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ORIGINAL ARTICLE

Temperature sensitivity of nutrient release from dung along elevation gradient on the Qinghai–Tibetan plateau

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Abstract The temperature sensitivity of nutrient release from dung decomposition will influence ecosystem nutrient recycling in the future global warming. However, the relationship between temperature and nutrient release is not well understood. We conducted a 2-year-long study to understand the yak dung decomposition and its potential response to climate change along an elevation gradient from 3,200 to 4,200 m above sea level on an alpine meadow on the Qinghai–Tibetan plateau. Mass loss of different chemical components of dung [organic carbon (C), cellulose, hemicellulose, lignin, N, P, potassium (K), calcium (Ca) and magnesium (Mg)] significantly decreased with elevation. The ratios of C:N and N:P in the remaining dung increased significantly with decrease in elevation. The average temperature sensitivities (% $°C^{-1}$) (i.e., increase of the mass loss (%) per 1°C temperature increase among elevations) were approximately 37, 75, 168, 41, 29, 37, 29, 34, and 31% per 1°C warming within a 273-day decomposition period, which decreased with decomposition time, for organic C, cellulose, hemicellulose, lignin, N, P, K, Ca, and Mg, respectively. The temperature sensitivity of organic C mass loss is positively correlated to the C:N ratios in dung. The average temperature sensitivity of phosphorus mass loss was higher than that of nitrogen mass loss for the first 273 days and thereafter this situation was reversed.

Keywords Temperature sensitivity · Nutrient release · Dung decomposition · Elevation gradient · Alpine meadow

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Introduction

The temperature sensitivity of dung decomposition will influence the ecosystem nutrient recycling in the future global warming. In natural grazing ecosystems, litter fall and dung from grazing animals are the two important processes by which minerals contained are returned to the soil through decomposition (Anderson and Coe 1974; Cornelissen et al. 2007; Fierer et al. 2005; Herrick and Lal 1995, 1996; Hirata et al. 2008). Temperature is often the primary factor determining litter decomposition (Anderson 1991; Couteaux et al. 1995, 1999; Fierer et al. 2005; Hobbie 1996; Silver and Miya 2001). Studies on plant–herbivore indirect interactions via nutrient recycling have led to the hypothesis that herbivores with a low nitrogen:phosphorus (N:P) ratio, feeding on plants with higher N:P ratio, recycle relatively more N than P through dung and urine, driving plants into P limitation (Sterner 1990; Daufresne and Loreau 2001). However, less attention is paid to the temperature sensitivity of release of different nutrients from dung. The deposition of dung in grasslands and its subsequent decomposition has a variety of important effects on functions in grassland ecosystems (Herrick and Lal 1995, 1996; Ma et al. 2006, 2007; MacDiarmid and Watkin 1972; White et al. 2001).

As the largest grassland area on the Eurasian continent, the Qinghai–Tibetan plateau is situated at 3,500 m or more above sea level, and covers an area of ~2.5 million km^2 (Zheng et al. 2000). Evidence shows that the Qinghai–Tibetan plateau is predicted to experience increases in surface temperatures in the future (Giorgi et al. 2001; IPCC 2007). Concurrent with climate changes, there are profound changes to the pastoral land-use dynamics on the plateau that result in increased grazing pressures on the alpine meadow (Duan et al. 2005, 2006; Zhou et al. 2005). Many studies from tundra ecosystems (Jonasson et al. 1993; Schmidt et al. 1999, 2002; Shaver et al. 1998) suggest that altered nutrient cycling may be a key response in the alpine ecosystems in response to climate and grazing perturbations. In this region, where open grazing in excess of 13.3 million domestic yaks and 20,000 wild yaks and 50 million sheep is practiced (Gerald et al. 2003; Yao et al. 2006), large amounts of animal excreta are deposited directly onto alpine grasslands because of overgrazing (Zhou et al. 2005). Knowledge about the role of dung decomposition in nutrient cycling and response to climate change in alpine ecosystems is still rudimentary. The specific aims of this study were to determine: (1) if mass losses of chemical components in dung decreased with an increase in elevation; (2) if the temperature sensitivity of mass losses of different chemical components in dung varied; and (3) if mass loss of nitrogen was faster or slower than that of phosphorus in dung, potentially driving a nitrogen or phosphorus limitation for plants in the region when affected by future global warming.

