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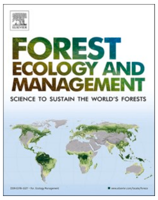

Timing of leaf fall and changes in litter nutrient concentration compromise estimates of nutrient fluxes and nutrient resorption efficiency

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ABSTRACT

Nutrient resorption in the canopy and return to soil with litterfall are two major nutrient processes in forested ecosystems. However, leaf-fall phenology and seasonal dynamics of canopy nutrient concentration have not been comprehensively quantified, compromising the confidence in estimates of litterfall nutrient fluxes and nutrient resorption efficiency. Here, we used high-frequency litter collections for 28 species in nine plots for a temperate deciduous broadleaved forest in northeastern China. Based on leaf-fall phenology and temporal shifts in nitrogen (N) and phosphorus (P) concentrations in leaf litter for major tree species, we quantified the errors in canopy nutrient flux and resorption efficiency for 15 species and nine plots. The day of year (DOY) of start of leaf-fall, DOY of peak leaf-fall, and the length of leaf-fall period differed dramatically among tree species. Concentrations of N and P in leaf litter usually declined during the summer and autumn seasons. Annual nutrient fluxes in total canopy litterfall at the ecosystem level were 65.70 ± 6.14 kg N ha^{-1} and 4.70 ± 0.80 kg P ha^{-1} of which leaf litterfall accounted for 78 and 76%, respectively. The N (NRE) and P (PRE) resorption efficiencies at the ecosystem level calculated based on the percentage of nutrient pool resorbed from canopy leaves were 49.8 ± 3.9 and 48.0 ± 7.1%, respectively. Calculating nutrient fluxes with species-specific nutrient concentration at the DOY of peak leaf-fall (Nu_{peak}) underestimated N and P fluxes by an average of 11 and 14%; the corresponding errors in N and P fluxes estimated using plot-specific Nu_{peak} were –5 and –7%. In addition, NRE and PRE for major species based on Nu_{peak} were overestimated by an average of 9 and 12%, and those for nine plots by 11 and 17%; using plot-specific Nu_{peak} lowered mean errors in NRE and PRE to 10 and 11%. These results indicate that estimating canopy nutrient fluxes and resorption efficiency using litterfall collected at the DOY of peak leaf-fall can lead to non-negligible errors, and species-specific combined litterfall collected at and slightly before the DOY of peak leaf-fall may be a better metric for estimating nutrient flux and resorption efficiency at both species and ecosystem scales.

1. Introduction

Canopy litterfall transfers aboveground organic matter from primary producers to soil, thus playing a vital role in carbon and nutrient cycles in forest ecosystems (Vitousek, 1982; Neumann et al., 2018). The forest nutrient cycle is strongly influenced by nutrient resorption before leaf abscission and by mineralization after abscission (Deng et al., 2018). Therefore, the dynamics of canopy litterfall and its nutrient concentration are critical to the understanding of nutrient cycling in forest ecosystems.

Seasonal pattern of litterfall is closely related to forest canopy dynamics, but the linkage between nutrient concentration and resorption and leaf fall phenology is still poorly understood. Significant differences in litterfall patterns were observed between forest types (Hou et al., 2013; Zhang et al., 2014) and between tree species within a forest community (Yang et al., 2004). For instance, leaf abscission in temperate summer-green broadleaved species is generally concentrated in autumn (Zhang et al., 2014). Nevertheless, the timing of peak leaf-fall varied dramatically across species within a site (Niinemets and Tamm, 2005; Yuan et al., 2010). Additionally, changes in climatic factors such as temperature, rainfall and light intensity may also affect the senescence and shedding of leaves in summer and autumn (Estiarte and Peñuelas, 2015; Dai et al., 2021). However, most litterfall studies in

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Nomenclature

Nu_{total}	Annual nutrient flux
Nu_{total_peak}	Annual nutrient flux estimated with Nu_{peak}
Nu_{wm}	Mass-weighted mean nutrient concentration
Nu_{peak}	Nutrient concentration at the DOY of collected peak of leaf-fall
MLCF	Leaf mass loss correction factor
N	Nitrogen
NRE	Nitrogen resorption efficiency
NuRE	Nutrient resorption efficiency
P	Phosphorus
PRE	Phosphorus resorption efficiency

temperate forests adopt a sampling frequency of a month (Jia et al., 2018; Ukonmaanaho et al., 2020), which limits the understanding of litter-fall phenology and of the associated nutrient dynamics in temperate forests (Niinemets and Tamm, 2005; Tateno et al., 2005; Liu et al., 2009).

The two major output pathways of canopy nutrients, i.e., leaf nutrient resorption before and return to soil with litterfall, are rarely estimated simultaneously in species-rich forests. Most studies of litterfall nutrient fluxes in forests are based on nutrient concentration measurements and multiple collections in a year (e.g., Neumann et al., 2018), but do not report species- and ecosystem-level leaf nutrient resorption efficiency (NuRE) or resorption flux. Most NuRE studies do not scale species-level measurements (e.g. as a trait of species) to ecosystem-level in mixed-species forests; this led to a recent calculation of global ecosystem-level NuRE based simply on dominant species (Du et al., 2020). Temporal changes in mass and nutrient concentrations in leaf litter have not been considered in measurements of NuRE and resorption fluxes.

The seasonal differences in mass and nutrient concentrations of leaf litter received attention in subtropical evergreen trees (Li et al., 2015; Zhou et al., 2021) because leaf litter in those ecosystems is produced year-round; this is not the case in temperate deciduous trees. A few studies (Niinemets and Tamm, 2005; See et al., 2019) showed that nutrient concentrations in leaf litter declined across the leaf-fall season, indicating that insufficient understanding of such temporal changes may compromise the estimates of nutrient fluxes and resorption.

It is also unclear how temporal patterns of litterfall in forests are related to nutrient partitioning between resorption and input to soil. It is well known that the seasonal dynamics of litterfall nutrient concentrations varies with forest type (Read and Lawrence, 2003; Ribeiro et al., 2020) and tree species (Robert et al., 1996; Shen et al., 2018). Litterfall is often collected with a monthly or bi-weekly frequency (Ukonmaanaho et al., 2020) for litterfall nutrient flux studies (Neumann et al., 2018), while many studies on NuRE use only one litter collection (e.g., Chen et al., 2021; Reed et al., 2012; Zeng et al., 2017). Errors in estimates of resorption efficiency and flux (both at species and ecosystem levels) using one seasonal litter collection have been largely ignored (Li et al., 2015). Yet, seasonal differences have been reported, notably for a subtropical tree species *Castanopsis eyrei* in China, in which NRE and PRE at the time of peak leaf-fall in autumn were 5.1 and 6.8% higher than those in spring (Li et al., 2015). The NuRE increased throughout the season for temperate deciduous trees because of declining N and P concentrations in leaf litter (Niinemets and Tamm, 2005). Therefore, using nutrient concentration in leaf litter at a single point in time would bias nutrient estimates for the whole litterfall period (See et al., 2019). The errors in NuRE involved in leaf-fall phenology (start, peak, and end of leaf-fall; expressed in day of year, DOY) and temporal changes in litter nutrient concentrations have been rarely quantified at either species or ecosystem scale, hindering accurate measurements of nutrient cycling in temperate forests.

Here, we collected litterfall with a high frequency (up to every five days in autumn) in a temperate deciduous forest (Liu et al., 2019), and determined leaf-fall phenology and N and P concentration dynamics for major tree species in nine plots to quantify potential errors in nutrient fluxes and NuRE at both species and plot scales. We hypothesized that (1) leaf-fall phenological parameters (e.g., DOY of start, peak, and end of leaf-fall, and length of leaf-fall period) vary highly among tree species, and that length of leaf-fall period is largely dependent on DOY of start of leaf fall, (2) N and P concentrations in leaf litter decrease with different rates and differ among species, and (3) there is a representative sample for nutrient concentration determination to simultaneously measure annual nutrient fluxes in leaf litterfall and NuRE. The results of this study provide insights into leaf-fall phenology and guidelines for litterfall nutrient studies, and inform about accuracy of ecosystem nutrient estimates.

