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Flower litters of alpine plants affect soil nitrogen and phosphorus rapidly in the eastern Tibetan Plateau

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Abstract

Litters of reproductive organs have been rarely studied, despite their role in allocating nutrients for offspring reproduction. This study determines the mechanism through which flower litters efficiently increase the available soil nutrient pool. Field experiments were conducted to collect plant litters and calculate biomass production in an alpine meadow of the eastern Tibetan Plateau. Carbon, nitrogen, phosphorus, lignin, cellulose, and their relevant ratios of litters were analyzed to identify their decomposition features. A pot experiment was performed to determine the effects of litter addition on soil nutrition pool by comparison between the treated and control samples. Litter-bag method was used to verify decomposition rates. The flower litters of phanerophyte plants were comparable with non-flower litters. Biomass partitioning of other herbaceous species accounted for 10%–40% of the aboveground biomass. Flower litter possessed significantly higher N and P levels but less C/N, N/P, lignin/N, and lignin and cellulose concentrations than leaf litter. Flower litter fed soil nutrition pool more efficiently because of their faster decomposition rate and higher nutrient contents. Litter-bag experiment confirmed that the flower litters of *Rhododendron przewalskii* and *Meconopsis integrifolia* decomposes approximately three times faster than mixed litters within 50 days. Moreover, the findings of the pot experiment indicated that flower litter addition significantly increased the available nutrient pool. Flower litter influenced nutrition cycling in alpine ecosystems, as evident by its non-ignorable production and significantly faster decomposition. The underlying mechanism can enrich nutrients, which return to the soil, and non-structural carbohydrates, which feed and enhance the transitions of soil microorganisms.

Key words alpine ecosystem, flower litter, chemical property, decomposition rate, nitrogen, phosphorus

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59 The growth and health of plants in their life history have been considerably influenced
60 by variations in the physical, chemical, and biological properties of soil, particularly
61 around the rhizosphere, although soil properties can also be mediated by plants. Plant
62 properties directly affect the productivity and function of an ecosystem (Chapin et al.,
63 1986; Chapin, 2003; Berendse and Aerts, 1987; Grime, 1998). In a natural
64 environment, plants continuously lose N and P in their whole life history and even
65 during litter production and decomposition (Laungani and Knops, 2009; Richardson
66 et al., 2009). N is a major constituent of several important plant substances (Vitousek
67 and Howarth, 1991). Most plants absorb N through soil compounds to support their
68 growth. In addition to the mineralization of soil organic matter, the decomposition of
69 plant residues can supply available N to plants and microorganisms. Similar to
70 nitrogen, P is closely associated with numerous vital plant processes. Nevertheless, in
71 most circumstances, P is limited because of its small concentration in soil; this
72 element is released slowly from insoluble P but is highly demanded by plants and
73 microorganisms (Bieleski, 1973; Richardson et al., 2009). As decomposition is a
74 prolonged process, plants contain concentrated nutrients comparable with soil, which
75 have significant effects on the biogeochemical cycle and feedbacks of plant–soil
76 interaction. However, these nutrients cannot be simply absorbed again to the soil
77 nutrient pool supplied by plants and microorganisms (Bieleski, 1973; Berendse and
78 Aerts, 1987).

79 In cold life zone ecosystems, plant biomass production is limited by N (Körner,
80 2003). Litter tends to be recalcitrant in cold environments (Aerts, 1997). In addition,
81 N is a key factor that determines the outcome of interspecific competition in
82 temperate-zone ecosystems (Laungani and Knops, 2009). Several studies reported that
83 litter can mediate the interactions between neighboring plants in infertile communities
84 (Nilsson et al., 1999, Xiong and Nilsson, 1999). In a succulent desert ecosystem in
85 Africa, fertile islands are formed in nutrient enrichment zones beneath shrubs; this
86 formation is attributed to a range of interactions between physical and biotic
87 concentrating mechanisms (Stock et al., 1999). In China, an experiment performed in
88 an alpine meadow ecosystem, the eastern Tibetan Plateau, indicated that soil N

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availability and supply rates, as well as microbial biomass, can be enhanced by *Stellera chamaejasme* L., which is an unpalatable poisonous weed that seriously deteriorated the local rangeland (Sun et al., 2009). Another study in the gully region of the Loess Plateau demonstrated that black locust improves most soil properties (Qiu et al., 2010). Plants enhance the microbial immobilization of N when they provide C to soil microorganisms. The nature of litter determines its palatability to soil organisms, thereby influencing their composition and activity levels. Furthermore, a few apparent effects of N may be caused by the low levels of polyphenols, which is associated with high N concentrations in litter (Haynes 1986). The rate of decay and concentrations of nutrients in the litter determine the rate of nutrient release, which creates a positive feedback to site fertility. Hence, the chemical properties of litters from different plant organs and their correlations with decomposition rate must be determined.

Although inflorescences comprise only a small fraction of plant biomass and production in Arctic and alpine vegetation, the inflorescence production can be a significant proportion of the total production of species under certain special circumstances (Martínez–Yrízar et al., 1999, Fabbro and Körner, 2004; Wookey et al., 2009). Reproductive tissues present chemical composition that differs from vegetative parts, resulting in a markedly faster decomposition and nutrient release, with repercussions on nutrient cycling and patchiness (Buxton and Marten, 1989; Lee et al., 2011). High contents of N and P exist in the reproductive organs of plants probably because of their essential roles in plant growth and formation (e.g., high protein content). Alpine ecosystems are thermally restricted and characterized by a low material turnover rate (Körner, 2003). In a high altitude region, plants grow in a harsh habitat that restricted their effective utilization of resources; in this regard, the total available resource is less compared with that of plants in other regions (Fabbro and Körner, 2004; Hautier et al., 2009). In long-term evolution, the allocation of accumulated carbohydrates to reproduction is an adaptation strategy, leading to the partitioning of reproductive organs, that is, the availability and timely mobilization of adequate resources from the vegetative plant body to reproductive structures (Arroyo

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et al., 2013). Thus far, probably due to reproductive organs' comparatively minor biomass production and difficult to be collected, studies on their decomposition have been limited particularly compared with those on leaf and other vegetative organs.

A fast decay of N-rich litters suggests that litter decay rates increase with increasing N content. The initial rate of nutrient release is positively correlated with the initial concentrations of N or P (MacLean and Wein, 1978; Aber and Melillo, 1980; Berg and Ekbohm, 1983; Yavitt and Fahey, 1986; Stohlgren, 1988). In agricultural systems, addition of fresh residues can stimulate the decomposition and net release of N from indigenous soil organic matter (Haynes, 1986; Scott et al., 1996). Long-term increases in N availability have also been reported following the additions of C to forests (Groffman, 1999). Recently, a common-garden decomposition experiment in a wide range of subarctic plant types demonstrated that structural and chemical traits are better predictors for several high-turnover organs than structural traits alone (Freschet et al., 2012). Decomposition rate of plant litters slightly differ because of their species-specific traits and various organs, whose chemical qualities vary in a wide range of plant types and environments. Thus, field investigation, pot experiment of litter addition, and litter-bag experiment were conducted in this study to address the following:

1) Should decomposition of flower litter be considered according to inflorescence biomass production, and/or allocation?

2) What are the unique chemical properties of flower litters that influence their faster decomposition rate compared with leaf litters?

