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Effect of inflorescence litter from distinct species and life forms on soil nutrients and microbial biomass in the eastern Tibetan Plateau

Jinniu Wang [a,b,e], Bo Xu [a,c], Yan Wu [a], Jing Gao [d], Fusun Shi [a,*], Ning Wu [a,e,**]

[a] Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China
[b] Mangkang Ecological Station, Tibet Ecological Safety Monitor Network, Changdu 854500, China
[c] Aba Teachers University, Aba 623002, China
[d] School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
[e] International Centre for Integrated Mountain Development (ICIMOD), G.P.O. Box 3226, Kathmandu, Nepal

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ABSTRACT

The influence of plant litter on soil varies with soil depth, species composition, and life forms of plants. Recalcitrant indexes are significantly lower in inflorescence litter as compared to leaf litter (C/N, N/P, lignin, cellulose, lignin-cellulose index, and lignin/N), with a majority of the interactions occurring between species and litter types. In a field pot experiment, N exchangeable pool and soil solutions with and without litter addition differed significantly with increased soil dissolvable inorganic nitrogen (DIN) and available phosphorus (A−P) at 0–5 cm shallow soil layer in samples with added litter. However, there was an unexpected decline in soil organic matter (SOM) after inflorescence litter addition as higher content of non-structural carbohydrates triggered faster decomposition of SOM. Exchangeable pool had significant interactions between litter addition and soil depth. Furthermore, different NH_4^+−N and Organic−N in soil solution were developed from litter addition, but the differences in SOM was mainly determined by soil depths. Both microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were improved with inflorescence litter addition in the shallow soil layer. After sorting the inflorescence litters according to life forms, A−P was the most dominant nutrient and DIN was the least dominant nutrient in phanerophytes while a completely contrasting trend was seen in geophytes. Thus, chemical properties of inflorescence litter were remarkably different from those of leaf litter, which elicited species-specific and life form-specific effects on soil nutrient pool, and efficiently modified soil nutrients.

1. Introduction

Plants modify and regulate the physico-chemical properties and biological composition of soil through different mechanisms. Litter production and decomposition are the main pathways by which aboveground nutrients return to the soil pool (West, 1979; Vitousek, 1984; Edwards et al., 2015), which can be influenced by a series of factors, such as mortality of plant parts (Persson, 1980; Facelli and Pickett, 1991; Fuentes-Ramirez et al., 2018), herbivore (Wardle et al., 2002), leaching from aboveground organs (Facelli and Pickett, 1991; Wieder et al., 2009), seed and pollen production (Lee et al., 1996; Perez-Moreno and Read, 2001), and root exudation (Kuzyakov

* Corresponding author.
** Corresponding author at: Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China.
E-mail addresses: shifs@cib.ac.cn (F. Shi), wuning@cib.ac.cn (N. Wu).

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et al., 2007). The quantity and composition of plant litters influences ecosystems due to their crucial role in nutrient cycling and soil formation (Vitousek, 1984; Orwin et al., 2006; Quested and Eriksson, 2006). It is also associated with diverse chemical and physical properties of plant litter's availability to decomposer communities (Swift et al., 1979; Aerts, 1997). The diversity range of decomposition is indicated by the decay rates of different plant organs; for example, the decay rates of fruits and leaves are higher than those of woody plant parts (Swift et al., 1979; Kögel-Knabner, 2002). Previous studies also supported that inflorescence, being a reproductive organ, significantly affects soil fertility and biogeochemical cycling in Mountainous ecosystem and alpine ecosystem (Lee et al., 2010; Wang et al., 2016). However, the influence of decomposition of inflorescence litter on gradients of soil depth, species-specific effects, and sorted life form for soil nutrients and soil microbial organism was not investigated in detail.

The quantity and quality of plant litter are the key factors regulating carbon (C) loss and nutrient feeding in the plant–soil interface (Cornwell et al., 2008; Djukic et al., 2018; Singh et al., 2021). In general, tissues with high lignin, polyphenol, wax contents, lignin: N and C: N ratios decompose more slowly than those with opposite indexes do (Jiang et al., 2014; Zhu et al., 2016). The decomposition rate is closely correlated with the C/P ratio of the litter due to limitation of insufficient P; as such, a low content of P corresponds to high amounts of litter (Kaspari andYanoviak, 2008). The ratio of lignin: cellulose (lignin–cellulose index, LCI) is also an appropriate predictor of the decomposition rate of litter; substrate quality, such as lignin content, is the main regulator of the decomposition rate of plant litter in coniferous forests (Taylor et al., 1991). Inflorescence litters are characterized by a distinct physical texture; for this reason, their chemical indexes significantly differ from those of other litters (Wang et al., 2016). This characteristic can be considered to establish models, and to predict nutrient cycling and source–sink relationships. It is also essential to figure out interactions between species and litter types for their unique properties, which may induce species-specific effects on available soil nutrients and soil microbes.

Trade-off of resource allocation occurs between vegetative growth and reproduction (Piquot et al., 1998). For example, Sanches et al. (2008), reported the mass of reproductive litter in a tropical semi-deciduous forest in the southern Amazon Basin accounted for approximately 10% of the total litter in January–August and 13–26% in September–December, respectively. Similarly, Mantovani and Iglesias (2009) found that the reproductive parts of *Tillandsia stricta* constitute 12–37% of the total biomass. Lee et al. (2010) report that *Robinia pseudoacacia* flower litter constituted 30–50% of the total litter production and decomposed rapidly. Our previous study found that inflorescence litter from phanerophyte were comparable with their non-flower litter. Biomass partitioning of some herbaceous species accounted for 10–40% of the aboveground biomass (Wang et al., 2016). Thus, inflorescence litter needs to be reassessed for better comprehension and modeling biogeochemical cycling. Some previous studies found that differences of soil nutrient and microbial biomass among soil depths being of variation along elevation gradients (Zuo et al., 2018; Sun et al., 2018). 13 C-labeled analysis revealed that fine root litter decomposition slows with soil depth (Hicks et al., 2018). In addition, one case study in mountain grassland belts observed most significant depth variation in Q10 of soil extracellular enzyme activity at low elevation (Zuo et al., 2021). Studies have also found that leaf litter and roots release nutrients (nitrogen and phosphorus) in the decomposition process which is faster in palatable grasses with high-nutrient than in unpalatable grass with low-nutrient (Moretto et al., 2001). It is critical to address that how the growth plants grow in alpine ecosystem, and obtain sufficient nutrients from soils to support growth and development. However, the extent of the complementary effects of plant litter at different soil depths has yet to be fully elucidated. Nutrient release and related biochemistry cycling also need to be understood to determine the spatial-specific effects along soil depth gradients on soil nutrient pool.

