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Warm season bias of branched GDGT temperature estimates causes underestimation of altitudinal lapse rate

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ABSTRACT

The temperature trend estimated from the distribution of bacterial branched glycerol dialkyl glycerol tetraethers (brGDGTs) in soil (i.e. the MBT–CBT or MBT′–CBT index) was studied along an altitude transect from 1850 m to 5139 m in the southeast Tibetan Plateau. Measured temperature values from weather stations in the area showed increasing seasonality with increasing elevation. The measured lapse rate of mean annual air temperature (MAAT) in the region was −7.2 °C/km, whereas that estimated from the MBT- or MBT′–CBT index was lower, with only −3.2 °C/km for the MBT′–CBT estimate. At elevation >4 km, MBT′–CBT temperature values were increasingly higher than measured MAAT values. We hypothesized that the systematic changes in the length of the warm season, as well as the seasonal period of brGDGT production, with elevation are likely the cause of overestimation of the MBT′–CBT temperature at high elevation sites, and hence the underestimation of lapse rate. The hypothesis was supported by a similar lapse rate of −3.1 °C/km calculated from the measured mean warm season temperature (MWST) that only included monthly temperature values >0 °C. This suggests that care should be taken in interpreting brGDGT derived temperature values in environments with large seasonal contrasts.

1. Introduction

The branched glycerol dialkyl glycerol tetraethers (brGDGTs; I–III, Fig. 1) are a type of acidobacterial lipids (Weijers et al., 2009) distributed ubiquitously in terrestrial settings such as peat bogs and soil (Weijers et al., 2006), but also in sedimentary settings receiving significant terrigenous input (e.g. Hopmans et al., 2004). Based on the distribution of brGDGTs in soil, their degree of cyclization (i.e. the CBT index) has been related to soil pH, and the degree of methylation (i.e. the MBT or the revised MBT′ index) to mean annual air temperature (MAAT) and soil pH (Weijers et al., 2007a; Peterse et al., 2012). Accordingly, a combined application of the two indices (i.e. the MBT–CBT or MBT′–CBT index) has been proposed as a proxy for estimating MAAT. These indices and parameters are calculated according to the following equations:

$$\mathrm{CBT} = -\log[(\mathrm{Ib} + \mathrm{IIb})/(\mathrm{Ia} + \mathrm{IIa})] \quad (1)$$

$$\mathrm{MBT} = (\mathrm{Ia} + \mathrm{Ib} + \mathrm{Ic})/(\mathrm{Ia} + \mathrm{Ib} + \mathrm{Ic} + \mathrm{IIa} + \mathrm{IIb} + \mathrm{IIc} + \mathrm{IIIa} + \mathrm{IIIb} + \mathrm{IIIc}) \quad (2)$$

where Roman numerals refer to the structures in Fig. 1. Soil pH and MAAT were calculated using the empirical equations based on a global calibration given by Weijers et al. (2007a):

$$\mathrm{CBT} = 3.33 - 0.38 \times \mathrm{pH} \quad (3)$$

$$\mathrm{MBT} = 0.122 + 0.187 \times \mathrm{CBT} + 0.020 \times \mathrm{MAAT} \quad (4)$$

The revised MBT′ index and the mean annual temperature (MAAT′) introduced by Peterse et al. (2012) were calculated according to the following equations:

$$\mathrm{MBT'} = (\mathrm{IIa} + \mathrm{IIb} + \mathrm{IIc})/(\mathrm{Ia} + \mathrm{Ib} + \mathrm{Ic} + \mathrm{IIa} + \mathrm{IIb} + \mathrm{IIc} + \mathrm{IIIa}) \quad (5)$$

$$\mathrm{MAAT'} = 0.81 - 5.67 \times \mathrm{CBT} + 31.0 \times \mathrm{MBT'} \quad (6)$$

Although it has been widely used for reconstruction of mean annual temperature, the MBT- or MBT′–CBT index was also

