(1) Title

Nitrogen resorption efficiency of 13 tree species of a cool temperate deciduous forest in Central Japan

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Abstract

The nitrogen (N) concentration of green and senescent leaves, and the N resorption efficiency of 13 dominant species from three distribution patterns along a slope (Ridge, Valley, and Uniform types) and two types of leaf emergence pattern (determinate and indeterminate flush types) were examined in a cool temperate natural forest in central Japan. Ridge species tended to have lower N concentrations of green and senescent leaves and higher N resorption efficiency than those of Valley species, and those of Uniform species were intermediate to other types with some exceptions. Furthermore, indeterminate flush species tended to have higher N concentrations in green and senescent leaves and lower N resorption efficiency than those of the determinate type. The N concentration of senescent leaves, which is an index of leaf-level N use efficiency (NUE), was significantly correlated with N concentrations in green leaves and with N resorption efficiency. The concentration in green leaves was not correlated with N resorption efficiency, suggesting that interspecific variation in the N concentration was not a major determinate of the N resorption efficiency at this study site. Rather N resorption efficiency was positively correlated with the start date of leaf fall, suggesting that early leaf fall species, which tended to have intermediate leaf flush types (with some exceptions), were not proficient in N resorption. Thus, the patterns in NUE and N resorption efficiencies were affected not only by the distribution pattern along the slope but also by leaf phenology in this cool temperate deciduous forest.

Key words: Beech forest, Leaf fall phenology, Nitrogen use efficiency, Retranslocation, Topography

Introduction

Nitrogen (N) availability limits plant growth in many ecosystems (Vitousek and Howarth 1991), so efficient N utilization is important to plant competition (Chapin 1980; Vitousek 1982, 1984; Berendse and Aerts 1987; Eckstein et al. 1999; Aerts and Chapin 2000). Resorption of N from senescing leaves reduces N loss, which may be an important mechanism for N conservation (Chapin 1980; Chabot and Hicks 1982; Aerts 1996; Eckstein et al. 1999; Niinemets and Tamm 2005; Millard and Grelet 2010; Sun et al. 2016). N resorption efficiency, which can be calculated from the N concentrations in green and senescent leaves, is higher at sites with low-N availability than those with high-N availability (Small 1972; Flanagan and van Cleve 1983; Enoki and Kawaguchi 1999; but see Lajtha 1987; Aerts 1996), but this is still controversial. N storage in plants and its remobilization to plant organs for growth, maintenance and reproduction could be important determinates of the N resorption efficiency (Lajtha 1987; Millard and Grelet 2010). N resorption efficiency increases with stand age due to increasing N requirements (Sun et al. 2016). Furthermore, Estiarte and Peñuelas (2015) recently suggested that warming and drought due to climate change affect the nutrient resorption efficiency. Understanding of plant N utilization, including the N use efficiency (NUE) and N resorption efficiencies, is important for forest management under a changing climate and increasing N deposition (Millard and Grelet 2010; Estiarte and Peñuelas 2015).

NUE can be defined as dry matter productivity divided by plant N uptake (Hirose 1971, 2011; Vitousek 1982). Ideally, dry matter productivity should include plant dry mass (including litterfall) and respiratory consumption in non-photosynthetic tissues, including stems, roots, and reproductive organs (e.g., Hirose 2011). Many studies have assumed a steady state and have simply used dry matter lost (i.e., leaf fall or litterfall weight) as an index of dry matter productivity (e.g., Vitousek 1982; Hirose 2011), given the complexity of estimating NUE and its components in natural environments, especial for canopy tree species. Likewise, plant N uptake from soil is equivalent to N loss, such as N content lost to leaf fall or litterfall (leaf fall or litterfall weight × N concentration of senescent leaves or organs). Thus, the inverse N concentration of leaf fall or litterfall is an index of NUE (e.g., Vitousek 1982).