The interaction among substrates, microbial factors, and abiotic conditions co-determine the persistence of reduced organic C in the environment (Cornwell et al., 2008; Kleber, 2010; Zhou et al., 2020). Soil microorganisms not only play an important role in soil interaction networks (Prin et al., 2009; Fuentes-Ramirez et al., 2018; Zhou et al., 2020), but also facilitate fundamental ecosystem functions, such as soil aggregation and nutrient cycling, and contribute substantially to soil organic matter content. Variation in microbial decomposer communities can be attributed to biotic interactions and shifting substrate availability during litter decomposition (Chapman et al., 2013). Therefore, litter quality indicated by the proportions of labile and relatively recalcitrant compounds can alter the direct effect of climate on decomposition by affecting microbial community composition (Suseela and Dukes, 2013). In agro-ecosystems, making organic amendments can be an effective approach to replenish depleted soil microbial biomass in comparison to inorganic fertilizer (Kallenbach and Grandy, 2011). Moreover, the abundance of soil microbes varies with the effects of the allelopathic potential of weeds and crops (Wurst and van Beersum, 2009). Hence, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and their ratios are appropriate indicators that can be used to predict and identify the stimulatory or inhibitory effects of plant litter addition on soil nutrient status.

This study addresses the three questions stated below.

1) Do chemical properties of inflorescence litter remarkably differ in comparison with leaf litters, and are there any significant interactions between litter types and plant species?
2) How does inflorescence litter supplement affect SOM, soil nutrients, and soil microbial biomass at different soil depths?
3) What are the differences of SOM, DIN, A−P, MBC, and MBN in soil with inflorescence litter addition among life forms at two soil depths?

2. Materials and Methods

2.1. Study area

The experiment site is located at the foot of Mt. Kaka (32° 59′ N, 103° 40′ E, see Fig. 1) in the middle section of the Minshan

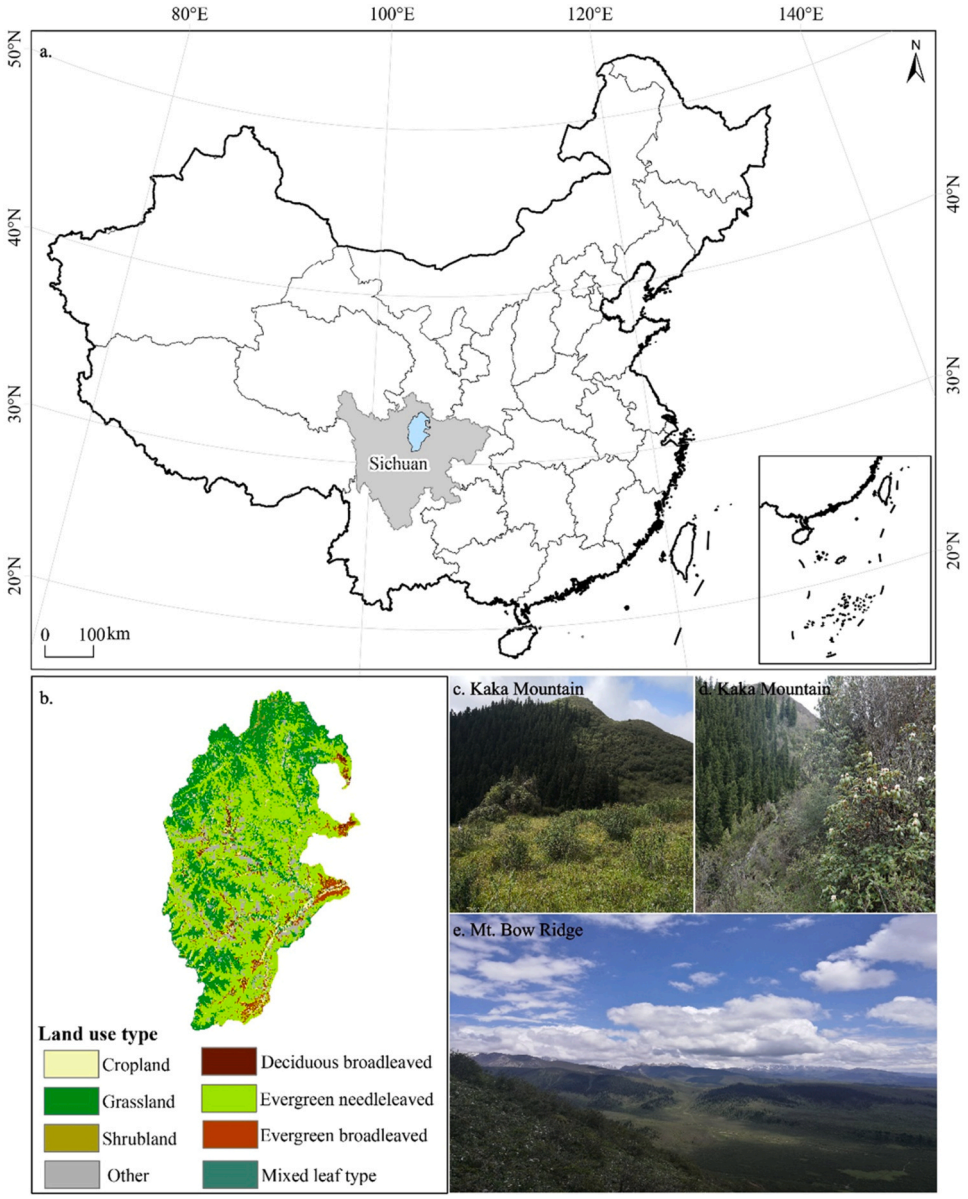

Fig. 1. Schematic overview and photographs of the study sites in Mt. Kaka and Mt. Bow Ridge, a) location of study sites; b) vegetation types; c) and d) typical plants in Mt. Kaka; e) landscape in Mt. Bow Ridge.

