

論文 (Original article)

Nutrient budgets in four Japanese forests based on short- and long-term methods

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Abstract

Estimation of the nutrient accumulation rate in tree biomass is important for understanding the nutrient budgets of forest ecosystems but choosing a suitable method can be challenging. In this study, we compared the nutrient budgets of four forest ecosystems in Japan (Oyasan, Kamigamo, Kiryu, and Takatori) and estimated the nutrient accumulation rates in tree biomass using two methods. For short-term estimates, the nutrient content of tree biomass was measured at two points in time over several years; for long-term estimates, the nutrient content was divided by forest age. The nutrient accumulation rates estimated using the long-term method was lower than those using the short-term method. Weathering rates for potassium, magnesium, and calcium estimated using the long-term method were lower than those using the short-term method. Weathering rates determined using the short-term method were high and could be overestimates in nutrient-limited forests. Soil nitrogen release values were lower with the long-term method than those with the short-term method and could be overestimated when using the latter method in nitrogen-limited watersheds. In conclusion, weathering rates and soil nitrogen release values determined using the long-term method are useful for assessing the sustainability of nutrient cycling in forest ecosystems although the rate of nutrient accumulation in tree biomass is assumed to be constant.

Key words : base cation, nitrogen, nutrient accumulation, stream runoff, weathering

1. Introduction

Rock weathering rates of base cations influence forest productivity and acid buffering capacity (Van Breemen et al. 1984, Asano et al. 2000, Fujii et al. 2008, Inagaki et al. 2019). Rock weathering rates of base cations can be estimated from input-output budgets by assuming a steady state (Fig. 1) (Van Breemen et al. 1984) and previous studies have investigated these rates in many forest ecosystems worldwide (White and Blum 1995, Watmough et al. 2005). In Japan, several studies have compared the input-output budgets of base cations (Asano and Uchida 2005, Yoshinaga et al. 2011) but information about rock weathering rates is still limited (Tokuchi and Ohte 1998, Asano et al. 2000, Inagaki et al. 2019).

Estimation of the nutrient accumulation rate in plant biomass (ΔNB) is crucial for calculating element budgets in forest ecosystems. Aboveground biomass is usually estimated using allometric equations for felled trees (Ando et al. 1977, Satoo and Madgwick 1982) and the nutrient content of annual increments in aboveground biomass can be calculated (Tsutsumi 1977). However, it can be challenging to choose an allometric equation as the most suitable equation varies among forest ecosystems (Satoo and Madgwick 1982, Inagaki et al.

2020).

Generally, there are two methods for calculating ΔNB . In the short-term, ΔNB can be calculated based on measurements taken at two time points (initial and final) over time. For long-term estimates, ΔNB is calculated based on one measurement and the accumulation rate is estimated as the nutrient content of the plant biomass divided by forest age. This method assumes a constant rate of ΔNB but requires less effort than the short-term method. Although these two methods have different advantages and disadvantages, it is not clear how the methods affect estimates of rock weathering rates in Japanese forests and comparisons are needed in diverse forest ecosystems. In this study, the two methods of measuring ΔNB were compared in four forest ecosystems with varying geological characteristics and climates in Japan. The weathering rates of cations were estimated using the two methods based on the element budget. Nitrogen is generally not derived from rocks but nitrogen release from long-term storage can be estimated using the same calculation as for rock weathering rates of base cations (Fig. 1). Using these comparisons, the study aimed to propose a method for the calculation of nutrient budgets in forest ecosystems.