Furthermore, NUE can be divided into mean residence time (MRT) and nitrogen productivity (NP) (Berendse and Aerts 1987; Eckstein et al. 1999; Hirose 2011). MRT can be defined as the mean standing plant N during the growth period (N_{mean}) divided by the plant N uptake, and NP can be defined as the dry matter productivity divided by N_{mean} (Berendse and Aerts 1987; Eckstein et al. 1999; Hirose 2011). The N_{mean}, which is the numerator and denominator of MRT and NP, respectively, can be the product of biomass, growth period, and the N concentration of plant organs. If we assume that biomass and organ concentration do not change over the growth period and that the N concentration of organs equals the leaf N concentration, MRT can be explained simply as a function of the growth period and N resorption efficiency, and NP can be simply explained as a function of the N concentration of the green leaves and the growth period. Thus, an increased growth period and N resorption efficiency increase MRT; similarly, an increased growth period and N concentration in green leaves decrease NP.

Leaf longevity, which varies widely from several months to several years (Kikuzawa 1983, 1984; Reich et al. 1992; Osada et al. 2001), is also related to the

NUE (Eckstein et al. 1999) and soil N availability (Pornon et al. 2011). Major acclimations to soils with low-N availability include increased leaf longevity and lower leaf N concentration (Aerts and Chapin 2000). Leafing duration, which refers to the period of leaf holding on the crown and differs from leaf longevity due to turnover of leaves and abrupt leaf fall during the growing season, is also an important parameter for NUE and its components in deciduous forest ecosystems. In temperate deciduous tree species, which flush their leaves in the spring and shed them in the fall, leaf longevity is less than 1 year (Kikuzawa 1983, 1984; Aikawa et al. 2002). The reported leafing duration of cool temperate deciduous species in central Japan ranged from 150 to 200 days and was determined mostly by the leaf fall dates rather than by the leaf flushing dates (Aikawa et al. 2002). In cool temperate forests, abrupt early leaf fall resulted in incomplete N resorption and low NUE (Yasumura et al. 2002). Thus, leaf phenology is also important as an N conservation mechanism. More recently, plant phenology has been considered a crucial factor affecting vegetation feedback by influencing the seasonality of albedo, surface roughness length, canopy conductance and canopy water and energy fluxes in future climate changes (Richardson et al. 2013).

Trees of the temperate region exhibit two types of leaf emergence: determinate growth (producing the bulk of their foliage in a short spring flush) and indeterminate growth (producing new leaves in spring but also late into the growing season; Kikuzawa 1983). Species of the indeterminate growth type tend to drop their leaves earlier than do those of the determinate growth type (Aikawa et al. 2002; Tateno et al. 2005). Leaf emergence patterns of tree species are correlated with shade tolerance, i.e., pioneer species have indeterminate growth and climax species have determinate growth (Kikuzawa 1983, 1984; Hirayama and Sakimoto 1999). In terms of differences in growth strategy, plants may change their N utilization patterns; however, few studies have investigated the effects of leaf phenology on NUE and N resorption efficiency (but see del Arco et al. 1991; Yasumura et al. 2002; Niinemets and Tamm 2005; Inagaki et al. 2008).

This study investigated the NUE and N resorption efficiencies of 13 dominant species (seven with determinate growth and six with indeterminate growth) in a cool temperate natural forest in central Japan growing on a wide range of soils. The focal species could be categorized into three types (Valley, Ridge, and Uniform species) according to their distribution along the topographic gradient (Tateno and Takeda 2003). This study investigated how tree distribution patterns, leaf emergence type, and leaf fall phenology affect plant NUE and N proficiency in a cool temperate forest.

Materials and Methods

Study site

This study was conducted in a cool temperate broadleaf deciduous forest at Ashiu Forest Research Station, Kyoto University (35°18'N, 135°43'E), Kyoto Prefecture, Japan. The mean annual temperature and precipitation are 10–11°C and 2895 mm, respectively, at a weather station (640 m elevation) about 1 km from the study site.

We established a 30 × 200 m (0.6-ha) transect plot extending from a valley bottom to the top of a northwest-facing slope. Diameter at breast height (DBH) was measured for all trees larger than 5 cm DBH. The details of the distributions of the species studied are reported elsewhere (Tateno and Takeda 2003). From this preliminary vegetation census, we selected 13 dominant tree species (Table 1), which accounted for more than 81% of the total basal area and 66% of the total number of trees in the study plot. Details of the leaf phenology of the species studied are reported elsewhere (Aikawa et al.2002; Tateno et al. 2005).

