EFFECTS OF SPRING EPHEMERAL HERBS AND SOIL MICROBES ON NITROGEN CYCLING IN A *QUERCUS MONGOLICA* FOREST

CHAE, H. M. – LEE, S. H. – YANG, K. C.*

Department of Smart Infrastructure Engineering, Kongju National University, Cheonan 31080, Korea

**Corresponding author
e-mail: yangkc@kongju.ac.kr*

(Received 31st Dec 2024; accepted 18th Mar 2025)

Abstract. The complex roles of soil microbes in forest N cycling require further research. We monitored N movement from 2010 to 2012 in a *Quercus mongolica* forest ecosystem. The net N uptake of spring ephemeral plants following snowmelt was 5.1 kg ha^{-1}, comparable to the amount of N leached from soil in early spring. Soil microbes stored N as microbial biomass N (MBN) at levels six times higher than the annual N leaching from the study site. However, in 2012, N storage by soil microbes decreased to 30% of the N uptake by spring ephemeral herbs, indicating a reduced capacity as stable N sinks. A significant correlation was found between N released from spring ephemeral herbs' decomposition and N uptake by summer green plants ($p < 0.001$, $r^2 = 0.4707$). Although soil microbes releasing 7–24 times more N, no significant correlation was observed with the N dynamics of summer green plants. Thus, spring ephemeral herbs serve as more stable N sinks and sources than soil microbes, regardless of environmental changes. This study highlights the critical role of spring ephemeral herbs in N cycling within the *Q. mongolica* forest ecosystem in Mt. Jeombongsan, Korea, emphasizing the need for detailed research on soil processes.

Keywords: *nitrogen sink, nitrogen source, microbial biomass nitrogen, summer green plants, Erythronium japonicum*

Introduction

In temperate regions characterized by distinct seasonal variations, a large quantity of leaf litter is accumulate during autumn. This accumulation of litter on the soil surface results from low winter temperatures, which limit microbial activity and slow decomposition. However, as temperatures and precipitation increase in spring, organic matter decomposition accelerates, leading to rapid mineralization and N loss from forest ecosystems through leaching (Zak et al., 1990; Zechmeister-Boltenstern et al., 2002; Tessier and Raynal, 2003; Castellano et al., 2013). Specifically, the concurrence of snowmelt, rise of soil temperatures, and mineralization of organic N during early spring (Williams and Melack, 1991; Bowman, 1992; Creed et al., 1996) leads to considerable N leaching from terrestrial ecosystems into groundwater and aquatic systems (Jeffries, 1990; Hornberger et al., 1994).

Plant growth is influenced by soil N, which is introduced into the soil through various processes, including leaf litter decomposition (Morgan and Connolly, 2013). During the growing season, plants absorb soil N and temporarily store it within their biomass. This highlights the considerable impact of N distribution and cycling in plant communities on N dynamics in forest ecosystems (Vitousek and Reiners, 1975; Morgan and Connolly, 2013).

In specific deciduous forests, N loss from the soil is reduced by the rapid growth and vigorous activity of spring ephemeral herbs and soil microbial communities prior to the

DOI: http://dx.doi.org/10.15666/aeer/2303_53275345

closure of the tree canopy. Muller and Bormann (1976) termed the process of N absorption and retention in spring ephemeral herbs as the “vernal dam” phenomenon. Spring ephemeral herbs contribute to this function by rapidly growing during the brief period between snowmelt and canopy closure (Muller, 1978; Blank et al., 1980; Peterson and Rolfe, 1982; Eickmeier and Schussler, 1993; Jandl et al., 1997; Anderson and Eickmeier, 2000; Pan et al., 2025). Furthermore, alpine plants (Mullen et al., 1998; Jaeger et al., 1999) and soil microbes (Zak et al., 1990; Groffman et al., 1993; Rothstein, 2000) have been recognized as important N sinks during spring. However, recent studies have investigated the phenology of spring ephemerals in relation to climate change (Hereford et al., 2017; Bucher and Römermann, 2021), and studies related to the ecosystem function, such as nitrogen cycling, are lacking.

Some researchers have reported that soil microbial biomass-N (MBN) can exceed the N absorbed by spring ephemeral herbs by a factor of 8–20 (Zak et al., 1990; Rothstein, 2000; Tessier and Raynal, 2003). This leads to an ongoing debate regarding the relative importance of soil microbes and spring ephemeral herbs in preserving soil nutrients. Moreover, some studies have indicated that the N absorption capacity of spring ephemeral herbs is negligible compared to N loss from the forest floor (Tremblay and Larocque, 2001; Mabry et al., 2008). Additional research has questioned the N release during the decomposition of spring ephemeral herbs, alongside their storage capacity (Muller and Bormann, 1976; Bormann et al., 1977). Despite these ongoing debates and the absence of frequent observation of the vernal dam phenomenon in terrestrial ecosystems, the role of spring ephemeral herbs in N cycling is widely recognized (Eickmeier and Schussler, 1993; Farnsworth et al., 1995; Jandl et al., 1997).

Against this background, we aimed to elucidate the functions of spring ephemeral herbs and soil microbes in the N cycling process. To achieve this, two specific objectives were established: (1) to assess the functions of spring ephemeral herbs and soil microbes as N sinks that mitigate substantial N loss during snowmelt in early spring, and (2) to determine whether spring ephemeral herbs act as N sources for other plants following the closure of the tree canopy.

From 2010 to 2012, we monitored N dynamics by quantifying the N contents in spring ephemeral herbs, soil microbes, and soil on a biweekly basis from April (the emergence of spring ephemeral herbs) to June (the disappearance of spring ephemeral herbs’ above-ground parts). Additionally, the growth and N content of summer green plants, along with changes in microbial N, were monitored until October, coinciding with the peak leaf litter season in autumn.

Materials and methods

Study site description

The study site, Mt. Jeombongsan (1424 m above sea level), is located on the border of Girin-myeon in Inje-gun and Seo-myeon in Yangyang-gun (38°0′–38°5′ N, 128°25′–128°30′ E, *Fig. 1*). Mt. Jeombongsan is situated to the north of Mt. Seoraksan and Hangyeryeong Pass, while it extends southward to the ridgeline of Gachilbong. In 1982, the Mt. Seoraksan region was designated as a Biosphere Reserve under the Man and Biosphere Project of UNESCO. Mt. Jeombongsan, situated at the southern end of Mt. Seoraksan National Park, is part of the core zone. The Mt. Jeombongsan area features well-developed mature oak forests. The canopy layer is primarily composed of *Q. mongolica* (Mongolian oak) and *Tilia amurensis* (Amur lime) trees, exhibiting diameters at breast height (DBH) ranging from 60 to 70 cm. The sub-canopy is primarily populated by *Acer pseudosieboldianum* (Korean maple) and *Carpinus cordata* (heartleaf hornbeam), which actively regenerate in forest gaps created by the mortality of dominant oaks. The herbaceous layer is dominated by *Sasa borealis* (Korean dwarf bamboo), *Rhododendron schlippenbachii* (royal azalea), and *Viburnum opulus* (guelder rose). The spring ephemeral herb layer includes various species, such as *Symplocarpus renifolius* (Asian skunk cabbage), *Erythronium japonicum* (dogtooth violet), *Anemone* spp. (windflower), and *Viola orientalis* (oriental violet) in early spring.