Materials and methods

Experimental site

The experimental site is located at the Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), a facility run by the Northwest Institute of Plateau Biology, Chinese Academy of Sciences. HBAMERS is situated at latitude 37°37′N, longitude 101°12′E. The station lies in the northeast portion of Tibet in a large valley surrounded by the Qilian Mountains. The station experiences a typical plateau continental climate, which is dominated by the southeast monsoon from May to September in summer and high-pressure systems from Siberia in winter. Summers are short and cool, and winters are long and severely cold. Mean annual temperature is −2°C, and mean annual precipitation is 500 mm, over 80% of which falls during the summer monsoon season. Mean elevation of the valley bottom is 3,200 m. A detailed site description can be found in Zhao and Zhou (1999).

Dung collection

The plant community at the experimental site at 3,200 m is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa* spp., *Carex* spp., *Scirpus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontopodium nanum*, *Blysmus sinocompressus*, *Potentilla nivea* and *Dasiphora fruticosa*. After grazing at the study site, yaks were enclosed at night and fresh dung samples from 20 yaks were collected from the corral the next morning on 6 August 2006. These samples were carefully mixed after collection. Eight fresh samples were immediately dried at 80°C for measurement of dry matter (DM) and chemical components. Other fresh dung samples were weighed to 125.6 g (which corresponded to a dry weight at 80°C of 22.195 g), and put into sealed plastic bags to be carried to the field plots.

Dung decomposition

Near HBAMERS, single plots of 10 × 20 m at the elevations of 3,200, 3,600, 3,800, 4,000 and 4,200 m above sea level along the southern side of the Qilian Mountains were fenced in Autumn 2005. The fresh dung samples were transferred to 0.5 mm mesh nylon bags in the field. In total, 32 dung bags were placed on the turf fixed with nails in each of the five fenced plots at spacings of 10–20 cm on 6 August 2006. On 14 September 2006, 7 May 2007, 24 July 2007, and 16 July 2008, eight samples were randomly selected, carefully taken back to the laboratory. There was almost no soil on the bottom surface of the nylon bags due to vegetation coverage being about 100% for all plots. The dung was removed from the bags and the samples were dried at 80°C to measure their mass losses, and then ground and passed through a 1 mm sieve. The concentrations of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) were determined following the methods of AOAC (1984). Dung chemistry was measured by sequentially digesting dung material into fractions that correspond with soluble cell contents, cellulose, hemicellulose, lignin and acid insoluble ash (Ryan et al. 1990; Van Soest 1963) on a forage fiber analyzer (ANKOM 200, Macedon, NY, USA). All nutrient concentrations were calculated on the basis of organic matter (i.e., dry matter minus crude ashes).

Air temperature

At the center of each plot, Hobo weather stations (Onset Computer Corporation, Japan) were used to monitor air temperature at a height of 2 m above the ground. The temperature sensors were connected to a CR1000 datalogger, and air temperatures were measured every minute and then 30 min averages were stored. Average annual air temperatures were 0.1, −1.2, −2.2, −3.8 and −5.3°C at 3,200, 3,600, 3,800, 4,000 and 4,200 m, respectively, from August 2006 to July 2007 (Fig. 1).

Statistical method

The General Linear Model-Univariate method (SPSS 13.0, SPSS Inc. Chicago, IL, USA) was used to assess the significance of the impacts of elevation, sampling date, and their interactions on dung components. For each sampling date, the significant difference between elevations was assessed by One-way ANOVA and Least Significance Difference (LSD). To test the correlations between the measured parameters of dung decomposition, Pearson's correlation analysis was performed. All significant differences mentioned in the text were at the $P = 0.05$ level.