The study species were categorized into two groups based on their type of leaf emergence: those with determinate (seven species) and indeterminate (six species) growth (Kikuzawa 1983, 1984; Hirayama and Sakimoto 1999; S. Morozumi personal observation for *Pterostyrax hispida* and *Lyonia ovalifolia*). Topography is one of the most important environmental gradients in terms of soil moisture and nutrients in cool temperate ecosystems and the distribution patterns of tree species often show a topographic tendency (Tateno and Takeda 2003). The distribution pattern of tree species reflects the soil habitat preference of a species (e.g., Chapin 1980). The sample species were categorized into the three types determined by Tateno and Takeda (2003) and are summarized in Table 1. Only one study species, *Aesculus turbinata*, was not categorized by Tateno and Takeda (2003) because of its low sample size; however, *Aesculus turbinata* is a riparian species in cool temperate forests (Kaneko et al. 1999) and thus was categorized as a Valley species.

Leaf sampling

To avoid the effects of light conditions on plant N utilization traits, we selected only canopy trees for this study, because the N resorption efficiency of canopy trees is different from that of subcanopy trees (Tateno and Kawaguchi 2002). We conducted leaf sampling in early September 1998, the end of the growing season, for measuring N concentration of green leaves. We sampled five trees for each species and collected one sunlit branch from the crown surface of each tree to minimize the variation in the N concentration in the crown within and outside the study plot. Uniform species were collected from a wide range of slope positions to avoid bias in soil conditions. All sampled branches included more than 10 current-year shoots, except for species with compound leaves (*Acanthopanax sciadophylloides* and *Aesculus turbinata*). For these species, we collected more than 10 compound leaves per tree from three or four shoots. A total of 10 shoots or 10 compound leaves were randomly selected from the sampled branch for each tree. Details of leaf sampling are reported elsewhere (Tateno et al. 2003). To collect senescent leaves, we gently shook the branches of sampled species beneath the crown to obtain newly shed leaves; we repeated this several times throughout the leaf-fall period of each species (from September to November).

All leaf samples (both green and senescent) were oven dried and ground into a powder, and then the total carbon (C) and N content of each species was determined using a C/N analyzer (NC-900, Shimadzu, Kyoto, Japan). N resorption efficiency was calculated using the following equation:

$$\text{N resorption efficiency (\%)} = (Ng - Ns) / Ng \times 100,$$

where Ng is the N concentration of green leaves and Ns is the N concentration of senescent leaves.

Statistical analysis

We used one-way ANOVA to test the effects of species on the N concentrations of green and senescent leaves and on N resorption efficiency. For multiple comparisons, we used Tukey’s HSD test to evaluate the N concentrations of green and senescent leaves and the Games–Howell test to evaluate N resorption efficiency depending on the results of Levene’s test. We also used one-way ANOVA with Games-Howell test to test the effects of distribution pattern and *t*-test to test the effects of leaf emergence pattern on the N concentrations of green and senescent leaves and on N resorption efficiency. We used linear regression to analyze the relationship between leaf fall timing and plant N parameters, such as the N concentrations of green and senescent leaves and N resorption efficiency, and to analyze the relationships among plant N parameters. Percentage data were arcsine transformed before the statistical analysis.

We used the start date of leaf fall (the day on which 10% of leaves were shed) as an index of leaf fall phenology, following Tateno et al. (2005), as summarized in Table 1. For some species that occurred at both upper and lower slope positions, we calculated the average start date across trees at both sites. We should note that leaf sampling was conducted in 1998, but leaf phenology was estimated in 2001. Leaf phenology tends to be similar from year to year, regardless of the species (Vitasse et al. 2009), so we assumed that sampling year effects were negligible. All statistical analyses were performed using IBM SPSS Statistics (IBM SPSS 22.0, IBM, Armonk, NY, USA).