3) Is pulsed effect evident on soil available N and P particularly in special temporal period and spatial location as determined through pot experiment?

Materials and Methods

Study area

The field site is located at the foot of Mt. KaKa, which belongs to the middle section of Minshan Mountain, eastern Tibetan Plateau (**Fig. 1**), with a mean annual precipitation of 720 mm. More than 70% of precipitation falls in summer from June to August. Snowfall usually occurs from the end of September to the next early May.

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Vegetation presents a typical alpine meadow with numerous and unique alpine plants. Mosses are abundant and cover most of the ground. The moss layer is dominated by *Polytrichum swartzii* and *Trematodon acutus* c. mull. Vascular plants include species mainly belonging to *Kobresia* and *Carex*. Other common species are *Festuca*, *Gentiana*, and *Leontopodium*. Plant roots in this ecosystem are generally confined to the surface A-horizon (2–20 cm). A few dwarf shrubs are scattered sporadically in the meadow, e.g., *Rhododendron* and *Salix*. The soil type is dominated by Mat Cry-gelic Cambisols (i.e., silty loam inceptisol, *Chinese Soil Taxonomy Research Group*, 1995).

Sampling

During the blooming period from the end of May until mid-June and from the end of July until early August, flower litters of 14 earlier flowering plants species and 15 later flowering plants species were carefully collected in 2012 at two sites, namely, Mt. KAKA (103°42′ E; 32°59′ N, 3500–3900 m a.s.l.) and Bow Ridge Mountain (103°42′ E; 33°1′ N, 3600–3850 m a.s.l.). These species were tentatively classified into five groups according to Raunkiaer's life-form system (i.e., chamephyte, geophyte, hemicryptophyte, phanerophyte, and therophyte; **Table 1**). Mixed litter of alpine meadows were sampled on the Mt. Kaka (3950 m. a.s.l.), and leaf litters of 13 dominant species were also collected to compare their chemical properties with flower litters. Both types of litters were first spread on blotting paper for air drying. A small portion of each litter was further dried in an oven for 48 h to calculate dry matter content.

Experimental design

Polyvinyl chloride (PVC) pots (15 cm deep, 20 cm diameter at the top, and 12 cm diameter at the bottom) were filled with 2 kg of soils, which were collected in autumn of 2011. The collected soil samples were stored at 4 ℃. The samples were sieved through 2 mm mesh and then mixed thoroughly. The soil surface of each treatment was added with 5 g of flower litters or mixed litters (calculated as dry weight) on June 21 (14 species, earlier flowering plants) and Aug 11, 2012 (15 species, later flowering plants). The surface was covered with a thin layer of soil to avoid being blown by wind. Other two additional treatments were conducted without litter addition (control)

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and with mixed leaf litter addition, respectively. In total, the pot experiment consisted of 33 treatments with three replicates, with a total number of 99 pots. All of the pots were carefully buried 12 cm deep into the field to maintain the same soil temperature in the experimental field. The pots were randomly distributed, and their top edges were approximately 3 cm above the ground to prevent runoff from outside. All of the pots were rearranged every week to create a similar microclimate. After 50 days, soil samples were separately obtained from the PVC pots and mixed evenly by sieving through a 2 mm mesh. Soil samples were collected from three points of each pot in the center and then mixed to avoid the boundary layer effect. The samples were stored in an ice box prior to chemical determination.

Decomposition rate

A litter bag with a size of 14 cm × 20 cm was used to determine the decomposition rate of different plant litters. The bag was double faced and made from nylon net material with above (4.5 mm × 4.5 mm mesh) and below layers (0.8 mm × 0.8 mm mesh). The above layer with bigger mesh size allowed free access for most micro-arthropods, which dominate the soil fauna of alpine meadow in the eastern Tibetan Plateau, whereas the below layer with smaller mesh size can reduce litter spillage from the litter bags in the process. As representative species, flower litters of *R. przewalskii* and *M. integrifolia* and mixed litter were packed into litter bags with the edges sealed on June 21, 2012. The litterbag experiment was conducted to compare the decomposition rate of flower litters and mixed litter. Each treatment had eight replicates. After 7 weeks (August 8, 2012), litter was obtained from the litter bags and dried in an oven for decomposition calculation. Litter decomposition rates can be determined by the following equation.

$$\mathbf{DR = (P-R)/P \times 100}$$

where *DR* is the decomposition rate, *P* is primary litter mass in the litter bags, and *R* refers to residue litter before determining percentage mass loss.

Soil chemistry determination

Total dissolved N (TDN) contents were determined using unsieved fresh moist

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soil subsamples. Soil subsamples were extracted using 2 M KCl and shaken for 1 h at room temperature (20 ℃), with a soil-to-solution ratio of 1:5 (weight/volume). The extracted solution was filtered through filter paper before further determination (Jones et al., 2004). NH_4^+-N and NO_3^--N were analyzed with the indophenol blue colorimetric (Sah, 1994) and ultraviolet spectrophotometry methods (Norman et al., 1985), respectively. Dissolved organic nitrogen (DON) was calculated by subtracting dissolved inorganic N (NH_4^+-N, i.e., DHN and NO_3-N, i.e., DNN) from TDN. Soil solutions were extracted by centrifugal drainage, whereas the exchangeable pool was extracted with 2 M KCl by using the methods reported by Jones et al. (2004). Total phosphorus (TP) and A-P in soils were estimated by extraction with 0.5 M sodium hydroxide sodium carbonate solution (Dalal, 1973). Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) contents were determined through the chloroform–fumigation direct-extraction technique. Correction factors of 0.54 for N and 0.45 for C were used to convert the chloroform labile N and C to microbial N and C (Brookes et al., 1985).

Data analysis

One-way ANOVA was applied to compare values between the treatments and the control. Post-hoc multiple comparisons were adopted when the groups were three or more. Multivariate ANOVA was conducted to determine the effects of blooming time and different addition of litters and their interactions. To simplify the comparison of soil N and P between control (without flower litter) and the treated (with flower litter), we defined an index **α** as: **α** = Ln (N_2/N_1). $\alpha > 0$, $N_2 > N_1$; $\alpha < 0$, $N_2 < N_1$; $\alpha = 0$, $N_2 = N_1$. N_1 is the control treatment without flower litter, and N_2 indicated nutrition value (N or P) of flower litter treatment. Descriptive analysis was operated to demonstrate α values of different N and P fragments in various species litters addition treatment. The box plots provide the distribution of the values by the medians (central line), the quartiles 25% and 75% (box), and the ranges (whiskers) of ratios. Differences were tested at $P < 0.05$ by using Tukey multiple range test in SPSS 19.0 software package (SPSS Inc., Chicago, IL, USA). The normality of data was tested with one-sample K-S test and Q-Q plot. Otherwise, log-transformation was adopted to meet the

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normality requirement. Homogeneity of variance test was also utilized during the analysis. In the figures and tables, information is presented as means and standard errors of means. All of the differences were tested at the $P = 0.05$ level.

Results

Inflorescence information of alpine plants from different life forms

Table 1 General description of flower litters in the study.