2. Materials and methods

2.1. Site description

This study was carried out at the Maoershan Forest Ecosystem Research Station, in Harbin City, northeastern China (45° 24′ N, 127° 40′ E). The site has a continental monsoon climate with a warm-wet summer and a cold-dry winter. During 2008–2019, the annual mean temperature was 2.1 ± 0.8 ℃, and the annual mean precipitation was 726 ± 261 mm (Sun et al., 2021). Vegetation is a 70-year-old temperate species-rich deciduous broad-leaved forest.

2.2. Litterfall collection and nutrient measurement

Five traps (1 m × 1 m) with steel frame structure and nylon nets were placed in each of nine permanent plots (20 m × 30 m). Species composition for each plot is listed in Table A1. To reduce litter mass loss caused by leaching or decomposition (Wang et al., 2019), we collected litterfall with a high frequency. Because of snowpack and freezing temperatures in winter, the first collection taken on May 1 represented the whole winter after the previous collection in late-autumn of the previous year. Then litterfall was collected once a month in June and July, twice a month in August, and once every five days from September to October in 2015 (Liu et al., 2019). Thus, our collections (from May 1 to October 21) represented a full year.

Litterfall from each trap was sorted into leaves by tree species, woody tissue (twig and bark), reproductive organs, and miscellaneous materials (including insect and detritus), then dried at 70 °C to a constant mass and weighed to the nearest 0.01 g (Sun et al., 2021). Then the litter from five traps in each plot was combined to one sample by organ or species, and ground for nutrient measurements. This scheme reduced the labor but ignored the inter-trap variability in nutrient concentration within organ and species.

N and P concentrations were measured with a continuous flow analyzer (AA3, SEAL, Germany) after the sample was digested by concentrated sulfuric acid and hydrogen peroxide (AA3 manual). Finally, the samples were analyzed on a AA3 for N and P concentrations. The cross-check with a standard substance (GBW07603) indicated that the measurement errors were within ± 4%. In total, 682 samples from 26 species were measured for total N and P concentrations.

2.3. Statistical analysis

2.3.1. Leaf-fall phenology

Litter-fall phenology parameters (i.e., DOY of start, peak, and end of leaf-fall, and length of leaf-fall period) were estimated for 28 species, including 21 broadleaf tree species, five broadleaf shrub species, and two coniferous tree species (Refer to Table A2 for details). Basal area percentage shared by each species in the nine plots is given (Table A2).

Based on the high frequency litterfall data, leaf-fall phenology parameters can be fitted with a logistic model of accumulated leaf litterfall (Dixon, 1976):

$$F = P_1/[1 + exp^{(2.2/P_3)(P_2-t)}] \tag{1}$$

where F is the relative accumulated leaf litterfall (0 to 100%); P_1 is 100% relative accumulated leaf litterfall; P_2 is the DOY of peak leaf-fall; P_3 is the time between 10 and 50% of leaf-fall; t is day of year (DOY). Three additional important leaf-fall phenology parameters can be calculated using P_2 and P_3: the DOY of start of leaf-fall = $P_2 - P_3$, the DOY of end of leaf-fall = $P_2 + P_3$, and the length of leaf-fall period = $P_3 \times 2$. To reduce potential errors due to spatial heterogeneity, leaf litter mass was summed for species and plots for each collection date before regression.

The differences in leaf-fall phenology parameters between 21 broadleaved tree species and five broadleaved shrub species were analyzed with an independent sample t test. The relationships between leaf-fall phenology parameters were tested with Pearson correlation analysis.

2.3.2. Temporal variability in leaf litter nutrient concentration

Repeated measures analysis of variance was performed on N and P concentrations in leaf litterfall because results of Mauchly sphericity test ($P < 0.05$) indicated high levels of autocorrelation between repeated measurements. Three models, linear, exponential, and asymptotic exponential, were used to describe the rate of decline in litterfall nutrient concentrations between the first and the last collections for 15 major species (≥four measurement points of specific nutrient in time) (See et al., 2019):

$$\mathrm{Nu}_t = \mathrm{Nu}_i \times (1 + b \times t) \tag{2}$$

$$\mathrm{Nu}_t = \mathrm{Nu}_i \times e^{-kt} \tag{3}$$

$$\mathrm{Nu}_t = \mathrm{Nu}_i \times (A + (1 - A) \times e^{-kt}) \tag{4}$$

where Nu_t is the proportion of initial nutrient concentrations (Nu_i) remaining at time t (in days), and b is the linear rate of decline (in days), k is the exponential rate of decline, A is the asymptote and k is the exponential rate for the declining fraction $(1 - A)$.

We also calculated the percentage of decline in nutrient concentration since the initial (first) measurement. A linear regression was used to analyze the trend in N:P ratio for each species. One-way analysis of variance was used to analyze the inter-specific difference in nutrient concentration at peak of leaf-fall versus the mass-weighted mean nutrient concentration for major tree species.

2.3.3. Litterfall nutrient flux and nutrient resorption

For each collection and each trap, nutrient flux in litterfall was calculated for organs, and species. Plot means and standard deviations (SD) were calculated based on five traps per plot. With this method, variability in nutrient fluxes among the five traps was caused solely by species composition because nutrient concentration sample was combined at collection time; differences among plots were due to differences in species composition and nutrient concentration. Annual nutrient flux (Nu_{total}), mass-weighted mean nutrient concentration (Nu_{wm}), and leaf NuRE were calculated for each species with the following equations:

$$Nu_{\mathrm{total}} = \sum\nolimits_{t_1}^{t_n} \left[m_t(\mathrm{g}) \times Nu_t\left(\mathrm{mg\ g^{-1}}\right) \right] \tag{5}$$

$$Nu_{\mathrm{wm}} = \sum\nolimits_{t_1}^{t_n} \left[m_t(\mathrm{g}) \times Nu_t\left(\mathrm{mg\ g^{-1}}\right) \right] \Big/ \sum\nolimits_{t_1}^{t_n} [m_t(\mathrm{g})] \tag{6}$$

$$\mathrm{NuRE}(\%) = \left(1 - Nu_{\mathrm{litter}}/Nu_{\mathrm{green}} \times \mathrm{MLCF}\right) \times 100\% \tag{7}$$

where m is the litterfall collected each time (g); Nu_t is the litterfall nutrient concentration per unit mass for a specific collection time (mg g^{-1}); t_1 and t_n are the first and last sampling dates, respectively. Nu_{litter} and Nu_{green} are nutrient concentrations in leaf litter and green leaves, respectively. The Nu_{green} was obtained from (Wang et al., 2020), and measured for leaves sampled in August before the N and P concentrations started to decline (Yan et al., 2016). MLCF was the leaf mass loss correction factor, which was obtained from a previous comprehensive sampling at the same site (Wang et al., 2020). Species-specific leaf mass loss during leaf senescence, MLCF, and NuRE are found in Table A3. Leaf litter mass with concomitantly-measured nutrient concentration accounted for 78% of the annual leaf litter mass. Nutrient concentrations that were missing due to low litter mass were obtained by extrapolation using a specific temporal trend and specific annual means. Plot-level nutrient flux was calculated by summing all species and organs. Plot-level leaf NuRE was calculated as the percentage of the nutrient pool resorbed from canopy leaves.