Temperature sensitivity (% °C^{-1}) of nutrient mass losses is defined as increase of mass loss (%) per 1°C temperature increase. It was calculated using the relative differences of mass losses (%) among different elevations divided by the annual average air temperature difference (°C) of the corresponding elevations.

Results

Mass loss

Generally, mass losses for all measured variables in Table 1 were affected significantly by elevation, and the interactions between elevation and sample date except for the lack of interactive effects for hemicellulose, phosphorus (P) and magnesium (Mg). Percentages of mass losses of organic carbon, cellulose, hemicellulose, lignin, N, P, K, Ca, and Mg at the 3,200 m elevation through 705 days of decomposition were: 67.6, 93.4, 68.9, 55.7, 69.3, 80.7, 77.4, 66.8, and 78.2%, respectively. The remaining masses

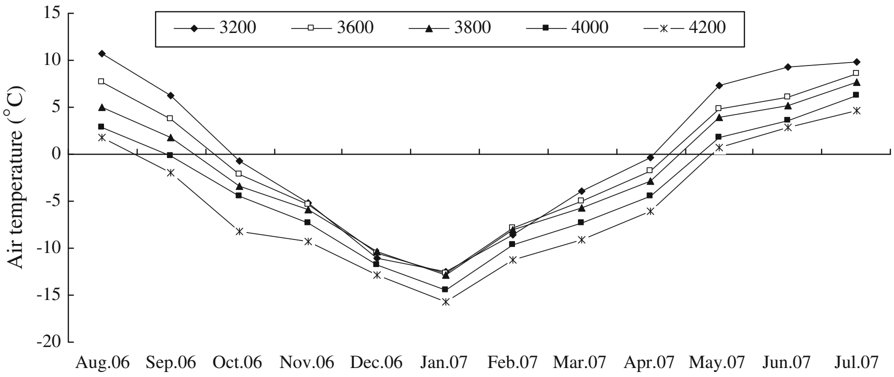

Fig. 1 Air temperature at different elevations above sea level from August 2006 to July 2007

Table 1 *P*-values of univariate analysis of variance of mass losses for the all measured variables using elevation and sampling date as fixed factors with GLM analysis of SPSS version 13

Remaining mass	Elevation (*E*)	Sampling date (*S*)	$E \times S$
Carbon	<0.001	<0.001	<0.001
Cellulose	<0.001	<0.001	0.003
Hemicellulose	<0.001	<0.001	0.088
Lignin	<0.001	<0.001	0.001
Nitrogen	<0.001	<0.001	<0.001
Phosphorus	<0.001	<0.001	0.692
Potassium	<0.001	<0.001	0.001
Calcium	<0.001	<0.001	<0.001
Magnesium	<0.001	<0.001	0.636
Ratio of C:N	<0.001	<0.001	0.085
Ratio of N:P	<0.001	<0.001	0.062

of all components decreased significantly with decrease in elevation and with dung decomposition time (Table 1 and Figs. 2, 3). In particular, the ratios of C:N and N:P in the remaining dung were affected significantly by elevation and sampling date (Table 1), and increased significantly with decrease in elevation (Fig. 4), suggesting that more organic N was mineralized relative to organic C, and more organic P was mineralized relative to organic N with decrease in elevation, respectively.