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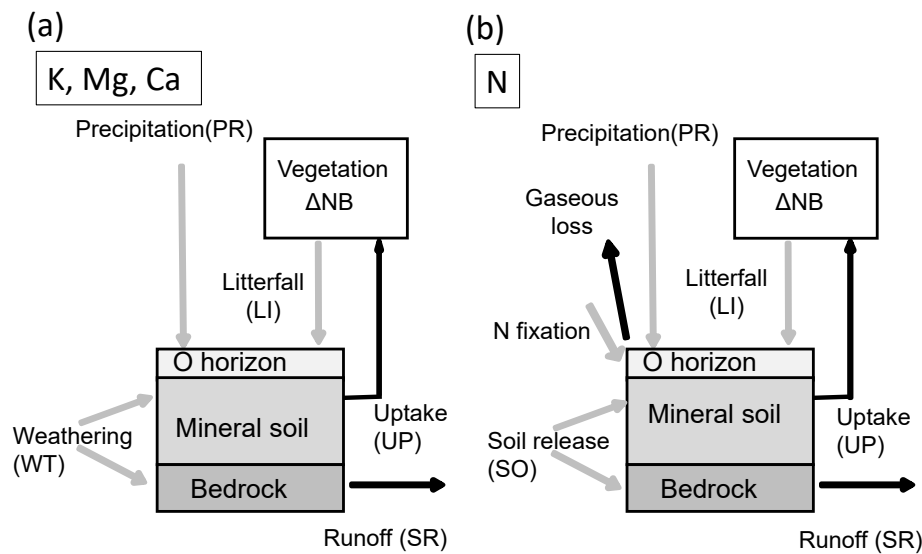


Fig. 1. Cycling of base cations (a) and nitrogen (b) in forest ecosystems.

2. Materials and Methods

2.1 Study sites

The present study compared nutrient cycling in four forest watersheds (Table 1) (Oyasan, Kiryu, Kamigamo, and Takatori) from published studies (Iwatsubo 1976, Ando et al. 1977, Tsutsumi 1977, Ohruai and Mitchell 1996, Inagaki et al. 2019).

Oyasan (36°34'N, 139°22'E) lies approximately 100 km northwest of the Tokyo Metropolitan area. Vegetation in the forest watershed (1.3 ha) is Japanese cedar (*Cryptomeria japonica*) planted in 1976 and the study was conducted when the forest was 14 to 18 years old (Ohruai and Mitchell 1996). Nitrogen fertilizer was applied seven times during the initial 11 years after planting. The amount of nitrogen in each application ranged from 33 to 154 kg N ha⁻¹ and the total amount was 585 kg N ha⁻¹ (Urakawa et al. 2012). In the watershed, nitrogen runoff in stream water was greater than nitrogen input from precipitation (Ohruai and Mitchell 1996, Mitchell et al. 1997) and the forest was considered to be in a nitrogen-saturated condition (Aber et al. 1989).

Kiryu (34°58'N, 136°00'E) is located in the Tanakami area of Shiga Prefecture. The parent materials in the area are granite and the soil is easily eroded. Exploitation of wood materials since the Heian period (8th century) has caused land degradation in the area but plantations to prevent soil erosion were established in the Edo period (17th century) (Yasuda 2010). The vegetation in this watershed (6.0 ha) is Japanese red pine (*Pinus densiflora*) and planted hinoki cypress (*Chamaecyparis obtusa*), planted 70 years previously (Nishimura 1973, Tsutsumi 1977).

Kamigamo (35°04'N, 135°46'E) is located in northern Kyoto city. The soil of the area is acidic and nitrogen limited (Nakanishi et al. 2009, Inagaki et al. 2011). Vegetation in the studied watershed (4.4 ha) is secondary evergreen hardwood forests dominated by *Ilex pedunculosa*, *Camellia japonica* and *Clethra barbinervis*. The age of the studied forest is not known. We assumed that regeneration started in 1949 when the area was designated as an experimental forest. The area might have been exploited heavily during World War II (1941–1945) judged from photographs published on the website of the Field

Table 1. Summary of the study sites

Site	latitude/longitude	Prefecture	MAT (°C)	MAP (mm)	Vegetation	Geology	reference
Oyasan	36°34'N/ 139°22'E	Gunma	13.2	1618	Japanese cedar plantation hinoki cypress plantation	Sandstone and shale	Ohruai and Mitchell 1996
Kiryu	34°58'N/ 136°00'E	Shiga	13.8	1645	Japanese red pine forest, hinoki cypress planation	Granite	Tsutsumi 1977
Kamigamo	35°04'N/ 135°46'E	Kyoto	14.6	1582	Evergreen hardwood forest	Sandstone and slate	Iwatsubo 1976; Tsutsumi 1977
Takatori	33°20'N/ 132°58'E	Kochi	13.3	2550	Momi fir and evergreen hardwood forest	Sandstone and mudstone	Ando et al. 1977; Inagaki et al. 2019

Science Education and Research Center, Kyoto University (<https://fserc.kyoto-u.ac.jp/zp/archive/kamigamo1950/>). An investigation of its vegetation was conducted in 1968 and the forest age was estimated as 19 years.