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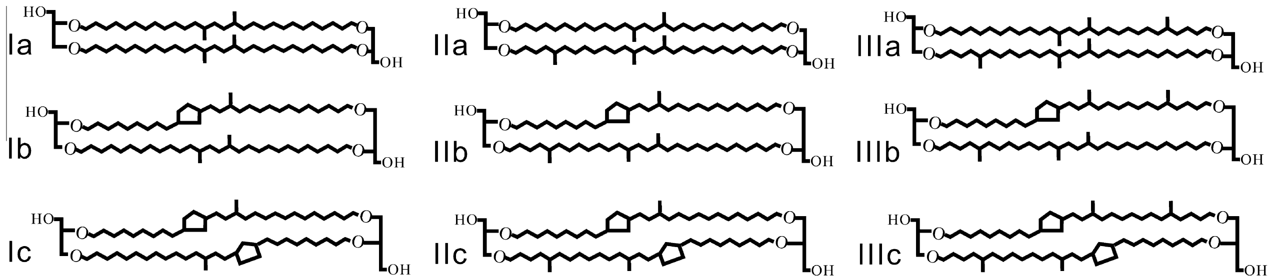

Fig. 1. Structures of brGDGTs.

surmised to reflect a temperature bias toward the warm season (e.g. Rueda et al., 2009; De Jonge et al., 2014), perhaps due to higher brGDGT production in organisms during warm periods.

In the troposphere, temperature generally decreases upward from the surface. The annual mean rate of temperature decrease with height, or lapse rate, at low latitudes is around −6.0 °C/km, varying from −5.0 to −8.0 °C/km (Stone and Carlson, 1979). Mountainous slopes therefore provide ideal places for testing the brGDGT-derived indices as a MAAT proxy in a wide temperature range within a limited distance. Indeed, studies along several mountainous slopes from Asia, Africa and South America have shown the altitudinal temperature trend from the brGDGT-derived indices in soil (Sinninghe Damsté et al., 2008; Peterse et al., 2009b; Ernst et al., 2013; Liu et al., 2013; Anderson et al., 2014; Coffinet et al., 2014; Yang et al., 2015). Among them, two studies, one at Mt. Gongga, China and the other at Mt. Rungwe, Tanzania, showed that temperature estimates from the MBT–CBT index (Eq. 4) were consistent with instrumental data and reflected local lapse rate well (Peterse et al., 2009b; Coffinet et al., 2014). In Meghalaya, NE India, the MBT′–CBT index based on Eq. 6 was preferred by authors due to its improved accuracy of MAAT estimates; however, the MBT′–CBT based lapse rate (−3.0 °C/km according to reported data therein) was lower than that from measured MAAT (−4.7 °C/km) (Ernst et al., 2013). On the Eastern Cordillera of Colombia and Mt. Shennongjia of China, brGDGTs IIIb and IIIc were not detected in most soil samples, and thus the data for MBT′ were reported (Anderson et al., 2014; Yang et al., 2015). Based on the data of these authors, we obtained MBT′–CBT based lapse rates of −3.4 °C/km for the Eastern Cordillera and −4.1 °C/km for Mt. Shennongjia, which are also lower than local measured ones, i.e. −4.9 °C/km and −6.2 °C/km, respectively. On Mt. Kilimanjaro, Tanzania, both absolute temperature values and lapse rates determined from the MBT–CBT proxy were higher than measured ones by ~3.1 °C (−1.1 °C to +6.1 °C range) and 1.6 °C/km (−6.9 °C/km vs. −5.3 °C/km), respectively (Sinninghe Damsté et al., 2008). We estimated MAAT′ temperature values by substituting their reported data of MBT for MBT′ in Eq. 6 (this is feasible because brGDGTs IIIb and IIIc are usually below detection limit and, if present, do not exceed 1% of total brGDGTs on average; Peterse et al., 2012) and found that the estimated MAATs are more accurate for in situ MAATs, with a mean offset of ca. 2.1 °C (0–4.8 °C), than the MBT–CBT estimates; however, the lapse rate based on the estimated MATs is only −4.1 °C/km. So it is evident that lapse rates from MBT′–CBT based temperatures are lower than in situ measured ones although the MBT′–CBT index seems more accurate than the MBT–CBT index in most studies. The reason for the lower MBT′–CBT lapse rate has yet to be explained. We hypothesized that it might be caused by seasonal bias in the brGDGT proxy, which may exhibit different extents at different elevations. Here, this hypothesis is tested by analyzing brGDGT distributions in surface soils along an altitude transect from 1850 to 5139 m above sea level (asl) on the southeast Tibetan Plateau.

2. Material and methods

2.1. Study area and sample collection

A total of 23 surface soils was analyzed. They were collected with a shovel with a depth of less than 5 cm along the Sichuan-Tibet Highway in the southeastern margin of the Tibetan Plateau (90.25–99° E, 28.9–32.43° N) in July–August, 2013 at various elevations, ranging from 1850 m to 5139 m (Fig. 2). Upon arrival at the laboratory, they were stored at −20 °C until analysis.