Temperature sensitivity of mass loss

The temperature sensitivity of mass losses of different measured variables varied with the decomposition time (Appendix 1, 2). The slopes of the regression equations between temperature sensitivity and the days of decomposition reflect the extent of temperature sensitivity over time. Generally, temperature sensitivity of mass losses for all measured variables decreased sharply over the 273-day decomposition period and then tended to reach relative stability except for hemicellulose (Fig. 5). For example, the average temperature sensitivities were approximately 37, 75, 168, 41, 29, 37, 29, 34, and 31% $°C^{-1}$ for organic C, cellulose, hemicellulose, lignin, N, P, K, Ca and Mg, respectively, for the first 273 days; but only 8, 9, 63, 19, 21, 14, 12, 10 and 13% $°C^{-1}$, respectively, after 705 days (the end of the experiment) (Fig. 5). Simple correlation analysis indicate that significant positive correlations exist between temperature sensitivity of mass loss of organic C and that of cellulose ($r = 0.998$**), P ($r = 0.984$**), K ($r = 0.994$**), Ca ($r = 0.997$**) and Mg ($r = 0.985$**), respectively; and there were no significant correlations between temperature sensitivity of mass losses of hemicellulose, lignin and N and that of other all variables ($P > 0.05$). These results suggest that with future global warming, the increase of mass losses of chemical components in dung decomposition may be

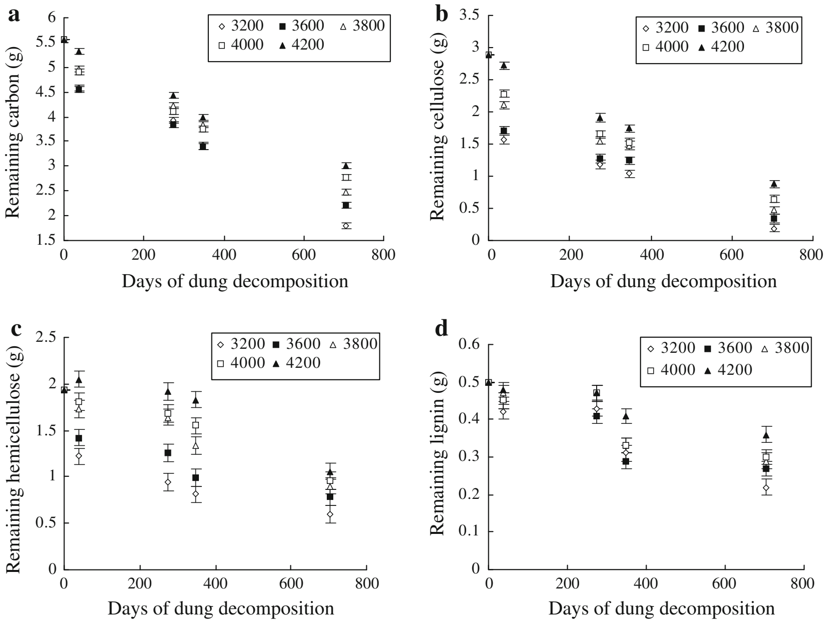

Fig. 2 Remaining masses (mean ± SE) of organic carbon, cellulose, hemicellulose and lignin in dung by elevation and days of decomposition