To determine errors in nutrient flux and NuRE calculations using litterfall samples collected at DOY of peak leaf-fall only, the error (either positive or negative) from the reference values was calculated as:

$$\text{Error in nutrient flux}(\%) = \left(Nu_{\mathrm{total\_peak}} - Nu_{\mathrm{total}}\right)/Nu_{\mathrm{total}} \times 100\% \tag{8}$$

$$\text{Erro in NuRE}(\%) = \left(\mathrm{NuRE_{peak}} - \mathrm{NuRE_{total}}\right)/\mathrm{NuRE_{total}} \times 100\% \tag{9}$$

where $Nu_{\mathrm{total\_peak}}$ was the nutrient flux value estimated using nutrient concentration at DOY of collected peak leaf-fall (Nu_{peak}); $\mathrm{NuRE_{peak}}$ and $\mathrm{NuRE_{total}}$ were NuRE calculated by Eq. (7) with concentrations at peak of fall and Nu_{wm}, respectively. We presented the errors of the nutrient flux and NuRE (Table A3) for 15 species, with the remaining species excluded due to the low mass of litterfall. The 15 species accounted for 91% of the total leaf litter mass. Both statistical significance (one sample t-test) and magnitude of relative error were considered for assessing an error, because of our high intra- and inter-plot variations.

All statistical analyses were accomplished with SPSS 22.0 software (IBM Corp., NY, USA).

3. Results

3.1. Leaf-fall phenology

The pattern of accumulated leaf litterfall varied noticeably among species (Fig. 1). The 28 species could be roughly grouped into three types based on the timing of leaf-fall: early leaf-fall (*Betula platyphylla*, *Ulmus laciniata*, and *Padus racemosa*, Fig. 1a), intermediate leaf-fall (most species, Fig. 1b-c), and late leaf-fall (Fig. 1d). The logistic model fitted the mass of accumulated leaf litterfall well, with the determination coefficient (R^2) > 0.927 (Table 1). The ranges of species differences in DOY of start, peak, and end of leaf-fall reached 89 d, 52 d, and 41 d, respectively; the difference in the length of leaf-fall period reached 74 d. The independent sample t test showed that trees started leaf-fall earlier than shrubs (248 DOY versus 269 DOY), while the DOY of peak and end leaf-fall were similar between the two growth forms (Table 2). Consequently, the period of leaf-fall for trees was significantly longer than that for shrubs (32 d versus 12 d, Table 2).

Simple linear regressions across all species showed that the length of leaf-fall period mainly depended on the start rather than the end of leaf-fall (Fig. 2). Peak leaf-fall was delayed (greater DOY) with start of leaf-fall, while the length of leaf-fall period decreased with the DOY of start of leaf-fall. The end of leaf-fall was delayed with the DOY of start and peak leaf-fall, but was not significantly related to the length of leaf-fall period. The length of leaf-fall extended with DOY of peak leaf-fall.

3.2. Dynamics of nutrients in leaf litter

Collection date, tree species, and their interaction significantly affected the concentrations of N and P in leaf litter (Table 3). For most

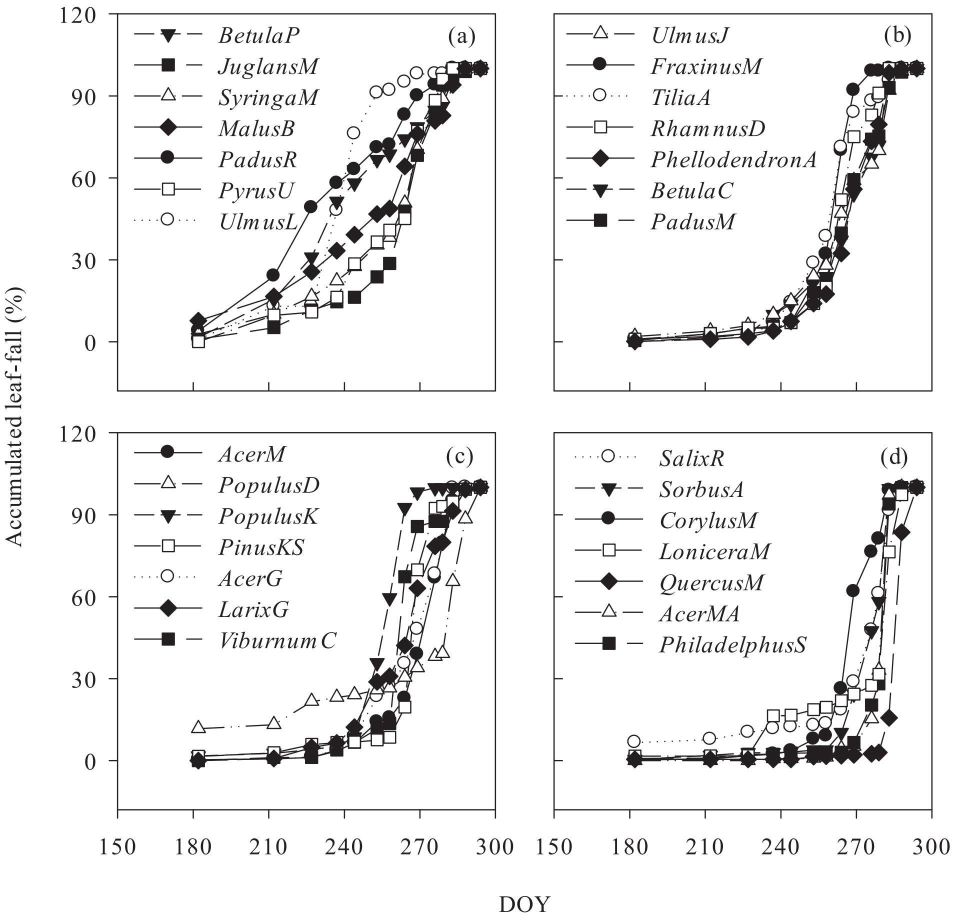

Fig. 1. Seasonal patterns of accumulated leaf-fall by species. The 28 species are divided into three groups: early (a), intermediate (b, c), and late (d) leaf-fall. The species within each panel are listed in the order of percentage of basal area. Species abbreviations: *BetulaP*: *Betula platyphylla*, *JuglansM*: *Juglans mandshurica*, *SyringaM*: *Syringa reticulata* var. *amurensis*, *MalusB*: *Malus baccata*, *PadusR*: *Padus racemosa*, *PyrusU*: *Pyrus ussuriensis*, *UlmusL*: *Ulmus laciniata*, *UlmusJ*: *Ulmus davidiana* var. *japonica*, *FraxinusM*: *Fraxinus mandshurica*, *TiliaA*: *Tilia amurensis*, *RhamnusD*: *Rhamnus davurica*, *PhellodendronA*: *Phellodendron amurense*, *BetulaC*: *Betula costata*, *PadusM*: *Padus maackii*, *AcerM*: *Acer mono*, *PopulusD*: *Populus davidiana*, *PopulusK*: *Populus koreana*, *PinusKS*: *Pinus koraiensis*, *AcerG*: *Acer ginnala*, *LarixG*: *Larix gmelini*, *ViburnumC*: *Viburnum opulus* var. *calvescens*, *SalixR*: *Salix rorida*, *SorbusA*: *Sorbus alnifolia*, *CorylusM*: *Corylus mandshurica*, *LoniceraM*: *Lonicera maackii*, *QuercusM*: *Quercus mongolica*. *AcerMA*: *Acer mandshuricum*, *PhiladelphusS*: *Philadelphus schrenkii*. The two coniferous species, *Pinus koraiensis* and *Larix gmelini*, exhibited intermediate leaf-fall timing.

Table 1
Parameters of leaf-fall phenology for 28 species. The regression model is calculated with Eq. (1). Growth form: BLT: broadleaved tree, BLS: broadleaved shrub, ConT; coniferous tree. The species are ranked in the order of DOY of peak leaf-fall.