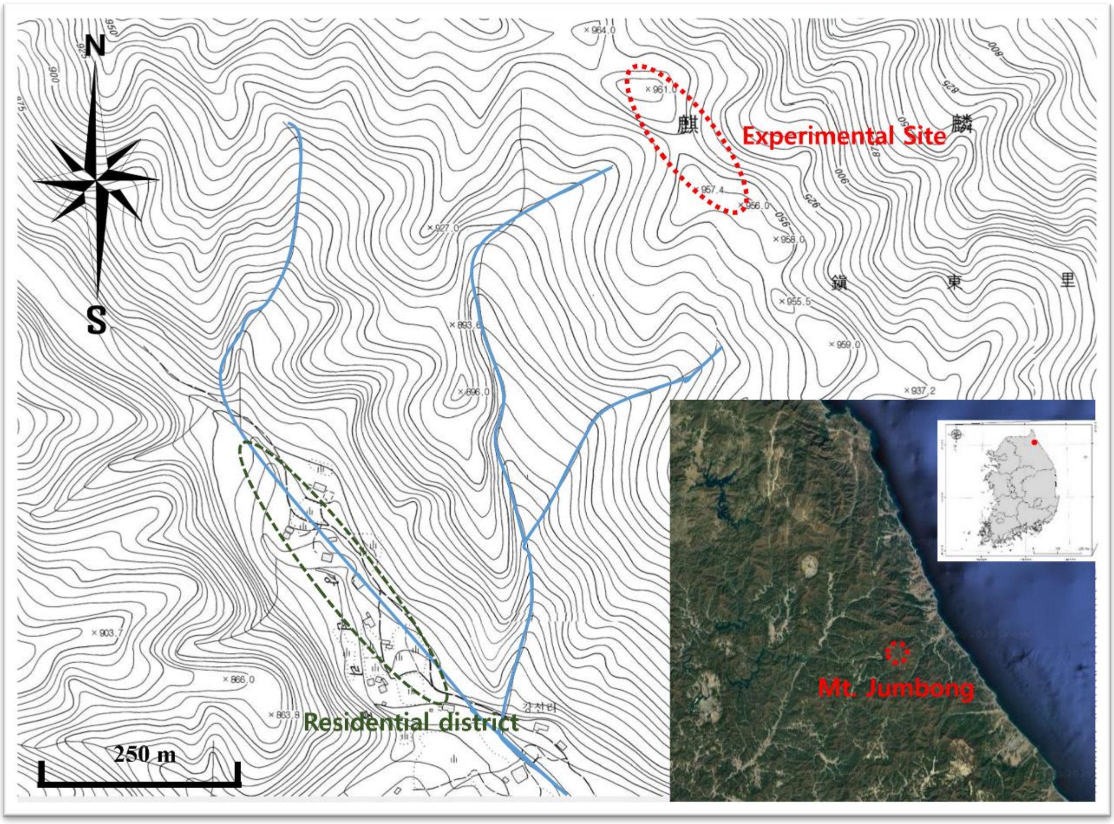

Figure 1. *Location of study area. The circle indicates the location of the Q. mongolica forest at the study site*

In autumn, some species, including *Aster scaber* (Korean aster), *Geranium thunbergii* (Thunberg’s geranium), *Ainsliaea acerifolia* (maple-leaf ainsliaea), and *Astilbe rubra* (red astilbe), dominate. Additionally, this region is home to numerous rare plants, including *Hanabusaya asiatica* (Asiatic bellflower), *Megaleranthis saniculifolia* (sanicle-leaved megaleranthis), *Aster altaicus* (Altai aster), and *Campanula takesimana* (Korean bellflower). Furthermore, high-value wild edible plants, including *E. japonicum, Angelica utilis* (Japanese angelica), and *Ligularia fischeri* (Handaeri ragwort), are prevalent, indicating a need for targeted conservation strategies (Lee and Cho, 2000). In addition, leguminous plants involved in biological N fixation, such as *Lespedeza bicolor* (shrub lespedeza) and *Lespedeza maximowiczii* (Korean lespedeza), have been identified; however, their low coverage and density indicate a minimal contribution to N fixation.

According to data from the Inje weather station near the study site, Mt. Jeombongsan exhibits typical inland climatic characteristics, and the annual mean temperature is 10.1°C, with mean maximum and minimum temperatures of 16.5°C and 4.7°C, respectively. January, the coldest month, has a mean temperature of -5.2°C, with the mean minimum falling to -11.0°C. August, the warmest month, has a mean temperature of 23.3°C, with a mean maximum of 28.7°C. The observed patterns reflect a continental climate characterized by extreme heat during summer and severe cold in winter. The mean annual precipitation is 1210.5 mm, with 60.0% (726.9 mm) occurring between June and August, indicating a notable summer precipitation peak.

During the study period (2010–2012), the annual total precipitation was 1354 mm, 1779 mm, and 1024 mm, respectively, with a mean precipitation of 1386 mm. The mean annual temperatures were 10.2°C, 9.3°C, and 10.0°C, respectively (*Fig. 2*). Compared to the 30-year climatological normal (1980–2010), temperatures exhibited no significant annual deviations. However, precipitation exceeded the climatological normal by 567 mm in 2011. Notably, rainfall increased considerably between April and July, recording 879 mm above the climatological normal, whereas August and September experienced substantially lower rainfall. These shifts in precipitation patterns are expected to influence N cycling within the *Q. mongolica* forest ecosystem on Mt. Jeombongsan.

To investigate N cycling in the *Q. mongolica* forest, we installed ten quadrats measuring 10 × 10 m. From 2010 to 2012, we quantified N input into the forest ecosystem through standing biomass, tree productivity, litterfall production, and rainfall, alongside N output via soil N leaching. The results are summarized in *Table 1*.

Table 1. *Nitrogen budget (kg $ha^{-1}yr^{-1}$) of the Q. mongolica forest at the study site*

		2010	2011	2012	Average
Plant uptake		151.5	152.4	141.7	148.6
Litterfall		84.8	65.9	70.7	73.8
Atmospheric N input (rainfall)		-	7.9	3.2	5.6
Internal N input	Throughfall	-	15.5	4.2	9.9
	Stemflow	-	1.3	0.3	0.8
	Decomposition	29.9	32.1	32.5	31.5
	Total	-	48.9	37.0	42.2
N output	N leaching	-	25.8	11.1	18.5

Experimental design

This study modified the experimental design of Rothstein (2000) to quantitatively evaluated N cycling and its processes in a representative temperate deciduous forest dominated by *Q. mongolica* from 2010 to 2012 (*Fig. 3a, b* and *c*). Seasonal measurements of N distribution and movement within the forest were performed over three years. Four quadrats, each measuring 3 × 3 m, were established to investigate N dynamics in herbs and soil. To quantify N leaching from the forest ecosystem, four lysimeters were installed at the center of each quadrat. The lysimeters collected soil leachate, which was analyzed for NO_3^--N and NH_4^+-N to assess N inputs and outputs in the Q. mongolica forest. Plants were sampled biweekly from April (when spring ephemeral herbs emerge) to June (when their above-ground parts disappear) to analyze the relationship between N leaching resulting from early spring snowmelt and N cycling in herbs and soil microbes. Soil samples were collected in 10 cm increments to a depth of 30 cm for evaluating MBN. Moreover, to investigate N dynamics after the decline of spring ephemeral herbs and canopy closure, summer green plants were seasonally sampled from May to late October, and their N contents were analyzed for changes. Variations in N content among spring ephemeral herbs, summer green plants, and soil microbes were analyzed to clarify N dynamics and interactions within the Q. mongolica forest ecosystem.