The area is characterized by a typical monsoon climate, with wet and warm conditions during boreal summer and dry and cold conditions during boreal winter. However, the duration of the warm season tends to become progressively shorter with height. This can be clearly seen from the monthly temperature data at nearby weather stations in the study area (Fig. 2; Table 1). For example, the months with temperature values >0 °C persist from January to December at the Batang station (2598 m asl), while they are short lived from May to September at Anduo station (4800 m asl). The MAAT at these stations ranges from 12.7 °C at the lowest station (Batang) to −2.8 °C at the highest station (Anduo), displaying a lapse rate of −7.2 °C/km (Fig. 4). Regional annual precipitation is low, ranging between 410 and 470 mm/yr, except for the obvious higher value of 688 mm/yr at the Linzhi Station, showing no trend with altitude (Table 1).

2.2. GDGT analysis

Sample pretreatment was according to regular procedures in our lab (Jia et al., 2012), with reference to Schouten et al. (2007). Briefly, frozen soil samples were first freeze dried and homogenized, and then ultrasonically extracted for lipids (6×) with MeOH (2×), dichloromethane (DCM)/MeOH (1:1, v/v; 2×) and DCM (2×), and all extracts were combined after centrifugation. The solvent was removed using vacuum rotary evaporation and each extract was purified and separated into an apolar fraction and a polar fraction over an activated alumina column by elution with *n*-hexane and DCM/MeOH (1:1, v/v), respectively. The polar fraction contained the GDGTs. A known amount of internal C_{46} GDGT standard was added to the polar fraction (Huguet et al., 2006). After the solvent was removed under N_2, the polar fraction was dissolved via sonication (5 min) in hexane/propanol (99:1, v/v) and filtered through a 0.45 μm, 4 mm diameter PTFE filter.

GDGTs were analyzed using high performance liquid chromato graphy–atmospheric pressure chemical ionization mass spectrometry (HPLC–APCI-MS) with an Agilent 1200 HPLC instrument-6410 TripleQuad MS instrument according to Schouten et al. (2007). Procedures described by Hopmans et al. (2000) and Schouten et al. (2007) were applied. Detection patterns were via selected ion monitoring (SIM) of $[M+H]^+$ ions (in MS1). Separation was achieved with a Prevail Cyano column (2.1 × 150 mm, 3 μm diameter