	Life form	Size of inflorescence (cm)	Dominant (Y/N)	Color	Dry matter content (%)
Caragana jubata	C	1-1.5	N	white	29.81
Primula orbicularis	H	1.5	Y	yellow	23.29
Potentilla anserina	G	1-1.8	Y	yellow	51.9
Rhododendron capitatum	P	2-3	Y	purple	32.84
Viola rockiana	H	1	N	yellow	25.22
Myricaria squamosa	P	0.5-1	N	pink	30.95
Potentilla saundersiana	G	1-1.4	N	yellow	54.01
Taraxacum lugubre	H	3-4	Y	yellow	14.97
Aster tongolensis	H	4-5	N	blue	28.72
Cardamine tangutorum	G	0.8-1.5	N	lavender	13.08
Spiraea alpina	P	0.5-0.7	Y	fallow	32.58
Caltha scaposa	H	3-4	Y	yellow	30.43
Rhododendron przewalskii	P	4-5	Y	pink	33.33
Meconopsis integrifolia	H/T	5-7	N	yellow	21.79
Stellera chamaejasme	C	0.5	N	red	28.11
Potentilla fruticosa	P	2-3	Y	yellow	30.43
Meconopsis punicea	H/A	5-8	N	red	33.57
Meconopsis violacea	H	4-6	N	purple	35.70
Sibiraea angustata	P	0.8	Y	white	29.50
Polygonum macrophyllum	H	0.2	Y	pink	21.79
Pedicularis megalochila	C	0.8-1	N	red	33.57
Ligularia virgaurea	C	1.5	N	yellow	16.78
Pilose Asiabell	C	2-2.5	N	pale green	22.26
Oxytropis ochrocephala	C	1	N	fallow	28.72
Pedicularis longiflora	C	0.8	N	yellow	28.11
Hedysarum vicioides	C	1	N	pink	30.02
Gentiana sino-ornata	C	3-5	Y	purple	44.10
Leontopodium sinense	C	0.2-0.5	Y	white	56.92
Cremanthodium lineare	G	1.2-1.7	Y	yellow	48.93

Note: C, H, G, P, and T represent chamaephyte, hemicryptophyte, geophyte (one of subdivided groups in Cryptophytes), phanerophyte, and thermophile, respectively. Y and N indicate whether the species is dominant or not in the community.

Twenty-nine species were reported in this study, and these species were divided into

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two groups based on blooming time, that is, earlier flowering species and later flowering species. According to Raunkiaer's life-form system, earlier flowering species mainly consisted of hemicryptophyte, geophyte, and phanerophyte, whereas more than half of later flowering species comprised chamaephyte. Nearly half of the tested species were dominant or co-dominant in their respective communities. The dry matter content of flower litters in all of the species was ranked from 10% to 60%. Various sizes of inflorescence were distributed from 0.2 cm to 8 cm in diameter.

Flower litter production of dominant species and their biomass allocation

Among 13 dominant species, the flower litters of phenerophyte plants, whose flower litters are comparable with non-flower litters, were calculated through comparison with non-flower litters during the flower litter collection (**Fig. 2 (a)**). The dry weights of flower litters per unit area were 10–40 g m^{-2}, whereas their non-flower litters were only 5–25 g m^{-2}. Although neither of the flower litters of *S. angustata* nor *R. capitatum* were significantly different compared with their non-flower litters ($P > 0.05$), the difference between the two remained noticeable, whose values were 28.03 ± 3.56 g m^{-2} versus 13.21 ± 1.49 g m^{-2} for *R. capitatum* and 19.58 ± 3.50 g m^{-2} versus 12.95 ± 0.61 g m^{-2} for *S. angustata*, respectively. The production of flower litters was higher than that of non-flower litters. The other three species significantly produced more flower litters than non-flower litters (*R. przewalskii*: $F = 15.76$, $P < 0.001$; *P. fruticosa*: $F = 4.76$, $P < 0.05$; *S. alpine*: $F = 10.18$, $P < 0.01$). The flower litters of the eight herbaceous species were compared with their individual aboveground biomass (**Fig. 2 (b)**), which ranked from 10% to nearly 40%. This finding indicated that flower litter should be considered to determine the effect of plants on soil nutrition pool during growing season.

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Comparison of chemical properties between flower and leaf litters

Total C content was not significantly different between flower and leaf litters (**Fig. 3 (a)**, $F = 1.80$, $P = 0.199$). However, the levels of cellulose, lignin, and structure C of leaf litter were significantly higher than those of flower litter ($F = 6.74$, $P < 0.05$; $F = 5.77$, $P < 0.05$; $F = 10.99$, $P < 0.01$). Hence, flower litter probably contains more non-structure C than leaf litter.

Both N and P contents of flower litters were significantly higher than those of leaf litters (**Fig. 3 (b)**). N in flower litters was nearly doubled to that of leaf litter (23.17 ± 1.52, 11.87 ± 0.77; $F = 45.70$, $P < 0.001$). More than twice the amount of P were also present in flower litters compared with that in leaf litters (2.95 ± 0.25, 1.12 ± 0.12; $F = 43.87$, $P < 0.001$).

For the implication of the ratio of different chemical properties, C/N, N/P, and lignin/N were determined to compare flower and leaf litters. All the three indicators of leaf litter were significantly higher than those of flower litters (**Fig. 3 (c)**). As parameters used to demonstrate decomposition rate, C/N and lignin/N of leaf litter were nearly double to those of flower litter (39.27 ± 4.16, 19.80 ± 1.39, $F = 37.78$, $P < 0.001$; 21.09 ± 2.25, 12.79 ± 1.15, $F = 7.91$, $P < 0.01$). Furthermore, N/P of flower litter was significantly higher than that of leaf litter (8.42 ± 0.42, 11.60 ± 0.56; $F = 20.62$, $P < 0.001$). These findings indicated that flower litter can supply more P per unit N than leaf litter.

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297 **Effects of flower litter on different fragments of soil nitrogen pool**

298 Earlier flowering species exerted positive effects on soil DIN, DON, TN, DNN, and
299 DHN (**Fig. 4 (a)**), with the addition of their flower litters according to their size of **α**
300 values. Most parameters were higher than 0, which indicated that $N_2 > N_1$. Flower
301 litter increased soil N pool. All of the minimum **α** values of five indices were also
302 higher than 0 (**Table 2**, 0.42–1.29), which indicated that flower litter addition
303 significantly increased different fragments in soil N pool ($P < 0.001$). Among the later
304 flowering species, except *G.* sino-*ornata* and *L. sinense*, soil N indices were
305 significantly improved with flower litter addition, as demonstrated through **α** values
306 higher than 0 (**Fig. 4 (b)**, **Table 2**). Later flowering species differed from earlier
307 flowering species, with minimum **α** values lower than 0, which resulted from the
308 exceptions of *G.* sino-*ornata* and *L. sinense*. However, all of the mean **α** values were
309 higher than 0, which presented general results after flower litter addition (0.36–1.49).
310 Different fragments of soil N pool were significantly enhanced only after 50 days ($P <$
311 0.001). Interactions between flowering time and litter addition for DIN, DNN, and
312 DHN were significant ($F = 5.043$, $P < 0.05$; $F = 7.947$, $P < 0.01$; $F = 24.143$, $P < 0.05$,
313 respectively) but not for TN and DON ($F = 0.470$, $P = 0.496$; $F = 2.798$, $P = 0.100$,
314 respectively). Flower litters from the two categories of plants with different flowering
315 times were processed and compared in the addition experiment; as such, the effects of
316 both factors and their interactions were evaluated. Different flowering times
317 significantly affected DIN, DNN, and DHN (**Table 3**, $P < 0.01$) but did not
318 significantly influences DON and TN ($F = 0.47$, $P = 0.50$; $F = 2.80$, $P = 0.10$,
319 respectively). As illustrated in **Fig. 4**, litter addition had significant effects on all of
320 the N fragments, which was in accordance with the results in **Table 3**. The interaction
321 of flowering time and litter addition exerted similar effects on different N fragments
322 in soil with flowering time solely.
323

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Table 2 α values of different nitrogen fragments in various species litters addition treatment (n = 14 and n = 15 in earlier flowering species and later flowering species, respectively).