Takatori (33°20'N, 132°58'E) is located in the Shimanto River basin on the island of Shikoku. Surface soil in the forest was moderately acidic and contained well-decomposed organic matter, as indicated by a low C/N ratio (Urakawa et al. 2015, Inagaki et al. 2017). Vegetation is dominated by momi fir (*Abies firma*) and some evergreen hardwood species (*Quercus salicina*, *Cleyera japonica* and *Illicium anisatum*). The forest was approximately 145 years old, estimated from the oldest age of felled Japanese fir trees. Measurement of stream water chemistry was conducted in an adjacent watershed (18.7 ha) (Inagaki et al. 2019).

2.2 Calculation of nutrient cycling

Nutrient cycling in forest ecosystems (Fig. 1) was determined using two methods that estimate ΔAB (aboveground biomass production, $\text{Mg ha}^{-1} \text{ yr}^{-1}$) and NB ($\text{kg ha}^{-1} \text{ yr}^{-1}$). ΔAB for short-term estimate (ΔAB_s) was obtained from previous studies (Iwatsubo 1976, Tsutsumi 1977, Ohruai and Mitchell 1996), while that for long-term estimates, ΔAB_L was calculated from the aboveground biomass divided by the forest age. For short-term estimates, ΔNB_s was defined as the differences in the nutrient content of aboveground biomass at two points in time. Therefore, ΔNB_s was equal to sum of biomass increment of each organ multiplied by its nutrient concentration. Data were obtained from previous studies (Iwatsubo 1976, Tsutsumi 1977, Ohruai and Mitchell 1996). For the Kiryu and Takatori sites, detail information about methods was not described in Tsutsumi (1977) but we considered ΔNB_s was determined by the conventional methods. For long-term estimates, ΔNB_L was calculated by dividing the nutrient content of the total aboveground biomass with the forest age.

Nutrient uptake by trees (UP) ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) was estimated using the following equation:

$$UP = LI + \Delta NB \quad \text{Eq. (1)}$$

where, LI represents the sum of the nutrient content of the litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) and nutrient leaching from the canopy ($\text{Mg ha}^{-1} \text{ yr}^{-1}$). Nutrient leaching from the canopy was defined as nutrient content in throughfall minus that in bulk precipitation (Tsutsumi 1977) and these data were obtained from the previous studies. At the Oyasan, Kiryu, and Kamigamo sites, LI was calculated from the sum of litterfall and nutrient leaching (Tsutsumi 1977, Ohruai and Mitchell 1996). At the Takatori site, UP was estimated from data for

felled trees, i.e., sum of nutrient in current year leaves and that in the increment of branches and stems (Ando et al. 1977) but throughfall nutrient content was not measured. At this site, LI was estimated as UP minus ΔNB_L . The nutrient accumulation rate estimated using the long-term method was more accurate than that estimated using the short-term method (see results and discussion).

The weathering rate of base cations (WT) ($\text{kg ha}^{-1} \text{ yr}^{-1}$) was estimated using the following equation:

$$WT = \Delta NB + SR - PR \quad \text{Eq. (2)}$$

where SR represents nutrient loss to stream runoff ($\text{kg ha}^{-1} \text{ yr}^{-1}$) and PR represents nutrient input from bulk precipitation ($\text{kg ha}^{-1} \text{ yr}^{-1}$) in the published studies (Tsutsumi 1977, Ohruai and Mitchell 1996, Inagaki et al. 2019).

Generally, the weathering rate of nitrogen is negligible and nitrogen release from the soil (SO) ($\text{kg ha}^{-1} \text{ yr}^{-1}$) is calculated from the following equation.

$$SO = \Delta NB + SR - PR \quad \text{Eq. (3)}$$

The origin of SO is not known but may include biological nitrogen fixation, past nitrogen fertilizer application, or stored organic nitrogen.