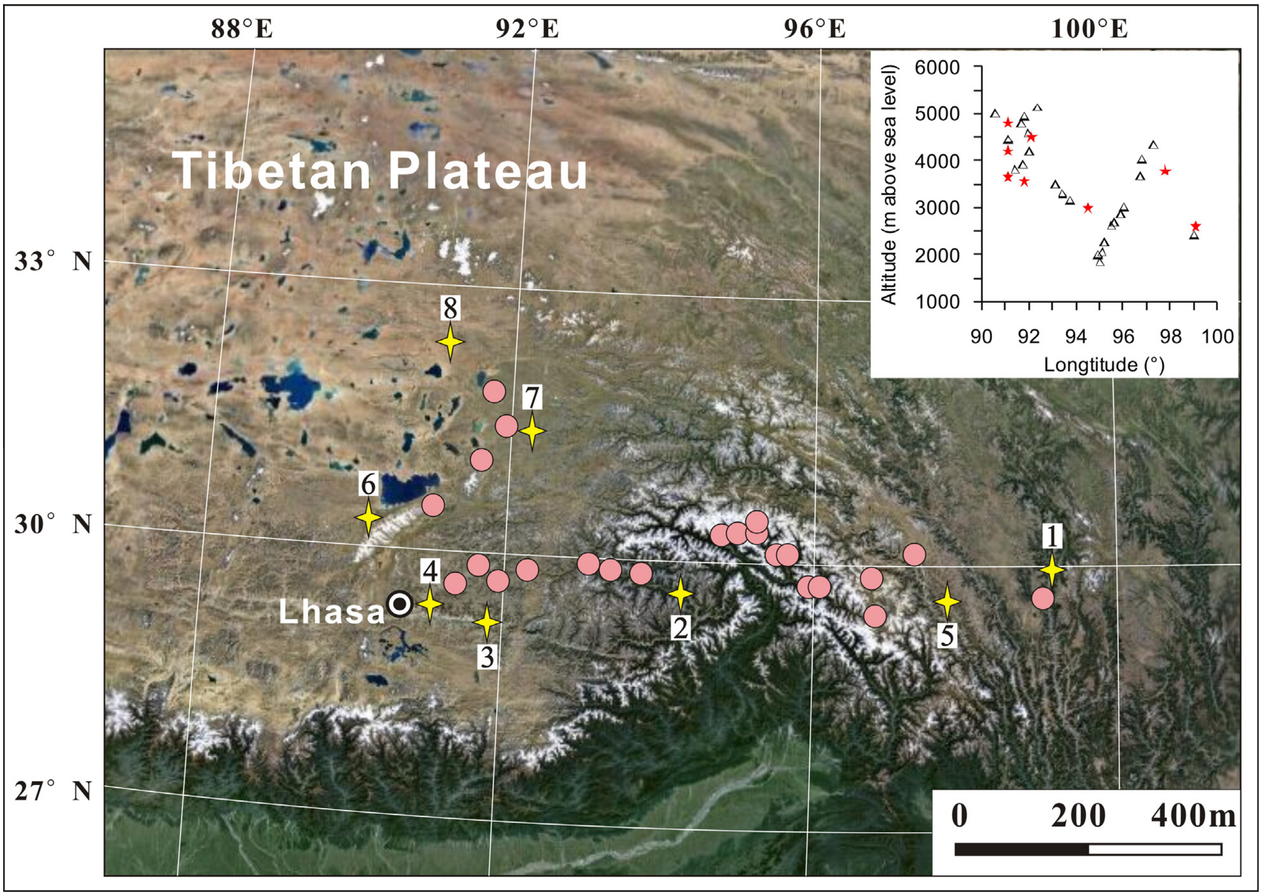

Fig. 2. Sampling sites (dots) and weather stations (stars). Weather stations are numbered as in Table 1. The insert shows elevation change of at sampling sites (triangles) and weather stations (stars) with longitude.

Table 1
Monthly and mean annual air temperature (MAAT, °C) and mean annual precipitation (MAP, mm/yr) measured at nearby weather stations from 1971 to 2000 (bold numbers indicate monthly temperature >0 °C; data from www.weather.com.cn).

St.	Name	Alt. (m)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	MAT	MAP
1	Batang	2598	**4.0**	**7.2**	**10.5**	**13.4**	**17.5**	**19.9**	**19.5**	**18.8**	**16.7**	**13.2**	**8.1**	**3.9**	12.7	470
2	Linzhi	2991	**1.3**	**3.1**	**6.3**	**9.5**	**12.5**	**15.5**	**16.6**	**16.5**	**14.7**	**10.9**	**5.9**	**2.4**	9.6	688
3	Naidong	3560	0	**2.2**	**5.4**	**8.7**	**12.5**	**15.7**	**15.6**	**14.8**	**13.3**	**9.1**	**3.5**	0	8.4	410
4	Lhasa	3648	−1.6	**1.5**	**5.2**	**8.4**	**12.3**	**15.9**	**15.7**	**14.7**	**12.9**	**8.7**	**2.9**	−1.2	8.0	427
5	Zuogong	3780	−5.6	−3.2	**0.7**	**4.2**	**8.8**	**12.9**	**12.9**	**12**	**10.2**	**5.6**	−0.6	−5.0	4.4	451
6	Dangxiong	4201	−9.3	−6.0	−2.0	**1.8**	**5.2**	**10.3**	**10.9**	**10.1**	**7.8**	**2.7**	−3.7	−8.3	1.6	460
7	Naqu	4509	−12.6	−9.8	−5.4	−1.2	**3.5**	**7.7**	**9.0**	**8.4**	**5.6**	−0.2	−7.2	−11.8	−1.2	430
8	Anduo	4800	−14.6	−11.8	−7.1	−2.6	**2.2**	**6.3**	**7.8**	**7.3**	**4.3**	−2.0	−9.4	−13.8	−2.8	436

particles; Grace, USA), maintained at 30 °C. GDGTs were eluted isocratically with 99% hexane and 1% propanol for 5 min, followed by a linear gradient to 1.8% propanol in 45 min. Flow rate was 0.2 ml/min. Injection volume was 10 µl. GDGTs were quantified by integration of the peak areas.