Results

The N concentration of green leaves ranged from 17.1 ± 1.5 mg g^{-1} (mean ± SD) in *Clethra barbinervis* to 30.7 ± 1.3 mg g^{-1} in *Pterostyrax hispida* (Table 1). Especially in Valley species of the indeterminate leaf flush type, the N concentration in green leaves was higher than that in species of the other types. Overall mean of Ridge, Uniform and Valley species were 17.1 ± 1.3, 21.3 ± 3.0 and 26.3 ± 4.3 mg g^{-1}, respectively, which were significantly different each other (one-way ANOVA with Games-Howell test, $p < 0.05$). Overall mean of indeterminate and determinate leaf flush type were 25.2 ± 5.2 and 20.6 ± 2.7 mg g^{-1}, respectively, and there was a significant difference between leaf flush type (t-test, $p < 0.05$).

The N concentration of senescent leaves ranged from 10.1± 2.0 mg g^{-1} in *Sorbus alnifolia* to 28.9 ± 0.8 mg g^{-1} in *Pterostyrax hispida* (Table 1). Especially in Valley species of the indeterminate leaf flush type, the N concentration in senescent leaves was higher than that in species of the other types, similar to the case with green leaves. Overall mean of Ridge, Uniform and Valley species were 12.3 ± 2.5, 14.1 ± 3.3 and 22.0 ± 6.3 mg g^{-1}, respectively, and Valley species had lower N concentrations in senescent leaves than Valley species and Uniform species (one-way ANOVA with Games-Howell test, $p < 0.05$). However, these pattern included some exceptions, for example, the N concentration in senescent leaves of *Aesculus turbinata,* which is categorized as a Valley species, was low. Overall mean of indeterminate and determinate leaf flush type were 20.8 ± 6.3 and 13.5 ± 3.6 mg g^{-1}, respectively, and there was a significant difference between leaf flush type (t-test, $p < 0.05$).

The N resorption efficiency ranged from 6.0 ± 2.7 % in *Pterostyrax hispida* to 49.1 ± 12.0 % in *Sorbus alnifolia* (Table 1). Overall mean of Ridge, Uniform and Valley species were 30.8 ± 10.7, 35.3 ± 9.6 and 21.5 ± 13.5 %, respectively. Significant differences were only found between Valley and Uniform species (one-way ANOVA with Games-Howell test, $p < 0.05$). Thus the N resorption efficiency did not show consistent patterns with habitat preference. Overall mean of indeterminate and determinate leaf flush type were 23.0 ± 12.1 and 34.7 ± 11.2%, respectively, and there was a significant difference between leaf flush type (t-test, $p < 0.05$). However, these pattern included some exceptions, for example, the N resorption efficiency of *Acer mono* and *Fagus crenata* were low among determinate species and those of *Acanthopanax Sciadophylloides* were high among indeterminate species.

The N concentration and N resorption efficiency were negatively correlated in senescent leaves (Fig. 1b, $r^2 = 0.762$, $p < 0.001$) but showed no linear correlation in green leaves (Fig. 1a, $p > 0.05$). In addition, there was a significant linear correlation between N concentrations in senescent and green leaves (Fig. 1c, $r^2 = 0.752$, $p < 0.001$), and between N resorption efficiency and the start date of leaf fall (Fig. 2a, $r^2 = 0.506$, $p < 0.001$), but not between N concentrations of green and senescent leaves and the start date of leaf fall (Fig. 2b, c, $p > 0.05$).

Discussion

Leaf emergence patterns are often correlated with shade tolerance; the leaf N concentration tended to be higher in indeterminate species than in determinate species in this study. Pioneer species tend to have higher leaf N concentrations than do shade-tolerant climax species (Ellsworth and Reich 1996). Differences in leaf N concentration between leaf emergence type could reflect their shade tolerance, because shade-intolerant pioneer species show indeterminate growth and shade-tolerant climax species show determinate growth (Kikuzawa 1983, 1984; Hirayama and Sakimoto 1999). However, the green leaf N concentration was not related to the N resorption efficiency. Rather, leaf fall occurred earlier in indeterminate species than in determinate species, which could explain the low N resorption efficiencies found in indeterminate species. Niinemets and Tamm (2005) suggested that the inherent potential of N resorption in tree species depends not on the initial N content, but on the greater N losses associated with earlier leaf fall. Thus, indeterminate species did not re-translocate N efficiently before leaf shedding.

