})	KCl extractable ammonium (g N m^{-2})	Water extractable ammonium (g N m^{-2})	Nitrate[†] (mg N m^{-2})	Total water extractable inorganic N (g N m^{-2})	Total free amino acid (mg N m^{-2})
4–8 Aug 1999						
Organic	116 ± 40 (n = 7)					
Mineral						
2003[‡]						
Organic		0.48		5		
Mineral		6.0		77		
11 Aug 04						
Organic						
Mineral	608					
10 Aug 05						
Organic		0.74 ± 0.57 (n = 3)		10 ± 1 (n = 3)		
Mineral	866	0.35 ± 0.13 (n = 3)		313 ± 44 (n = 3)		
15 Aug 06						
Organic	99					
Mineral	617 ± 261 (n=3)					
6 Jun 09						
Organic						
Mineral		2.5 ± 0.8 (n = 4)		89 ± 18 (n = 4)		
21 Aug 09						
Organic						
Mineral		10.5 ± 0.9 (n = 4)		307 ± 226 (n = 4)		
7 Jun 10						
Organic						
Mineral		0.35 ± 0.39 (n = 3)				
1 Aug 10						
Organic		5.7 ± 4.6 (n = 3)		54 ± 45 (n = 3)		
Mineral		6.7 ± 3.1 (n = 3)		918 ± 925 (n = 3)		
17 Aug 10						
Organic						
Mineral		14.3 ± 4.9 (n = 3)	1.3 ± 1.1 (n = 3)	330 ± 371 (n = 3)	1.6	
15 Jun 11						
Organic		0.18 ± 0.06 (n = 3)	0.1 ± 0.1 (n = 6)	69 ± 72 (n = 9)	0.17	53 ± 100 (n = 6)
Mineral		1.5 ± 0.64 (n = 3)	0.15 ± 0.22 (n = 6)	361 ± 126 (n = 9)	0.51	221 ± 262 (n = 6)
1 Jul 11						
Organic		0.07 ± 0.03 (n = 3)	ND[§] (n = 6)	1 ± 2 (n = 9)	1.0	32 ± 46 (n = 6)
Mineral		1.6 ± 0.25 (n = 3)	0.35 ± 0.66 (n = 6)	42 ± 37 (n = 9)	0.39	408 ± 591 (n = 6)

(continued)

Table 2. Continued.

| Data Layer | Bulk N | Soil N pool | | | | |
		KCl extractable ammonium	Water extractable ammonium	Nitrate[†]	Total water extractable inorganic N	Total free amino acid
21 Jul 11						
Organic		0.14 ± 0.01 (n = 3)	0.06 ± 0.05 (n = 6)	5 ± 4 (n = 9)	0.06	10 ± 15 (n = 6)
Mineral		3.0 ± 0.35 (n = 3)	1.4 ± 0.55 (n = 6)	197 ± 45 (n = 9)	1.6	432 ± 485 (n = 6)

[†] Both water extractable nitrate and KCl extractable nitrate were averaged because there was no difference between them. Average of this values and SD were shown.
[‡] Data from Koide *et al*. (2010), sampling date not specified.
[§] ND, not detected.

to-year variation, and it was up to 75 times larger than nitrate. Large seasonal variation in the soil KCl-extractable inorganic N pool was found in the soil mineral layer. KCl-extractable ammonium in the mineral soil layer increased from 2.5 on 6 June to 10.5 g N m^{-2} on 21 August in 2009, from 0.354 on 7 June to 14.3 g N m^{-2} on 17 August in 2010, and from 1.5 on 15 June to 3.0 g N m^{-2} on 21 July in 2011. As seen in Table 2, in the beginning of the growing season (June until the middle of July), the inorganic N content in the soil was low. It increased by August due to increase in the amount of ammonium in the KCl-extractable soil N pool.

Water-extractable ammonium was two to ten times less than KCl-extractable ammonium. In the beginning of the growing season, the amount of water-extractable ammonium in the soil mineral layer was low (151 mg N m^{-2} on 15 June 2011), and it increased to 1.4×10^3 mg N m^{-2} on 21 July 2011. Unlike water-extractable ammonium, nitrate did not show a clear increase from June to August.