Flowering period	Index	Mean	Std. Error	Minimum	Maximum	*F*	*P*
Earlier flowering	DIN	1.66	0.07	1.07	2.20	578.88	0.000
	DON	1.76	0.26	0.67	4.46	46.45	0.000
	TN	1.67	0.06	1.29	2.05	719.05	0.000
	DNN	1.67	0.07	1.08	2.23	563.90	0.000
	DHN	0.97	0.12	0.42	2.06	68.25	0.000
Later flowering	DIN	1.07	0.17	-0.63	1.50	40.29	0.000
	DON	1.49	0.29	-0.18	3.29	27.04	0.000
	TN	1.29	0.21	-0.37	2.40	38.37	0.000
	DNN	1.11	0.18	-0.75	1.55	37.77	0.000
	DHN	0.36	0.05	-0.09	0.72	60.64	0.000

Table 3 Multifactorial analysis of variance for the effects of flowering time, litter addition, and their interactions on different nitrogen fragments.

Source of variation	DIN		DON		TN		DNN		DHN	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Corrected Model	31.74	**0.00**	23.62	**0.00**	59.25	**0.00**	69.24	**0.00**	54.07	**0.00**
Flowering time	5.05	**0.03**	0.47	0.50	2.80	0.10	7.93	**0.01**	24.36	**0.00**
Litter addition treatments	86.44	**0.00**	70.24	**0.00**	173.47	**0.00**	194.34	**0.00**	117.00	**0.00**
Flowering time × Litter addition treatments	5.05	**0.03**	0.47	0.50	2.80	0.10	7.93	**0.01**	24.36	**0.00**

Note: ***P*** values for significant effects and interactions are in bold.

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Effects of flower litter on soil TP and A-P

Table 4 α values of TP and A-P with flower litter added treatments (n=14 and n=15 in earlier flowering species and later flowering species, respectively).

Flowering period	Index	Mean	Std. Error	Minimum	Maximum	*F*	*P*
Earlier flowering	TP	0.02	0.03	-0.04	0.08	8.498	**0.007**
	A-P	0.31	0.17	0.67	0.13	47.39	**0.000**
Later flowering	TP	0.03	0.11	-0.20	0.12	0.97	0.33
	A-P	0.50	0.23	0.06	0.37	68.82	**0.000**

Table 5 Multifactorial analysis of variance for the effects of flowering time, litter addition, and their interactions on TP and A-P.

Source of variation	TP		A-P	
	F	*P*	*F*	*P*
Corrected Model	1.07	0.37	43.01	**0.00**
Flowering time	0.02	0.90	6.44	**0.01**
Litter addition treatments	3.17	0.08	114.14	**0.00**
Flowering time × Litter addition	0.02	0.90	6.44	**0.01**

Note: *P* values for significant effects and interactions are in bold.

Flower litters exerted different effects on soil TP and A-P. Soil TP increased in treatment with early flowering litters (**Fig. 5**, **Table 4**, $F = 8.498$, $P = 0.007$) but not in later flowering litters. The minimum **α** values were lower than 0 (−0.04 and −0.20, respectively). However, A-P of both litter treatments was significantly positively stimulated ($F = 47.39$, $P < 0.001$; $F = 68.82$, $P < 0.001$), whose **α** values were both higher than 0 (0.67–0.13 and 0.06–0.37, respectively). Multifactorial analysis indicated that soil TP was not significantly different between treated with flower litter and control in general (**Table 5**, $F = 1.07$, $P = 0.37$). No significant interaction was evident between flowering time and litter addition treatments on soil TP ($F = 0.01$, $P = 0.93$). Litter addition treatments alone only had a marginal significant effect on soil TP ($F = 3.17$, $P = 0.08$). Moreover, both minimum **α** values were lower than 0, but TP was not significantly different between treatments with later flowering litters and control treatment ($F = 0.97$, $P = 0.33$), which mainly resulted from *G. sino-ornata*, *L. sinense*, and *C. lineare*. Nevertheless, A-P increased significantly after flower litter addition ($F = 43.01$, $P < 0.001$), with a significant interaction between flowering time and litter addition ($F = 6.44$, $P < 0.05$).

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356 **Comparison of decomposition rate between flower litter and mixed litter**

357 Two typical plant species, which are widely distributed and easily collected, were
358 assessed to compare the decomposition rate of flower litter and mixed litter.
359 Differences in decomposition rate among flower litter of two species and mixed litter
360 were supposed to be significant (**Fig. 6**, $F = 130.34$, $P < 0.001$). The flower litters of
361 *R. przewalskii* and *M. integrifolia* decomposed greatly faster than mixed litter.
362 However, within only 50 days, more than 20% of *R. przewalskii* and *M. integrifolia*
363 flower litters decomposed, whereas the decomposition rate for mixed litter was
364 approximately 6% (i.e., the former was nearly three times faster). Moreover, no
365 significant differences were evident in the decomposition rates of the flower litter of *R.*
366 *przewalskii* and *M. integrifolia* ($P = 0.371$).

367

368 **Discussion**

369 Plant litter decomposition is a critical step in the formation of soil organic matter,
370 mineralization of organic nutrients, and C balance in terrestrial ecosystems (Austin
371 and Ballaré, 2010). Species-specific variations in plant phenology can affect
372 production of litter fall, which is noticeable during the growing season from the aspect
373 of nutrient cycling although the peak of litter fall happens in autumn. Thus, the early
374 litter fall of alpine plants during the study period from May to August can be a
375 potential nutrient source when nutritional demands increase for rapid growth and
376 development. In particular, the amount of flower fall in study area exceeds the leaf
377 fall during the flowering season. A previous study indicated that reproductive litter
378 production accounted for < 10% of the total litter in January–August and 13%–26% in
379 September–December (Sanches et al., 2008), which was mainly triggered by rainfall
380 variability that directly altered litter production dynamics and indirectly altered forest
381 floor litter. In addition, the flowers are more nutritional than the leaves in terms of
382 nutrients necessary for plant growth (Lee et al., 2011). In this study, summit
383 production of flower litters are booming during special periods for both earlier
384 flowering and later flowering species. Flower biomass of herbaceous plants accounts

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for 10% to approximately 40% of total aboveground biomass. Moreover, these flower litters produced considerably earlier than other aboveground litters that dropped at the end of growing season. Furthermore, flower litters and non-flower litters (mainly constituted of leaves) of woody plants were 10–40 g m^{-2} and 5–25 g m^{-2}, respectively, which clearly implies that flower litter can be a comparable decomposition substrate in alpine ecosystems even for phenerophyte plants.