Habitat preference with respect to topography is also a potential factor affecting the NUE and N resorption efficiencies of tree species, as these traits are important for acclimation to infertile soil environments (e.g., Aerts and Chapin 2000). In this study, N concentrations in green leaves showed clear patterns with topographic preference. However, the N resorption efficiency did not show consistent patterns with habitat preference. At this study site, leaf fall occurred slightly earlier on the upper slope than on the lower slope (Tateno et al. 2005), suggesting that incomplete N resorption tends to occur more on upper slopes, where soil N availability is lower (Tateno and Takeda 2003), than on lower slopes. However, at least at the stand level, N resorption efficiencies were negatively correlated with N availability in the soil (Tateno and Takeda 2010), although previous studies have demonstrated that N resorption efficiency is not always correlated with soil N conditions (e.g., Lahja 1987). This inconsistency of correlation may be due partly to the range in timing of the start of leaf fall, which overlaps considerably between species on upper and lower slopes (Tateno et al. 2005). Late leaf fall species may also be more dominant on upper slopes than on lower slopes. At the species level, the pattern of N resorption was affected not only by soil habitat preference, but also by leaf fall phenology. Thus, the timing of leaf fall appears to affect the N utilization strategy of each species.

The N resorption efficiency among the studied species showed wide variation, from 6.0% to 49.1%, which is slightly lower than the worldwide range reported by Aerts (1996). In contrast to the variation in the N resorption efficiency among the species evaluated, the variation in leaf longevity differed among tree species thought to be relatively less in deciduous trees. For example, Kikuzawa (1983) reported that leaf longevity of cool temperate tree species ranged from 90 to 170 days. The reported leafing duration of cool temperate deciduous species, which is not accurately consistent with leaf longevity, was 150–200 days in this site (Aikawa et al. 2002). In the present study, indeterminate species tended to have shorter leafing durations than those of determinate species (Aikawa et al. 2002), and the difference in leaf longevity between the two leaf emergence types may be larger because indeterminate species produce and shed leaves throughout the growing season (Kikuzawa 1983). Overall, the variation in leaf longevity and leafing duration among species was less than twofold, which was considerably less than the variation in N resorption efficiency. MRT could be increased with leafing duration and N resorption efficiency, with a greater contribution of changing N resorption efficiency relative to leafing duration in deciduous tree species.

Furthermore, the variations in leaf longevity and leafing duration in deciduous trees were not accounted for in the calculation of N uptake or re-translocation on an annual basis. More precisely, with even earlier or later leaf shedding, the N re-translocated before winter will be utilized for next year’s production. In this sense, the total amount of re-translocated N is more important for temperate deciduous trees, considering annual-based production and N cycling. Several studies have suggested that leaf longevities are more important in explaining interspecific variation in the MRT, especially in evergreen species (Escudero et al. 1992; Eckstein et al. 1999); however, the differences in N resorption efficiency could be relatively more important for the effective utilization of N in a cool temperate deciduous forest.

The inverse of the N concentration in senescent leaves has been used as an index of NUE (e.g., Vitousek 1982). In the present study, both N concentration in green leaves and N resorption efficiency were correlated with the N concentration in senescent leaves, as previously reported (Aerts and Chapin 2000; Tateno and Kawaguchi 2002). However, the N concentration of green leaves was not correlated with N resorption efficiency. Killingbeck (1996) proposed that the N resorption proficiency, the level to which leaf N is reduced during senescence, is for acclimation to infertile soil conditions. N resorption proficiency is basically the same as leaf-level NUE, which can be defined as the inverse of the N concentration in senescent leaves (Vitousek 1982). If plants re-translocate N more proficiently at the time of leaf abscission, the plant leaf-level NUE will increase (Killingbeck 1996). However, the low N resorption proficiency of some species in this study could be related to early leaf fall, probably due to abrupt water stress, wind and cold. Niinemets and Tamm (2005) suggested that large N losses are associated with earlier leaf fall. Furthermore, Yasumura et al. (2002) suggested that abrupt early leaf fall leads to low N resorption efficiency in *Fagus crenata* in temperate deciduous forests in northern Japan. Conversely, an extended delay in the senescence period due to climate change can result in more proficient resorption (Estiarte and Peñuelas 2015). Further study is needed to investigate the interrelationship between N utilization traits and leaf phenology under climate change and increasing N deposition.