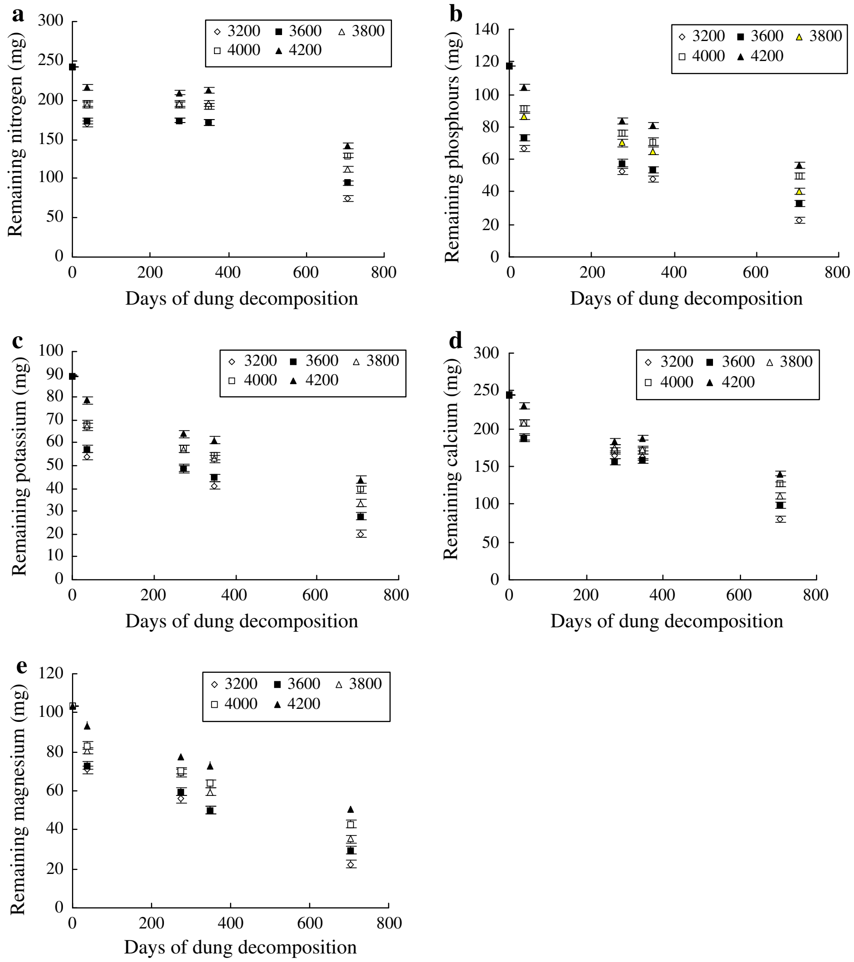

Fig. 3 Remaining masses (mean ± SE) of total nitrogen, phosphorus, potassium, calcium and magnesium in dung by elevation and days of decomposition

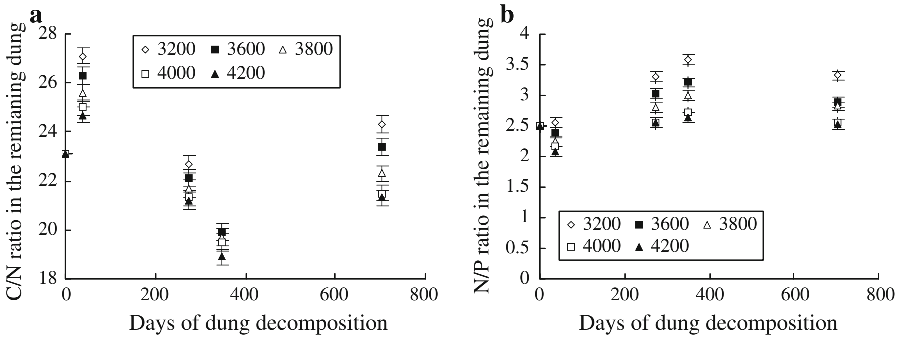

Fig. 4 The ratios of carbon:nitrogen and nitrogen:phosphorus in dung by elevation and days of decomposition

different, and the temperature sensitivity of more easily degraded structural carbohydrate (i.e., hemicellulose vs. cellulose or cellulose vs. lignin) is higher. In particular, during the early stage of dung decomposition (i.e., before the 273 day sample), higher P mass loss relative to N indicates that there is a potential for more N limitation for plants in the region, whereas after 273 days of decomposition, this situation is reversed.