Mountain, eastern Tibetan Plateau, which is northwestern Sichuan province, China with humid continental climate. The area is the headstream of Minjiang and Peijiang Rivers. It is characterized by a mean annual precipitation of 720 mm. Almost 70% of the total precipitation falls during June–August. From late September to May, Snowfall usually occurs, and permanent snow-cover forms at the end of December. The annual mean temperature of the site is 2.8 °C, with mean values of −7.6 °C and 9.7 °C in January and July, respectively. The annual mean solar radiation is 1827 h. The annual mean accumulative temperature above 0 °C is 1833.9 °C (Wang et al., 2014). With monthly percent possible sunshine ranging from 31% in September to 57% in December, the county receives 1831 h insolation annually. The area has subalpine forests, dominated by *Abies faxoniana* with mosaic spruce and some shrubs. A typical alpine meadow exists above the treeline with numerous and unique alpine plants. Most of the ground is covered by abundant mosses, which are dominantly composed by *Polytrichum swartzii* and *Trematodon acutus.* Vascular plants include species mainly belonging to genus *Kobresia* and *Carex*. Other common species are plants in *Festuca* spp., *Gentiana* spp., and *Leontopodium* spp. (Wang et al., 2014). Plant roots in this ecosystem are mainly distributed at the surface A-horizon Dwarf shrubs of *Rhododendron* and *Salix* are scattered sporadically in the meadow. The soil type is dominated by Mat Crygelic Cambisols (i.e., silty loam inceptisol, *Chinese Soil Taxonomy Research Group*, 1995).

2.2. Sampling

In the blooming period of plants from late May to mid-June in 2012, a field investigation was carried out to collect inflorescence litters and leaf litters of early summer 14 plant species, at two sites, namely, Mt. Kaka (103° 42′ E; 32° 59′ N, 3500–3900 m a.s.l.) and Mt. Bow Ridge (103° 42′ E; 33° 1′ N, 3600–3850 m a.s.l.), to determine their chemical properties, assess the C, N, P, lignin, and cellulose contents and their ratios, and also to explain the underlying mechanisms. Four litter traps were placed under the canopy of each individual shrub in the study. Five to eight individuals for each shrub species to collect enough inflorescence litters were selected. After inserting legs of litter trap into the soil, plant litter was collected twice weekly, which was later sorted as inflorescence litter and other types during the blooming period. Inflorescences of herbaceous individuals were just plucked at the end of flowering phase for their small size (Wang et al., 2016). These species were tentatively classified into five groups based on their life forms according to Raunkiaer's system (i.e., chamaephyte, geophyte, hemicryptophyte, phanerophyte, and therophyte). More than half of these plants were dominant species, and the whole group of experimental species was mainly composed of geophyte (G), hemicryptophyte (H), and phaenerophyte (P), except one species from chamaephyte (C). In addition, all the species were also sorted to be herbaceous and woody plants these two kinds of life forms. A mixed leaf litter of alpine meadows was sampled on Mt. Kaka (3950 m. a.s.l). Both kinds of litters were spread on blotting papers for air-dry. A small portion of each litter was separated and dried in an oven for 48 h to calculate their dry matter content.

2.3. Experimental design

In this study, to verify whether the vertical spatial enhancement of soil nutrient pool is stimulated by inflorescence litters at species level, we established a simulated pot experiment by adding different kinds of plant litters. Polyvinyl chloride (PVC) pots with a depth of 15 cm, a top diameter of 20 cm, and a bottom diameter of 12 cm were filled with 2 kg of soil. The soil was collected in autumn in 2011, stored at 4 °C, sieved through a 2 mm mesh, and mixed thoroughly. Afterward, 5 g (calculated as dry weight) of flower litters or mixed litters was added to the soil surface of each treatment on June 21, 2012 (also see Wang et al., 2016). Each treatment was covered with a thin soil layer to prevent wind erosion. A control treatment was prepared without additional litter. Sixteen treatments with three replicates were prepared. All the pots were buried into the experimental field carefully to maintain soil temperature. The pots were also distributed randomly in the experimental field and their top edges were about 3 cm above the ground to avoid runoff from outside. The pots were rearranged weekly to create a similar microclimate. After two months, soil samples in the PVC pot were taken out from 0 to 5 cm and 5–10 cm two soil depths, respectively, and mixed evenly by sieving through 2 mm mesh. Furthermore, soil samples were collected from three triangle points from the center of each pot and combined to avoid boundary layer effect. Soil samples were stored in an ice box for chemical determination later. Moreover, pooled data with life forms sorted were also investigated to study the effects of inflorescence litters on soil organic matter (SOM), soil nutrients, and soil microbial biomass.

2.4. Chemical analysis of soil and plant samples

For soil samples, total dissolved N (TDN) contents were determined using unsieved fresh moist soil subsamples. Soil subsample extractions were shaken for 1 h with 2 M KCl at room temperature (20 °C) and a soil-to-solution ratio of 1:5 (weight/volume); subsequently, the extracted solution was filtered through a 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. TDN subtracted dissolved inorganic N (NH_4^+−N and NO_3^-−N) equaling dissolved organic nitrogen (DON). We extracted soil solutions and the exchangeable pool with centrifugal drainage and 2 M KCl in respect to the methods in Jones et al. (2004), respectively. Total phosphorus (TP) and available phosphorus (A−P) (Wang et al., 2016) in soils were estimated by extraction with 0.5 M sodium hydroxide sodium carbonate solution (Dalal, 1973). MBC and MBN contents were determined by the chloroform-fumigation direct-extraction technique. The 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). For plant samples, the contents of C and N were determined by dry combustion with a CHNS auto-analyser system (Elementar Analysensysteme, Hanau, Germany) (Brodowski et al., 2006). The content of P was obtainedcolorimetrically by the chloromolybdo-phosphoric blue color method after wet digestion in a mixture of

HNO_3, H_2SO_4, and $HClO_4$ solution (Institute of Soil Academia Sinica, 1978). Lignin and cellulose were estimated by the method described by Melillo et al. (1989).