Conclusions

Leaf emergence patterns and habitat preference of deciduous tree species affected N concentrations in green and senescent leaves and N resorption efficiencies in a cool temperate natural forest in central Japan. The N concentration in senescent leaves, which is an index of leaf-level NUE, was correlated significantly with N concentrations in green leaves and N resorption efficiency, whereas the concentration in green leaves was not correlated with N resorption efficiency. These results suggest that interspecific variation in the N concentration in green leaves was not a major determinate of N resorption efficiency at this study site. Rather, N resorption efficiency was correlated positively with the start date of leaf fall, suggesting that species that experience early leaf fall, which tend to have intermediate leaf flush types (with some exceptions), were not proficient in N resorption. Early leaf fall, probably due to abrupt water stress, wind, and cold, could lead to lower N resorption efficiency and NUE. Thus, the patterns observed in N utilization, such as the NUE and N resorption efficiencies, were affected not only by the distribution pattern along the slopes, but also by leaf phenology, such as the leaf emergence type and timing of leaf fall, in this cool temperate deciduous forest.

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Figure legends

Fig. 1 Relationship between the N concentration of green leaves (Ng) and N resorption efficiency (NRE) (a), N concentration of senescent leaves (Ns) and NRE (b), and Ng and Ns (c) of 13 tree species. Closed symbols indicate determinate flush type and open symbols indicate indeterminate flush type. Squares, circles, and triangles indicate Valley, Uniform and Ridge species, respectively. Solid lines indicate the significant linear regression equations. (b) The regression was $y = -1.495\, x + 55.353$ ($r^2 = 0.769$, $p < 0.001$). (c) The regression was $y = 1.197\, x -10.324$ ($r^2 = 0.752$, $p < 0.001$).

Fig. 2 Relationship between N resorption efficiency (NRE) and start date of leaf fall (a), N concentration of green leaves (Ng) and start date of leaf fall (b), and N concentration of senescent leaves (Ns) and start date of leaf fall (c) of 13 tree species. Closed symbols indicate determinate flush type and open symbols indicate indeterminate flush type. Squares, circles, and triangles indicate Valley, Uniform and Ridge species, respectively. Solid lines indicate the significant linear regression equation. (a) The regression was $y = 0.441\, x -47.371$ ($r^2 = 0.506$, $p < 0.01$).