The total free amino acid in the soil pool observed in 2011 in the mineral layer was higher than that in the organic layer; however, the difference was statistically not significant. Soil pools of amino acid tended to decrease (from 53 to 10 mg N m^{-2}) in the organic layer and increase in the mineral soil layer (from 221 to 432 mg N m^{-2}) from June to July.

3.1.3. N collected by ion exchange resins

Similarly to soil extracts, the amount of collected total N varied greatly from 50 to 475 mg N m^{-2} period^{-1} (Table S2). The amount of ammonium captured by ion exchange resins was also larger than that of nitrate in most of samples. Ammonium to nitrate ratio was from 1.7 to 2.8 except for the ratio of 18.8 observed for the period from 3 August 2005 to 6 August 2006. The observations that covered late summer and fall (August and September) showed larger amounts of inorganic N than those observed during other periods.

Table 3 Soil inorganic nitrogen (N) pools before and after incubation experiments and calculated production calculated for the mineral soil layer 0–50 cm for the period of incubation (g N m^{-2})

| Date | Soil inorganic N[†] | | Production[§] (g N m^{-2} period^{-1}) |
	Before incubation[‡] (g N m^{-2})	After incubation[‡] (g N m^{-2})	
22 Aug 2009–17 Aug 2010	10.8	36.0	26.0
18 Aug 2010–21 Jul 2011	14.6	1.1	–13.6

[†] Total amount of ammonium and nitrate extracted with potassium chloride (KCl) solution.
[‡] Soil inorganic N before and after incubation experiments were shown.
[§] Production was calculated from the difference between initial (before incubation) and final (after incubation) N pools.

3.1.4. Inorganic N production

A high production of ammonium (26.0 g N m^{-2} period^{-1}) was observed in the first incubation period from 22 August 2009 to 17 August 2010 covering a full year, and the rate decreased with depth (Table 3 and Table S3). On the other hand, in the second incubation from 18 August 2010 to 21 July 2011, ammonium was consumed (–13.6 g N m^{-2} period^{-1}). Consumption rate was the highest at the top of the mineral soil layer, and it decreased with depth. The second incubation experiment did not cover the whole year, particularly late July and August. This indicates the relative importance of late summer for N production.

3.2. Tracer experiments

Results of the amino acid tracer labeling experimental results are shown in Fig. 1. No significant change in needle δ^{15}N was observed in the control and amino acid-treated trees during both experiments. On the other hand, δ^{15}N of needles from ^{15}N-ammonium
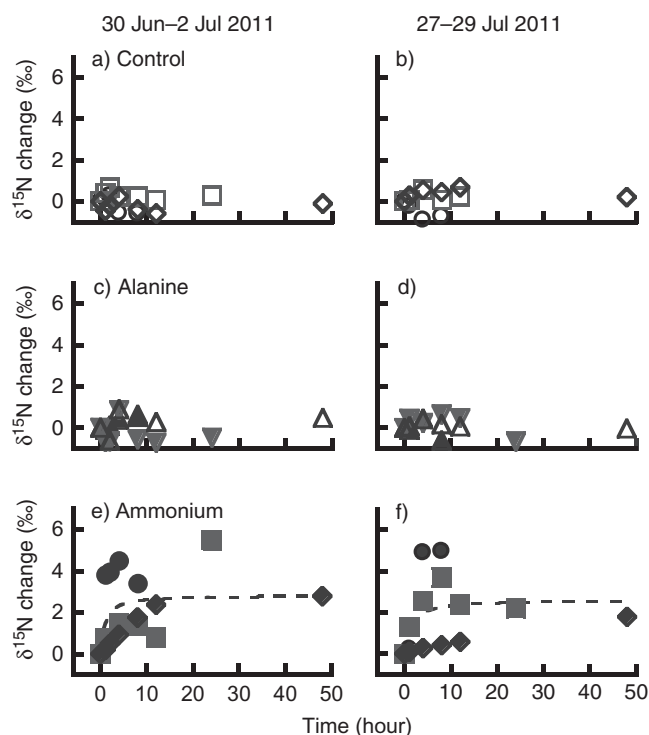
Figure 1 The change in larch (*Larix cajanderi* Mayr.) needle $\delta^{15}N$ observed during amino acid and ammonium tracer experiments held from 30 June to 2 July (a, c, and e) and from 27 to 29 July 2009 (b, d, and f), calculated from needle $\delta^{15}N$ of each sample tree before the tracer application, ranged from –5.2 to 0.2‰. Different markers (*open* or *closed square, triangle*, or *circle*) indicate each sample tree. A *broken line* indicates the average $\delta^{15}N$ change (e and f). Although the same markers were used to indicate individual trees in two experiments, the trees are not the same.