Species	Growth form	R^2	Peak leaf-fall (DOY)	Start of leaf-fall (DOY)	End of leaf-fall (DOY)	Length of leaf-fall (d)
Padus racemosa	BLT	0.967	233.4	193.4	273.3	79.9
Ulmus laciniata	BLT	0.989	237.4	223.7	251.1	27.5
Betula platyphylla	BLT	0.968	245.7	211.3	280.0	68.6
Populus koreana	BLT	0.987	257.6	246.4	268.8	22.5
Syringa reticulata var. *amurensis*	BLT	0.959	258.1	232.0	284.1	52.0
Fraxinus mandshurica	BLT	0.995	259.5	251.1	268.0	16.9
Tilia amurensis	BLT	0.983	261.1	241.8	280.5	38.6
Juglans mandshurica	BLT	0.978	263.7	247.5	279.9	32.4
Pyrus ussuriensis	BLT	0.954	264.5	247.7	281.2	33.5
Betula costata	BLT	0.974	264.6	250.5	278.7	28.2
Ulmus davidiana var. *japonica*	BLT	0.975	265.6	242.7	288.5	45.8
Pinus koraiensis	ConT	0.995	266.2	261.5	271.0	9.6
Padus maackii	BLT	0.990	266.9	249.2	284.6	35.3
Rhamnus davurica	BLT	0.989	267.1	256.4	277.8	21.4
Phellodendron amurense	BLT	0.987	267.3	258.6	276.0	17.4
Malus baccata	BLT	0.962	267.7	249.9	285.4	35.5
Larix gmelini	ConT	0.994	267.8	253.4	282.2	28.7
Acer mono	BLT	0.983	268.6	254.6	282.6	28.0
Acer ginnala	BLS	0.985	270.0	258.5	281.4	22.8
Viburnum opulus var. *calvescens*	BLS	0.995	272.1	268.7	275.5	6.9
Corylus mandshurica	BLS	0.984	273.6	265.8	281.4	15.6
Populus davidiana	BLT	0.927	274.5	256.9	292.0	35.1
Salix rorida	BLT	0.957	275.0	266.4	283.6	17.2
Sorbus alnifolia	BLT	0.972	276.1	268.1	284.1	15.9
Philadelphus schrenkii	BLT	0.978	279.3	274.1	284.6	10.5
Acer mandshuricum	BLS	0.990	279.6	276.6	282.6	5.9
Lonicera maackii	BLS	0.994	282.0	279.1	284.9	5.8
Quercus mongolica	BLT	0.998	285.7	282.7	288.8	6.1

Table 2
Comparisons of the parameters of leaf-fall phenology between broadleaved tree species and shrub species.

Parameter	Tree ($N = 21$)	Shrub ($N = 5$)	t	P
Start of leaf-fall (DOY)	248.0 ± 20.4	269.2 ± 7.9	2.260	0.033
Peak of leaf-fall (DOY)	263.8 ± 12.7	275.4 ± 5.1	1.976	0.060
End of leaf-fall (DOY)	279.6 ± 8.9	281.6 ± 3.8	0.478	0.637
Length of leaf-fall period (d)	31.6 ± 18.5	12.3 ± 7.0	2.266	0.033

species, both concentrations of N and P in leaf litter declined during the seasons. N concentration in leaf litter of *B. platyphylla* declined first and then fluctuated slightly (Fig. 3a), while P concentration declined first and then increased (Fig. 3b). Both N and P concentrations in *Juglans mandshurica* declined first and then rebounded (Fig. 3c and 3d). The rate of decline in N and P concentrations varied with species; the percentages of the concentration declining since the first to the last collection were in the range of 4 to 80% for N and 10 to 90% for P, with the lowest and highest decreases occurring in *J. mandshurica* and *Populus davidiana*, respectively. The best fitting models for the proportions of decline in leaf litter nutrient concentrations were exponential or linear (Table A4 and A5). The temporal trends in N:P in leaf litter diverged among species, and only five species had significant linear trends over time (Fig. 4). Leaf litter N:P for *U. davidiana* var. *japonica*, *Fraxinus mandshurica* and *Syringa reticulata* var. *amurensis* increased significantly with time, while that for *B. platyphylla* and *P. koreana* significantly declined.

At the ecosystem level, N and P concentrations at the end of leaf fall declined by 68 and 69% compared with the initial concentration at 152 DOY (Fig. 5a); both were best fitted with the linear and asymptotic exponential functions. The N:P in leaf litter also declined from summer to autumn, when the earliest point was excluded (Fig. 5b).

3.3. Annual nutrient flux in total and leaf litterfall

Mean annual total litterfall mass was 4898.7 ± 172.9 kg ha^{-1} for the nine plots (i.e., ecosystem-scale). Leaves, woody tissue, reproductive organs, and miscellaneous litter accounted for 76, 14, 3, and 7%, respectively. Annual nutrient fluxes in total litterfall were 65.7 ± 6.1 kg N ha^{-1} and 4.7 ± 0.8 kg P ha^{-1} (Table A6). Leaf litter contributed 78% (51.1 ± 4.8 kg ha^{-1}) and 76% (3.6 ± 0.8 kg ha^{-1}) to the total litterfall N and P fluxes (Table A6). Miscellaneous materials accounted for both 10% of the total fluxes, while woody tissue and reproductive organs together accounted for 12% of total N and 14% of total P.

Annual nutrient flux in leaf litter was generally overestimated when calculated using Nu_{peak} instead of using temporal integration (Fig. 6). On average, N and P fluxes calculated with species-specific Nu_{peak} were underestimated by 11% and 14%, respectively ($P < 0.002$). The error in P flux was greater than that in N flux for most plots (except Plots #9, Table A6). For the 15 major tree species, Nu_{peak} tended to be lower than or similar to the mass-weighted mean nutrient concentration, except that N Nu_{peak} of *B. platyphylla* was significantly higher than the mass-weighted mean ($P = 0.005$, Table 4). Using plot-specific Nu_{peak}, mean errors in N and P fluxes at the ecosystem level were also negative (–5% and –7%, respectively), but had large ranges (Table A6).

3.4. Leaf nutrient resorption efficiency

NRE and PRE were overestimated when calculated with peak leaf-fall nutrient concentration instead of mass-weighted mean nutrient concentration (Fig. 7). The annual NRE and PRE of 15 tree species calculated based on annual mass-weighted mean concentration were on average 44.7 and 45.3%, respectively, and the mean ratio of NRE to PRE

Table 3
Repeated measures analysis of variance for leaf litterfall nutrient concentration of major species.

Nutrient	Sampling date (t)		Species (S)		$t \times S$	
	F	P	F	P	F	P
N	641.744	< 0.001	32.286	< 0.001	2.250	< 0.001
P	615.680	< 0.001	43.071	< 0.001	2.448	< 0.001