Litter production and decomposition are controlled by biological and physical processes, such as the activity and composition of soil and litter fauna and climate variations (Meentemeyer, 1978; Cornejo et al., 1994; Wieder and Wright, 1995; Aerts, 1997; Cleveland et al., 2004). An integration of index or traits has been recommended to indicate process and rate of litter decomposition. Generally, tissues with high lignin, polyphenol, and wax contents and higher lignin:N and C:N ratios exhibit slow decomposition. The effect of litter quality on decomposition rates was extensively discussed in the literature, and C/N and lignin/N ratios have been commonly accepted as main explanatory factors (Melillo et al., 1982; Berg, 2000). Leaf litter with C/N ratios lower than 30 is known to decompose easily and yield a mull humus type, whereas C/N ratios above 30 result in N immobilization (Heal et al., 1997) and decomposition retardation. In the present study, flower litter had significantly less C/N ratio (19.80 ± 1.39, less than 30) than leaf litter (39.27 ± 4.16, more than 30). Lignin content in flower litters was significantly less than that in leaf litters (211.37 ± 8.63 mg kg^{-1} and 237.88 ± 6.89 mg kg^{-1}, respectively; F = 5.77, P = 0.02), similar to cellulose (266.93 ± 4.92 mg kg^{-1} and 283.75 ± 4.21 mg kg^{-1}, respectively; F = 6.74, P = 0.01), which is one of the major cell-wall constituents. All of the results are in accordance with previous studies. Decomposition rate is negatively correlated with the concentration of lignin, which is a group of complex aromatic polymers that serves as a structural barrier impeding microbial access to labile C compounds (Swift et al., 1979; Taylor et al., 1989; Austin and Ballaré, 2010; Talbot and Treseder, 2012). Moreover, greater non-structural carbohydrates existed in flower litters than those in other litters, as indicated by the absence of significant differences of total C content between flower litters and other litters. However, the structural carbohydrates of

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415 flower litters were significantly less than that of leaf litters. This finding can be
416 inferred from the contents of lignin and cellulose (**Fig. 3 (a)**). Hence, flower litters
417 can promote nutrients that easily complement soil (Parton et al., 2007) for plants in
418 their whole life history. Decomposition rates of leaf litters have been considered
419 recently from their lignin/N or lignin/cellulose (Talbot and Treseder, 2012; Cornwell
420 et al., 2008). Furthermore, in the present study, lignin/N was less in flower litters
421 (almost 50% in leaf litters, i.e., 12.79 ± 1.15 and 21.09 ± 2.25, respectively), whereas
422 N/P was higher than that of leaf litters.
423 A litterbag experiment was adopted and confirmed that the decay rates of flower
424 litters were significantly faster than that of other litters, which is in accordance with
425 the fast decomposition of *R. pseudoacacia* flower from an experiment performed in
426 Korea (Lee et al., 2010). Flower litters contained significantly higher N and P
427 contents than leaf litters (**Fig. 3 (b)**). Plant litter available to the decomposer
428 community encompasses a broad range of issues that differ in chemical and physical
429 properties (Swift et al., 1979). P has to be highlighted because it has been regarded as
430 essential for a long time, which causes a limited attention on mechanisms that drive P
431 limitation and their interactions with the N cycle (Vitousek et al., 2010). Although soil
432 generally contains a large amount of total P, only a small proportion is immediately
433 available for plant uptake from the soil solution. In most soils, the concentration of
434 orthophosphate in solution is low (Richardson et al., 2009). P is derived mainly from
435 rock weathering and related biogeochemical cycle, and ecosystems begin their
436 existence with a fixed complement of P, and even very small losses cannot be readily
437 replenished (Walker and Syers, 1976). The present study indicated that decomposition
438 of flower litter can be one of the beneficial source of soil A-P in alpine ecosystems.
439 Nevertheless, the current study regarding the characteristics and driven mechanism of
440 this source remains at the first stage. Variation in soil physical-chemical properties,
441 vegetation types, and microbial activities can significantly affect chemical
442 compositions and forms and biological availability of soil P directly or indirectly.
443
444

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445 **Table 6** Comparison medium values of soil solution pool and soil microbial biomass
446 between litter addition treated (flower litter and mixed litter) and control.

Treatments	Soil solution pool (mg g^{-1})		Soil microbial biomass (mg kg^{-1})		
	Nitrate-N	Ammonium-N	MBC	MBN	MBC/MBN
Flower litter	46.8	0.55	102.05	73.02	1.40
Mixed litter	32.4	0.45	68.08	69.29	0.98
Control	30.93	0.53	46.25	67.13	0.69

447 Decay rates of different plant organs reflect the diversity that fruits decompose faster
448 than leaves, which in turn decompose faster than woody plant parts (Swift et al., 1979;
449 Kögel–Knabner, 2002). Flower litters decompose rapidly with higher N and P levels
450 supplied to soil, particularly from nitrate-N in soil solution pool (**Table 6**). The soil
451 solution pool has been improved noticeably from 30.93 mg g^{-1} to 46.8 mg g^{-1} in
452 flower litter treatment compared with the control. Histogram for **α** values of DIN and
453 A-P also presented soil available nutrients positively stimulated by flower litter (**Fig.**
454 **7**) for their values distributed at an interval greater than 0. The high DOC values in
455 flower litter may influence N and P in soil through C substrate supplement for soil
456 microorganisms to enhance N immobilization. Recent empirical studies noted that the
457 changing microbial community composition significantly affects ecosystem processes,
458 such as litter decomposition (Strickland et al., 2009; Ramirez et al., 2012). Shifts from
459 bacterial-dominated to fungal-dominated decomposition happened over short (days to
460 a few months) periods (Poll et al., 2008; McMahon et al., 2005). Although the present
461 study did not present the precise analysis of microbial community, both MBC and
462 MBN differed greatly between different treatments (**Table 6**). Litter addition
463 increased them obviously, which is evident not only in microbial biomass C and N but
464 also in their C:N ratios (1.40, 0.98, and 0.69 for flower litter, mixed litter, and control,
465 respectively). Therefore, microbial community composition varied depending on
466 nutrient supplement from litters. Flower litter contains more than twice MBC
467 (increased from 46.25 to 102.05); hence, microbial biomass and their activities
468 enhance potentially.
469 Several unexpected species in the experiment reduced soil available nutrients

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probably because their specific chemical properties, which change as a result of microbial activities and nutrient dynamics (Karmarkar and Tabatabai, 1991), may negatively affect soil microorganism biomass or activities (Wardle et al., 1998, Cipollini et al., 2012). Furthermore, soil microbial communities can be modified through time in response to allelopathic plants with known or potential effects on plant communities (Cipollini et al., 2012, Inderjit and Weiner, 2001). Mineralization and nitrification can be subdued by inhibitory compounds from the exudates of a certain plant species, which come from a negative aspect and mainly result from suppression of related microbes (Cipollini et al., 2012). In another positive perspective, considering "*priming effect*" once flower litter is added in moderate treatments causes strong short-term changes in the turnover of soil organic matter and nutrient release follows litter decomposition (Jenkinson et al., 1985; Kuzyakov et al., 2000; Blagodatskaya and Kuzyakov, 2008). Hence, N and P availability in the soil of alpine ecosystem can be maintained in part by tissue chemistry favorable to microbial decomposition and release of nutrients.