3. Results and Discussion

3.1 Nutrient accumulation rate of plant biomass (ΔNB)

Properties of the aboveground biomass at the study sites are presented in Table 2. The aboveground production rate calculated using the long-term method (ΔAB_L) was smaller than that using the short-term method (ΔAB_s), the ratio of ΔAB_L to ΔAB_s ranged from 0.32 to 0.66. The rate of tree death is one of the factors affecting ΔAB . In the Kamigamo site, ΔAB_s did not include the death rate of trees (Iwatsubo et al. 1976). The presence of many small trees is expected in

Table 2. Aboveground biomass and annual increments in aboveground biomass estimated by short- (ΔAB_s) and long-term methods (ΔAB_L).

Site	Oyasan	Kiryu	Kamigamo	Takatori
Forest age (yr)	18	70	19*	145
AB (Mg ha^{-1})	136.2	148.2	88.4	501.0
ΔAB_s ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	11.4	n.d.	13.3	10.9
ΔAB_L ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	7.6	2.1	4.7	3.5
$\Delta AB_L / \Delta AB_s$	0.66	n.d.	0.35	0.32

Italic letters: data from the original references shown in Table 1.

*Forest age: estimated from the land use history of the site. See methods and materials section. n.d.: no data.

naturally regenerated forests, and their mortality rate should be high (Masaki et al. 2021). At the Oyasan site, the ratio of ΔAB_L to ΔAB_S (0.66) was larger than that for the other forests, which may be because the rate of tree death is low as the forest is young and weeding was conducted after planting (Ohrui and Mitchell 1996). Another reason for the larger ΔAB_S value is related to the allometric equations. Generally, leaf and branch biomass are estimated from tree height and diameter at breast height but these biomass values are overestimated when the increments of leaf and branch biomass are inhibited due to closure of the forest canopy (Satoo and Madgwick 1982, Inagaki et al. 2020). The changes of crown length should be considered for the accurate estimation of branch and leaf biomass (Inagaki et al. 2020).

The nutrient accumulation rate based on the long-term method (ΔNB_L) was lower than that based on the short-term method (ΔNB_S) (Table 3, Fig. 2a). The $\Delta NB_L/\Delta NB_S$ ratio differed considerably between forest ecosystems but showed similar values between elements within a forest. The $\Delta NB_L/\Delta NB_S$ ratio was similar to the $\Delta AB_L/\Delta AB_S$ ratio, which suggests that the rate of aboveground biomass production is the primary factor determining the $\Delta NB_L/\Delta NB_S$ ratio. The $\Delta NB_L/\Delta NB_S$ ratio is also affected by biomass allocation and nutrient concentration in leaves and woody organs (Ando et al. 1977). In the short-term method, nutrient content was calculated for the increment of leaves and woody organs whereas in the long-term, it was calculated for the total aboveground biomass. Therefore, the contribution of stems to the aboveground biomass in the long-term method becomes greater in old forests (Fukuda et al. 2003). For example, the nitrogen concentration of biomass increment obtained using the long-term method in the Takatori site was lower than that obtained

using the short-term method because the former should have higher contribution of woody organs. This difference caused the $\Delta NB_L/\Delta NB_S$ of nitrogen to be lower than $\Delta AB_L/\Delta AB_S$. On the contrary, the $\Delta NB_L/\Delta NB_S$ of calcium in the Takatori site was larger than $\Delta AB_L/\Delta AB_S$. These results suggest lesser and greater accumulation of nitrogen and calcium in woody organs at this site, respectively.

3.2 Rock weathering rates (WT) and soil nitrogen release (SO)

The nutrient budgets based on ΔNB_L and ΔNB_S are presented in Table 4 and Table 5. WT using the long-term method (WT_L) was smaller than that using the short-term method (WT_S) (Fig. 2b). SO using the long-term method (SO_L) were smaller than those using the short-term method (SO_S) (Fig. 2b). The relationship between ln-transformed stream runoff and WT (WT_L/WT_S) and SO (SO_L/SO_S) ratios estimated using short- and long-term methods is shown in Fig. 3. In

Table 3. Accumulation rate of nutrients in tree biomass estimated using short- (ΔNB_S) and long-term methods (ΔNB_L) ($\text{kg ha}^{-1} \text{yr}^{-1}$)

	Oyasan	Kiryu	Kamigamo	Takatori
ΔNB_S				
K	22.5	4.5	28.3	48.3
Mg	3.8	2.4	12.9	5.8
Ca	51.2	23.6	40.3	41.6
N	33.9	8.2	36.8	23.3
ΔNB_L				
K	15.8	1.88	9.4	12.8
Mg	2.3	0.84	4.6	1.3
Ca	33.0	7.49	13.8	15.5
N	24.5	3.85	12.1	6.5
$\Delta NB_L/\Delta NB_S$				
K	0.70	0.42	0.33	0.27
Mg	0.60	0.36	0.36	0.22
Ca	0.64	0.32	0.34	0.37
N	0.72	0.47	0.33	0.28

Italic letters: data from the original references shown in Table 1.