Discussion

The temperature sensitivity of dung decomposition will influence the rates of ecosystem carbon sequestration in a warmer world. A number of studies have shown that the temperature sensitivity of litter decomposition can vary depending on litter type and extent of decomposition (Couteaux et al. 1995; Hobbie 1996;

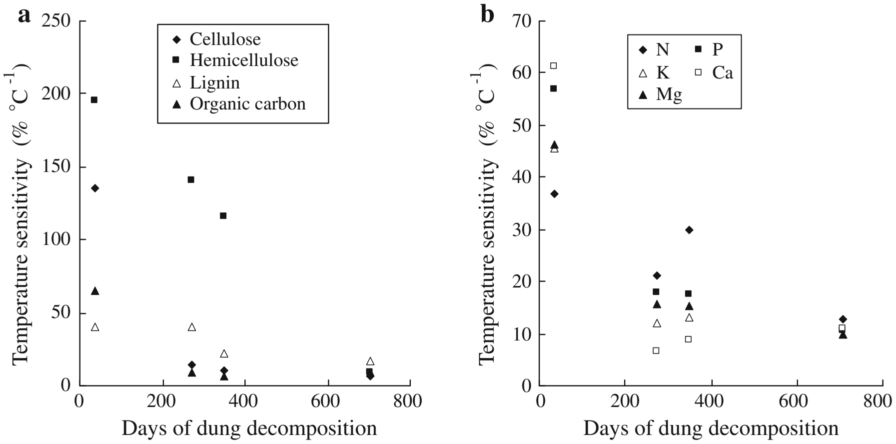

Fig. 5 Temperature sensitivity of mass loss rates (% °C^{-1}) of organic carbon, cellulose, hemicellulose and lignin (**a**) and total nitrogen, phosphorus, potassium, calcium and magnesium (**b**) in dung by days of decomposition

Silver and Miya 2001; Fierer et al. 2005). However, dung decomposition is not well understood. Fierer et al. (2005) found using a 53-day short-term litter incubation that, as decomposition progressed over time, the relative quality of the catabolized C substrates tended to decrease, while the temperature sensitivity of decomposition increased, suggesting that the temperature sensitivity of microbial decomposition is inversely related to litter carbon quality. Our results showed that the C:N ratio was the highest after the 37-day dung decomposition period, which corresponds to the highest temperature sensitivity of organic carbon mass loss. During this decomposition period, a higher C:N ratio could result from a faster release of soluble N from dung. As decomposition proceeded over time, the decreased the C:N ratio in the remaining dung until the 348-day sample date resulted in the decrease of the temperature sensitivity of organic C mass loss. Thereafter, the temperature sensitivity of organic C mass loss increased due to N limitation that caused increase of C:N ratio at the end of the experiment. Thus, we found that the temperature sensitivity of organic C mass loss is positively correlated to C:N ratio in dung, i.e. inversely related to dung quality because the higher C:N ratio is in dung, and the lower the quality for decomposers is (Eiland et al. 2001).

During the last decade, the stoichiometric approach has also focused on indirect interactions between plants and herbivores via nutrient recycling (Daufresne and Loreau 2001; Elser and Urabe 1999; Sterner 1990). N and P have been mostly considered, because these elements are known to limit primary production in most terrestrial and aquatic ecosystem. However, how these relationships will change with future warming is not well understood. Our results indicate that more P was released during dung decomposition as compared to N within the 273-day dung decomposition period, which will drive N limitation for plants in the region during global warming. However, the temperature sensitivity of N mass loss was higher than that of P after 273 days of decomposition, which may drive the extent of P limitation.

In our study, temperature sensitivity of mass losses of structural carbohydrates is higher than that of non-structural carbohydrates, because the temperature sensitivity of mass loss of total organic carbon (including non-structural carbohydrate and structural carbohydrates) (average 22.2% °C^{-1}) was lower than that of structural carbohydrate (average 63% °C^{-1}). Most of the structural carbohydrate in dung is indigestible plant cell walls that are comprised of a complex array of carbohydrate fractions including hemicellulose (8.7% of dry matter (DM)), cellulose (15.2% of DM), and lignin (2.2% of DM) in our study. Although cellulose is the predominant component of plant fiber, digestion of cellulose is limited by the hemicellulose-lignin encasement. The cellulose microfibrils are tightly bonding in a matrix of other fibers, particularly hemicellulose and lignin (Jeffries 1990; Mullahey et al. 1991). Digestion of non-cell wall organic matter fractions (non-structural carbohydrates plus protein and lipid) averages 85% in forages. However, digestion of the cell wall fraction is much lower, typically ranging between 40 and 70%, with an average of roughly 60% (Zinn and Ware 2007).