This study provides evidence that plant species, through tissue chemistry, biomass allocation, and phenology, affect local soil properties in alpine ecosystem. Soil has specific susceptibility to decomposition of biochemical compounds in plant tissues, on a spectrum from quickly decomposed labile to relatively recalcitrant. Decomposition rates can be markedly affected by particle size, surface area, and mass characteristics (Angers and Recous, 1997). In addition, physical toughness (lignin, dry matter content, or C content) can be suitable predictors of decomposition across all of the organs. Structural (lignin, DMC) and chemical (N) traits together are proposed to be better predictors for several high-turnover organs than structural traits alone (Freschet et al., 2012). Flower litters have these intuitive benefits chemically and physically, but physical components of litter quality have received little attention in the research on litter quality. Future climate changes in temporal patterns are likely to have important direct and indirect consequences on litter dynamics as well as on phenology and decay process temporally and spatially. In brief, the question of the essentiality and fundamentality of litter decomposition, especially under natural

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conditions, remains unresolved although the key role of litter quality in decomposition and in ecosystem function is generally clear.

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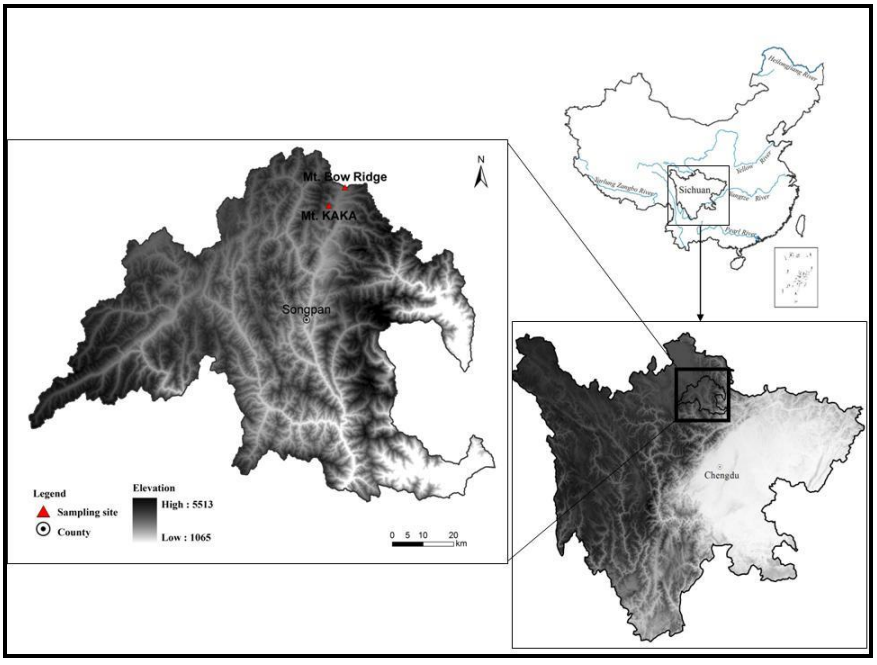
625 **Figures**



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627 **Fig. 1** Location of the study sites.

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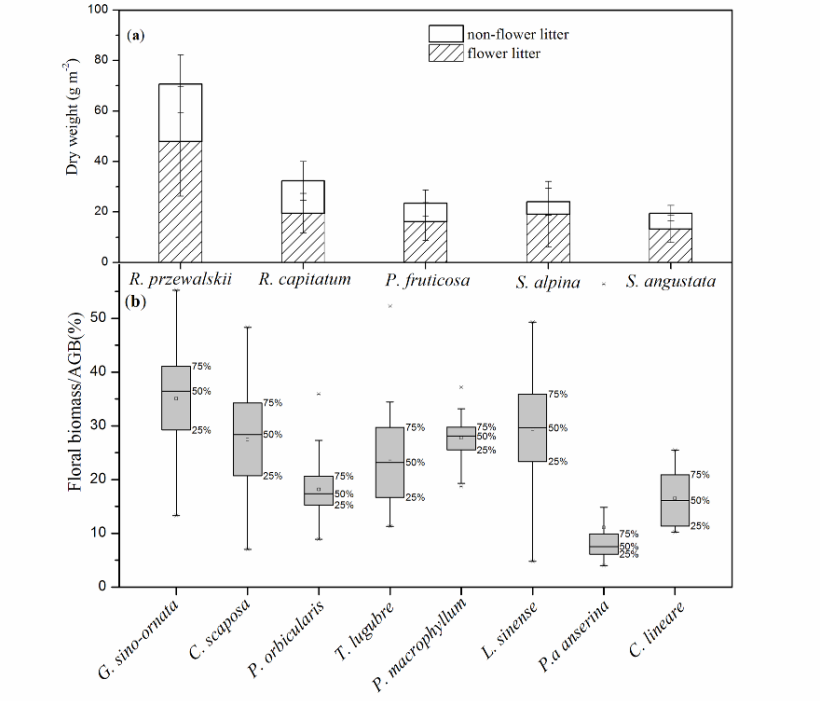

Fig. 2 Production of flower litters and biomass allocation of representative dominant species. (a) Production of flower litters and non-flower litters of shrubs (phaenerophyte) per unit area (m^2); and (b) floral biomasses and their allocation in the aboveground biomass.

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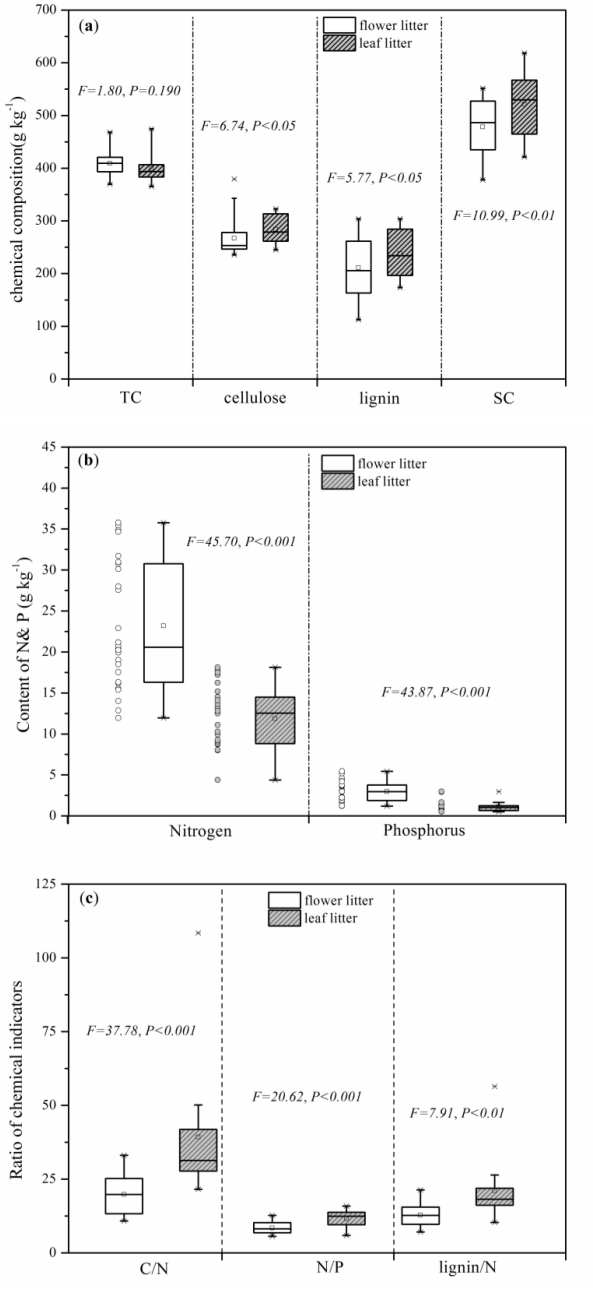

Fig. 3 Chemical composition and their comparison between flower and leaf litters.

