Does rise in temperature adversely affect soil fertility, carbon fractions, microbial biomass and enzyme activities under different land uses?

Dibyendu Chatterjee[1,*], Rukuosietuo Kuotsu[1], Merasenla Ao[1], Saurav Saha[2], Sanjay Kumar Ray[1] and S. V. Ngachan[3]

[1]Indian Council of Agricultural Research, Research Complex for North Eastern Hill Region, Nagaland Centre, Jharnapani, Medziphema 797 106, India
[2]Indian Council of Agricultural Research, Research Complex for North Eastern Hill Region, Mizoram Centre, Kolasib 796 081, India
[3]Indian Council of Agricultural Research, Research Complex for NEH Region, Umiam 793 103, India

We studied the variable dynamic response of different soil properties under the exposure of three elevated temperature treatments on six land-use systems. After one month of incubation, the associated changes were measured in terms of soil fertility, carbon, microbial biomass and soil enzymes. Our results confirmed the significant increase ($P < 0.05$) in soil available nitrogen content (by 1.85–49.32%) with the subsequent rise in incubation temperature for soils collected from orchards and agriculture land uses. We observed a steady decrease in total organic carbon (TOC) levels with increase in incubation temperature varying between 4.1% and 31.4% ($P < 0.05$) across different soil types and land-use systems, resulting in a significant rising trend for microbial biomass carbon and labile carbon : TOC ratio up to 3°C elevation from maximum temperature. Among the soil enzymes, dehydrogenase, fluorescein diacetate hydrolase and β-glucosidase activity increased significantly with increase in incubation temperature from the ambient temperature, while acid phosphomonoesterase and arylsulphatase activity decreased. Our current research findings will provide new insights regarding temperature control on soil C dynamics and nutrient availability in terms of modified soil enzyme activity that will be useful to model the dynamics of soil organic matter and associated nutrient availability in acid soils.

Keywords: Carbon, land use, microbial biomass, soil enzyme activity, temperature effects.

IN the post-industrial revolution era, technological advancement of modern human civilization invades the obvious negative consequences of increasing anthropogenic greenhouse gas (GHG) emission with a significant atmospheric warming trend, worldwide. The level of atmospheric carbon dioxide (CO_2) is expected to reach about 570 ppm by 2050, with the concomitant increase in average global air temperature by 1.8–6.4°C by 2100 AD, depending on the emissions scenario in the next few decades[1,2]. This warming trend in India over the past 100 years (~0.6°C) is comparable to the increase in global mean temperature in the past 100 years[3]. Soils act as the major source and sink of carbon (C) that have the potential to sequester sizable quantities of atmospheric CO_2, and soil C is a consequential necessity for maintaining soil fertility. The natural feedback mechanism of atmospheric warming mostly relies on two probable consequences for our warmer globe, viz. either significant C influx from atmosphere to soil that will reduce the net atmospheric C load and nullify the warming trend (negative feedback), or increase in heterotropic respiration that may further accelerate the warming process (positive feedback)[4]. The microbial decomposition process of soil organic matter (SOM) is highly sensitive to such a change in surrounding environmental condition (temperature increase), which has the potential to modify the enzyme kinetics and associated nutrient availability in the soil system through alteration in resource allocation strategy and community composition of the soil biota[5,6]. The modified dynamics of soil microbial activity in warmer environment may determine the effective direction and net magnitude of C flux among the source–sink components of the global carbon cycle as well as the status of soil C pools, available nutrient status and soil C stock that ultimately affect crop production[7,8].

Land-use pattern and soil management factors have the key functional control on dynamics of soil C stock over the long run. Rabbi *et al.*[9] reported that properties like soil texture, soil density and pH had robust associations with soil organic carbon (SOC) fractions under different land-use systems. Shrestha *et al.*[10] and Saha *et al.*[11] reported higher SOC stock status of surface soils in grasslands followed by forest and agricultural lands respectively, under the humid subtropical climate of the

*For correspondence. (e-mail: dibyenducha@gmail.com)

Himalaya for a wide range of soil pH values (varying from 4.7 to 6.9). Soil enzyme activities are useful to monitor changes in soil quality as well as nutrient availability to plants. Irrespective of the level of fertilizer application, intensification of land use from grasslands to agricultural lands yielded contrasting results of either increase[12] or decrease[13] in soil nutrient content with significant reduction in soil enzyme activities[14]. Mganga *et al.*[15] observed that the traditional agroforestry systems promoted soil fertility with enhanced soil microbial biomass C and associated enzyme activities, than monocropping with agricultural crops (maize) for neutral to slightly acidic soils of tropical Africa. The beneficial role of minimum disturbance in different land-use systems enhanced soil enzyme activities involved in carbon, nitrogen, phosphorus, sulphur cycling[14], that resulted in an increase in net nutrient availability for acid soils in different land-use systems (orchards, grasslands and agricultural land) of subtropical China[16].