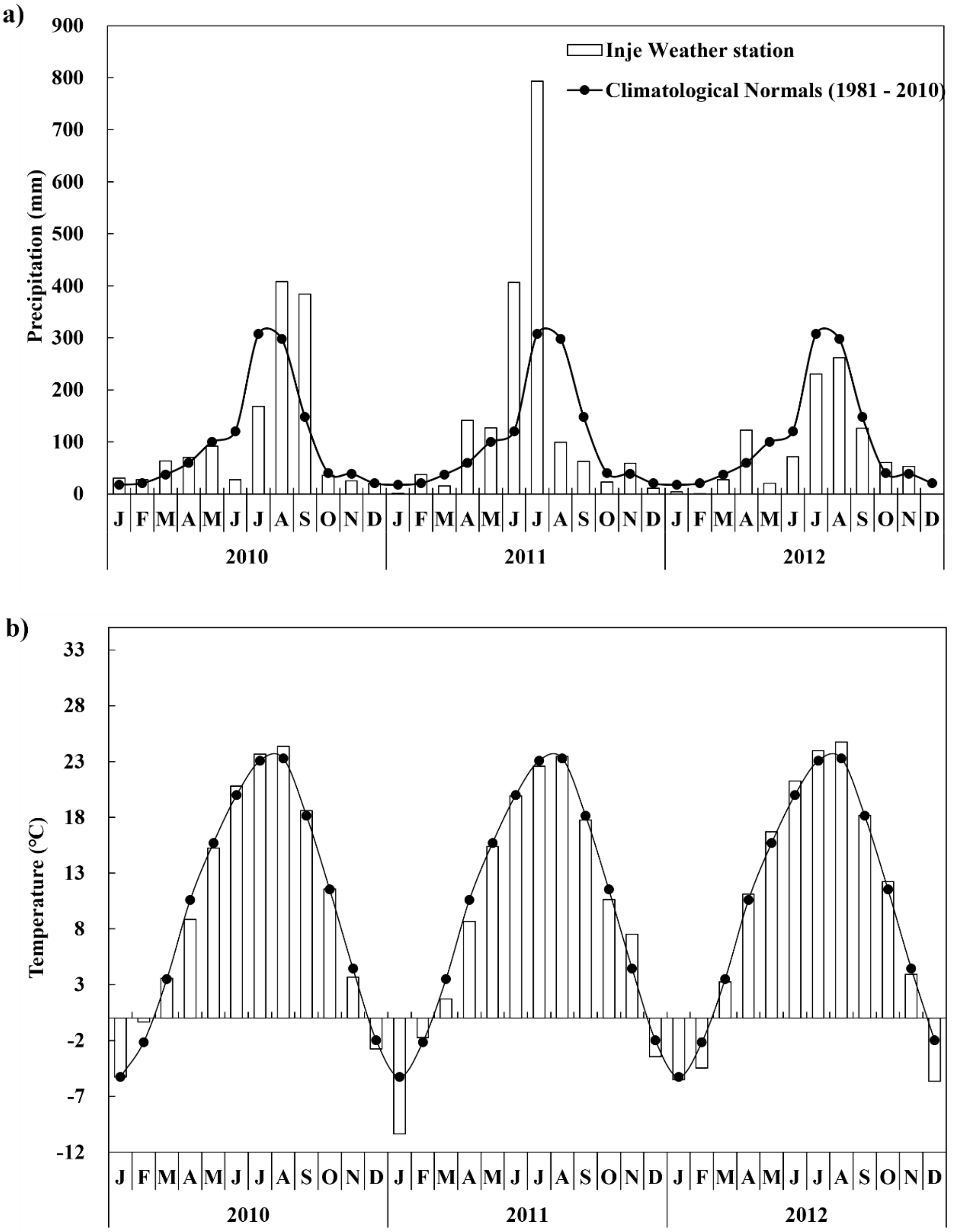

Figure 2. *Seasonal patterns of a) precipitation (mm) and b) temperature (℃) from 2010 to 2012 and climatological normals (1981-2010) at the Inje weather station*

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2303_53275345

***Figure 3.** Photos of study sites and plants. Study site in (a) March, (b) April, and (c) May. Spring epermeral herbs (d) E. japonicum and (e) A. raddeana. Summer green plants (f) M. urticifolia, (g) A. acerifolia and (h) C. siderosticta*

Establishment of quadrats and lysimeters

In April 2010, four quadrats (3 × 3 m) were established within the *Q. mongolica* forest at Mt. Jeombongsan. The quadrats were located on level ground wherever feasible, avoiding irregular terrain and areas with large, dead trees. The quadrats were spaced at least 10 m apart. Within each quadrat, nine subplots (1 × 1 m) were arranged in a grid pattern, and herb density was surveyed in eight subplots (excluding the center). The density survey identified *E. japonicum* as the predominant species, with *Anemone raddeana* Regel (many-sepal anemone) co-occurring (*Fig. 3d* and *e*). After the mid-May decline in the growth of spring ephemeral herbs, summer green plants, including *Meehania urticifolia* Makino (nettle-leaf mint), *Carex siderosticta* Hance (creeping broad-leaf sedge), and *A. acerifolia* Sch. Bip (Ainsliaea) emerged as the dominant species (*Fig. 3f*, *g* and *h*). The densities observed within the study site are presented in *Table 2*.

***Table 2.** Average stem density of spring ephemeral herbs and summer green plants in the Q. mongolica forest from 2010 to 2012*

	Spring Ephemeral herbs		**Summer green plants**		
	E. japonicum	***M. urticifolia***	***M. urticifolia***	***C. siderosticta***	***A. acerifolia***
Stem density (stem m^{-2})	21.5 ± 1.8	23.6 ± 5.0	7.1 ± 1.7	11.3 ± 6.5	3.9 ± 0.5

To measure N leaching from the soil, a lysimeter (20 cm in diameter and 314 cm^2 in surface area) was installed at a depth of 50 cm in the center of each quadrat in June

2010, resulting in a total of four lysimeters. This selected depth corresponds to the primary distribution of plant roots within the top 50 cm of soil, thereby allowing the lysimeters to capture N that was not absorbed by plants but rather leached through the soil (Gale and Grigal, 1987; Rothstein, 2000). The collected soil leachate was measured for volume in the field and subsequently transported to the laboratory for the analyses of NO_3^- and NH_4^+ contents.

Plant sampling and N analysis

Herbaceous plants were sampled from the area surrounding the quadrats between April 2010 and October 2012. From April to mid-June, during the emergence of spring ephemeral herbs, specific species, such as *E. japonicum* and *Anemone raddeana*, were sampled every 2–3 weeks. Following the disappearance of the above-ground parts of spring ephemeral herbs, summer green plants were sampled on two occasions: once during their peak growing season in summer and again during the leaf-fall period that marked the end of the growing season. For each plant species, 5–20 whole plants, encompassing both shoots and roots, were sampled in four replicates from the quadrats. The collected samples were transported to the laboratory in sealed containers, cleaned of soil, separated into above-ground and below-ground components, and dried at 80°C. The dried plant material was subsequently weighed and ground using a Wiley mill (Thomas Scientific, 3383L10) with a 0.1-mm mesh for N content analysis.

Total N content in the plant samples was determined using the Kjeldahl method as follows: A 0.5 g subsample of ground plant material was placed in a 250 ml digestion tube accompanied by two Kjeltab tablets (FOSS) and 10 ml of sulfuric acid. The samples underwent digestion at 400°C for 120 min using a Tecator digestion system (FOSS, Hillerod, Denmark), followed by a minimum cooling period of 15 min. After digestion, the samples underwent distillation using a Kjeltec 8100 distillation unit (FOSS, Hillerod, Denmark) into a 4% boric acid solution. The N content was subsequently quantified through titration using 0.05 N hydrochloric acid. To estimate N content per unit area, plant density (*Table 2*) was multiplied by dry biomass per unit area, and this value was subsequently multiplied by the N concentration to calculate the total N per unit area.

Soil N leaching

N leaching from the soil was monitored from 2011 to 2012. During the growing season of spring ephemeral herbs (April to June), soil leachate was collected every 2–3 weeks using lysimeters. Outside this period, leachate was collected after rainfall events exceeding 5 mm. The collected leachate volume was measured in the field using a volumetric flask, filtered on-site, and transported to the laboratory in sterile 50-ml conical tubes. The NO_3^- and NH_4^+ concentrations in the leachate were analyzed using a flow injection analyzer (FIAstar 5000, FOSS, Hillerod, Denmark). N leaching amounts were calculated based on the leachate volume, lysimeter collection area, and measured NO_3^- and NH_4^+ concentrations.

Soil sampling and microbial biomass N

Soil samples were collected from 2010 to 2012, coinciding with the timing of plant sampling. Soil was extracted in 10 cm increments to a depth of 30 cm using a soil corer.

Soil samples were collected from adjacent areas outside the quadrats to minimize disturbance to the herbs and lysimeters within the quadrats. The collected soil samples were sealed on-site and transported to the laboratory for analysis.

In the laboratory, fresh soil was passed through a 2-mm-mesh sieve and used to measure moisture content, NH_4^+-N, NO_3^--N, and MBN. NH_4^+-N and NO_3^--N contents in soil were measured using a flow injection analyzer (FIAstar 5000; FOSS, Hillerod, Denmark). Specifically, 5 g of fresh soil was mixed with 50 ml of 2 M KCl for 30 min, and the resulting extract was filtered using Whatman No. 42 filter paper. The measured concentrations were adjusted to a dry-soil basis, accounting for soil moisture content.