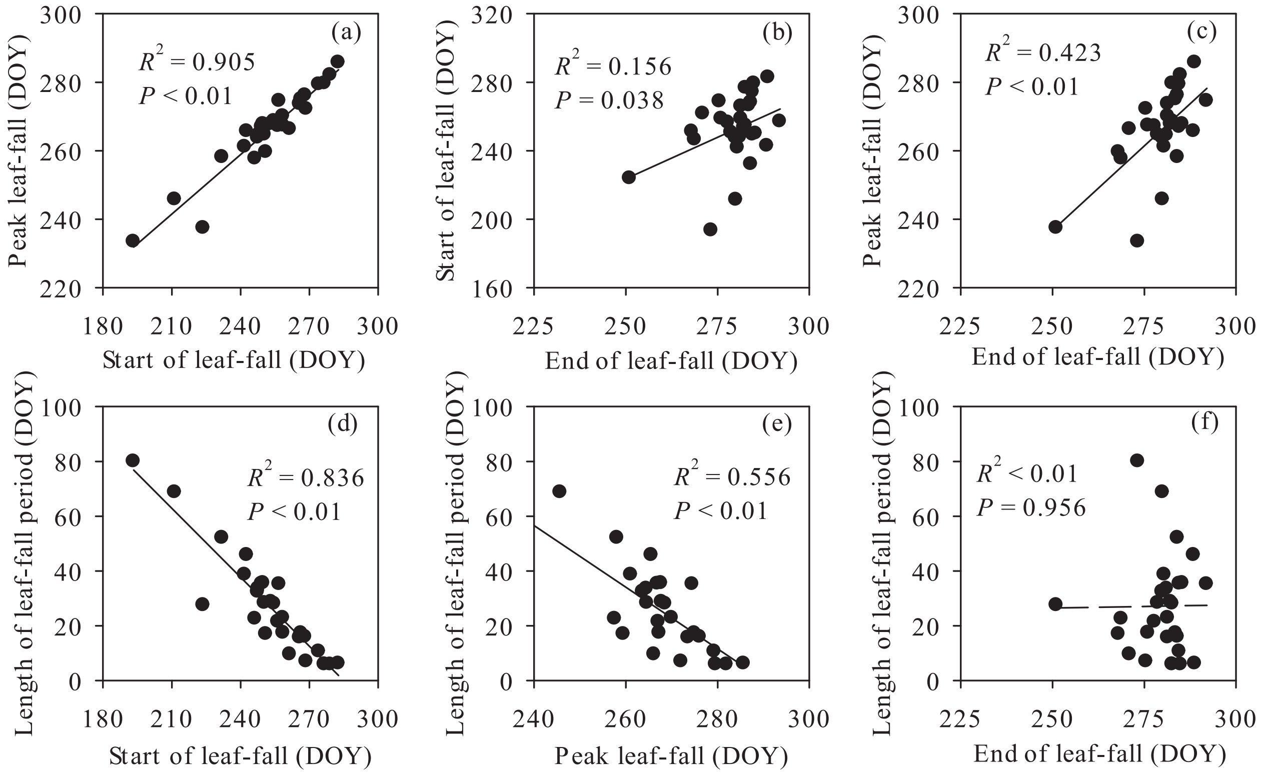

Fig. 2. Relationships between leaf-fall phenology parameters. The solid line indicates a significant relationship, while the dashed line indicates an insignificant one.

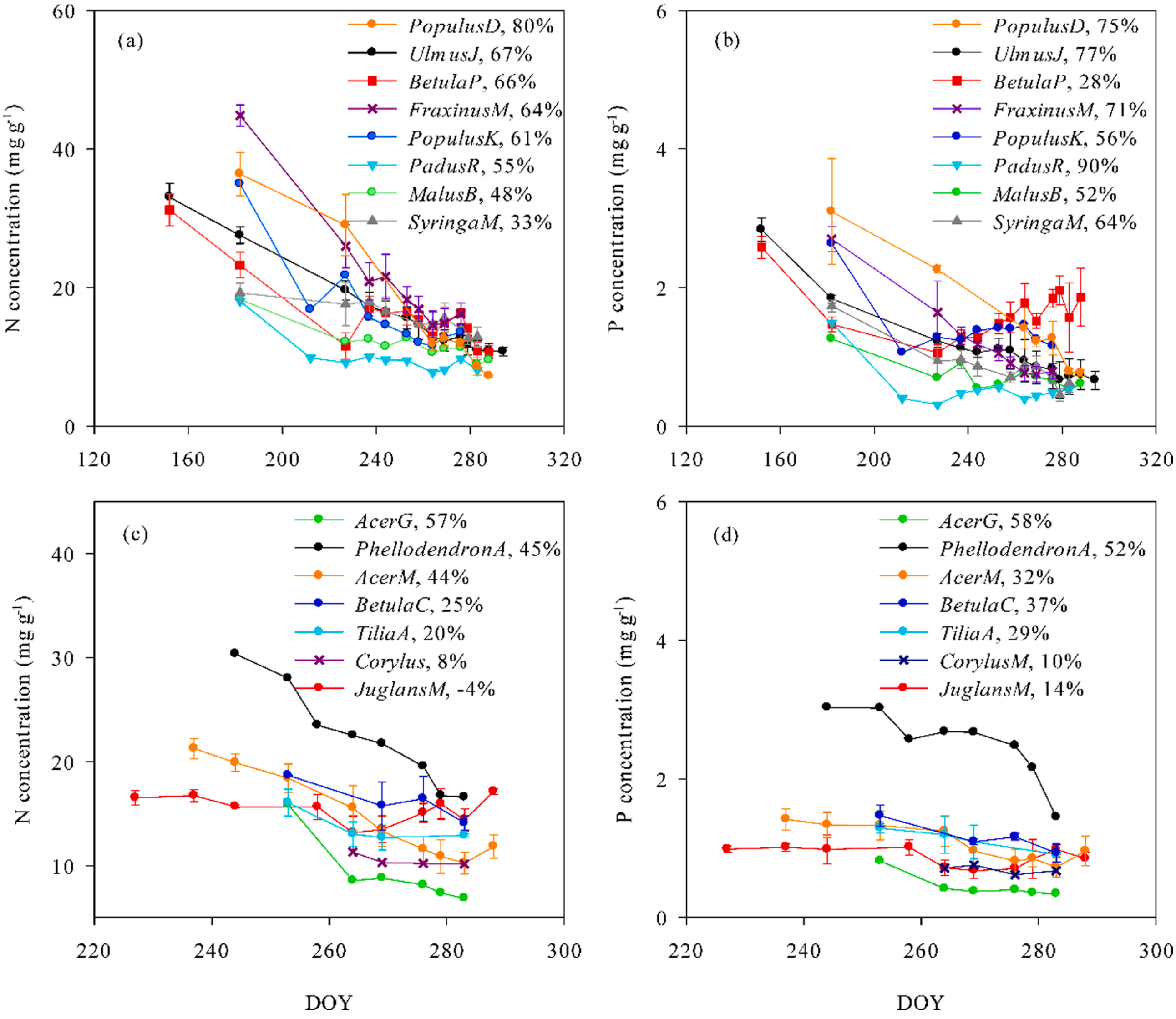

Fig. 3. Changes in nutrient concentration in leaf litter between summer and autumn for nine species. Species abbreviations are given in Fig. 1. The declining percentage from the initial concentrations to the concentration at the final collection to is given. The species are graphed according to declining percentage in N concentration. The error bars represent the standard error of the nutrient concentration for nine plots.

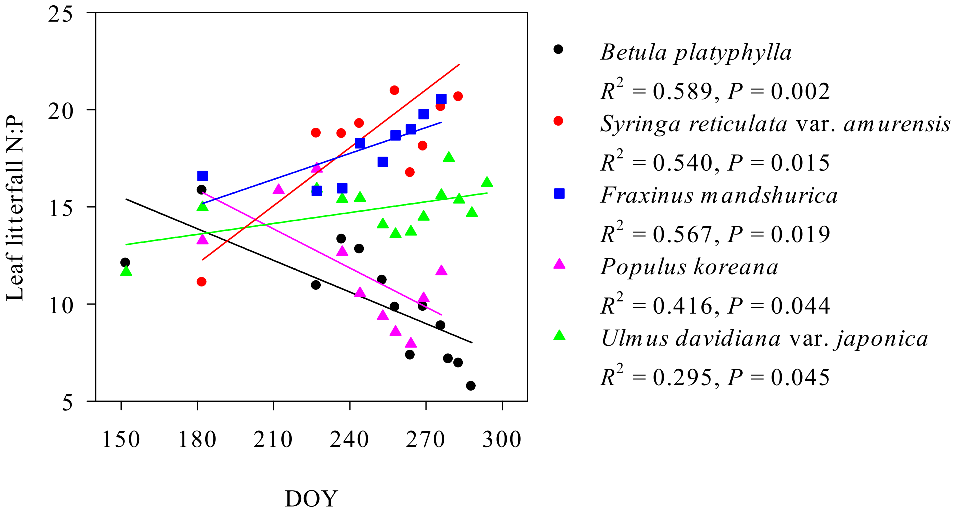

Fig. 4. Linear trend of N:P ratio in leaf litter from summer to autumn. Only five species with significant trends are shown.