treated trees gradually increased beginning 1 h after the experiment started. In the experiment performed in June, the maximum change observed in $\delta^{15}N$ was +5.5‰, whereas it was +5.0‰ in July (Fig. 1e and f). The needle $\delta^{13}C$ of individual trees showed no significant change in experiments for both control and labeled trees with alanine and ammonium (data not shown).

The results of the inorganic ^{15}N labeling experiments are summarized in Table 4. The $\delta^{15}N$ of needles from trees labeled with ^{15}N-ammonium (127 ‰) was about 1.5 times larger than that of trees labeled with ^{15}N-nitrate (84‰) on Day 26 after application of the tracer, although the difference was statistically insignificant.

4. DISCUSSION

4.1. Preference of N form

The results of amino acid tracer labeling experiments showed no change in $\delta^{15}N$ (Fig. 1). This means that larch trees did not uptake the amino acid (alanine) directly in this site, and it also showed that the amino acid did not turn into an inorganic form available for plants within 48 h, which means inorganic N production

Table 4 Needle $\delta^{15}N$ observed in ammonium and nitrate tracer experiments and soil nitrogen (N) pool.

Needle $\delta^{15}N$ (‰)[†]	Soil inorganic N (mg N) [‡]	
^{15}N-ammonium experiment		
127 ± 38	KCl-extractable ammonium	72.0
	Water-extractable mmonium	9.5
^{15}N-nitrate experiment		
84 ± 17	Nitrate	2.1

[†]Mean $\delta^{15}N$ values observed on Day 26 for all experiment trees and standard error were shown. Repeated number was 9 for both labeling experiments.
[‡] Data for potassium chloride (KCl)-extractable ammonium and nitrate was obtained on 6 June 2009, the closest observation day to the tracer application day (28 May 2009). Amount for water-extractable ammonium was estimated using Eq. (1) in 4.3 for 6 June 2009, because no observation was made. Soil volume in which tracers were spread was assumed to be a column of mineral soil layer with a diameter of 30 cm and 0 to10 cm depth.

was still slow in the middle of the growing season or amino acid was immobilized by microorganisms. In contrast, inorganic N in the form of ammonium was quickly assimilated and was transported to the needles of larch saplings within 2 h. Since these tracer experiments were conducted with the addition of ammonium, we cannot

rule out the possibility of interference of added ammonium in the uptake rate of amino acid, because it has been suggested that direct uptake of amino acid may take place favorably under limited supply of inorganic N (Jones *et al.* 2005). However, even if the uptake of amino acid were suppressed by the addition of ammonium, the importance of amino acid as a source of N would have been minor, because the natural abundance of amino acid was one order smaller than that of ammonium in the earlier half of the growing season. In addition, it should be noted that the level of ammonium concentration in the tracer experiment is naturally observed in the latter half of the growing season, as we describe in the next section. Therefore, from results of these tracer experiments no uptake of amino acid is expected.

From the inorganic ^{15}N labeling experimental results (Table 4), it can be said that larch trees uptake both forms of inorganic N. These results also indicate another important fact: Added ^{15}N-labeled ammonium was possibly diluted only by the soil solution. Because of the considerable amounts of ammonium and nitrate in the soil pool, dilution of the tracers must be considered. Generally, it is not easy to determine the exact extent of the volume of dilution in the soil. Therefore, we assumed that the labeling solution was uniformly spread in the volume of mineral soil with diameter of 30 cm and 10 cm deep. Using the data observed on 6 June 2009, one week ahead of the tracer application, the amount of KCl-extractable ammonium and nitrate in this volume of soil described above were calculated to be 72.0 and 2.1 mg N, respectively (Table 4). These data showed that 34 times more ammonium than nitrate existed in the soil. Since the same amount of tracer was applied in the form of ammonium and nitrate, a small difference in δ^{15}N of needles indicated a similar magnitude of uptake of labelled material from the soil pool. There are three possibilities to explain these observations: (1) dilution occurs only in the soil solution; (2) ammonium was taken up 34 times more than nitrate, or (3) nitrate was immobilized by microbes 34 times more intensively than ammonium. As we describe in Section 4.2, microbial activities are expected to be low in the first half of the growing season. Although we cannot exclude the possibility of a 34-fold increase in the uptake of ammonium or 34 times more intensive immobilization of nitrate than ammonium, we expect that the reason of dilution of the tracer label only in the soil solution is the most likely explanation.