2.5. Data analysis

One-way ANOVA was applied to compare the values between the treated and control. The general linear model (*GLM*) was processed to determine the pooled effects of species or life forms and soil depths on soil nutrients and soil microbial biomass as well as their interactions. Mean comparison was calculated with One-Way ANOVA statistics for the separate effects of different indicators. Post hoc multiple comparisons were adopted once no fewer than three groups are existed. Multivariate ANOVA was conducted to estimate the effects of litter type and soil depths and their interactions by SPSS 19.0 (SPSS Inc., Chicago, IL, USA). All differences were tested at $P < 0.05$ using a Tukey multiple range test. The normality of data tested with One-Sample K–S test and Q–Q plot, or log-transformation was adopted to meet the normality requirement. Homogeneity of variance test was also processed during the analysis process. In the figures and tables, information is presented as the means and the standard errors of means. All differences were tested at $P = 0.05$ level.

3. Results

3.1. Comparison of chemical properties between inflorescence litter and leaf litter

Higher C, N, and P contents were observed in inflorescence litters than those in leaf litters ($P < 0.05$, see Table 1 and Table S1). Both lignin and cellulose in inflorescence litters were significantly lower than those in leaf litters (lignin, 211.37 ± 53.88 and 237.88 ± 43.002, F=25.92, $P < 0.001$; cellulose, 266.93 ± 30.76 and 283.75 ± 26.30, F=29.68, $P < 0.001$, respectively), so were C/N, N/P, LCI, and lignin/N. Moreover, we did not find significant interactions of N/P (F=0.696, $P = 0.675$) and lignin/N (F=1.931, $P = 0.111$) between species and litter types.

Table 1
Comparision of chemical composition between inflorescence litter and leaf litter.

	Inflorescence litter				Leaf litter				Corrected model	
	Minimum	Maximum	Mean	Std. Deviation	Minimum	Maximum	Mean	Std. Deviation	F	*P*
C (mg g^{-1})	369.73	468.50	410.66	24.16	365.27	474.81	400.44	25.98	3.34	0.002
N (mg g^{-1})	11.95	35.41	22.17	7.18	4.38	18.12	12.19	3.90	12.48	0.000
P (mg g^{-1})	1.20	4.59	2.753	1.09	0.52	2.96	1.17	0.64	13.71	0.000
C/N	11.62	33.08	20.54	6.86	21.53	108.40	38.49	21.92	6.30	0.000
N/P	5.58	12.68	8.57	2.17	5.90	15.84	11.36	2.83	3.52	0.001
Lignin (mg g^{-1})	112.70	304.10	211.37	53.88	173.40	304.10	237.88	43.00	25.92	0.000
Cellulose (mg g^{-1})	235.70	379.30	266.93	30.76	245.20	322.80	283.75	26.30	29.68	0.000
Lignin/cellulose (LCI)	0.26	0.55	0.44	0.08	0.37	0.53	0.45	0.04	27.65	0.000
Lignin/N	7.10	21.37	12.75	3.63	10.35	32.45	20.03	6.07	5.96	0.000

3.2. Effects of inflorescence litters on different soil N fragments

After the inflorescence litters were added, the NO_3^-–N content in exchangeable pool was significantly modified at two depths (Fig. 2(A), B, and C. F= 9.34, $P < 0.001$), which was attributed to significant litter addition (F=6.12, $P < 0.001$) and different soil depths (F=154.67, $P < 0.001$). Besides, a significant effect on the interaction between litter addition and soil depth (F=2.10, $P < 0.05$) were observed. The soil NO_3^-–N of inflorescence litter treatments, with values ranging from 36.98 to 53.85, was greater than that of mixed-litter addition (29.90 ± 0.37). The non-addition control contained the least soil NO_3^-–N (29.09 ± 1.02 mg kg^{-1}) at the first soil layer. In addition, a significant difference was observed in soil NH_4^+–N (F=4.14, $P < 0.001$) with litter addition at different soil depths, whose differences were taken up both by litter addition (F=5.37, $P < 0.001$) and soil layers (F=4.98, $P < 0.05$), as well as their interactions (F=2.74, $P < 0.01$). However, non-addition treatment was not the one with the least NH_4^+–N (2.42 ± 0.74), while it existed in NO_3^-–N. Similar result was also observed in DON, whose values of flower litters treated were between 74.7 and 114.62, with significant differences at two soil depths after litter addition (F=4.03, $P < 0.001$).

A similar trend was observed in contents of different N fragments in soil solutions compared with those in exchangeable pool (Fig. 2D, E, and F; Table 3). All the N fragments in soil solutions were significantly different at two soil depths after litter addition, which were mainly from litter addition without interaction between litter addition and soil depth. Nevertheless, soil NH_4^+–N varied gently at different soil layers in soil solutions. Values of DON in soil solutions fall between 5.23 and 24.09 in comparison with mixed litter (5.52 ± 2.13) and non-addition (3.62 ± 0.13).