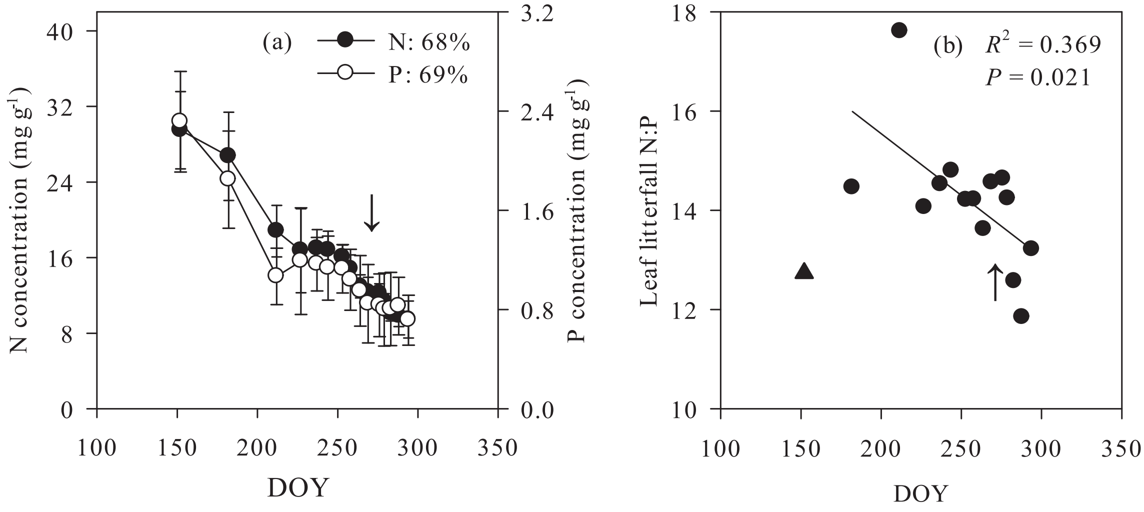

Fig. 5. Changes in leaf litter nutrient concentrations at the ecosystem-level between summer and autumn. The black arrow indicates DOY of peak leaf fall. The error bars represent standard error of the nutrient concentration for nine plots. The declining percentage from the initial concentrations to the concentration at the final collection to is given in (a). The filled triangle (at the DOY of 152) in (b) indicates data excluded from regression analysis. The best fitting model with the proportion of initial concentration at ecosystem level is a linear decay model ($Nu_t = Nu_i \times (1 - 0.0048\, t^{***})$, AIC = –53.73, $P < 0.001$) and asymptotic exponential model ($Nu_t = Nu_i \times (0.22 + (1 - 0.22)\, e^{-0.013t})$, AIC = –49.32, $P < 0.05$), respectively for leaf litter N and P concentrations.

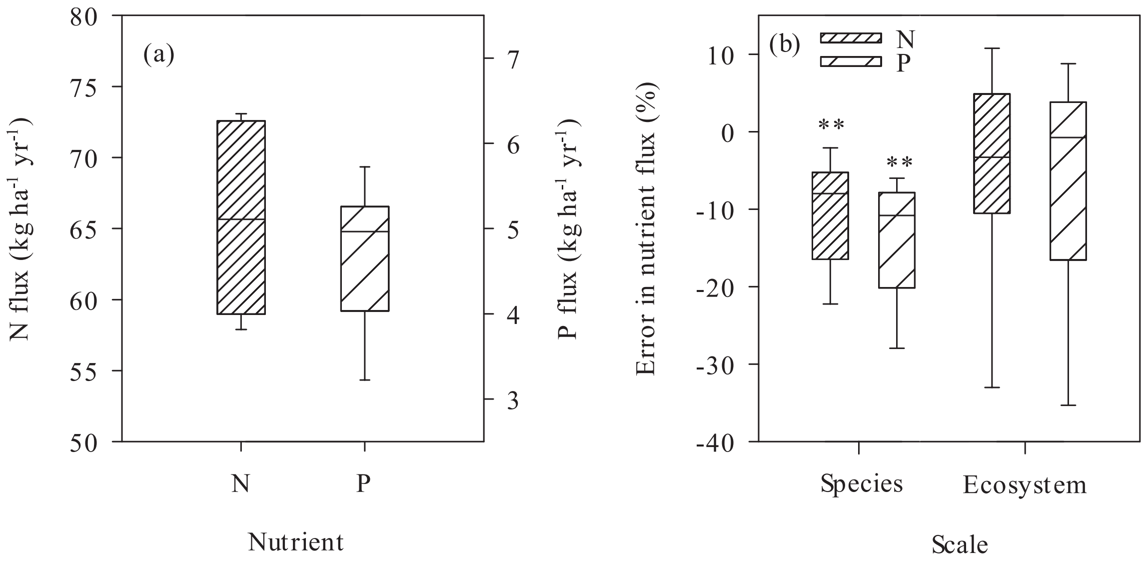

Fig. 6. Box plot of annual ecosystem nutrient flux (a) and the error with using nutrient concentrations at the DOY of peak leaf fall (b) in nine plots. Nutrient flux in leaf litterfall (temporal accumulation) calculated with Eq. (5) was used as reference, and error was calculated with Eq. (8). Species and ecosystem levels were based on concentrations at species-specific and plot-specific DOY of peak leaf fall, respectively. Boxes indicate 25 and 75 percentiles; bars indicate 10 and 90 percentiles. The solid line in the box indicates the median. ** indicates a significant difference from zero at the 0.01 level.

(NRE:PRE) was 1.0. The relative errors in NRE and PRE estimated with nutrient concentration at DOY of peak leaf-fall ranged from –19 to 46% and from –19 to 56%, respectively, with the mean of 9 and 12%, respectively. The range of relative errors in NRE:PRE was –40 to 23% (Table A3).

At the ecosystem level, NRE and PRE calculated based on the percentage of the nutrient pool resorbed from canopy leaves were 49.8 ± 3.9 and 48.0 ± 7.1%, respectively, and ranged from 44.6 to 57.0% and from 41.0 to 63.4%, respectively, across the nine plots (Table A7). Using concentration at DOY of ecosystem-level peak leaf-fall, NRE and PRE for the nine plots were averaged to 54.4 ± 8.2 and 52.9 ± 10.3%, with mean errors of 10 and 11%, respectively (Table A7).

4. Discussion

We found that the errors in nutrient flux and resorption efficiency were non-negligible when using species or ecosystem-level Nu_{peak}; errors were mainly due to the asymmetry in the rate of change in nutrient concentration in leaf litter before and after peak leaf-fall, i.e., early litterfall had a disproportionately higher nutrient concentration than late litterfall.

4.1. Interspecific differences in leaf-fall phenology

Although leaf-fall in this temperate forest at canopy scale concentrated in autumn, the DOY of start and peak leaf-fall differed across species (Table 1). Similarly, the peak of leaf-fall varied between September and October, while the timing of peak leaf-fall differed

Table 4

Comparison of nutrient concentrations of leaf litter at DOY of peak leaf-fall and annual mass-weighted means. The mass-weighted mean nutrient concentration is calculated with Eq. (6). Different lowercase letters represent significant differences at the $\alpha = 0.05$ level. The species are listed in the order of the difference in N concentration between DOY of peak leaf-fall and annual mass-weighted mean as in Table A9. *Populus koreana*, *Padus racemosa*, and *Phellodendron amurense* have only one collection in time.