Thus, contrary to our expectation, ^{15}N-ammonium was not diluted by the large KCl-extractable soil N pool, but rather by that in the soil solution (9.5 mg N). Apparently, the exchange and thus equilibration between adsorbed ammonium and ammonium in the soil solution

were slow. Although we cannot reject the possibility that nitrate was taken up much more quickly than ammonium, an equal preference for ammonium and nitrate, and a slow exchange between adsorbed ammonium and ammonium in the soil solution, seem to be explanations that are more reasonable. Dörr *et al.* (2012) also reported a long retention period of added ammonium in a temperate Norway spruce (*Picea abies* (L.) Karst.) forest, which is consistent with the idea of a slow release of adsorbed ammonium.

4.2. Seasonal dynamics of N in soil

The existence of permafrost affects the temperature and moisture in the surface soil layer and, as a result, many physiological processes. In our study, the soil inorganic N pool seemed to exhibit seasonality, depending on the soil temperature. To confirm this, the observed inorganic N soil pool was plotted against the cumulative degree days of soil temperatures at 20 cm (°C day). The inorganic N soil pool demonstrated clear non-linear seasonality, and it increased with soil temperature cumulative degree days (Fig. 2). In the beginning of the summer, the soil inorganic N pool was small. The increase in the pool started at some point in August, when the soil temperature degree days reached 300°C day. The soil inorganic N pool increased rapidly in August; then by the next June it was small again. The soil temperatures reach about 9–10°C when soil inorganic N pool begins to increase. Nadelhoffer *et al.* (1991) reported that in a laboratory experiment, between 3 and 9°C N mineralization rates of arctic soils in Alaska were relatively unaffected by temperatures but they increased significantly
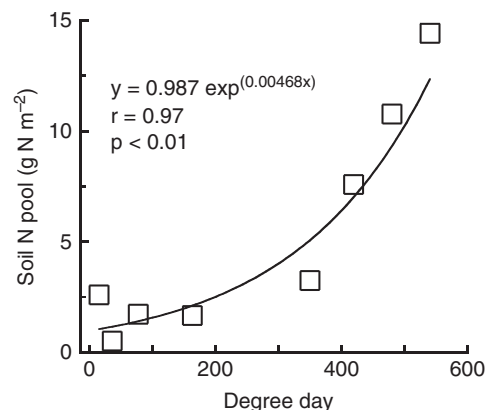
Figure 2 The relationship between inorganic nitrogen (N) soil pool and soil temperature cumulative degree day. *Open squares* indicate potassium chloride (KCl)-extractable inorganic N pool (mineral soil layer 0–50 cm) observed from 2009 to 2011 (data shown in Table 2). A fitted line was also shown. Degree days were calculated for each observation date from the soil temperatures above 0°C observed at 20 cm from 2009 to 2011.

between 9 and 15°C. Dependency of inorganic N production on temperature has also been shown by Hobbie (1996). Therefore, it is quite reasonable that active inorganic N production begins in the late summer and causes a rapid increase in the inorganic N in August at our site. Microbial activity in the late summer was also supported by a result of high soil respiration rate observed in August by Kononov (2006) at our study site.

Microbial consumption (immobilization) should be taken into consideration to explain the seasonality observed at our site. A large decrease of inorganic N pool size was observed in the second incubation experiment, which ended on 21 July 2011 (Table 3), indicating that microbial immobilization occurred during the period of incubation. As soil inorganic N pool is a result of two opposite processes – production and consumption of inorganic N – the size of the pool changes depending on their relative rates. As described above, the rate of production of inorganic N increased in late summer (mid-July and August), while the rate of microbial consumption is expected to increase subsequently after that. Ivanova *et al.* (2006) reported an increase in number of cellulolytic microorganisms (actinomycetes and fungi) from the beginning of September at our study site. The number of those was increasing until the beginning of October. Since the N source for those microorganisms would be inorganic N from the soil pool, a continuous increase in rate of consumption of inorganic N is expected in fall. A similar seasonal pattern for production and consumption was observed in the soil in a temperate beech (*Fagus sylvatica* L.) forest and explained by the availability of dissolved C for microorganisms (Kaiser *et al.* 2011). When the rate of consumption of inorganic N exceeds the rate of its production, the size of the inorganic N soil pool decreases. We observed the increase in the soil inorganic N pool in the late summer, which means the rate of production of inorganic N exceeded the rate of its consumption. In the fall the rate of inorganic N consumption is expected to prevail,