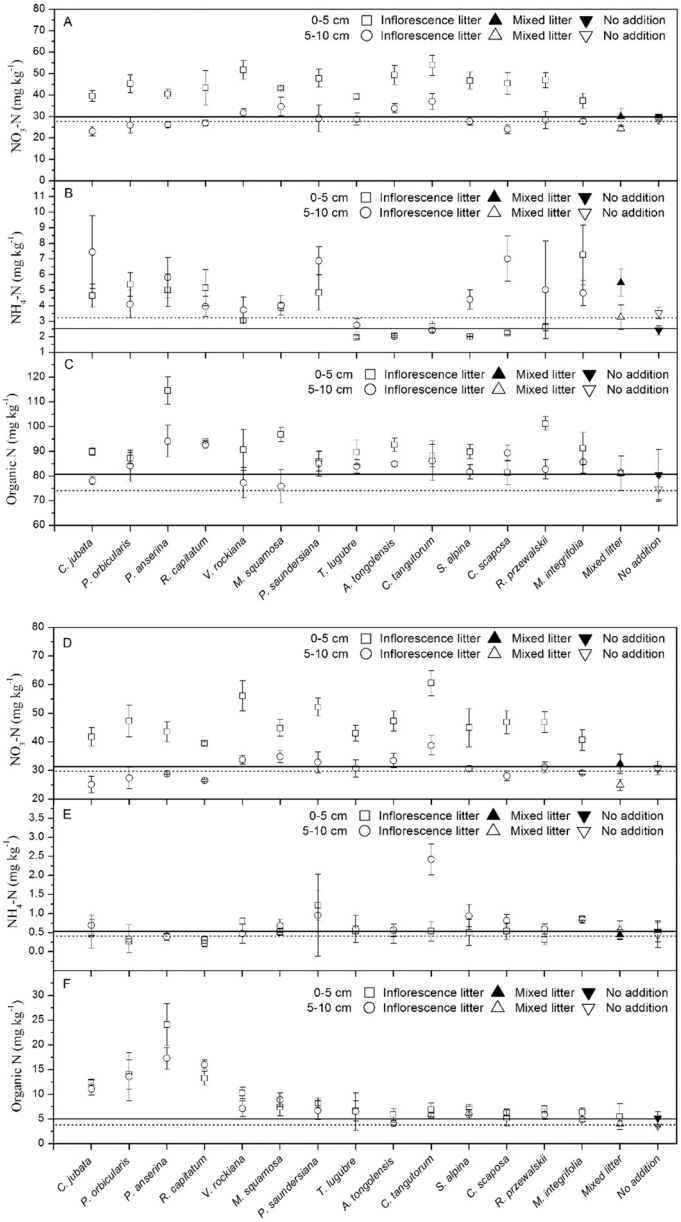

Fig. 2. Different nitrogen components in exchangeable pool (A, B, and C) and soil solutions (D, E, and F) after litter-addition treatment.

3.3. Effects of inflorescence litter addition on SOM and P contents

Soil organic matter (SOM) generally decreased in the treatment with inflorescence litters addition in comparison with non-addition treatment (Fig. 3A), while not the same with mixed-litter addition. The significant differences of SOM after litter addition were mainly from soil depths (F=11.65, $P < 0.05$) and marginal significant difference from litter addition (F=3.40, $P = 0.07$) but without significant interactions (F=1.14, $P = 0.34$). However, inflorescence litters addition of four species *Myricaria squamosal*, *Aster tongolensis*, *Rhododendron przewalskii*, and *Meconopsis integrifolia* had greater SOM than control treatment at shallow soil layer. Both TP and A−P were significantly affected by litter addition. In addition, they were more noticeable at the first depth (Fig. 3B and C, Table 3). Non-addition control contained significantly lower TP (1.18 ± 0.03 g kg^{-1}) in soil than the other litter-addition treatments (Fig. 3B, Table 3; F=3.04, $P < 0.001$). Likewise, total soil A−P increased significantly with litter-addition treatments (Fig. 3C, F=10.63, $P < 0.001$), whose variances were attributed to significant differences of litter addition (F=4.72, $P < 0.001$) and soil depths (F=40.79, $P < 0.001$). Neither T − P nor A−P had significant interactions between litter addition and soil depth (F=1.15, $P > 0.05$).

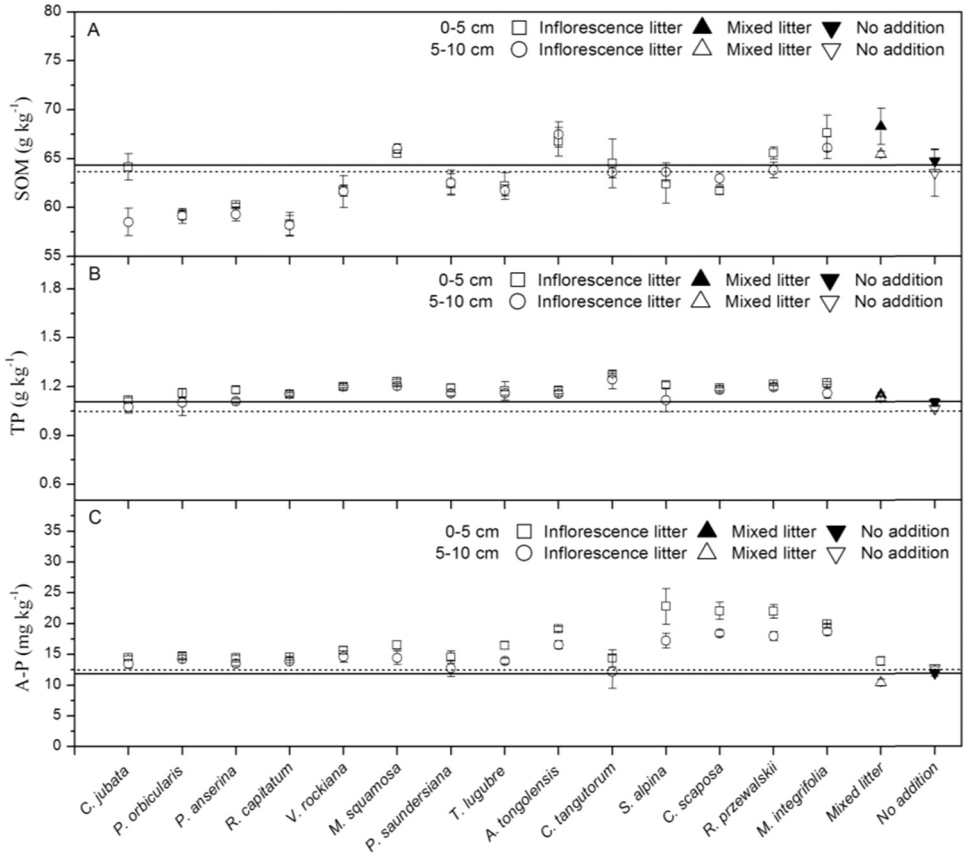

Fig. 3. SOM, T-P and A-P between inflorescence litter, other litters, and non-addition treatment at two soil depths.

3.4. MBC and MBN at different soil depths after inflorescence litter addition

Inflorescence litters increased soil MBC with a mean value of 97.07 mg kg^{-1} at the first soil layer. Their values were also greater than those treated with mixed litters (68.32 mg kg^{-1}), except for *Potentilla anserina* (67.64 mg kg^{-1}). Besides, at the soil sub-layer, the minimum and maximum values of soil MBC with inflorescence litters were 55.25 and 123.03 mg kg^{-1}, respectively, which were greater than those in non-addition control (50.21 ± 1.59 mg kg^{-1}). Values of MBN in soil were between 49.16 and 74.41 mg kg^{-1} at the first layer, which were all greater than those of non-addition control (48.32 ± 0.84 mg kg^{-1}). It was not the same in the sub-layer with values between 42.36 and 62.65 mg kg^{-1}, whereas MBN of the control was 46.70 ± 3.33 mg kg^{-1}. Both MBC and MBN were improved with inflorescence-litter addition than non-addition control (Fig. 4, Tables 2; F=6.28, $P < 0.001$ and F=5.78, $P < 0.001$, respectively). Though MBC and MBN were significantly different at different soil layers ($P < 0.05$), MBC/MBN did not present the same result (F=3.39, $P = 0.07$). Different types of litter addition resulted in significant differences for all three indicators (MBC, F=6.94, $P < 0.001$; MBN, F=9.86, $P < 0.001$; MBC/MBN, F=9.48, $P < 0.001$).