Soil MBN was quantified using the fumigation-extraction method (Ross and Sparling, 1993). Fresh soil samples (20 g) were fumigated with 25 ml ethanol-free $CHCl_3$ in a vacuum desiccator for 24 h at 23°C in the dark. Subsequently, $CHCl_3$ was removed from the soil through repeated cycles of vacuum aspiration and pressure restoration. Both fumigated and non-fumigated soil samples (10 g each) were shaken with 40 ml of 0.5 M K_2SO_4 for 30 min and filtered using Whatman No. 42 filter paper. The resulting filtrates were used to assess MBN via the ninhydrin-reaction method (Joergensen and Brookes, 1990). In the analysis, 0.7 ml of the 0.5 M K_2SO_4 soil extract, blank, and standard solution were allocated to individual test tubes. Ninhydrin reagent (1.2 ml) and citric acid (1.75 ml) were introduced into each tube, followed by a reaction in boiling water for 25 min. After cooling, 4.5 ml of ethanol-water solution (1:1) was added to each tube, and absorbance was recorded at 570 nm using a spectrophotometer (DU650, Beckman, CA, USA). The MBN was calculated using the formula $MBN = 5.0 \times EN$, where EN represents the difference in absorbance between fumigated and non-fumigated samples.

N uptake and release of spring ephemeral herbs and soil microbes

The N contents of plant samples and soil MBN were converted to N per unit area. N uptake and release were calculated by analyzing variations in total N over the sampling periods. The net N uptake was calculated as the difference between the maximum N content during the growing season and the initial N content at the beginning of the growth phase. The net N release was calculated as the difference between the maximum N content during the growing season and the N content at the end of the season.

Statistical analysis

One-way analysis of variance (ANOVA) was performed, followed by Tukey’s HSD post-hoc test, to evaluate differences of biomass, N uptake and release between each species of spring ephemeral herbs and summer green plants, and soil microbes by depth. Furthermore, statistical significance of the differences between total spring ephemeral herbs, summer green plants, and soil microbes was determined by ANOVA and T-test. Correlation analysis was employed to investigate the effects of spring ephemeral herbs, summer green plants, and soil microbes on N leaching and soil inorganic N (NH_4^+ and NO_3^-). Additional correlation analysis was performed to examine the relationship between N uptake by summer green plants and N release by spring ephemeral herbs and soil microbes. The significance of the correlations was assessed using Pearson’s correlation coefficient, and linear regression analysis was performed to further explore these relationships. All statistical analyses were conducted using PASW Statistics 18 software (SPSS Inc., Chicago, USA).

Results

Changes in soil NO_3^- and N leaching

From 2011 to 2012, measurements were taken of the N contents in herbaceous plants, soil NO_3^- concentrations, and NO_3^- leaching in alignment with the lifecycle of herbs in the *Q. mongolica* forest understory to monitor changes in plant growth, N content, and soil N dynamics. Sampling was conducted biweekly from April to May, coinciding with the overlapping life cycles of spring ephemeral herbs and summer green plants. The results are presented in *Figure 2*. In 2011, NO_3^- concentrations in the topsoil (0–20 cm) were at their lowest in early April (4.97 mg kg^{-1}), coinciding with the onset of growth in spring ephemeral herbs. Concentrations increased until May 13, subsequently declining and stabilizing. This variation in soil NO_3^- concentration correlated with the onset of early spring thawing. The decrease in NO_3^- during this period was linked to a significant increase in N leaching. A similar pattern was observed in 2012. Soil NO_3^- concentrations were initially low in April, increased after May 11, and subsequently stabilized. Concurrently, NO_3^- leaching peaked in April and decreased as soil NO_3^- concentrations increased. Following these springtime changes, NO_3^- leaching was observed during heavy rainfall periods in July and August 2011 and between July and September 2012. However, this leaching did not significantly impact soil NO_3^- concentrations (*Fig. 4*). Throughout the study period, no statistically significant correlation was observed between soil NO_3^- concentrations and NO_3^- leaching, indicating that elevated NO_3^- concentrations in the soil did not directly influence leaching rates.

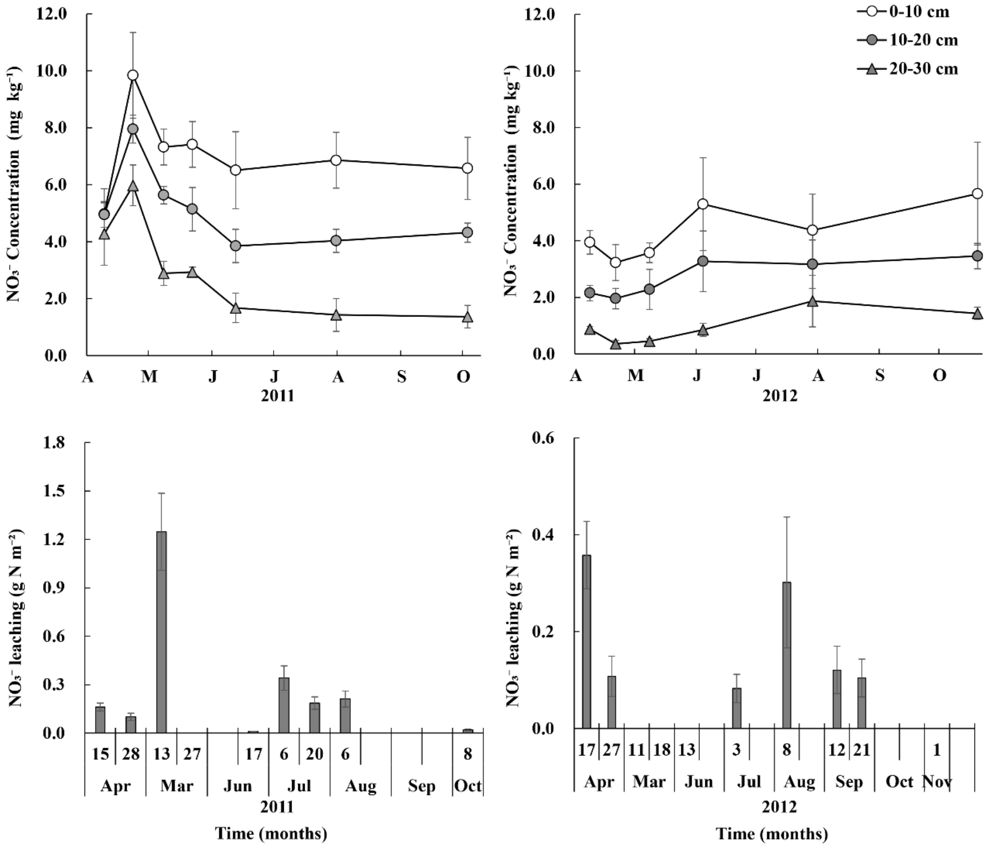

Figure 4. *Comparison of NO_3^- concentration (mg kg^{-1}) in soil and amount of NO_3^- leaching (g N m^{-2}) in 2011 and 2012*

N fluxes in herbs and soil microbes

The annual means of biomass, net N uptake, and net N release for spring ephemeral herbs, summer green plants, and soil microbes for 2010–2012 are presented in *Table 3*. The mean biomass of spring ephemeral herbs was 627.7 kg ha^{-1}, which higher than that of summer green plants, 511.7 kg ha^{-1}, but statistical significant was not found. The other hands, the mean biomass of *E. japonicum* was statistical significantly higher than that of the other four species ($p < 0.001$). Net N uptake was 5.1 kg ha^{-1} for spring ephemeral herbs, 3.8 kg ha^{-1} for summer green plants, and 214.0 kg ha^{-1} for soil microbes, indicating a significantly higher uptake for the latter ($p < 0.001$). Net N release followed a similar trend, with 3.4 kg ha^{-1} released by spring ephemeral herbs and 177.4 kg ha^{-1} by soil microbes. Soil microbes exhibited net N uptake ($p < 0.001$) and release rates ($p < 0.05$) that were 5 to 24 times higher than those of spring ephemeral herbs. The annual mean N leaching was 18.5 kg ha^{-1}yr^{-1}. Soil microbes absorbed between 1.5 and 5 times the amount of N that was leached, whereas spring ephemeral herbs absorbed approximately 28% of the leached N. This highlights the comparatively lower ecological function of spring ephemeral herbs in mitigating N leaching compared to soil microbes. The net N release from spring ephemeral herbs accounted for 89% of the net N uptake by summer green plants, whereas soil microbes released 7 to 23 times more N.