leading to an observed decrease in the size of inorganic N pool in the beginning of each growing season. It should be noted that the year-to-year variations of inorganic N production and consumption rates affect the size and the timing of build-up of the soil inorganic N pool.

Microbial activity during the winter has not been well understood so far. However, some researchers have suggested there is microbial activity in the winter. According to Kielland *et al.* (2006) microbial processes continue in the soil even after the soil temperatures dip below zero degrees. At our site, some microorganisms were found in the beginning of the spring (Ivanova *et al.* 2006). Although microbial activity during the winter has not been proven, a large soil inorganic N pool observed in late summer was consumed until the early summer of the following year.

It has been reported that the inorganic N pool showed year-to-year variation depending on mean air temperature in July in Central Siberia (Tokuchi *et al.* 2010). Although a year-to-year variation in the soil inorganic N pool is expected in our site, the contribution of seasonal variation (Fig. 2) might be of greater magnitude than that of the year-to-year variation (Fig. 3). It should be noted that this pattern of seasonality makes it inconvenient for plants to uptake N because of the discrepancy in timing between inorganic N production (starting from late summer) and active transpiration or growth of plants. The build-up of a large amount of inorganic N in the soil in fall is too late for plants, resulting in a decrease in the availability of N for plants.

4.3. Availability of N for plants
4.3.1. N budget

The main fluxes and pools of N observed in our study are summarized in Fig. 4. To describe variations of pools and fluxes in the ecosystem, we used the average annual N throughfall shown in Table 1, the highest observed values of bulk N and the soil inorganic N pool presented
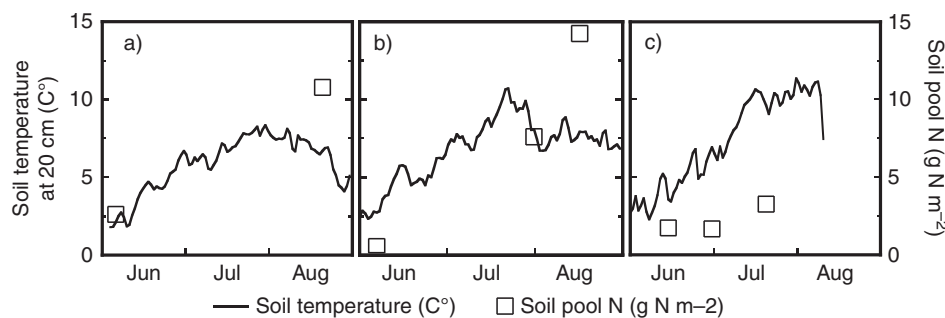
Figure 3 The seasonal changes in the size of the soil inorganic nitrogen (N) pool observed in 2009 (a), 2010 (b), and 2011 (c). A *solid line* represents daily average soil temperature observed at 20 cm depth, *open squares* denote potassium chloride (KCL)-extractable soil inorganic N pool size. "Layer" indicates the soil mineral layer, 0–50 cm.
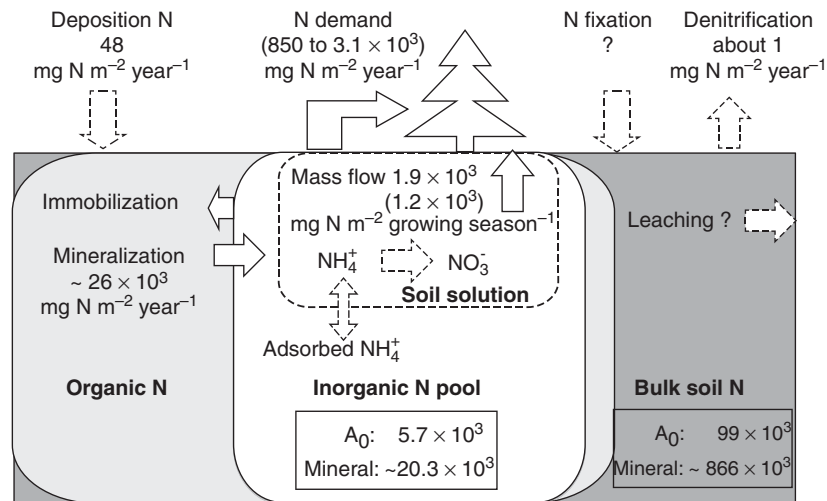
Figure 4 The schematic figure for nitrogen (N) pools in the soil (mg N m^{-2}) and ecosystem fluxes. *Areas outlined with solid lines* represent the following: *dark grey,* bulk soil N pool; *light grey,* organic N pool, *white,* potassium chloride (KCL)-extractable inorganic N pool. *Areas outlined with dashed lines* represent the water-extractable part of the inorganic N pool in the soil solution. The maximum sizes of the pools are described in the figure as *outlined values.* "A$_0$" and "Mineral" denote pools in organic layer and mineral soil layer (0–50 cm). respectively. Fluxes within the ecosystem or larch (*Larix cajanderi* Mayr.) trees (*in parentheses*) are shown by arrows with *open values. Solid arrows* are major fluxes, whereas *dashed arrows* are those expected to be minor or negligible. The maximum net mineralization rate (Table 3) shown here was calculated from the incubation that covered almost one year. N demand and mass flow estimation were explained in sections 4.2 and 4.3, respectively. "Growing season" indicates the period from 1 June to 31 August. The value for denitrification was calculated from Koide *et al.* (2010). Values of N fixation and leaching are not indicated here but are expected to be minor (Shugalei and Vedrova 2004).