3.5. Effects of plant litter on SOM, DIN, A−P, and SMB after life forms sorted

In terms of SOM, DIN, A−P, MBC, and MBN in soil with inflorescence litter addition, SOM did not have significant differences among life forms at two soil depths, neither between herbaceous and woody plants (Fig. 5(a) and (f), $P > 0.05$). Litter addition with three life forms affected A−P substantially at two soil depths (Fig. 5(b); F= 2.97, $P = 0.04$), which were mainly from soil depths (F=4.67, $P = 0.04$) and life forms (F=4.72, $P = 0.02$) but without their significant interactions (F=0.18, $P = 0.84$). There were no significant differences of the effects of inflorescence litters on soil A−P between herbaceous and woody plants (Fig. 5(g)), with marginal significant differences resulted at two soil depths (F=4.02, $P = 0.06$) while not from life forms ($P > 0.05$). DIN had significant differences between three life forms (F=22.52, $P < 0.05$), resulting from soil depths (F=101.12, $P < 0.05$) while not life forms (F=1.43, $P = 0.26$) and their interactions. It is the similar pattern for DIN between herbaceous and woody plants that significantly differences (F=38.27, $P < 0.05$) were also merely resulted from soil depths (F=102.34, $P < 0.05$). For MBC and MBN in the soil after litter addition, both values of MBC with herbaceous plants litter addition were significantly greater than those with woody plants at shallow soil layer (Fig. 5(i), MBC, 114.61 ± 6.44 and 87.33 ± 5.44, F= 4.20, $P = 0.02$; Fig. 5(j), MBN, 79.09 ± 6.15, and 93.91 ± 10.87, F= 8.75, $P < 0.05$) and sub-layer (MBC, 69.08 ± 2.32, 62.07 ± 2.70, MBN, 54.39 ± 2.20, 52.16 ± 2.02). At both soil

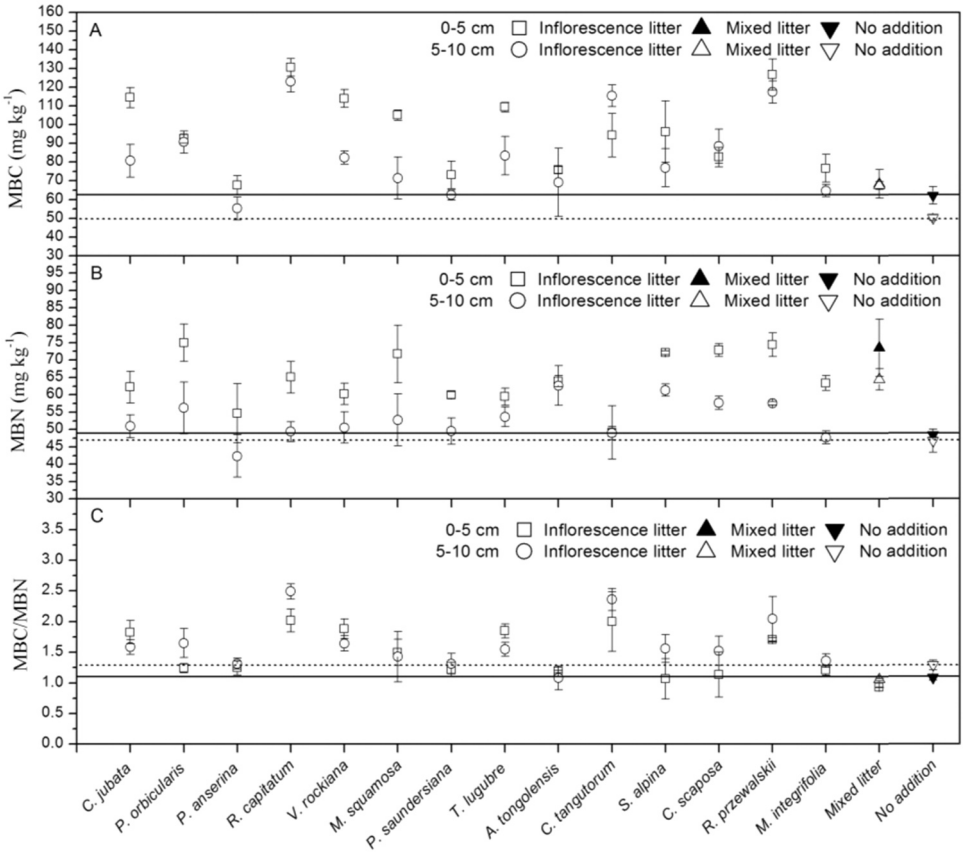

Fig. 4. MBC, MBN, and MBC/MBN at two soil depths after different litter-addition treatments.

Table 2
Multi-factor ANOVA on N exchangeable pool and soil solutions in soil after litter addition.

	Exchangeable pool						Soil solutions					
	NO_3^--N		NH_4^+-N		Organic-N		NO_3^--N		NH_4^+-N		Organic-N	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Corrected model	9.34	0.00	4.14	0.00	4.03	0.000	8.90	0.00	1.88	0.01	8.13	0.00
Litter addition	6.12	0.00	5.37	0.00	4.18	0.000	6.14	0.00	2.30	0.01	15.66	0.00
Soil depth	154.67	0.00	4.99	0.03	16.71	0.000	143.94	0.00	2.87	0.09	2.82	0.10
Litter addition × Soil depth	2.10	0.02	2.74	0.00	3.11	0.00	1.91	0.04	1.44	0.15	0.95	0.52

Table 3
Multi-factor ANOVA on SOM, A-P, TP, MBC, MBN, and MBC/MBN after litter addition at two soil depths.