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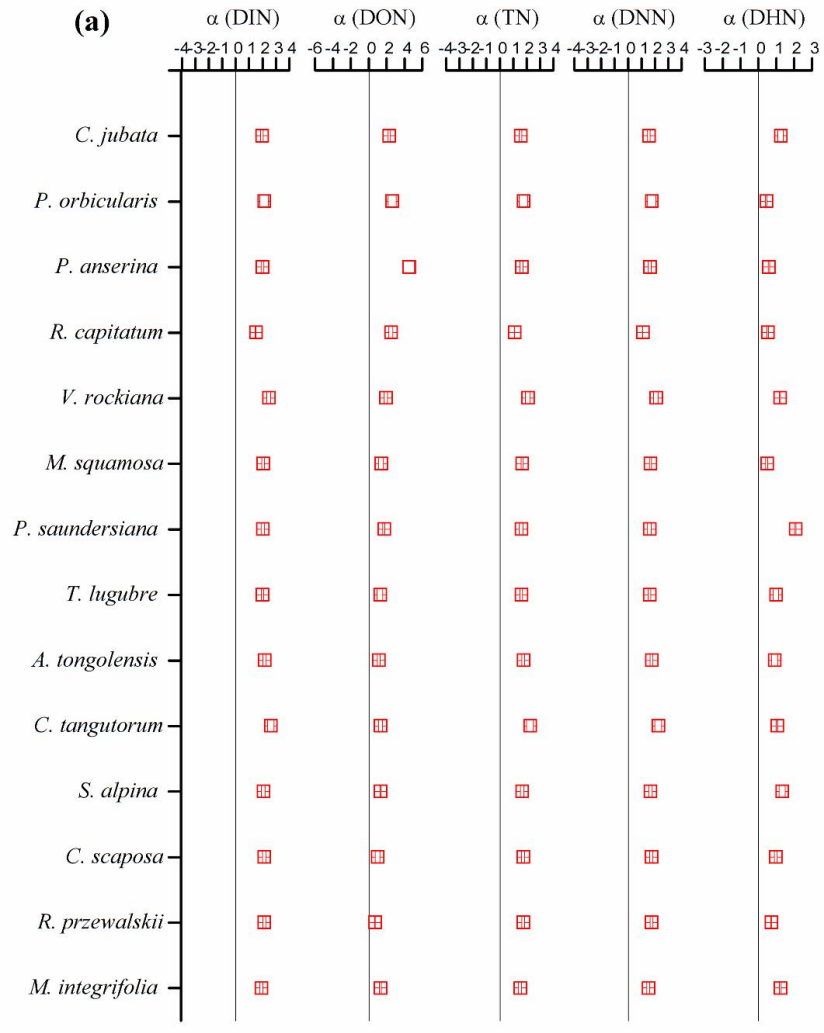

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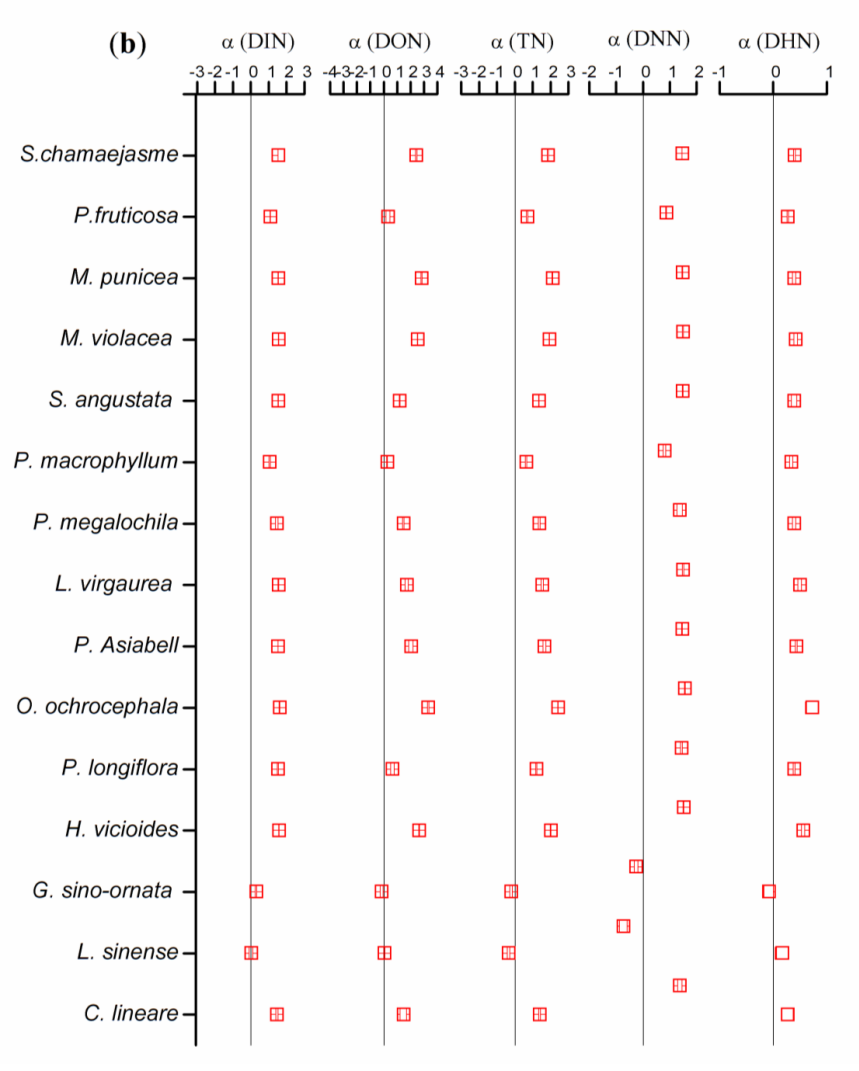