Recently, a new set of brGDGT isomers, which differ in the position of methyl moieties on the alkyl chains, was identified by substituting four Alltima Silica columns in tandem for the traditional one Prevail Cyano column in HPLC–APCI-MS analysis (De Jonge et al., 2014). Based on the extended family brGDGT members, a new temperature index, i.e. MAT_{mr}, that uses linear combinations of the fractional abundances of the 15 brGDGTs was recommended (De Jonge et al., 2014). We could not observe the new set of brGDGT isomers in our analysis, so the MBT- or MBT′–CBT calibration (Weijers et al., 2007a; Peterse et al., 2012) was applied. But according to De Jonge et al. (2014), in most cases, the MBT′–CBT based temperatures approximate the MAT_{mr} based values. In addition, the use of MBT- and MBT′–CBT calibrations enables this study to be comparable with previous results.

3. Results and discussion

3.1. BrGDGT abundance

BrGDGTs were detected in all the samples (Table 2). Except for the highest value of 3.26 µg/g dry weight (dwt), the total concentration varied between 0.04 and 1.30 µg/g dwt, with an average of 0.52 µg/g dwt. There was no trend in brGDGT concentration with altitude. Among the nine brGDGTs, the abundances of IIIb and IIc were quite low, i.e. ca. 1.4% and 0.3%, respectively, of the total brGDGTs on average, and brGDGT IIIc in particular was below

Table 2
Soil brGDGT concentration and related parameters, southeast Tibetan Plateau.

Sample	Lat. (N)	Long. (E)	Alt. (m)	Conc (μg/g dwt)	CBT	MBT	MAT	MBT′	MAT′	BIT
QZ-75	30.06	95.03	1850	0.22	0.15	0.28	6.45	0.29	8.91	0.95
QZ-74	29.99	94.95	2012	0.08	0.34	0.39	10.12	0.39	11.13	0.99
QZ-76	30.10	95.10	2062	0.41	0.07	0.32	9.29	0.33	10.61	0.94
QZ-77	30.08	95.21	2268	0.85	0.34	0.44	12.53	0.44	12.57	0.99
QZ-109	29.78	99.01	2436	0.06	0.56	0.26	1.63	0.27	5.96	0.67
QZ-80	29.93	95.51	2631	0.54	0.17	0.23	4.02	0.24	7.37	0.77
QZ-81	29.91	95.62	2688	1.30	−0.01	0.24	5.77	0.25	8.49	0.85
QZ-82	29.79	95.90	2872	0.26	0.72	0.45	9.88	0.46	10.84	1.00
QZ-83	29.74	96.05	3026	0.19	0.77	0.49	11.11	0.49	11.68	1.00
QZ-67	29.85	93.75	3165	0.04	0.56	0.18	−2.45	0.18	3.24	0.96
QZ-64	29.85	93.43	3306	0.46	1.17	0.56	10.97	0.56	11.56	0.99
QZ-62	29.88	93.12	3493	0.13	1.19	0.36	0.99	0.37	5.39	0.97
QZ-96	30.03	96.72	3678	0.05	0.82	0.13	−7.24	0.13	0.27	0.63
QZ-46	29.67	91.41	3811	0.02	0.94	0.26	−1.82	0.26	3.62	0.78
QZ-49	29.84	91.75	3929	3.26	0.72	0.35	4.83	0.35	7.72	0.98
QZ-93	30.55	96.80	4049	1.07	0.22	0.16	−0.18	0.16	4.64	0.85
QZ-51	29.70	92.00	4211	0.11	1.24	0.37	0.94	0.37	5.34	0.95
QZ-100	30.19	97.31	4352	0.23	0.56	0.17	−2.93	0.17	2.95	0.62
QZ-38	30.50	91.13	4460	0.95	0.49	0.19	−1.47	0.19	3.83	0.88
QZ-27	31.43	91.97	4585	0.48	0.24	0.10	−3.50	0.10	2.55	0.73
QZ-31	31.07	91.69	4808	0.04	0.73	0.14	−5.71	0.15	1.19	0.70
QZ-21	31.78	91.79	4959	0.95	0.37	0.10	−4.58	0.10	1.86	0.94
QZ-54	29.81	92.34	5139	0.83	1.56	0.23	−9.34	0.23	−0.97	1.00

detection limit in 8 samples. The most dominant brGDGTs were Ia (avg. 19.7%), IIa (avg. 39.3%) and IIIa (av. 20.1%). The analysis showed a typical soil distribution, i.e. dominated by brGDGTs, with a minor but varying amount of crenarchaeol, resulting in high BIT index values (i.e. 0.62–1.0; Table 2). The CBT index ranged from 0 to 1.56. Both MBT and MBT′ varied between 0.10 and 0.56, with only slight differences between the two indices for each sample.