Therefore, our study on the temperature sensitivity of dung decomposition and feedback to climate change may have important implications for predictions about future contributions of alpine or cold regions to carbon dynamics and nutrient cycling worldwide.

Conclusion

Our study shows that warming and/or interaction between warming and decomposition time will increase dung decomposition and nutrient release from dung. The temperature sensitivity of mass losses of different chemical components in dung varied, decreased with decomposition time, and then tended to relative stability except for hemicellulose. In particular, the average temperature sensitivity of mass loss of phosphorus was higher than that of nitrogen within the 273-day decomposition period, and thereafter this situation was reversed. The temperature sensitivity of organic carbon mass loss was positively correlated to the ratio of carbon to nitrogen in dung.

With respect to climate warming, our results suggest that (1) faster nutrient release may promote nutrient recycling through dung decomposition; (2) different temperature sensitivities of mass losses of nitrogen and phosphorus over different dung decomposition periods may drive nitrogen or phosphorus limitation for plants and change the structure and function of the community; (3) a decrease of the ratio of carbon to nitrogen in dung (i.e., increase of forage quality) may reduce the temperature sensitivity of the mass loss of chemical compositions in dung. Therefore, our study on the temperature sensitivity of dung decomposition and feedback to climate change may have important implications for predictions about future contributions of alpine or cold regions to carbon dynamics and nutrient cycling worldwide.

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Appendix 1

See Fig. 6.

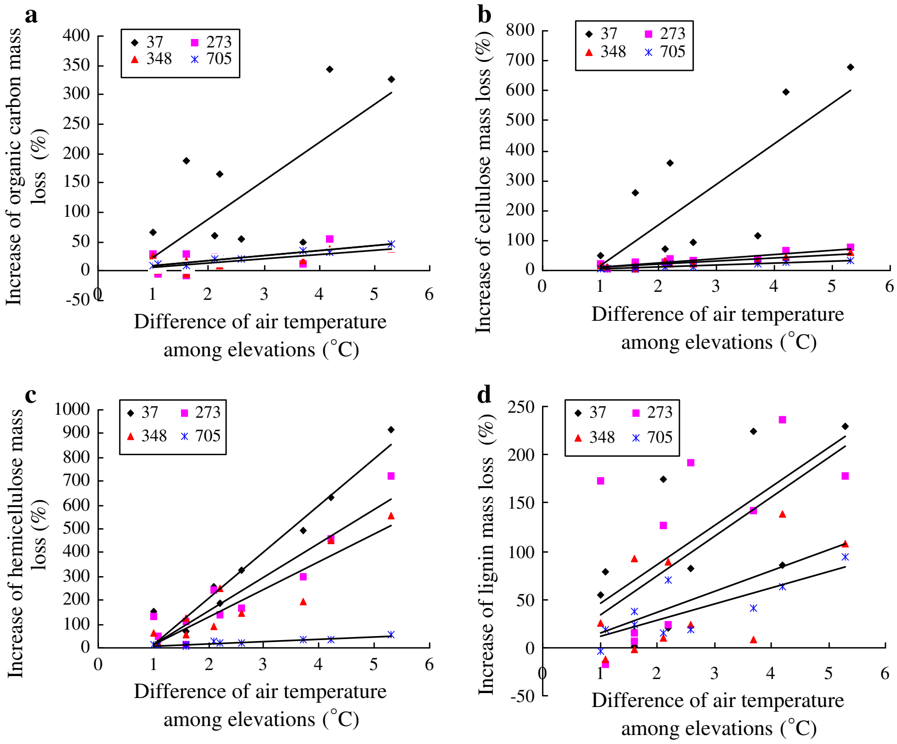

Fig. 6 Increase of mass losses for organic carbon, cellulose, hemicellulose and lignin by difference of air temperature among elevations and days of decomposition

Appendix 2

See Fig. 7.