Table 3. *Comparison of biomass, net N uptake, and N release of spring ephemeral herbs, soil microbes and summer green plants*

		Biomass (kg ha^{-1})	**Net N uptake (kg ha^{-1})**	**Net N release (kg ha^{-1})**
Spring Ephemeral herbs	*E. japonicum*	549.0 (87.5)a**	4.4 (86.3)a**	2.5 (73.5)a*
	A. raddeana	78.7 (12.5)b**	0.8 (26.5)b**	0.9 (26.5)a*
	Total	627.7 (100)*NS*	5.1 (100)A**	3.4 (100)A*
Summer green plants	*M. urticifolia*	161.7 (31.6)b**	1.6 (42.1)b**	
	C. siderosticta	186.9 (36.5)b**	1.1 (28.9)b**	
	A. acerifolia	163.0 (31.9)b**	1.0 (26.3)b**	
	Total	511.7 (100)*NS*	3.8 (100)A**	
Soil microbes	0-10 cm		89.4 (41.8)c**	81.9 (46.2)b*
	10-20 cm		95.2 (44.5)c**	68.5 (38.6)b*
	20-30 cm		29.3 (13.7)ac**	27.0 (15.2)ab*
	Total		214.0 (100)B**	177.4 (100)B*

Numbers in parentheses are percentages of the total
Different lowercase indicate a significant difference between species, and soil microbes by depth as a result of post-hoc analysis (Tukey`s HSD, *: $p < 0.05$ **: $p < 0.001$)
Different uppercase indicate a significant difference between total of species and total soil microbes as a result of post-hoc analysis or t-test (Tukey`s HSD, *: $p < 0.05$ **: $p < 0.001$, *NS*: not significant)

Figure 5 illustrates the N uptake and release of spring ephemeral herbs, soil microbes, and summer green plants, calculated for each sampling period over three years. Spring ephemeral herbs absorbed N in April and commenced releasing N into the soil by mid-May. Summer green plants started N uptake in May, coinciding with the N release period of spring ephemeral herbs. Despite some quantitative differences, the timing of N release by spring ephemeral herbs and N uptake by summer green plants was highly synchronized. Conversely, the timing of N uptake by summer green plants did not align with N release by soil microbes, which absorbed N until September and released it during winter. In 2010, soil microbes continued absorbing N until September and released it during winter. In 2011, while summer green plants commenced N uptake on May 13, soil microbes continued to absorb N from the soil. In 2012, soil microbes released N on May 18 but resumed N uptake shortly thereafter. These observations confirm that the timing of N uptake by summer green plants and N release by soil microbes are independent processes that do not coincide.

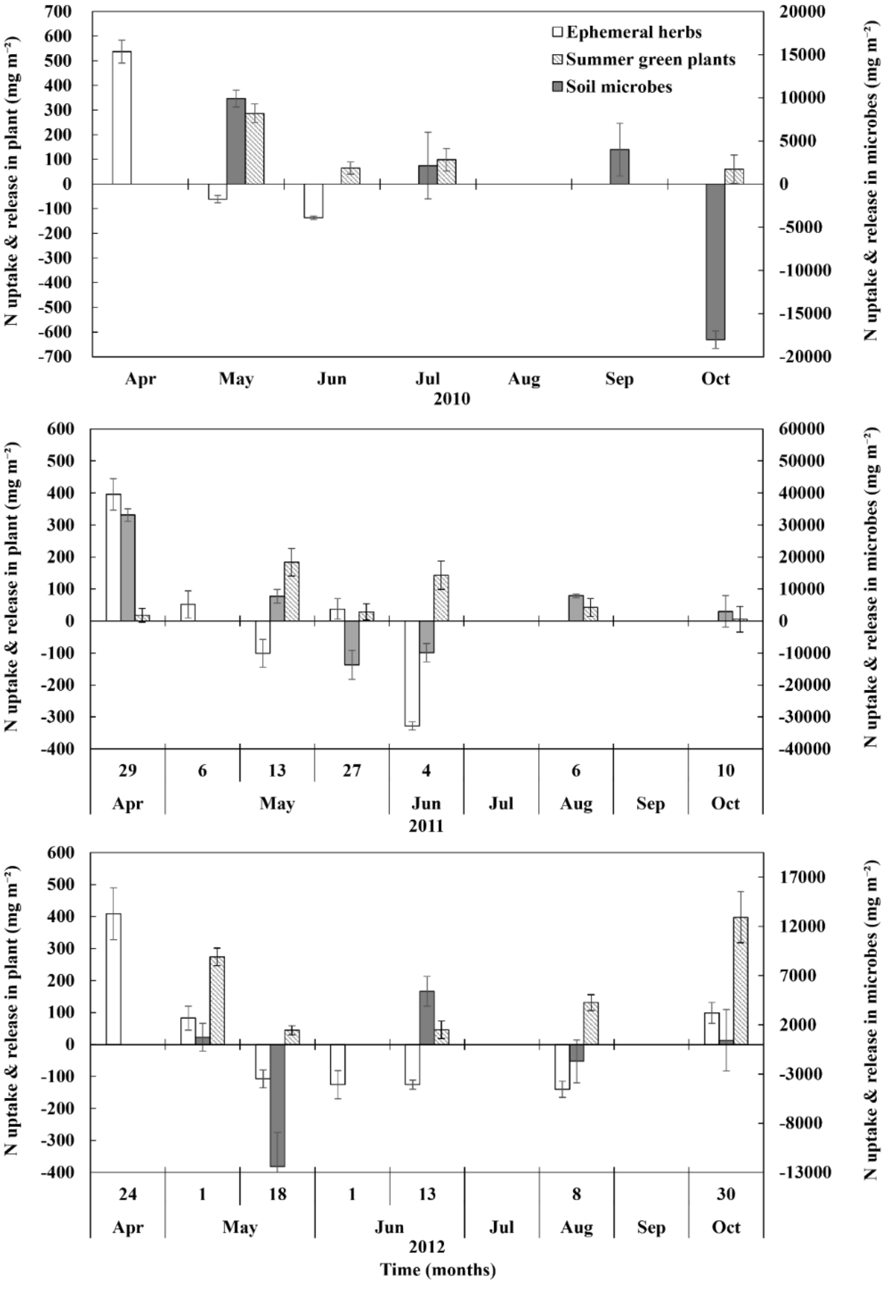

Figure 5. *Comparison of N uptake and release in ephemeral herbs, soil microbes, and summer green plants from 2010 to 2012. On the y-axis, positive values indicate N uptake and negative values indicate N release*

Relationship between soil N leaching, herbs, and soil microbes

A correlation analysis was conducted to investigate the effects of soil N leaching and soil inorganic N on the N dynamics of spring ephemeral plants, summer green plants, and soil microbes. The results are summarized in *Table 4*. No significant correlations were observed between N leaching and the N uptake or release of spring ephemeral herbs at any of the sampling points. However, partial correlations were observed for summer green plants, contingent upon the form of leached N. For instance, the N uptake and release of *M. urticifolia* were positively correlated with NH_4^+ leaching ($p < 0.05$, $r = 0.335$), whereas those of *Carex siderosticta* and *A. acerifolia* were positively correlated with NO_3^- leaching ($p < 0.05$, $r = 0.389$ and $p < 0.05$, $r = 0.341$, respectively). Moreover, soil N leaching was positively correlated with soil MBN ($p < 0.01$, $r = 0.400$) and microbial N uptake and release ($p < 0.01$, $r = 0.422$), indicating that soil microbes play a critical role as N sinks, thereby mitigating leaching.

No significant correlations were observed between inorganic soil N (NH_4^+-N and NO_3^--N) and the N uptake or release of spring ephemeral herbs. However, the N uptake and release of *Carex siderosticta* and *A. acerifolia* were negatively correlated with the total inorganic N ($p < 0.05$, $r = -0.281$ and $p < 0.05$, $r = -0.278$, respectively). Soil MBN was positively correlated with soil NO_3^- ($p < 0.01$, $r = 0.382$) and negatively correlated with NH_4^+ ($p < 0.05$, $r = -0.258$). Similarly, microbial N uptake and release were negatively correlated with NH_4^+ ($p < 0.05$, $r = -0.278$).