3.2. BrGDGT derived temperature

MBT and MBT′ are supposed to relate to MAAT and soil pH (Weijers et al., 2007a; Peterse et al., 2012). However, the MBT- or MBT′–CBT temperature proxy likely works less well in arid environments with mean annual precipitation (MAP) < 500 mm (e.g. Peterse et al., 2012). A number of studies have noted that the MBT or MBT′ proxy showed no correlation with MAAT but significant correlation with MAP or aridity index in arid environments, e.g. in areas with MAP < 800 mm (Dirghangi et al., 2013; Menges et al., 2014). All the study sites here are in a relatively dry climate, with MAP generally < 500 mm as measured at nearby weather stations. In our results, however, MBT and MBT′ did not correlate with MAP, which is rather constant along the transect, but showed a moderate decreasing trend with elevation rise (Fig. 3a). Similarly, the CBT index exhibited a moderate increasing trend, likely suggestive of soil pH decrease, with increasing elevation (Fig. 3b). The decrease of MBT or MBT′ with increasing elevation is, therefore, very likely associated with decreases of temperature and soil pH, which suggests that the MBT- or MBT′–CBT index may be valid for temperature estimation. The validity of MBT or MBT′ as a temperature proxy in this arid area is different from previous findings (Peterse et al., 2012; Dirghangi et al., 2013; Menges et al., 2014), which might be associated with a strong monsoon climate. Summer monsoon accounts for 80% annual precipitation in the area, leading to relatively wet conditions in summer. So, if soil brGDGT production is warm and wet season biased, as discussed below, the application of annual precipitation, which encompasses monthly data as low as zero in an extremely cold and arid season, would be invalid as an aridity indicator for assessment of brGDGT derived proxies.

The MBT–CBT derived temperature varied from 12.53 to −9.34 °C with increasing elevation, showing a lapse rate of −5.0 °C/km (r^2 0.61). Both the CBT–MBT temperature and lapse rate were obviously lower than the measured values at nearby weather stations (Fig. 4). The MBT′–CBT derived temperature values showed a range between 12.58 and −0.97 °C. This MBT′–CBT temperature range generally agreed better with the measured values at nearby stations and showed less scatter, as indicated by smaller standard errors for the slope and intercept in the regression analysis (Fig. 4). So, the MBT′–CBT index may be more suitable for this study area, and thus is preferred here. However, the lapse rate of MBT′–CBT temperature was only −3.2 °C/km (r^2 0.62), even lower than that of the MBT–CBT estimates. A lower lapse rate from the MBT′–CBT estimates than that from the MBT–CBT estimates has also been reported or may be assessed from other studies. For example, at Mt. Kilimanjaro and Mt. Rungwe in East Africa the CBT–MBT temperature lapse rate was −7 °C/km (Sinninghe Damsté et al., 2008; Coffinet et al., 2014), whereas the MBT′–CBT temperature lapse rate decreased to ca. −4 °C/km (Coffinet et al., 2014, and our remarks in the Introduction); in Asia, the MBT–CBT temperature lapse rate ranged between −4.8 and −6.3 °C/km (Peterse et al., 2009b; Ernst et al., 2013; Liu et al., 2013), whereas the recalculated MBT′–CBT temperature lapse rate by Ernst et al. (2013) averaged −3.6 ± 0.6 °C/km. The lower lapse rate of the MBT′–CBT temperature than that of the MBT–CBT temperature, as well as the higher MBT′–CBT temperature than the MBT–CBT temperature in cold, high elevation sites (Fig. 4), is likely associated with the shallower slope of the MBT′–CBT calibration. Similar interpretation has been made by Peterse et al. (2014) for their findings that the application of the MBT′–CBT calibration resulted in higher MAATs in the Arctic than that using the original MBT–CBT calibration. Since the MBT′–CBT calibration overestimated measured MAAT at cold, high elevation (this study) and Arctic area (Peterse et al., 2014), it seems that the MBT–CBT calibration might be better suited to generating reliable MAAT estimates in cold areas. However, considering the large error (±5 °C) in the calibrations, it would be precarious to determine a suitable calibration based solely on limited data comparison of estimates with measured values.