in Table 2, and the inorganic N production observed in the first incubation experiment, which covered almost one year (Table 3). The amount of N in the litterfall and the amount of available N for plants is estimated later in this section.

Our results showed that a large amount of bulk N, up to 866 and 99 g N m^{-2} for the 0–50 cm mineral layer and the surface organic layer, respectively (Table 2), is stored in the soil mostly as organic matter. The inorganic N pool was up to 14.6 and 5.7 g N m^{-2} for the mineral layer and the organic layer, respectively, which accounts for 1.7 and 5.8% of bulk N in each layer. A major component of the soil inorganic N pool was ammonium in our study site (Table 2), and most of it exists in a form adsorbed on soil particles extractable with KCl. The large variation that is observed in the soil inorganic N pool (Table 2) indicates dynamic production and consumption of inorganic N in the soil. It has been reported that the contribution of N fixation to the inorganic N soil pool was minor in the larch forests in central Siberia (Shugalei and Vedrova 2004), and the rate of N loss due to denitrification was also very low (Koide *et al.* 2010; Matsuura and Hirobe 2010).

4.3.2. Plant N demand

In Lambers *et al.* (2008) and Shaver and Chapin (1991), nutrient recycling before senescence and new uptake

were considered to supply new growing parts. To evaluate the amount of recycled nutrients, we estimated N demand for our 150-year-old larch stand. In previous reports (Schulze *et al.* 1995; Shibuya *et al.* 2004), in northeastern Siberia, forest aboveground biomass becomes saturated at the age of 120–130 yr and does not change much after that. Therefore, we assume that the biomass production reported for 120 and 125-year-old stands (Schulze *et al.* 1995; Shibuya *et al.* 2004) was similar to that of our 150-year-old study site. The annual production of woody biomass required 240 to 1.0×10^3 mg N m^{-2} year^{-1}, and for the production of new needles 3.1×10^3 to 4.0×10^3 mg N m^{-2} year^{-1} was additionally needed. However, considering the reallocation of N from senescing larch needles, which has been reported to be about 70% (Gower and Richards 1990; Matsuura and Hirobe 2010), the estimated annual loss of N with litterfall would be only 930 to 1.2×10^3 mg N m^{-2} year^{-1}. The amount of N lost with the litterfall observed at our study site was about 500 mg N m^{-2} year^{-1} (A. Sugimoto, unpublished data), which was much lower than the estimated range above. Belowground production was not considered in many of the previous works, mainly because of the difficulty of such estimation in the field. Calculation of N demand based on the estimation of larch belowground production (Pozdnyakov *et al.* 1969) accounted for about