Species	N (mg g^{-1})		P (mg g^{-1})	
	Concentration at DOY of peak leaf-fall	Annual mass-weighted mean concentration	Concentration at DOY of peak leaf-fall	Annual mass-weighted mean concentration
Populus davidiana	8.86 ± 1.11b	14.89 ± 2.52a	0.84 ± 0.11b	1.27 ± 0.21a
Acer mono	11.81 ± 1.15b	14.13 ± 1.81a	0.85 ± 0.17b	1.01 ± 0.15a
Betula platyphylla	17.16 ± 1.34a	15.13 ± 1.32b	1.27 ± 0.09b	1.46 ± 0.18a
Betula costata	14.56 ± 0.39b	15.93 ± 0.78a	0.95 ± 0.05b	1.22 ± 0.14a
Ulmus davidiana var. *japonica*	11.00 ± 1.40b	14.08 ± 2.06a	0.72 ± 0.26a	0.95 ± 0.24a
Juglans mandshurica	13.14 ± 1.61b	14.79 ± 0.80a	0.72 ± 0.11a	0.80 ± 0.07a
Fraxinus mandshurica	14.77 ± 2.02a	16.72 ± 1.94a	0.78 ± 0.12a	0.90 ± 0.14a
Syringa reticulata var. *amurensis*	15.62 ± 2.20a	15.62 ± 1.20a	0.86 ± 0.15a	0.85 ± 0.08a
Tilia amurensis	13.38 ± 0.92a	13.70 ± 1.10a	1.20 ± 0.17a	1.13 ± 0.17a
Corylus mandshurica	10.32 ± 1.10a	10.56 ± 0.68a	0.76 ± 0.11a	0.70 ± 0.02a
Malus baccata	10.57 ± 0.36a	11.36 ± 0.33a	0.78 ± 0.06a	0.84 ± 0.07a
Acer ginnala	8.14 ± 0.56a	8.94 ± 1.43a	0.40 ± 0.01a	0.44 ± 0.03a
Populus koreana	11.60	13.42	1.46	1.47
Padus racemosa	9.15	9.54	0.31	0.48
Phellodendron amurense	21.73	21.69	2.48	2.41

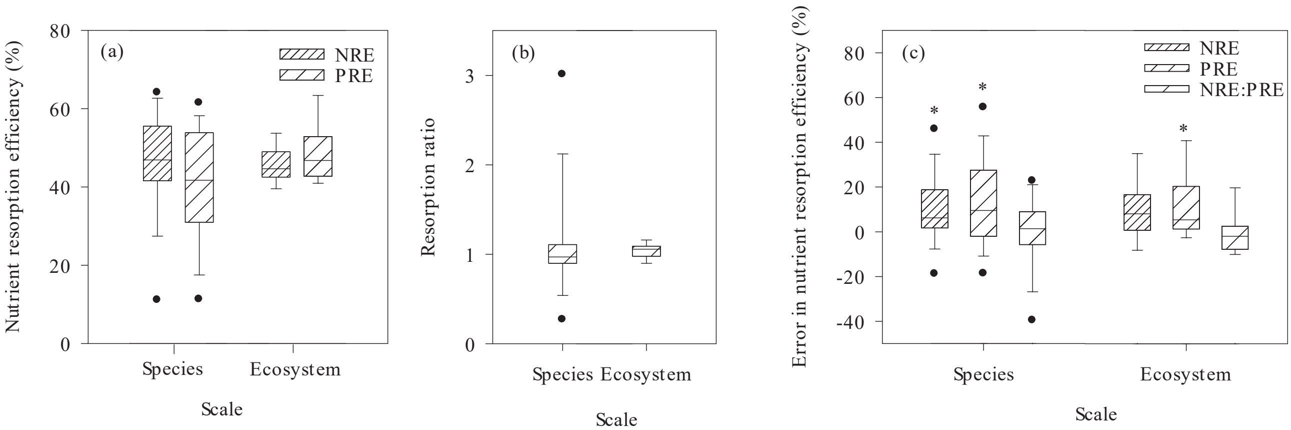

Fig. 7. Box plot of nutrient resorption efficiency (a), resorption ratio of nitrogen to phosphorous (b), and the error using nutrient concentration at the species-specific DOY of peak leaf fall (c) in nine plots. Nutrient resorption efficiency is calculated with Eq. (7) and the relative error is calculated with Eq. (9). Species and ecosystem levels are based on concentrations at species-specific DOY of peak leaf fall. Boxes indicate 25 and 75 percentiles; bars indicate 10 and 90 percentiles. The solid line in the box indicates the median. * indicates significant difference from zero at the 0.05 level.

among major tree species in a mixed broadleaf-Korean pine forest in Changbai Mountain, northeastern China (Yuan et al., 2010);leaf-fall in *Pinus koraiensis* and *T. amurensis* peaked in mid-September and then lasted for a long time, while that in *Q. mongolica*, *U. davidiana* var. *japonica* and *A. mono* concentrated in early October. Start of leaf-fall for *B. pendula*, *Q. robur* and *Q. rubra* in a deciduous mixed forest in northern Belgium (Staelens et al., 2011) was consistent with the congeneric species in this study, but the end of leaf-fall for the three species was later than in our forest, and we attribute this to the higher autumn temperature in Belgium. The start and end of leaf-fall in *B. pendula*, *Corylus* spp. and *F. excelsior* (except *Lonicera xylosteum*) in a warmer mixed deciduous forest in Estonia (Niinemets and Tamm, 2005) was later than in our forest. Climate variability leads to overall differences in leaf-fall phenology among sites, while species respond to inter-specific differences in leaf-fall phenology within sites. Large inter-specific differences in leaf-fall phenology (Table 1) caused difficulties in field collection and nutrient measurement in species-level nutrient studies. If the objective is to measure NuRE using leaf litter samples about the DOY of peak leaf-fall, sampling time should consider phenological differences. However, if the plan is to simultaneously estimate species- and ecosystem-level nutrient partitioning into resorption and litterfall, a multiple collection scheme should be considered for both litter mass and nutrient concentration (Refer to section 4.3 for details).

The start of leaf-fall largely determined the duration of leaf-fall in the Maoershan forest in this study. Species with an earlier start of leaf-fall usually reached peak of leaf-fall earlier, though not the end of leaf-fall, leading to a relatively long period of leaf-fall compared with species with a later start of leaf-fall. This indicated that the canopy duration of species with an earlier start of leaf-fall should be carefully used to calculate leaf lifespan. We also noted that leaf-fall often started at the lower part of the canopy (older leaves) for species with an earlier start of leaf-fall (e.g., the light-demanding species *B. platyphylla* and intermediate species *J. mandshurica* and *P. racemosa*), but not so for species with intermediate and later start of leaf-fall. The earlier leaf-fall from the lower part of the canopy for light-demanding and intermediate species may indicate a shorter leaf lifespan and a different nutrient use strategy compared with other species. The later start of leaf-fall in shrubs can help improve light capture of the whole ecosystem.

4.2. *Temporal variability in nutrient concentrations in leaf litter*

Nutrient concentration in leaf litter declined through the seasons for most species studied in temperate broad-leaved forest (Fig. 3; Niinemets and Tamm, 2005; See et al., 2019). Such declines in N and P concentrations may result from three mechanisms. First, a greater proportion of green litterfall in summer and early-autumn in temperate broadleaf forests led to a higher nutrient concentration in early-stage of leaf fall than at a later stage. Summer litterfall contains more leaf litter that was generated by insects, strong winds and/or rainstorm events than by natural senescence; such early litter had high nutrient concentrations. These stochastic events did not occur at the Maoershan forest in 2015 (except typhoons in 2020, Jiang et al. (2022)). However, the frequency of extreme climate events (such as typhoon and severe drought) is predicted to increase in mid-latitudes due to global warming (Trenberth, 2011; Altman et al., 2018), possibly altering the relative allocation of N and P to resorption or loss through litterfall.