Alternatively, the lower lapse rate from the MBT′–CBT estimates, as well as from the MBT–CBT estimates, than the measured one could reflect a bias toward warm season temperature, which occurs increasingly upslope. A plausible explanation for this

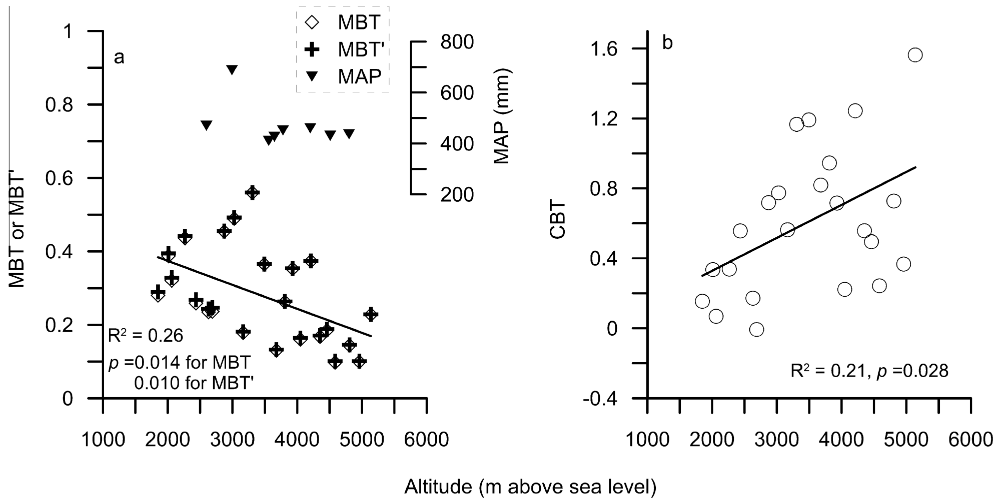

Fig. 3. Changes in (a) MAP, MBT, MBT′ and (b) CBT with altitude. Data for MAP are from the weather stations in Table 1.

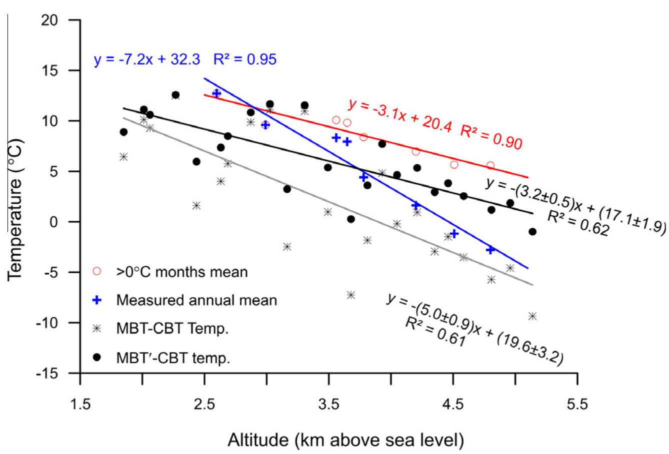

Fig. 4. Comparison between surface soil brGDGT derived temperature and measured temperature at nearby weather stations.

phenomenon would be the preferential production of brGDGTs in the warmer season relative to the seasons when the soil is frozen. This mechanism has been speculated as a cause of the wide scatter in brGDGT temperature calibrations (Peterse et al., 2009b, 2012; Rueda et al., 2009; Sun et al., 2011; De Jonge et al., 2014), although Weijers et al. (2011) did not observe a seasonal difference in the brGDGT distribution. Seasonal contrasts in temperature and hydrology that are synchronous and complementary are significant in our study area, with warm, wet conditions in summer and cold, dry conditions in winter. Moreover, degree of seasonality changes systematically with elevation rise. As can be seen in Table 1, not only the MAAT but also the length of the warm season, e.g. the number of months with temperature >0 °C, decrease with elevation rise. The monthly temperature is >0 °C throughout the year below ca. 3000 m, then the number of months with temperature >0 °C decreases upwards and the temperature is <0 °C for nearly half a year at ca. 4200 m. Thereby, we hypothesize that the systematic changes in the length of the warm and wet season, which controls the window length of brGDGT production, with elevation are likely the cause of lower lapse rate of the MBT′–CBT temperature at the high altitude.