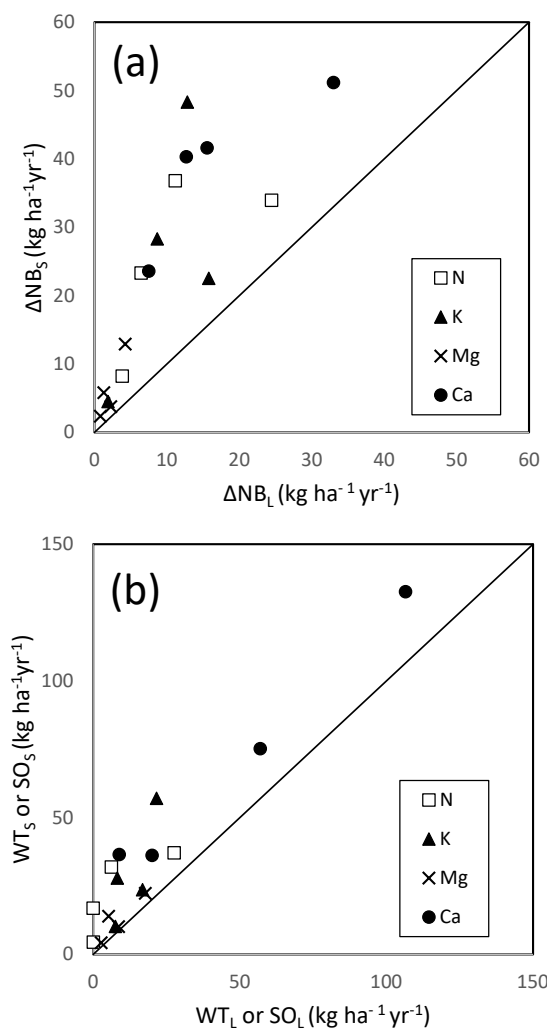


Fig. 2. Relationship between estimates of (a) nutrient accumulation in plant biomass (ΔNB), and (b) base cation weathering rate (WT) and soil nitrogen release (SO), using long- ($_L$) and short-term ($_S$) methods.

each forest, the ratio increased with increasing stream runoff ($r^2 = 0.521$, $P = 0.0016$, Fig. 3). WT and SO were calculated from nutrient accumulation in plant biomass (ΔNB), runoff by stream water (SR), and input by precipitation (PR) in Eqs (2) and (3). Therefore, some factors may have affected the ratio of estimates using short- and long-term methods. Firstly, nutrient input by precipitation was generally small in this study, and it may not have significantly affected the WT and SO estimates. Secondly, the stream runoff differs within a forest, and the difference in estimates between the two methods becomes greater in forests with lower stream runoff because

Table 5. Ratio of weathering rate (WT_L/WT_S) or soil nitrogen release (SO_L/SO_S) estimated using short- ($_S$) and long-term ($_L$) methods.

	Oyasan	Kiryu	Kamigamo	Takatori
K	0.71	0.74	0.32	0.38
Mg	0.85	0.64	0.40	0.80
Ca	0.76	0.56	0.27	0.80
N	0.74	0.01	0.23	0.00

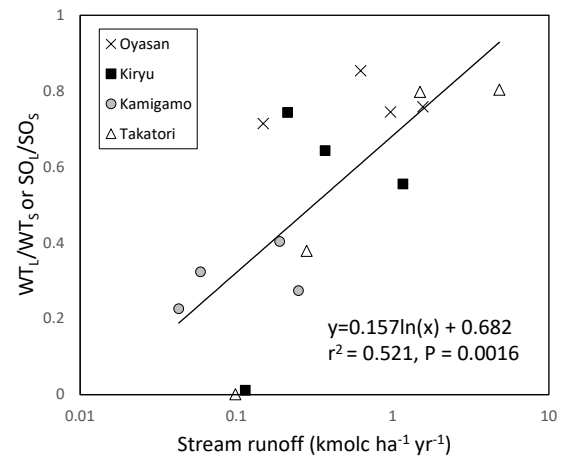


Fig. 3. Relationship between stream runoff and the ratio of estimates of rock weathering rates (WT) and soil nitrogen release (SO) using long- ($_L$) and short-term ($_S$) methods (WT_L/WT_S or SO_L/SO_S). Stream runoff was sum of four nutrients and expressed in $\text{kmolc ha}^{-1} \text{yr}^{-1}$.