Table 4. *Correlation coefficients of N fluxes between plant, soil leaching, soil mineral N, net mineralization, and soil microbes during the entire survey period from 2010 to 2012*

		Leaching			**Soil**		
		NO_3^-	**NH_4^+**	**Sum**	**NO_3^-**	**NH_4^+**	**Sum**
Spring Ephemeral herbs	*E. japonicum*	0.237	0.278	0.241	0.049	-0.004	0.013
	A. raddeana	0.219	0.355	0.224	0.011	0.122	0.127
	Total	0.248	0.295	0.253	0.045	0.022	0.037
Summer green plant	*M. urticifolia*	-0.098	0.335^*	-0.093	0.060	0.098	0.112
	C. siderosticta	0.389^*	-0.018	0.387^*	-0.156	-0.247	-0.281^*
	A. acerifolia	0.341^*	0.182	0.342^*	-0.262	-0.210	-0.278^*
	Total	0.156	0.217	0.158	-0.225	-0.194	-0.255^*
Soil microbes	Biomass N	0.405^{**}	-0.144	0.400^{**}	0.382^{**}	-0.258^*	-0.107
	N uptake & release	0.422^{**}	0.173	0.422^{**}	0.039	-0.278^*	-0.241

* $p < 0.05$; ** $p < 0.01$

Effects of spring ephemeral herbs and soil microbes on summer green plants

Table 5 displays the results of the correlation analysis between the N uptake of summer green plants and the N release of spring ephemeral herbs and soil microbes. Significant positive correlations were observed between spring ephemeral herbs and summer green plants. *E. japonicum* exhibited significant positive correlations with all three summer green plants examined (*Fig. 6a*), particularly with their overall N uptake ($p < 0.001$, $r^2 = 0.5072$). However, the correlation with *M. urticifolia* was relatively low ($p < 0.01$, $r^2 = 0.2441$). *Anemone raddeana*, another spring ephemeral plant species, exhibited no significant correlation with *M. urticifolia* or *A. acerifolia*; however, it

DOI: http://dx.doi.org/10.15666/aeer/2303_53275345

showed positive correlations with *Carex siderosticta* ($p < 0.001$, $r^2 = 0.3558$) and the total summer green plants ($p < 0.001$, $r^2 = 0.4655$) (*Fig. 6b*). The total N release from spring ephemeral herbs was significantly correlated with the N uptake of summer green plants (*Fig. 6c*), particularly with their total uptake ($p < 0.001$, $r^2 = 0.4707$). However, the correlation with *M. urticifolia* was relatively low ($p < 0.05$, $r^2 = 0.1533$). In contrast, no significant correlations were observed between the N release of soil microbes and N uptake of summer green plants, indicating that N released by soil microbes is rarely utilized for the growth of summer green plants (*Fig. 6d*).

Table 5. *Correlation coefficients between N fluxes of spring ephemeral herbs, summer green plants, and soil microbes during the entire survey period from 2010 to 2012*

		Ephemeral herbs			**Summer green plants**				**Soil microbes**
		E. japonicum	***A. raddeana***	**Total**	***M. urticifolia***	***C. siderosticta***	***A. acerifolia***	**Total**	
Spring Ephemeral herbs	*E. japonicum*	1	.669**	.917**	.494**	.479**	.641**	.712**	.102
	A. raddeana		1	.822**	.221	.597**	.384*	.682**	-.560
	Total			1	.410*	.543**	.499**	.682**	-.120
Summer green plants	*M. urticifolia*				1	.566**	.504**	.867**	-.240
	C. siderosticta					1	.516**	.816**	-.232
	A. acerifolia						1	.618**	-.254
	Total							1	-.214
Soil microbes									1

* $p < 0.05$; ** $p < 0.0$

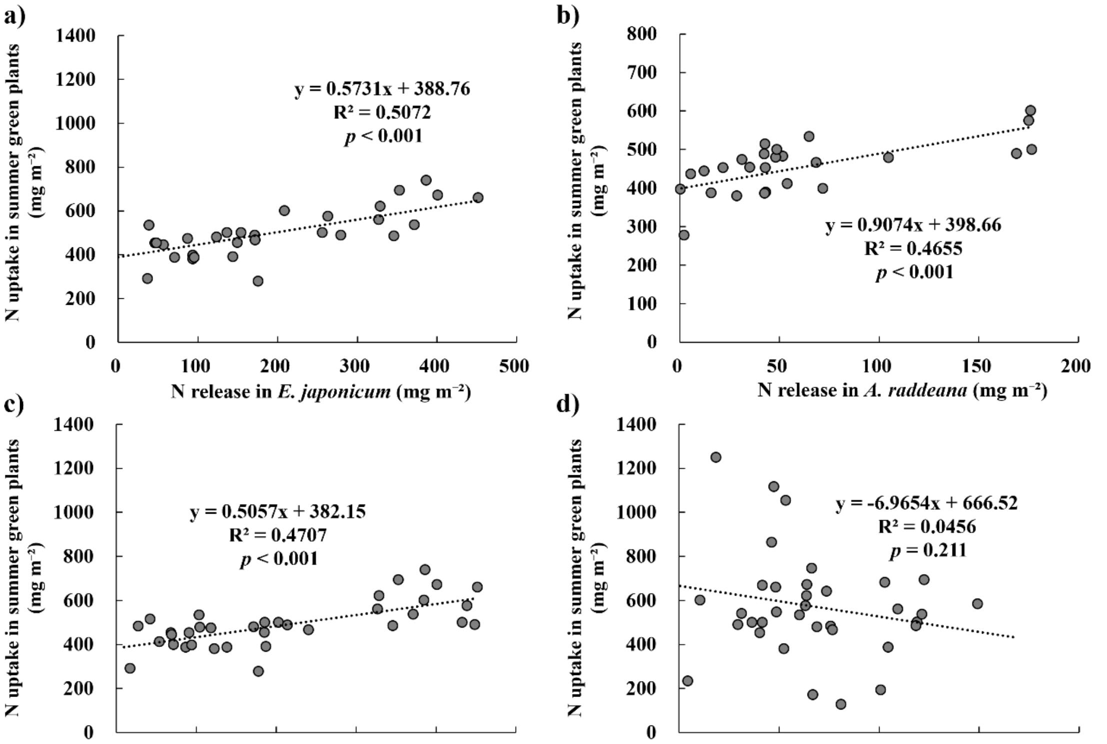

Figure 6. *Relationships of N fluxes between summer green plants and soil microbes and ephemeral herbs. (a) E. japonicum, (b) A. raddeana, (c) total ephemeral herbs, and d) soil microbes*

Overall, the timing and magnitude of N uptake by summer green plants correspond closely with N release by *E. japonicum*, highlighting its importance as a key N source for these plants. In contrast, despite their higher N release, soil microbes did not align temporally with the N uptake patterns of summer green plants.

Discussion

Relationship between soil N leaching and N uptake by spring ephemeral herbs and soil microbes

During the study period, the mean N uptake by spring ephemeral herbs was 5.1 kg ha^{-1} (*Table 3*), consistent with the range reported in previous studies: 1 kg ha^{-1} in a deciduous forest in New Hampshire (Muller and Bormann, 1976), 6 kg ha^{-1} in an Indiana beech-maple forest (Blank et al., 1980), 11 kg ha^{-1} in an Illinois oak-hickory forest (Peterson and Rolfe, 1982), and 4 kg ha^{-1} in a Michigan deciduous forest (Rothstein, 2000), with the findings from Michigan and Indiana most closely aligned with this result. Soil NO_3^- leaching resulting from snowmelt in early spring was measured at 5.4 kg ha^{-1} in 2011 and 4.7 kg ha^{-1} in 2012, values that were comparable to the N uptake by spring ephemeral herbs. However, in early spring 2011, heavy rainfall resulted in no statistically significant correlation between soil N leaching and N uptake by spring ephemeral herbs (*Table 4*). Interestingly, following the initiation of N release in May 2011, spring ephemeral herbs exhibited a brief resumption of N uptake after substantial N leaching occurred due to a rainfall event on May 13 (*Fig. 5*). This transient N uptake pattern observed exclusively in 2011 likely indicates a response to increased rainfall and highlights the significance of spring ephemeral herbs in maintaining ecosystem stability amid rapid environmental changes.