We calculated the mean warm season temperature (MWST) that only includes months with temperatures >0 °C at the 8 weather stations, and then determined a MWST lapse rate of −3.1 °C/km (Fig. 4). Clearly, this value is consistent with the apparently low lapse rate from the MBT′–CBT derived temperature values. Although the MWST is systematically higher than the MBT′–CBT temperature by 3.3 °C, the difference is still within the MBT′–CBT calibration error of 5.0 °C (Peterse et al., 2012). Further, local conditions might also have an effect on the difference. We therefore surmise that growth of the source bacteria for the brGDGTs may have been greatly depressed and thus have contributed little to the annual brGDGT production below ca. 0 °C. Although this scenario may be absent at low elevation sites where monthly temperature is always >0 °C, it would have occurred at high elevation sites. Accordingly, it is this change in the seasonality of brGDGT production with altitude, exhibiting a stronger bias to warm season at higher sites, that resulted in the low lapse rate of the MBT′–CBT temperature observed here. However, brGDGT concentration did not decease with elevation rise in our data. It should be pointed out that the warm season bias of brGDGT production does not necessarily mean low brGDGT concentration in cold, high elevation soils, because the concentration is determined by the balance between production rate and decomposition rate.

The scatter in the estimated temperature-altitude relationship here compares with the scatter reported from other mountain slopes showing r^2 values varying between 0.55 and 0.77 (Sinninghe Damsté et al., 2008; Peterse et al., 2009b; Ernst et al., 2013; Liu et al., 2013; Coffinet et al., 2014). Several factors, such as soil type, seasonality, soil moisture content, etc. have been suggested to contribute to the relatively wide scatter (Peterse et al., 2009b; Ernst et al., 2013). Recently, the finding of a new set of brGDGT isomers based on improved chromatography revealed that 6-methyl branched tetraethers may be the cause of the large scatter in the MBT- or MBT′–CBT temperature estimates (De Jonge et al., 2014; Yang et al., 2015); we believe this is also true for the scatter observed here. Moreover, our study sites were not from a single mountain slope but on a transect through different mountains at the margin of the Tibetan Plateau. Local temperature would be affected by not only elevation but also local morphology and microclimate, which likely also cause significant scatter.

4. Implications and conclusions

Our results for the MBT′–CBT derived temperature in soils with altitude in the SE Tibetan plateau suggest that seasonality in bacterial brGDGT production, and hence for the associated indices, in soil may increase with elevation rise and seasonal contrast. Thus, caution should be taken in applying brGDGT derived temperature and a global mean temperature lapse rate to paleoelevation estimates. Since the degree of seasonality is dependent on location, altitude and climate, a constant value for temperature lapse rate is likely inappropriate. However, if the warm-season lapse rate could be modeled, the brGDGT based indices may potentially work as a paleoelevation indicator.

Seasonality in brGDGT distributions in lake sediments and more extensive microbial production in warm seasons has been suggested in several studies (e.g. Sun et al., 2011; Shanahan et al., 2013; Wu et al., 2013; Peterse et al., 2014). However, the occurrence of this phenomenon is still unclear for soils. For example, Peterse et al. (2009a) found that MBT–CBT derived temperature was close to measured MAAT in high latitude Svalbard and Weijers et al. (2011) did not observe seasonal difference in the brGDGT distribution in mid-latitude soils. In Arctic soil bacteria have been shown to grow in frozen conditions (McMahon et al., 2009), although the contribution of their production of new cell membrane components to the annual amount is unknown. Nevertheless, there is no clear rationale for the absence of seasonality in soil brGDGT production, considering the occurrence of aquatic brGDGT seasonality, especially in areas with strong seasonal contrasts. In fact, there are implications for soil brGDGT seasonality in previous studies. For example, the wide scatter in calibrations for brGDGT indices has been attributed partly to seasonality (Weijers et al., 2007a; Peterse et al., 2012; De Jonge et al., 2014). A potential bias to summer temperature has been suggested in several paleotemperature reconstructions based on the MBT–CBT proxy (e.g. Weijers et al., 2007b; Rueda et al., 2009; Eberle et al., 2010; Peterse et al., 2011). Our suggestion of an increase in brGDGT seasonality with elevation is in agreement with these inferences and supports the idea that seasonality should be taken into account in interpreting brGDGT derived temperatures in environments with large seasonal contrasts.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.orggeochem.2016.03.004.

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