Table 4. Input-output budget for the study sites estimated using short- and long-term methods.

Site	Short-term method				Long-term method			
	Oyasan	Kiryu	Kamigamo	Takatori	Oyasan	Kiryu	Kamigamo	Takatori
K input								
PR	4.7	2.6	2.7	2.2	4.7	2.6	2.7	2.2
LI	24.8	27.6	64.5	108.0	24.8	27.6	64.5	108.0
WT	23.6	10.2	27.9	57.1	16.9	7.6	9.0	21.6
Sum	53.1	40.4	95.1	167.3	46.4	37.8	76.2	131.8
K output								
UP	47.3	32.1	92.8	156.3	40.6	29.5	73.9	120.8
SR	5.8	8.3	2.3	11.0	5.8	8.3	2.3	11.0
Sum	53.1	40.4	95.1	167.3	46.4	37.8	76.2	131.8
Mg input								
PR	1.2	2.6	1.3	1.7	1.2	2.6	1.3	1.7
LI	5.4	6.5	10.7	11.0	5.4	6.5	10.7	11.0
WT	10.2	4.3	13.9	22.3	8.7	2.7	5.6	17.8
Sum	16.8	13.4	25.9	35.0	15.3	11.8	17.6	30.5
Mg output								
UP	9.2	8.9	23.6	16.8	7.7	7.3	14.9	12.3
SR	7.6	4.5	2.3	18.2	7.6	4.5	2.3	18.2
Sum	16.8	13.4	25.9	35.0	15.3	11.8	17.6	30.5
Ca input								
PR	7.3	10.7	8.8	5.4	7.3	10.7	8.8	5.4
LI	59.1	57.3	48.6	55.7	59.1	57.3	48.6	55.7
WT	75.2	36.2	36.5	132.6	57.0	20.1	10.0	106.5
Sum	141.6	104.2	93.9	193.7	123.4	88.1	67.4	167.6
Ca output								
UP	110.3	80.9	88.9	97.3	92.1	64.8	62.4	71.2
SR	31.3	23.3	5.0	96.4	31.3	23.3	5.0	96.4
Sum	141.6	104.2	93.9	193.7	123.4	88.1	67.4	167.6
N input								
PR	10.4	5.4	5.5	7.8	10.4	5.4	5.5	7.8
LI	37.8	25.4	43.2	67.6	37.8	25.4	43.2	67.6
SO	37.1	4.4	36.8	16.9	27.7	0.1	7.2	0.0
Sum	85.3	35.3	85.5	92.3	75.9	30.9	55.9	75.4
N output								
UP	71.7	33.7	84.9	90.9	62.3	29.3	55.3	74.0
SR	13.6	1.6	0.6	1.4	13.6	1.6	0.6	1.4
Sum	85.3	35.3	85.5	92.3	75.9	30.9	55.9	75.4

Italic letters: data from the original references shown in Table 1.

the contribution of ΔNB to the WT and SO estimates becomes greater. Nitrogen loss from stream water is generally low and the estimates of nitrogen release can vary more depending on the methods than on other elements. In the present study, the exception was the nitrogen-saturated Oyasan site, where the nutrient runoff was higher than that of potassium. Finally, the difference in ΔNB between the methods affected $\text{WT}_\text{L}/\text{WT}_\text{S}$ and $\text{SO}_\text{L}/\text{SO}_\text{S}$. As previously mentioned, the stem contribution to aboveground production as well as nutrient concentration in different organs can affect the estimates of ΔNB .