	SOM		TP		A-P		MBC		MBN		MBC/MBN	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Corrected model	6.28	0.00	3.04	0.00	10.63	0.00	6.28	0.00	5.78	0.00	5.33	0.00
Litter addition	3.40	0.07	4.72	0.00	18.07	0.00	6.94	0.00	9.86	0.00	9.48	0.00
Soil depth	11.65	0.00	5.76	0.02	40.79	0.00	69.15	0.00	5.87	0.02	3.39	0.07
Litter addition × Soil depth	1.14	0.34	1.16	0.33	1.15	0.33	1.32	0.22	1.67	0.08	1.32	0.22

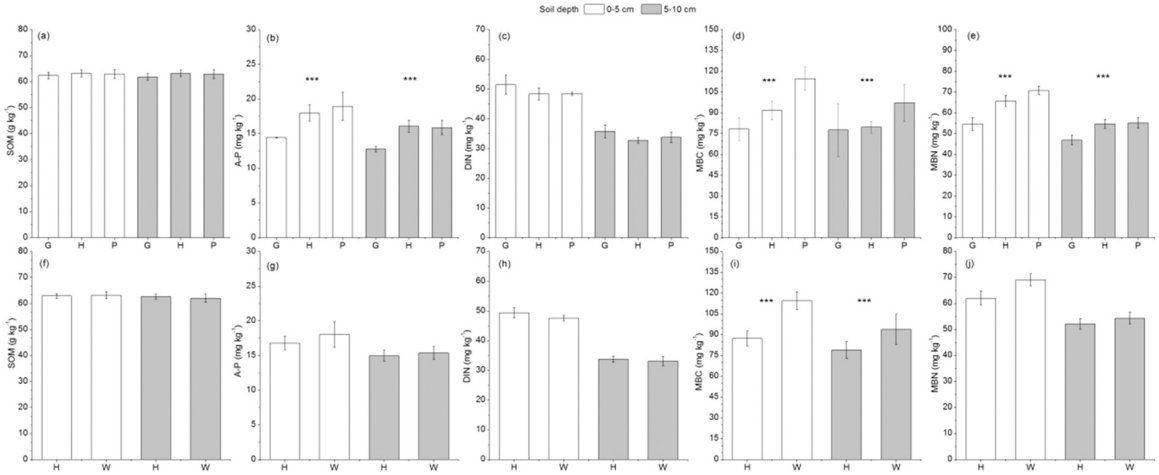

Fig. 5. Comparison of SOM, DIN, A-P, MBC, and MBN in soil with inflorescence litter addition after life forms sorted at different soil depths, a-e) G, H, and P refer to geophyte, hemicryptophyte, and phaenerophyte, respectively; f-j) H, and W refer to herbaceous and woody plants, respectively. * ** indicate significant differences between life forms.

depths, P had significant greater MBN (Fig. 5(e), F= 10.346, $P < 0.05$) than other two life forms (H and G) but not for MBC (Fig. 5(d), F= 2.22, $P = 0.09$).

4. Discussion

The decomposition of plant litter can contribute to various fluxes in ecosystem (Aerts, 1997; Heal et al., 1997; Heneghan et al., 1998; Fitter et al., 2005; Kaspari and Yanoviak, 2008; Djukic et al., 2018). In Arctic and alpine vegetation, although inflorescences constitute a small fraction of plant biomass and production, inflorescence production can be a significant proportion of a species' total production under special conditions, (Fabbro and Korner, 2004; Wookey et al., 2009) and were noticeably great particularly in a specific period of the growing season (Lee et al., 2010; Wang et al., 2016). The time of plant litter fall significantly influenced soil available N and P, and soil microbial biomass of alpine meadow on the Tibetan Plateau (Wang et al., 2016). Diverse blooming phenology may regulate the peak times of litter production, which can also be greatly influenced by climatic factors.

Biochemical compounds, from rapidly decaying to relatively recalcitrant labile, are present series of regimes in plant tissues with variations in terms of their decomposability (Djukic et al., 2018; Zhou et al., 2020). In this study, the inflorescence litters were composed of significantly greater total C content but less structural C-containing compounds being major cell-wall constituents, such as lignin and cellulose, than the leaf litters (Table 2). Physical toughness (dry matter content, or C content, and lignin) can be used as appropriate predictors of decomposition across all organs (Freschet et al., 2012; Wang et al., 2016). A critical N level was positively correlated with mass loss rate. Hence, the decay rate of flower litter was significantly faster due to its greater N content in comparison with leaf litters (19.80 ± 1.39 verses 39.27 ± 4.16, F=37.78, $P < 0.05$). Besides, C/N and lignin/N ratios were commonly proposed to explain the decomposition rate explanatory factors (Melillo et al., 1982; Heal et al., 1997, Berg, 2000). Our study indicated that C/N ratio of flower litter was below 30, which is significantly low than that of leaf litter, and C/N ratio lower than 30 can decompose easily and yield a mull humus type. A similar trend of lignin/N ratios (Table 2) was observed. Substrate quality measured as lignin content was the primary control on the decomposition rate of plant litter (Aber et al., 1990; Taylor et al., 1991). LCI is also a good predictor of the decomposition rate k of plant litter, and lignin/N was related to the decomposition rate. Both indicators were significantly less in flower litters than in leaf litters, which also supported flower litters' fast decomposition, improvement for soil nutrients, and stimulation effects on immobilization of soil organic matter.

Only a small proportion P in soil is directly available for plant uptake, although it contains a large amount of total P. Plants obtain P as orthophosphate anions, predominantly as HPO_4^{2-} and $H_2PO_4^{1-}$, from the soil solution. In most soils, the concentration of orthophosphate in a solution is low (Richardson et al., 2009). N and P synergistically affect many ecosystems (Elser et al., 2007), which act jointly in the ecosystem process (Sterner and Elser, 2002). Across a sample of 28 lowland forest stands in Peru and Panama, which was very closely correlated with C:P ratio of the litter and consistent with litter breakdown being limited by P, essentially, less P means more litter (Kaspari andYanoviak, 2008). Reproductive organs contain more P because their active growth needs greater ATP of nucleic acid synthesis. Thus, lower N/P in reproductive organs was observed. As testified from our study, inflorescence litter had significantly lower N/P than leaf litter (8.42 ± 0.42 and 11.60 ± 0.56, respectively; F=20.62, $P < 0.05$).