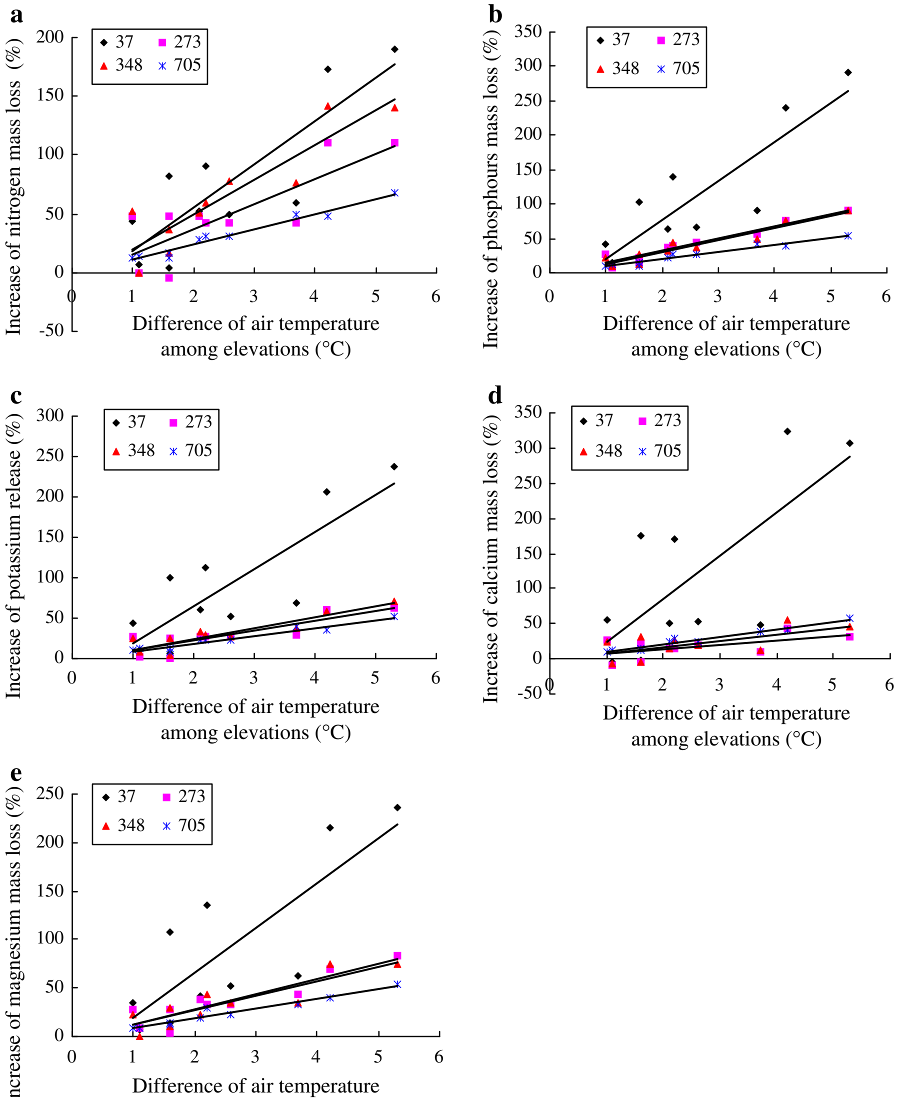

Fig. 7 Increase of mass losses for nitrogen, phosphorus, potassium, calcium and magnesium by difference of air temperature among elevations and days of decomposition

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