Fig. 1 Tateno and Takeda

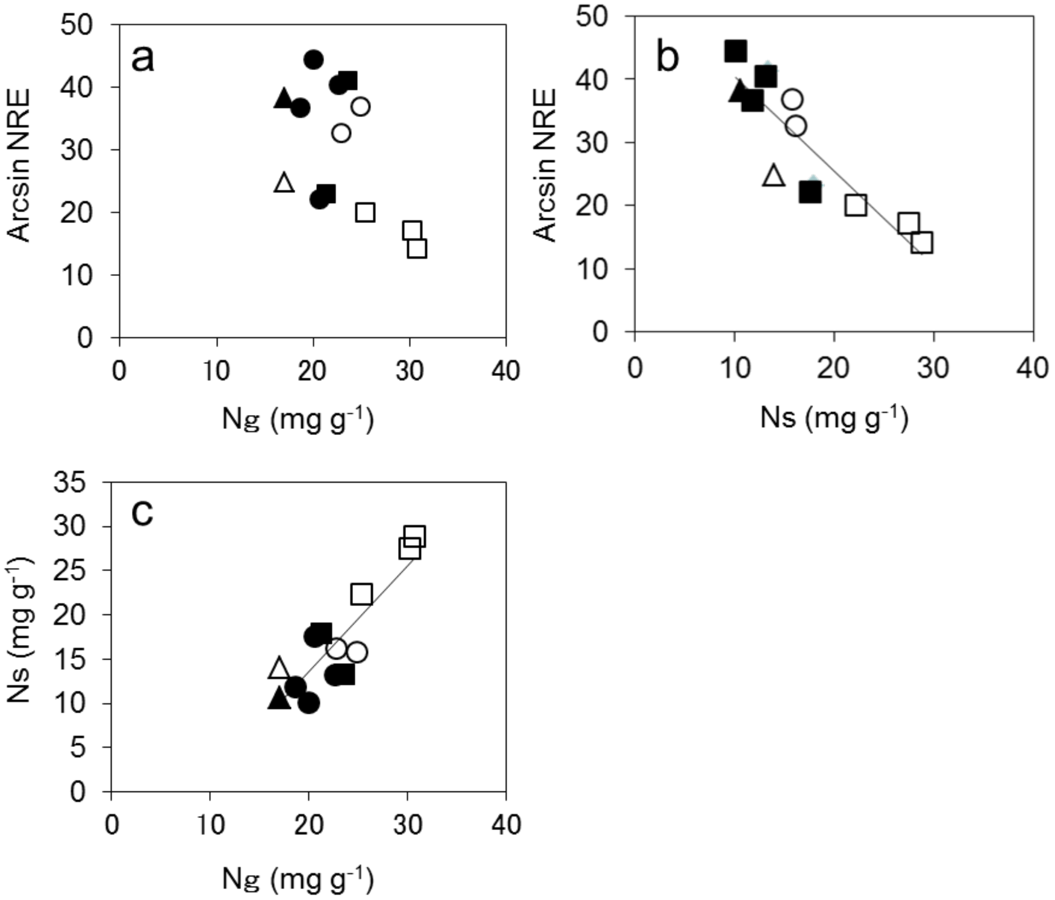

Fig. 2 Tateno and Takeda

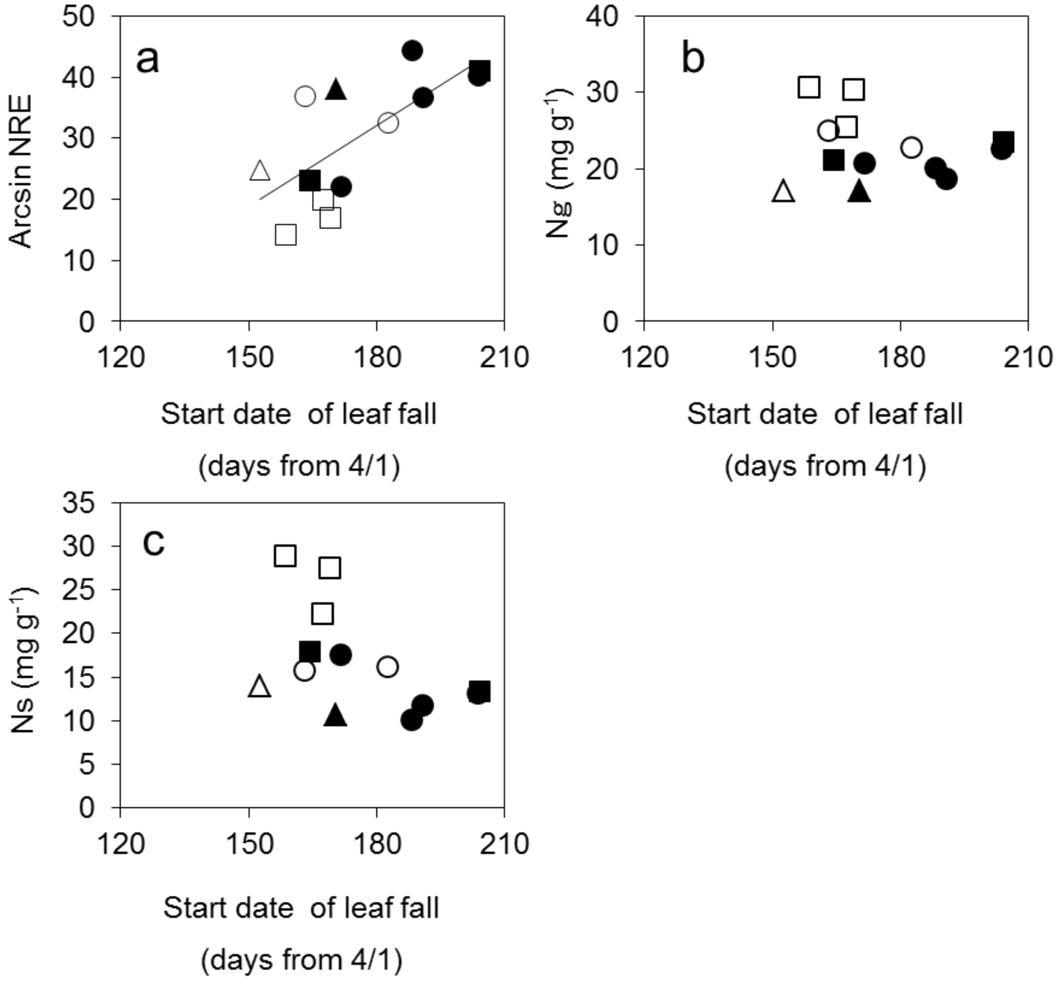

Table 1 Tateno and Takeda

Table 1 N concentration of green leaves (Ng), N concentration of senescent leaves (Ns), and N resorption efficiency (NRE) of the 13 study species. Different letter means there were no significant differeces ($P < 0.05$) according to Tukey's HSD test for Ng and Ns and Games-Howell test for NRE.

Species	Distribution pattern[1]	Leaf emergence type[2]	Ng (mg g^{-1})	Ns (mg g^{-1})	NRE (%)	Start date of leaf fall[3]	Relative dominance (%)[4]
Aesculus turbinata	Valley	Determinant	23.6 ±1.1 bcd	13.4 ±0.9 cde	43.2 ±3.1 cd	10/22	0.1
Acer mono var. marmoratum f. dissectum	Valley	Determinant	21.3 ±0.9 bcdef	18.0 ±3.2 bc	15.4 ±13.7 abcd	9/12	4.9
Fagus crenata	Uniform	Determinant	20.7 ±2.6 cdef	17.6 ±1.6 bc	14.1 ±6.1 ab	9/19	23.4
Quercus crispula	Uniform	Determinant	22.7 ±2.0 bcde	13.2 ±1.7 cde	42.0 ±5.3 cd	10/21	18.0
Acer sieboldianum	Uniform	Determinant	18.7 ±1.7 ef	11.8 ±1.5 de	35.7 ±13.3 abcd	10/8	4.3