The effects of inflorescence litters on soil nutrient pool were limited by various factors, such as spatial limitation, to a certain extent. At two soil depths, the influence from inflorescence litters on soil available N and P were mainly presented at the shallow soil depth (0–5 cm), probably due to limited leaching or diffusing effects. Soil NH_4^+−N in soil solutions varied lightly at different soil layers. N dynamics also change with depth in the soil profile (Melillo et al., 1989 ; Chi et al., 2021). In a field study conducted in nutrient-impacted marsh in southern Florida, USA, NH_4^+−N concentration is typically high in the litter layer, and this parameter

generally increases with soil depth (Debusk and Reddy, 2005). Nevertheless, in the natural ecosystem, it might be more complicated due to leaching or other factors. Decomposition rates may vary with depth in a soil profile. Patterns of root decomposition through a short grass steppe soil profile presented that mass loss rates decreased linearly from 10 cm to 1 m, so was result observed in patterns of total C and cellulose loss rates. Differences in the stabilization of lignin may be a consequence of differences in microbial community through a short grass steppe soil profile (Richard and Ingrid, 2002). In a boreal forest, ^{14}C and ^{15}N implied that fungi influence C and nutrient cycling at different soil depths variously. Within the deeper horizons, changes in the fungal community with soil depth could be observed, with some species found predominantly in the fragmented litter and humus and others being most common in the mineral soil(Lindahl et al., 2007; Sun et al., 2021)).

Inflorescence litters affected different N components in exchangeable pool and soil solution, particularly NO_3^-−N content (Fig. 2). Inflorescence litter accelerated soil microbial nitrification after addition. Theoretically, maximum C, N, and P were estimated using *R. przewalskii*, *R. capitatum*, and *S. alpina* species. The macronutrients released by the three species fall between 77.81 and 195.90, 4.41–11.10, and 0.56–1.41 kg ha^{-1}, respectively. This further implicated that inflorescence litter can compensate soil nutrient pool noticeably. In some forests, plant litters, particularly pollen, affect the soil biogeochemical cycle (Lee et al., 1996; Qiu et al., 2010; Wang et al., 2012; Fuentes-Ramirez et al., 2018). Previous experiment results of the decay rates presented that inflorescence litters significantly decomposed faster than that of the other litters (Lee et al., 2010; Wang et al., 2016).

Soil chemistry and community composition may be altered by C substrate identity and diversity, changing belowground ecosystem functions, such as decomposition and nutrient transfer, and triggered feedback may affect plant growth and the aboveground community ((McMahon et al., 2005)Orwin et al., 2006). Amendment quality and application rates are strong regulators of microbial biomass, and even small quantities of organic amendments can be used to rapidly restore MB across a range of cropping systems, but specific responses depend upon the type and rate of inputs, as well as on soil characteristics (Kallenbach and Grandy, 2011). As testified previously in our results, inflorescence-litter addition increased microbial biomass C and N by 42.09% and 32.25% at the shallow soil layer, respectively (Fig. 4). At the two sampling mountain sites, MBC in soil decreased and reached the minimum value from early May to late September (Fig. S1), which covers the growing season of the study region. C availability is the principal driver of MB in soils, and organic amendments increase soil microbial biomass (Wardle, 1992; Bowman et al., 2004; Fierer et al., 2009). Given that MB is closely related with the quantity and quality of C inputs, it presented an increased MBN that inferred that MB and its activities were mainly restricted by the available labial carbon (Bowman et al., 2004; de Graaff et al., 2010). Inflorescence litter input quickly decayed labile carbon and stimulated soil microbial activities and community composition, which enhance soil mineralization. High amounts of N and P can be released into the soil nutrient pool. This result has been applied to many agricultural practices as an effective way to facilitate soil nutrient cycling and contribute to a more soil organic matter (Diacono and Montemurro, 2010; Bhogal et al., 2011).

At the community level, diverse decay rates of plant litters were mainly caused by species-specific plant characteristics and their traits associated with decomposition (Quested et al., 2003; Dorrepaal et al., 2005). In this study, at shallow soil depth (0–5 cm), phaenerophyte feed more A-P but less DIN amount, while geophyte supplied more DIN but less A-P. Besides, it also implied that per unit P might be coupling with more N of phaenerophyte than geophyte (i.e., N: P). Both pooled life forms, i.e., G, H, and P, and herbaceous and woody plants, had greater influence on DIN at shallow soil depth than 5–10 cm depth. Significant effects were not attributed to the differences between herbaceous and woody plants. P availability is necessary to control microbial processes in many lowland tropical forests (William et al., 2009). This result was also observed in the inflorescence litters collected from the studied alpine ecosystem.

5. Conclusion

Available plant litter nutrient is associated with the decomposer community, which differs in terms of chemical and physical properties and decay rates. The higher amount of inflorescence litter than that of other litters is a prerequisite of soil nutrient supplementation and soil microbial regulation. The inflorescence litters with easily decayed labile quality were rapidly consumed by soil microorganisms and thus facilitated. After a short period, available N and P in soil increased significantly when a high nutrient content was present and the texture of the substrate was easily decayed. Phaenerophyte can release more N per unit P correlatively than geophytes. Both kinds of pooled life forms had greater influence on DIN at shallow soil depth. Therefore, the soil at shallow depth benefited better from inflorescence litter due to spatial limitations. These findings provided insights into the mechanisms by which the decomposition of diverse plant litters enhances soil nutrient pool, alters microbial communities, and mediates ecological processes under unique conditions. Individual plant species affect the local patterns of soil C and N dynamics. Hence, further studies should be conducted to link and up-scale these plant-induced heterogenetic patterns on a small scale with ecosystem-level N and C budgets in an environment exposed to changing environment. Abundant nutrients or non-structural carbohydrates from the inflorescence litters were probably introduced and transported to the community composition of soil microorganisms. It is essential to understand the mechanisms underlying soil organic matter stabilization and to estimate nutrient budgets on a large scale in the future.

CRediT authorship contribution statement

Jinniu Wang, Fusun Shi and Ning Wu conceived the paper and analyzed the data. Jinniu Wang, Bo Xu, and Jing Gao conducted the field work and lab procedure. Jinniu Wang, Fusun Shi and Yan Wu did map and plotting. All authors contributed substantially to the discussion and manuscript.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01825.

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