Soil microbes absorbed six times more N annually than the amount of soil NO_3^- leached, and a statistically significant correlation with N leaching was observed ($p < 0.01$, $r = 0.422$; *Table 3*). Their average N content was 1.4–3.0 times higher than that reported in previous studies (Zak et al., 1990; Holmes and Zak, 1994; Bohlen et al., 2001), indicating that the soil microbes at the study site functioned more effectively as N sinks than those in other regions. However, in 2012, soil microbial N uptake decreased to 30% of that by spring ephemeral herbs, shifting their function from an N sink to an N source (*Fig. 5*). This decrease is likely attributable to variations in early spring rainfall between 2011 (174.9 mm) and 2012 (21.1 mm) (*Fig. 2*). This indicates that soil microbial N uptake is more strongly influenced by rainfall than by snowmelt. Consequently, although spring ephemeral herbs possess a smaller capacity as N sinks compared to soil microbes, their ecological function as stable N sinks is more reliable.

These results indicate that soil microbes and spring ephemeral herbs contribute to forest N cycling under different environmental conditions and timeframes. Notably, after the record rainfall in 2011, MBN declined slightly during winter but remained higher than its peak activity in 2012 (*Fig. 5*). This result is consistent with that of Isobe et al. (2018), who reported that soil microbes maintained high activity during winter, thereby enhancing N cycling in temperate deciduous forests. Although microbial activity typically decreases at lower temperatures (Price and Sowers, 2004), evidence demonstrates that microbial growth and metabolism can persist even at freezing temperatures (Bakermans and Skidmore, 2011). High soil microbial activity is evident in winter, as demonstrated by leaf litter decomposition in snow-covered forests (Mullen et al., 1998; Jaeger et al., 1999; Schmidt et al., 2007), increased enzyme activity (Lipson et al., 2002; Kaiser et al., 2010; Voříšková et al., 2014), and elevated soil mineralization rates (Hishi et al., 2014; Zhang et al., 2014). This high biological activity observed during winter seems to be an adaptation aimed at minimizing competition for N with plants, suggesting that soil microbes and plants occupy temporally distinct ecological niches. Isobe et al. (2018) reported that microbial growth during plant dormancy in winter enables microbes to function as N sinks. Conversely, their N release during spring snowmelt provides an accessible N source for plants.

Relationship between the N release patterns of spring ephemeral herbs and soil microbes and the growth activity of summer green plants

Herbaceous plants in the forest understory are important for diversity and ecosystem function (Gilliam, 2007) and play an important role in storing and cycling nutrients such as nitrogen (Elliot et al., 2015). Shafer and Golay (2020) reported that early-flowering plants accumulate nitrogen nutrients primarily aboveground parts during flowering, and nutrients return to underground parts as the plants senesce. In this study, spring ephemeral herbs rapidly absorb N during the early spring snowmelt, corresponding to the amount of N leached from the soil. Starting in May, N is released back into the soil (*Fig. 5*), providing an N source for summer green plants during their leaf-out phase (Muller and Bormann, 1976). A significant positive correlation was observed between N release by spring ephemeral herbs and N uptake by summer green plants ($p < 0.001$, $r^2 = 0.4707$; *Fig. 6c*). Among the spring ephemeral herbs, *E. japonicum* exhibited the highest biomass and showed the strongest correlation with the growth of summer green plants ($p < 0.001$, $r^2 = 0.5072$; *Fig. 6a*), serving as an important N source for all three summer green species analyzed.

Spring ephemeral herbs demonstrated diverse responses to environmental changes, highlighting interspecies variations in N-cycling functions. For example, *E. japonicum* absorbed similar amounts of N in 2011 and 2012; however, its N release was significantly higher in 2011 (349.6 kg ha^{-1}) than in 2012 (252.2 kg ha^{-1}). In contrast, *Anemone raddeana* showed 3–4 times higher N uptake and release in 2012 than in 2011. These differences suggest interspecies variability in ecological functions associated with N cycling. This was consistent with findings by Blank et al. (1980), who reported interspecies differences in productivity and N uptake among six spring ephemeral species in Indiana. This variability may result from species with higher below-ground biomass depending on stored nutrients for early growth (Blank et al., 1980).

Conversely, soil microbes released 7–24 times more N than spring ephemeral herbs; however, no significant correlation was observed with the N uptake period of summer green plants (*Table 5*). These results suggest that the N released by soil microbes is not utilized by summer green plants during their growth phase (*Fig. 5*). This indicates that, although soil microbes act as efficient N sinks during early spring snowmelt, they do not function as N sources for summer green plants.

Impacts of spring ephemeral herbs and soil microbes on N cycling in forest ecosystems

Previous studies have questioned the role of spring ephemeral herbs as significant N sinks in forest ecosystems, noting that their N uptake is substantially lower than that associated with tree uptake, litterfall production, litter decomposition, soil microbial activity, and organic matter dynamics (Rothstein, 2000; Tremblay and Larocque, 2001; Mabry et al., 2008). In this study, the N uptake by spring ephemeral herbs accounted for only 3.4% of tree N uptake, 6.9% of N input from litter decomposition, and 5.7–17.3% of N uptake by soil microbes (*Tables 1* and *3*), which appears to align with previously expressed reservations. However, spring ephemeral herbs were found to play a crucial role as timely N sources during the leaf-out stage of summer green plants and other trees by releasing N stored in their biomass through the decomposition of their aboveground parts. Pan et al. (2025) reported that spring ephemeral herbs have a strong nutrient uptake capacity, and in our study, the N released by these accounted for 10.6% of the annual N input from leaf litter decomposition, indicating that the N released during their brief lifespan (1–2 months) is far from negligible (*Tables 1* and *3*). Therefore, given their brief growth period, the ecological role of spring ephemeral herbs as N sinks and sources—though previously questioned—should not be underestimated. They function as stable “vernal dams” and N sources, performing critical ecological functions even during rapid environmental changes, setting them apart from soil microbes.

Conclusions

The findings of this study confirm that spring ephemeral herbs serve as important N sinks and sources within temperate deciduous forest ecosystems. These herbs store N during the early spring snowmelt period, which is associated with the highest N loss in the *Q. mongolica* forest. Subsequently, they release this stored N during the leaf-out stage of summer green plants, thereby facilitating stable N cycling within the forest ecosystem. In contrast, soil microbes serve as major N sinks and buffer N loss during snowmelt and rainfall events; however, they do not contribute to N uptake in summer green plants because they occupy a distinct temporal niche compared to spring ephemeral herbs. This underscores the significance of spring ephemeral plants in the N cycling process, as they adapt to seasonal and short-term environmental changes.

This study also aimed to elucidate the role of soil microbes in forest N cycling by analyzing changes in microbial N content. However, because of the complexity and diversity of soil processes, more detailed and precise research is required to accurately quantify the functional roles and contributions of soil microbes to forest N cycling. In particular, further investigation is required to determine whether the observed increase in MBN during snowmelt and rainfall events mitigates N loss or, under specific conditions, promotes certain processes (e.g., denitrification and nitrification) that can amplify N loss.

Acknowledgements. This research was supported by the National University Development Project by the Ministry of Education in 2021 and Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2019R1A6A3A01096293).

REFERENCES

[1] Anderson, W. B., Eickmeier, W. G. (2000): Nutrient resorption in *Claytonia virginica* L.: implications for deciduous forest nutrient cycling. – Canadian Journal of Botany 78: 832-839.

[2] Bakermans, C., Skidmore, M. (2011): Microbial respiration in ice at subzero temperatures (-4°C to -33°C). – Environmental Microbiology Reports 3: 774-782.

[3] Blank, J. L., Olson, R. K., Vitousek, P. M. (1980): Nutrient uptake by a diverse spring ephemeral community. – Oecologia 47: 96-98.

[4] Bohlen, P. J., Groffman, P. M., Driscoll, C. T., Fahey, T. J., Siccama, T. G. (2001): Plant –soil–microbial interactions in a northern hardwood forest. – Ecology 82: 965-978.

[5] Bormann, F., Likens, G., Melillo, J. (1977): Nitrogen budget for an aggrading northern hardwood forest ecosystem. – Science 196: 981-983.

[6] Bowman, W. D. (1992): Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. – Arctic and Alpine Research 24: 211-215.

[7] Bucher, S. F., Römermann, C. (2021): The timing of leaf senescence relates to flowering phenology and functional traits in 17 herbaceous species along elevational gradients. – Journal of Ecology 109(3): 1537-1548.