110 mg N m^{-2} year^{-1}. On the other hand, for the 105-year-old larch stand in central Siberia, the demand of N for belowground production was about 850 mg N m^{-2} year^{-1} (Tokuchi *et al.* 2010), and no recovery of N from tree roots has been reported so far. Using the minimum and maximum values described above, in total roughly 850 to 3.1 × 10^3 mg N m^{-2} year^{-1} is the range of demand for above- and belowground production annually by a larch stand only (requirements for needles, above-, and belowground production), which has to be covered by nutrient uptake. This range is wide but still provides an understanding of the magnitude of larch N demand and it covers somewhat that estimated for the central Siberia *L. gmelinii* stand (1.1 × 10^3 mg N m^{-2} year^{-1}) (Tokuchi *et al.* 2010).

4.3.3.   N availability

Nutrient supply occurs mainly via mass flow and diffusion (Lambers *et al.* 2008). It is expected that mass flow driven by evapotranspiration is an important force to supply nutrients to plants. Here we assessed the available N for plants using observed data on water-extractable inorganic N as shown in Table 2. The idea of assessment with water-extractable N is also supported by the observed fact that the ammonium-to-nitrate ratio collected by ion exchange resin (Table S2) functioning as plant roots was close to that in the soil solution. The amount of water-extractable N in the mineral soil layer (0–50 cm) was expected to increase from June (512 mg N m^{-2} on 15 June 2011) to August (1.6 × 10^3 mg N m^{-2} on 17 August 2010) as the KCl-extractable ammonium pool increased with soil temperature. To estimate the seasonal variation of water-extractable N, the relationship between water-extractable inorganic N (Table 2) and the cumulative degree day of soil temperature at 20 cm was obtained:

$$N\,pool_{w} = 345.4 \times exp^{0.00317 \times Tdd}(r = 0.78, p < 0.1) \qquad (2)$$

where $N\,pool_{w}$ is the soil water-extractable inorganic N pool (mg N m^{-2}) and Tdd denotes the cumulative degree days calculated for positive soil temperatures at 20 cm. Using this equation, we estimated the amount of soil water-extractable inorganic N pool for each day during the growing season. We assumed that this water-extractable N was transported with soil water and taken up by plants.

The concentration of water-extractable N in the soil solution was estimated as follows:

$$N\,concentration = N\,pool_{w}/Wg \qquad (3)$$

where *N concentration* is the concentration of total water-extractable inorganic N in the mineral soil solution (mg N l-soil solution^{-1}), $N\,pool_{w}$ is the mineral soil water-extractable inorganic N pool (mg N m^{-2}), and Wg (l m^{-2}) is the daily average amount of water in the soil layer (0–50 cm). In our estimation, the N concentration in the soil solution varied from 3 to 30 mg N dm^{-3} during the growing season. It has been reported that at our study site the evapotranspiration was 1.5 to 2.3 mm per day (Ohta *et al.* 2008) and the understory contribution was 35% of that (Ohta *et al.* 2001). The amount of inorganic N transported with the soil solution to the plant root surface was estimated assuming a mean evapotranspiration rate of 1.9 dm^3 m^{-2} day^{-1} (mm day^{-1}) (Kelliher *et al.* 1997; Ohta *et al.* 2008) so that during the period from 1 June 2010 to 31 August 2010, about 174.8 mm m^{-2} of water was assumed to have been transpired. The total amount of inorganic N transported to the root surface with the mass flow during the growing season was calculated to be 1.9 × 10^3 mg N m^{-2} period^{-1}. The amount of available N for the larch and other tall trees was estimated to be 65% of that value or 1.2 × 10^3 mg N m^{-2} period^{-1} (Fig. 4).