Second, progressive nutrient resorption led to a declining trend in nutrient concentrations in green leaves in the canopy (Niinemets and Tamm, 2005; Yan et al., 2016). Efficient degradation of chlorophyll and full nutrient remobilization in early-falling non-green leaves is hindered by insufficient time and low temperatures (Hörtensteiner, 2006), and may be the main reason for the high nutrient concentration in early-shed leaves in this study. The two exceptions, a low nutrient concentration before or around the DOY of peak leaf-fall in *B. platyphylla* and *J. mandshurica*, suggest true leaf senescence and potential remobilization of nutrients from older to younger leaves which remained green on the tree.

Third, leaching from old leaves while still in the tree canopy in the late period of litterfall (Duchesne et al., 2001; Turpault et al., 2021) and pre-collection leaching may also reduce late leaf-fall nutrient concentration. Leaching in the canopy for the whole growing season (0.05 kg ha^{-1} yr^{-1}) (Sun, 2014) was negligible compared with leaf litter N flux to soil (51.1 kg ha^{-1} yr^{-1}). We found that percentages of the initial N and P concentrations in leaf litter declined with a wide range (Fig. 3) and were usually not well expressed with asymptotic exponential functions (c.f., See et al., 2019). At the ecosystem level, the gradually declining nutrient concentration in leaf litter since June was due primarily to a decline in concentration within species (Fig. 3) and, less importantly, across species (Wang et al., 2022). Our frequent collection minimized the pre-collection leaching (Wang et al., 2019).

The different decline rates of N and P concentrations among species led to various trends in N:P ratios over time (Fig. 4), and reflected the imbalance of N and P between resorption and loss from plants. The decreasing N:P in leaf litterfall in this study (Fig. 5b) was consistent with that in a temperate forest in Estonia (Niinemets and Tamm, 2005), but inconsistent with the increasing trends for all six studied species at the Hubbard Brook Experimental Forest (See et al., 2019). The ecosystem-level N and P concentrations and N:P for the final litter collection in this study indicated that the Maoershan forest (N $\approx$ 10 mg g^{-1}, P$\approx$ 0.8 mg g^{-1}, N:P $\approx$ 12, Fig. 5) and the temperate forest in Estonia (N $\approx$ 10 mg g^{-1}, P $\approx$ 0.7 mg g^{-1}, N:P $\approx$ 14) were weakly N-limited, whereas the Hubbard Brook Experimental Forest (N $\approx$ 7 – 12 mg g^{-1}, P $\approx$ 0.2 – 0.6 mg g^{-1}, N:P $\approx$ 17 – 35 for the three studied species) was strongly P-limited. The temporal trend in leaf litter N:P reflects higher resorption efficiency of a limiting element (Killingbeck, 1996; Reed et al., 2012; Du et al., 2020; He et al., 2020). A temporal change in N:P may be used as a complementary approach for detecting the relative limitation of N or P at species and ecosystem scales.

4.3. *Nutrient flux in leaf litter and nutrient resorption efficiency*

The N and P fluxes in total litterfall in the Maoershan forest were 65.7 ± 6.1 kg ha^{-1} yr^{-1} and 4.7 ± 0.8 kg ha^{-1} yr^{-1}, respectively, and relatively higher compared with those in European forests (44.9 kg N ha^{-1} yr^{-1} and 3.2 kg P ha^{-1} yr^{-1}) (Neumann et al., 2018). Leaf litter accounted for 78 and 76% of the total litterfall N and P fluxes, indicating that leaf litter was the main component of nutrient return to the soil (Yang et al., 2004; Hansen et al., 2009). Therefore, quantifying the error in estimating leaf litter N and P fluxes can greatly increase the accuracy of nutrient quantities cycling through litterfall.

We found that using Nu_{peak} instead of nutrient concentrations in season-total leaf litter on average underestimated true nutrient fluxes by 11% or more (Fig. 6) and overestimated NuRE by > 9% for the 15 tree species (Fig. 7). This was because early litterfall had a lower mass (Fig. 1) but disproportionately high nutrient concentrations than mid- and late-season litterfall (Fig. 3, Fig. 5). The ratio of leaf litterfall mass before the peak of leaf-litter production to that after was 1.29, while the corresponding ratios of N and P nutrient concentrations were both 1.40. In the Maoershan forest, the magnitude of errors in nutrient flux in leaf litterfall and NuRE calculated using nutrient concentration at the DOY of peak leaf-fall for these tree species was higher than or equivalent to the 7% underestimation of NuRE by ignoring leaf mass loss (Wang et al., 2020). These findings indicated that studies comparing NuRE between species groups (e.g., red-leaved deciduous species such as *Acer ginnala*; and yellow-leaved deciduous species such as *Betula platyphylla* in this study) need to carefully consider measurement errors in NuRE (Hughes et al., 2021), including the mass loss correction factor (Wang et al., 2020) and the effect of a temporal change in nutrient concentration in leaf litter (Fig. 8; Niinemets and Tamm, 2005).

There is a trade-off between measurement accuracy and labor/time cost in studies of canopy nutrient recycling. Using a combined leaf litter sample for all species can save time when litterfall nutrient flux measurements are of interest at the ecosystem level only. To determine a species contribution to the ecosystem-level nutrient flux, a species-specific season total sample is sufficient. However, to determine resorption efficiency or the maximum potential resorption as a plant trait (Killingbeck, 1996), the late-falling leaf litter may be better than litter collected at DOY of peak leaf-fall.

It is a challenge to simultaneously measure nutrient resorption fluxes (or NuRE) and litterfall nutrient fluxes at both species and ecosystem levels in mixed-species forests. The question remains whether we can use combined leaf-litter at and before leaf-fall peak to represent mass-weighted mean concentration across the seasons. In the deciduous broad-leaved forest in this study, peak leaf-fall in nine plots occurred mostly in late September or early October (Fig. A1), and N and P concentrations in leaf litterfall at the plot scale exhibited uniformly declining trends across the season (Figs. A2 and A3). At plot-level, the errors in N and P fluxes calculated using mass-weighted mean nutrient concentrations at peak and 10 days before peak leaf-fall underestimated nutrient fluxes on average by < 5% (Table A8), representing a reduction in error compared with that using Nu_{peak} only. For most tree species, NRE and PRE estimated using the nutrient concentration of combined samples at peak and 10 days before peak leaf-fall were also smaller compared with that obtained using Nu_{peak} (Table A9). These findings suggest that, to simultaneously measure leaf-litterfall nutrient and resorption fluxes in temperate deciduous forests, a species-specific combined litter fall collected at and slightly before the DOY of peak leaf-fall might have a better temporal representativeness than that using just the DOY of peak leaf-fall.

5. Conclusions

The start of and peak leaf-fall dominated the differences in leaf-fall phenology among species in the temperate deciduous forest in this study. The rate and pattern of decline in N and P concentrations and the trends in N:P ratios in leaf litter varied among species. The mean errors in N and P fluxes, NRE and PRE for major species and for the nine plots calculated with species-specific or plot-specific Nu_{peak} were generally higher than 10%. Such non-negligible errors resulted from had a disproportionately higher nutrient concentration in early litterfall than in late litterfall. Multiple collections of litterfall can help in accurate measurements of nutrient cycling processes in forest ecosystems, while a species-specific litter fall collected at and slightly before the DOY of peak leaf-fall may be better than a single collection at peak leaf-fall.

CRediT authorship contribution statement

Xingchang Wang: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Huimin Song:** Investigation, Writing – original draft. **Fan Liu:** Investigation, Writing – original draft. **Xiankui Quan:** Resources. **Chuankuan Wang:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120188.

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