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644 **Fig. 4** Variation in soil nitrogen pool after addition of flower litters.
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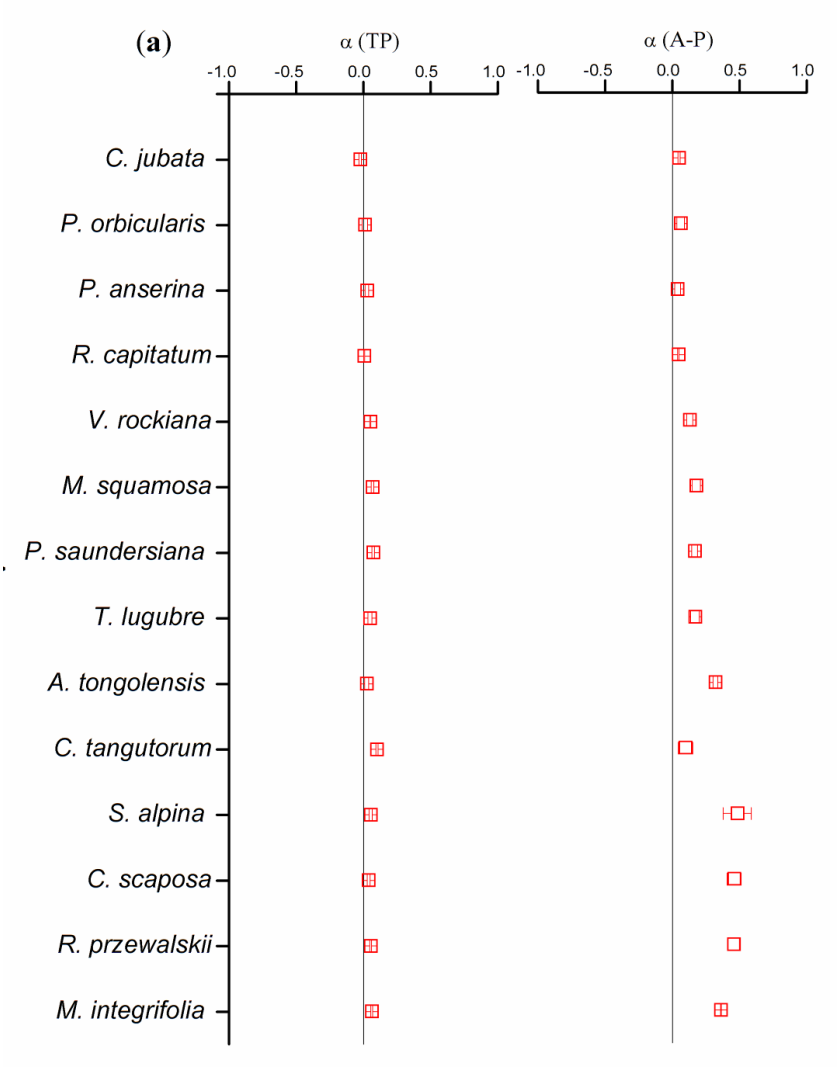

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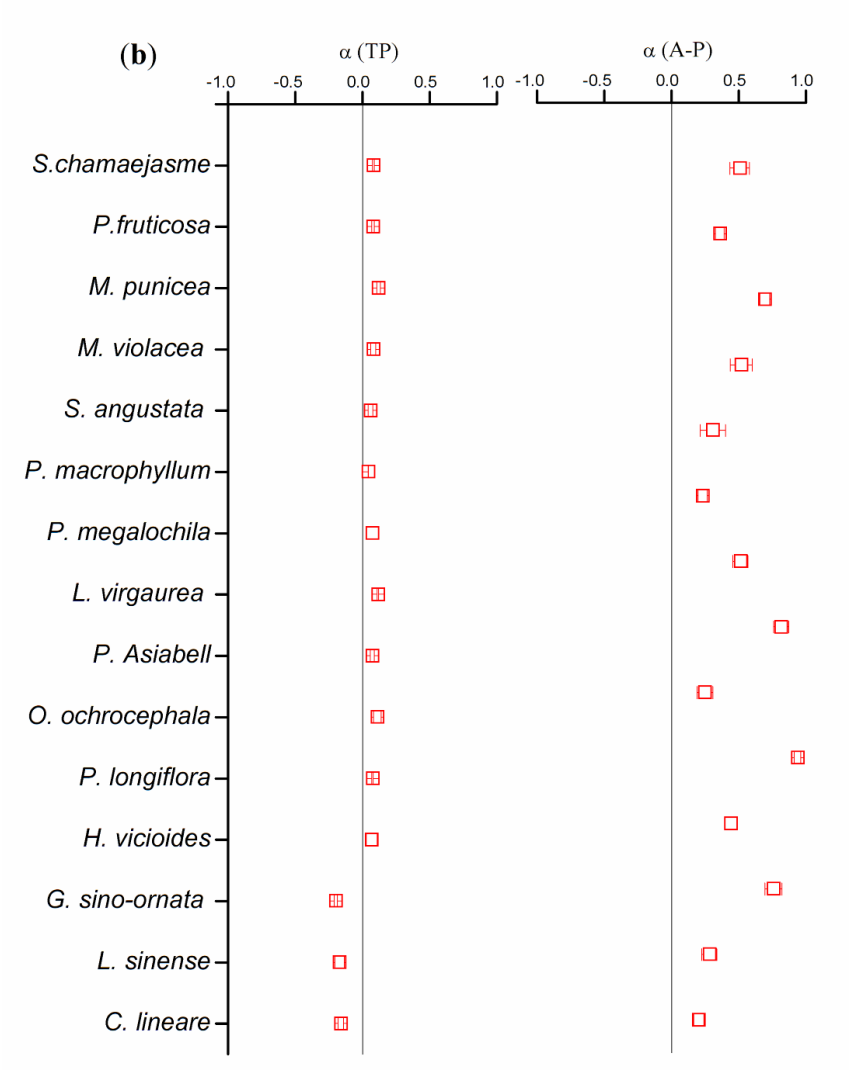

Fig. 5 Variation of TP and A-P in flower litter added treatments.

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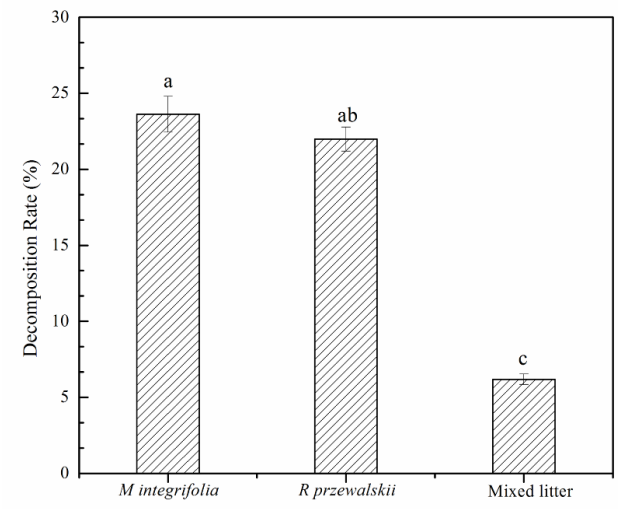

Fig. 6 Percentage of decomposed dry mass of *M. integrifolia* and *R. przewalskii* in a 50-day litter-bag study. *Column* represents mean, and bar indicates Standard Error (n = 8). Different lowercase letters indicate significant differences of decomposition rate between litter materials.

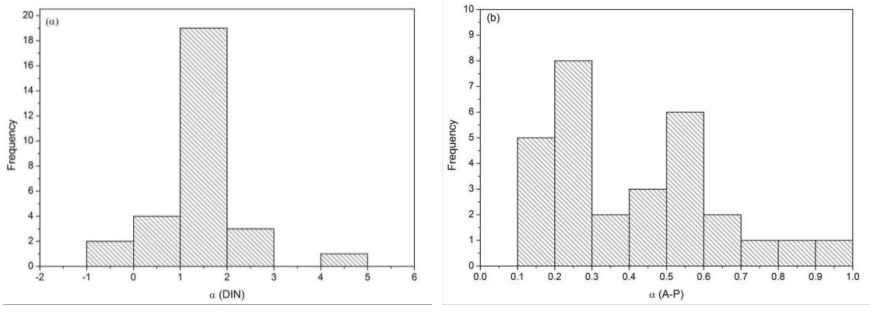

Fig. 7 Variation in soil nutrition pool with flower litters addition. Histogram for **α** values of DIN (a) and A-P (b) indicates the change between treatments and control.