[8] Castellano, M. J., Lewis, D. B., Kaye, J. P. (2013): Response of soil nitrogen retention to the interactive effects of soil texture, hydrology, and organic matter. – Journal of Geophysical Research: Biogeosciences 118: 280-290.

[9] Creed, I. F., Band, L. E., Foster, N. W., Morrison, I. K., Nicolson, J. A., Semkin, R. S., Jeffries, D. S. (1996): Regulation of nitrate-N release from temperate forests: a test of the N flushing hypothesis. – Water Resources Research 32: 3337-3354.

[10] Eickmeier, W. G., Schussler, E. E. (1993): Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the "vernal-dam" hypothesis. – Bulletin of the Torrey Botanical Club 120: 157-165.

[11] Elliot, K. J., Vose, J. M., Knoepp, J. D., Clinton, B. D., Kloeppel, B. D. (2015): Functional role of the herbaceous layer in Eastern deciduous forest ecosystems. – Ecosystems 18: 221-236.

[12] Farnsworth, E., Nunez-Farfan, J., Careaga, S., Bazzaz, F. (1995): Phenology and growth of three temperate forest life forms in response to artificial soil warming. – Journal of Ecology 83: 967-977.

[13] Gale, M., Grigal, D. (1987): Vertical root distributions of northern tree species in relation to successional status. – Canadian Journal of Forest Research 17: 829-834.

[14] Gilliam, F. S. (2007): The ecological significance of the herbaceous layer in temperate forest ecosystems. – BioScience 57(10): 845-858.

[15] Groffmann, P. M., Zak, D. R., Christensen, S., Mosier, A., Tiedje, J. M. (1993): Early spring nitrogen dynamics in a temperate forest landscape. – Ecology 74: 1579-1585.

[16] Hereford, J., Schmitt, J., Ackerly, D. D. (2017): The seasonal climate niche predicts phenology and distribution of an ephemeral annual plant, *Mollugo verticillata*. – Journal of Ecology 105(5): 1323-1334.

[17] Hishi, T., Urakawa, R., Tashiro, N., Maeda, Y., Shibata, H. (2014): Seasonality of factors controlling N mineralization rates among slope positions and aspects in cool-temperate deciduous natural forests and larch plantations. – Biology and Fertility of Soils 50: 343-356.

[18] Holmes, W. E., Zak, D. R. (1994): Soil microbial biomass dynamics and net nitrogen mineralization in northern hardwood ecosystems. – Soil Science Society of America Journal 58: 238-243.

[19] Hornberger, G. M., Bencala, K. E., McKnight, D. M. (1994): Hydrological controls on dissolved organic carbon during snowmelt in the Snake River near Montezuma, Colorado. – Biogeochemistry 25: 147-165.

[20] Isobe, K., Oka, H., Watanabe, T., Tateno, R., Urakawa, R., Liang, C., Senoo, K., Shibata, H. (2018): High soil microbial activity in the winter season enhances nitrogen cycling in a cool-temperate deciduous forest. – Soil Biology and Biochemistry 124: 90-100.

[21] Jaeger, C. H., Monson, R. K., Fisk, M. C., Schmidt, S. K. (1999): Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. – Ecology 80: 1883-1891.

[22] Jandl, R., Kopeszki, H., Glatzel, G. (1997): Effect of a dense *Allium ursinum* (L.) ground cover on nutrient dynamics and mesofauna of a *Fagus sylvatica* (L.) woodland. – Plant and soil 189: 245-255.

[23] Jeffries, D. S. (1990): Snowpack storage of pollutants, release during melting, and impact on receiving waters. – In: Norton, S. A., Lindberg, S. E., Page, A. L. (eds.) Acidic Precipitation: Soils, Aquatic Processes, and Lake Acidification. Springer, New York, pp. 107-132.

[24] Joergensen, R., Brookes, P. (1990): Ninhydrin-reactive nitrogen measurements of microbial biomass in 0.5 M K2SO4 soil extracts. – Soil Biology and Biochemistry 22: 1023-1027.

[25] Kaiser, C., Koranda, M., Kitzler, B., Fuchslueger, L., Schnecker, J., Schweiger, P., Rasche, F., Zechmeister-Boltenstern, S., Sessitsch, A., Richter, A. (2010): Belowground carbon allocation by trees drives seasonal patterns of extracellular enzyme activities by altering microbial community composition in a beech forest soil. – New Phytologist 187: 843-858.

[26] Lee, K. S., Cho, D. S. (2000): The effects of microenvironmental heterogeneity on the spatial distribution of herbaceous species in a temperate hardwood forest. – Korean Journal of Ecology and Environment 23: 255-266.

[27] Lipson, D. A., Schadt, C. W., Schmidt, S. K. (2002): Changes in soil microbial community structure and function in an alpine dry meadow following spring snow melt. – Microbial Ecology 43: 307-314.

[28] Mabry, C. M., Gerken, M. E., Thompson, J. R. (2008): Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests. – Applied Vegetation Science 11: 37-44.

[29] Morgan, J. B., Connolly, E. L. (2013): Plant-soil interactions: nutrient uptake. – Nature Education Knowledge 4(8): 2.

[30] Mullen, R. B., Schmidt, S. K., Jaeger III, C. H. (1998): Nitrogen uptake during snowmelt by the snow buttercup, *Ranunculus adoneus*. – Arctic and Alpine Research 30: 121-125.

[31] Muller, R. N. (1978): The phenology, growth and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. – Ecological Monographs 48: 1-20.

[32] Muller, R. N., Bormann, F. H. (1976): Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. – Science 193: 1126-1128.

[33] Pan, L., Wang, T., Gavrikov, V. L., Guo, X., Mu, L., Tang, Z. (2025): Trade-off strategies between growth and defense of spring ephemeral plants in early spring. – Frontiers in Plant Science 16: 1503169.

[34] Peterson, D. L., Rolfe, G. L. (1982): Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. – American Midland Naturalist 107: 325-339.

[35] Price, P. B., Sowers, T. (2004): Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. – Proceedings of the National Academy of Sciences of the United States of America 101: 4631-4636.

[36] Ross, D., Sparling, G. (1993): Comparison of methods to estimate microbial C and N in litter and soil under *Pinus radiata* on a coastal sand. – Soil Biology and Biochemistry 25: 1591-1599.

[37] Rothstein, D. E. (2000): Spring ephemeral herbs and nitrogen cycling in a northern hardwood forest: an experimental test of the vernal dam hypothesis. – Oecologia 124: 446-453.

[38] Schmidt, S. K., Costello, E. K., Nemergut, D. R., Cleveland, C. C., Reed, S. C., Weintraub, M. N., Meyer, A. F., Martin, A. M. (2007): Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. – Ecology 88: 1379-1385.

[39] Shafer, P., Golay, M. G. (2020): Seasonal storage of carbon, nitrogen, and phosphorus in two perennial forest herbaceous plants. – Flora 271: 151687.

[40] Tessier, J. T., Raynal, D. J. (2003): Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. – Plant and Soil 256: 443-453.

[41] Tremblay, N. O., Larocque, G. R. (2001): Seasonal dynamics of understory vegetation in four eastern Canadian forest types. – International Journal of Plant Sciences 162: 271-286.

[42] Vitousek, P. M., Reiners, W. A. (1975): Ecosystem succession and nutrient retention: a hypothesis. – BioScience 25: 376-381.

[43] Voříšková, J., Brabcová, V., Cajthaml, T., Baldrian, P. (2014): Seasonal dynamics of fungal communities in a temperate oak forest soil. – New Phytologist 201: 269-278.

[44] Williams, M. W., Melack, J. M. (1991): Solute chemistry of snowmelt and runoff in an alpine basin, Sierra Nevada. – Water Resources Research 27: 1575-1588.

[45] Zak, D. R., Groffman, P. M., Pregitzer, K. S., Christensen, S., Tiedje, J. M. (1990): The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. – Ecology 71: 651-656.

[46] Zechmeister-Boltenstern, S., Hahn, M., Meger, S., Jandl, R. (2002): Nitrous oxide emissions and nitrate leaching in relation to microbial biomass dynamics in a beech forest soil. – Soil Biology and Biochemistry 34: 823-832.

[47] Zhang, X., Wang, W., Chen, W., Zhang, N., Zeng, H. (2014): Comparison of seasonal soil microbial process in snow-covered temperate ecosystems of northern China. – PloS ONE 9: e92985.