In conclusion, the estimation of WT and SO using the two methods can vary greatly in nutrient-limited forests. Using the short-term method for estimating WT and SO is problematic as it can overestimate nutrient availability in nutrient-limited forests. In contrast, WT and SO from the long-term methods are useful for the evaluation of soil sustainability although the rate of nutrient accumulation in tree biomass is assumed to be constant. The calculation of rock weathering rate from the nutrient budget also assumes the constant rate of fluxes (Van Breemen et al. 1984). Therefore, the assumption of steady state should be satisfied for applying the method. In other words, the method cannot be applied for non-steady state ecosystems affected by severe disturbances. The results of this study are based on the published studies and the method of these studies would be different to some extent. This is the limitation of this study and further studies are required in the future.

From the following section, the estimation of WT and SO using the long-term method is discussed. The sum WTL of calcium, magnesium, and potassium in Oyasan, Kiryu, Kamigamo, and Takatori was 4.0, 1.4, 1.2, and 7.3 $\text{kmolc ha}^{-1} \text{yr}^{-1}$, respectively. The weathering rates of base cations in 24 forest ecosystems worldwide ranged from 0.66 to 14.50 $\text{kmolc ha}^{-1} \text{yr}^{-1}$ and in Japanese forests ranged from 4.97 to 7.64 $\text{kmolc ha}^{-1} \text{yr}^{-1}$ (Tokuchi and Ohte 1998). The weathering rates from the present study do not include sodium. The sodium weathering rates in Oyasan, Kiryu, and Takatori were 1.2, 2.0, and 2.6 $\text{kmolc ha}^{-1} \text{yr}^{-1}$, respectively (Ohrui and Mithcell 1996, Asano et al. 2000, Inagaki et al. 2019). When the weathering of sodium is included, the weathering rates of base cations in this study are in a similar range to those reported by Tokuchi and Ohte (1998). Sodium accumulation in plant biomass is not usually evaluated because sodium is not considered as a nutrient, however, it can affect the estimation of weathering rates.

At the Kiryu and Takatori sites, SO_L was close to zero. The calculation used in this study does not consider biological nitrogen fixation, dry deposition, or denitrification but the results suggest that the sum of these inputs and outputs is close to zero. At the Kamigamo site, SO_L was 7.2 $\text{kg ha}^{-1} \text{yr}^{-1}$. In the

calculation of nutrient budgets of the study (Table 4), difference between throughfall and bulk precipitation is considered as litter fraction derived from leaching from the canopy. However, the fraction can include nitrogen input by dry deposition. If we assume canopy leaching of nitrogen is negligible, dry deposition of the Kamigamo site is 3.5 $\text{kg ha}^{-1} \text{yr}^{-1}$ (Iwatsubo 1976). The SO_L considering this dry deposition rate is estimated as 3.7 $\text{kg ha}^{-1} \text{yr}^{-1}$. There was some uncertainty about forest age at the Kamigamo site (see Materials and Methods). The estimation of forest age in this study is based on the duration of protection and the regeneration of the vegetation could have possibly started earlier. These uncertainties may have resulted in an overestimate of SO_L at the Kamigamo site to some extent. In summary, PR, SR, and SO_L in the Kiryu, Kamigamo, and Takatori sites were low, which implies that nitrogen cycling in these forests is tight and closed.

At the Oyasan site, SO_L was 27.7 $\text{kg ha}^{-1} \text{yr}^{-1}$. Nitrogen fertilizer (585 kg N ha^{-1}) was applied for 18 years after planting. Measurement of nitrogen runoff started four years after planting in the study forest and was also conducted in the adjacent non-fertilized middle-aged forest (Fig. 4, Urakawa et al. 2012). The difference in nitrogen runoff between the study site and the middle-aged forest from ages 5 to 18 years was 74.4 kg ha^{-1} . The amount of nitrogen applied during the period was 454 kg ha^{-1} and approximately 16% of the applied nitrogen was lost via stream water. This result suggests that much of the applied nitrogen remained in the soil. Wakamatsu et al. (2001) investigated the fate of ^{15}N tracer in a Japanese cedar forest. After one year, 60% of the added nitrogen remained in the soil whereas only 8% leached from the rooting zone. ^{15}N tracer experiments in many forest ecosystems have shown that soil is a major sink of added ^{15}N (Tietema and Wright 1998, Nadelhoffer et al. 1999). These findings suggest that a large part of the nitrogen remained in the Oyasan site and the major source of SO_L was nitrogen fertilizer. In the study, some processes were not considered, such as dry deposition,