The amount of inorganic N supplied by mass flow barely covered the annual demand of the larch (850 to 3.1 × 10^3 mg N m^{-2} year^{-1}) estimated from annual biomass production. Despite the large amount of inorganic N produced in the soil, there are certain limitations of N availability for the larch. First, very little inorganic N exists in the soil pool in the beginning of the growing season, which is when plants require large amounts of nutrients. At the same time, a majority of the inorganic N exists in the form of ammonium adsorbed on soil particles. Aoki *et al.* (2012) showed the use of exudation of organic acids by plants to derive non-labile phosphate from phosphorus-poor soil. A similar mechanism might be used by plants to obtain adsorbed N, although the high expense for organic acids production required for it would limit the process. On the other hand, the inorganic N pool becomes large by the end of the growing season, when senescence starts and transpiration rate decreases, which also equates to a decrease in mass transport. Thus, there is a discrepancy between the timing of inorganic N production by microorganisms and the seasonal development of the larch, which leads to limitations in N availability for plants. In addition, competition for N among microorganisms and understory plants is expected to be very strong and is not considered in our estimation. It is obvious that the N budget for the larch is very tight and N availability must be limited.

The amount of N available for plants estimated in various boreal forests in the northern hemisphere at similar latitudes is presented in Table 5. N uptake estimated for

Table 5 Nitrogen (N) availability estimated in various types of boreal forest

Observation site	Latitude	Longitude	Dominant species[†]	Consumer of N	Nitrogen availability (mg N m^{-2} year^{-1})	Data from
Alaska	64°N	148°W	Spruce	Tree	920–1.4 × 10^3	Ruess *et al.* (1996)
Canada	46–48°N	89°W	Spruce	Ecosystem (aboveground)	(2.4–4.8) × 10^3	Gordon (1979)
Komi	61°N	50°E	Spruce	Ecosystem	6.0 × 10^3	Archegova *et al.* (1976)
Tunguska river basin	65°N	89°E	Larch	Ecosystem	(2.2–4.6) × 10^3	Shugalei and Vedrova (2004)
Kola peninsula	68°N	33°E	Spruce	Ecosystem	4.1 × 10^3	Lukina and Nikonov (1996)
Central Siberia	64°N	100°E	Larch	Tree	1.5 × 10^3	Tokuchi *et al.* (2010)
North-Eastern Siberia	62°N	129°E	Larch	Tree	1.2 × 10^3	This study

[†]Spruce species from observation site in: Alaska, *Picea glauca* (Moench) Voss; Canada, *Picea rubra* A. Dietr.; Komi, *Picea abies* (L.) H. Karst.; Kola peninsula, *Picea abies* (L.) H. Karst. Larch species from observation site in: Tunguska river basin, *Larix gmelinii* (Rupr.) Rupr.; Central Siberia, *Larix gmelinii* (Rupr.) Rupr.; North-Eastern Siberia, *Larix cajanderi* Mayr.

various boreal ecosystems differs from forest to forest, but it is somehow dependent on longitude. It is likely that in the Eurasian continent, the amount of N availability decreases from west to east or from spruce forest to larch forest. Differences in the methods for estimation of N availability make direct comparison difficult among the estimated values. This is because such processes as recovery of N from needles before litterfall, which accounted for a large amount of N at the scale of individual trees in this study, is not always taken into consideration in the methods based on net primary production. Nonetheless, all compared estimations are within the same order of magnitude, regardless of the method used for calculation. Among the ecosystems compared, our study in eastern Siberia and the study performed in Central Siberia showed the lowest utilization of N.

In the current study, we demonstrated the strong dependence of inorganic N production by microbiota on soil temperatures. According to the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (Solomon *et al.* 2007), it is expected that in the area of our study, the mean summer air temperatures are going to increase over the coming 70 to 80 years by 3–3.5°C. This considerable change would lead to an increase of soil temperatures and thus the production of inorganic N by microbes. On the other hand, the same report suggests a prospective significant increase in precipitation, especially during the winter (up to 50% of the current amounts). If this leads to later snowmelt, the timing of microorganism development and inorganic N production may be delayed.

5. CONCLUDING REMARKS

N transformation in soil is a very dynamic process with large seasonal variation: There was a rapid increase in the soil inorganic N pool in late summer followed by consumption by soil microbiota in the fall. Larch trees could not uptake organic N directly from the soil. The main source of

N for plants was the inorganic N (either ammonium or nitrate) that existed in the soil solution. The amount of N supplied by mass flow was barely enough to meet the demand of the larch trees. Soil temperature was one of the main factors limiting inorganic N availability.

6. SUPPLEMENTARY MATERIAL

Supplementary material for this article is available online at http://dx.doi.org/10.1080/00380768.2013.772495

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