Sorbus alnifolia	Uniform	Determinant	20.0 ±1.7 def	10.1 ±2.0 e	49.1 ±12.0 d	10/6	4.8
Lyonia ovalifolia var. elliptica	Ridge	Determinant	17.1 ±1.5 f	10.6 ±1.7 e	38.2 ±6.1 cd	9/18	5.6
Pterostyrax hispida	Valley	Indeterminant	30.7 ±1.3 a	28.9 ±0.8 a	6.0 ±2.7 a	9/6	0.3
Swida controversa	Valley	Indeterminant	30.3 ±3.2 a	27.5 ±2.6 a	8.6 ±8.3 abc	9/17	1.6
Carpinus tschonoskii	Valley	Indeterminant	25.4 ±2.0 b	22.3 ±2.6 b	11.7 ±13.6 abcd	9/15	3.5
Carpinus laxiflora	Uniform	Indeterminant	22.8 ±1.7 bcde	16.2 ±2.9 cd	29.2 ±9.9 abcd	9/30	7.2
Acanthopanax sciadophylloides	Uniform	Indeterminant	24.9 ±2.4 bc	15.8 ±1.5 cd	36.1 ±7.8 bcd	9/11	1.9
Clethra barvinervis	Ridge	Indeterminant	17.1 ±1.0 f	14.0 ±1.6 cde	17.6 ±11.3 abcd	8/31	5.9

mean ±SD

1: Categories are according to Tateno and Takeda (2003) and Kaneko et al. (1999).

2: Categories are according to Kikuzawa (1982), Hirayama and Sakimoto (1999) and S Morozumi personal observations.

3: Day of 10% of leaf fall occurred. Data from Tateno et al. (2005).

4: Relative dominance of each tree species at 0.6 ha plot based on basal area. Data from Tateno and Takeda (2003)