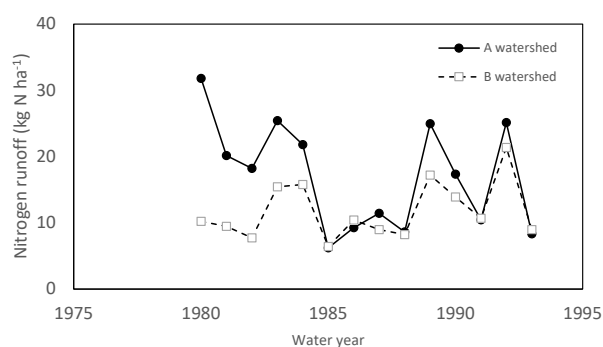


Fig. 4. Annual variation in nitrogen runoff from stream water in a young forest (A watershed) and a middle-aged forest (B watershed) at the Oyasan site (Urakawa et al. 2012).

biological nitrogen fixation, and denitrification. The input from dry deposition was $2.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Ohrui and Mitchell 1996) and the rate of denitrification was $19.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fang et al. 2015). Biological nitrogen fixation was not measured but a study conducted in a Japanese cedar forest revealed substantial nitrogen fixation activity ($2.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) due to non-symbiotic nitrogen fixation in the leaf litter (Nioh and Haruta 1986, Yamanaka et al. 2011). Because denitrification is substantial, the sum of these processes would give a net loss of nitrogen. In this situation, SO_L considering these processes would have a greater value.

A comparison of the four forests revealed that SO_L was very low in the three nitrogen-limited forests and was substantial at the nitrogen-saturated Oyasan site. Usually the degree of nitrogen saturation is evaluated by comparing nitrogen input from precipitation and output via stream water (Aber et al. 1989). The method used here is also useful for evaluating the input-output balance. If soil nitrogen release is substantial, it implies that nitrogen is decreasing in the forest ecosystem. In this situation, the forest is considered to be in a nitrogen-saturated state.

3.3. Choice of method for calculating nutrient budgets

Based on the findings of the study, we recommend that ΔNB is determined using the long-term method. This method is simple because it requires a one-time measurement. The method assumes steady state, and cannot be applied to non-steady state ecosystems affected by severe disturbances. It is important to choose a proper allometric equation for estimating branch or leaf biomass. An allometric equation based on the pipe model is applicable for diverse forests (Inagaki et al. 2020). For the calculation of ΔNB , plant samples should be collected and the nutrient concentration of leaves, branches, and stems should be measured.

The short-term method is more common and widely used. The results of this study indicate that estimations of biomass production can vary considerably due to the difficulties of estimating tree death. To avoid this problem, it is recommended that long-term tree censuses should be conducted over a wide area. Another finding of the study is that the weathering rates based on the short-term method were higher in nutrient-limited forests. This is problematic for evaluating soil sustainability in nutrient-limited forests. It is recommended that the long-term method is also used to calculate weathering rates when the short-term method is used.

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長期的と短期的な手法に基づく4つの日本の森林における養分収支

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要旨

森林生態系の物質収支を明らかにする際に樹木の養分蓄積速度を推定することが重要であり、適切な推定手法を選択することが必要である。本研究では日本の4つの森林（大谷山、上賀茂、桐生、鷹取）において養分循環を比較し、2通りの手法で樹木の養分蓄積速度を推定した。短期的な手法では数年間の2つの時期における樹木の養分含有量を算出するのに対して、長期的手法ではある時期の養分含有量を林齢で割って算出する。長期的手法による樹木の養分蓄積速度は短期的手法による推定よりも低い値を示した。長期的手法によるカリウム、マグネシウム、カルシウムの風化速度は短期的手法よりも低い値を示した。養分が乏しい森林では、短期的手法による風化速度は高く過大であった。土壌窒素放出速度は長期的手法で短期的手法よりも小さく、窒素制限の森林では短期的手法による推定が過大であった。これらをまとめると、長期的手法による風化速度と窒素放出速度は樹木の養分蓄積速度が一定であることを仮定するものの、森林生態系の養分の持続可能性を評価する際には有益であった。

キーワード：塩基性カチオン、窒素、養分循環、溪流からの流出、風化

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