A literature survey showed that separate research efforts on studying the impact of either temperature or land-use systems on soil C stock status, enzyme activities and associated soil nutrient dynamics. Collective reporting for the effect of these two factors on the acid soils of humid subtropical regions of North East India is scarce[17], as they are exclusively important to model the interaction mechanism between land use and global climate change[18]. There are large uncertainties and lack of knowledge on possible modification of the mechanistic link between microbial enzyme dynamics and associated nutrient pools as modified under elevated temperature exposure. Therefore, this research gap streamlined our present research objective of mechanistic evaluation of the effect of elevated temperature and different land-use systems on nutrient transformation, carbon dynamics, microbial biomass and enzymatic activities in the acid soils of Nagaland, NE India. Our result will enable us to identify potential land-use system(s) with high carbon accumulation potential with consequent rise in air temperature. Our hypothesis was that increase in incubation temperature would modify the soil biochemical properties that will affect the dynamics of soil carbon and storage of other nutrients through enhanced enzymatic activities that may negatively affect soil quality.

Material and methods

Collection of soils from various land-use systems under different soil orders

Composite soil samples (0–15 cm) were collected from six land-use systems distributed within two soil orders (Alfisols and Entisols) in three replications. The samples collected from various locations in Nagaland, varied widely in terms of elevation, system of cultivation and vegetation type. Table 1 provides details of the collected experimental materials and their properties.

Incubation experiment at elevated maximum temperature

We conducted a controlled incubation experiment at elevated temperatures in the ICAR Research Complex for NEH Region, Nagaland Centre, Medziphema, with the collected soil samples. For this, the composite soil samples were taken in a perforated container and kept in a petri plate containing distilled water. The soils were saturated overnight in an air-tight container to prevent evaporation loss, followed by draining out of excess water under gravitational pull to attain moisture content at field capacity. The soil samples were then transferred to a moisture-proof container and maintained for one month at various temperatures in a BOD incubator. The highest value of mean monthly maximum temperature at the study site varied from 34.7°C (2011), 36.5°C (2012), and 35.7°C (2013) with an average of 35.6°C (~36°C). Therefore, we selected a set of temperatures, viz. ambient temperature (27°C), maximum temperature (36°C), 3°C elevation from maximum temperature (39°C), and 6°C elevation from maximum temperature (42°C). The sealed containers were turned upside down daily, for uniform movement of water vapour inside the container. After a month, the entire soil samples were taken out from the incubation chamber and moist soils were used to analyse microbial biomass and soil enzymes; whereas for soil fertility and carbon fractions, processed air-dried soil samples were used.

Soil analysis for fertility, carbon fractions, microbial biomass and enzyme activities

The collected soil samples were air dried, ground and passed through 2 mm sieve to analyse soil pH, electrical conductivity (EC), available nitrogen (N), available phosphorus (P), available potassium (K) and oxidizable organic carbon, total organic carbon (TOC) and labile carbon (LC) under variable incubation temperature exposures. Fresh moist samples were used to determine microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and microbial biomass phosphorus (MBP), and the hydrolytic activities of different soil enzymes. pH in soil-water suspension (1 : 2.5) was measured using a combined electrode (glass and calomel) fitted with a digital pH meter. EC was measured in the supernatant liquid of the soil-water suspension (1 : 2.5) using conductivity bridge at 25°C (dS m^{-1}). Available nitrogen was measured by alkaline-$KMnO_4$ method[19]. Available phosphorus was extracted following Bray-Kurtz No. 1 method[20], followed by the measurement of blue colour development using ascorbic acid method[21]. Available potassium was extracted by 1 N neutral NH_4OAc and determined by flame photometer[22].

Table 1. Details of experimental soil sample collection sites and properties of the collected soil

Notation	Soil type	Vegetation	System of cultivation	Latitude (N)	Longitude (E)	Elevation (m)
AF	Alfisol	Forest trees	Natural forest	25°35′56.4″	93°53′8.7″	520.0
AO	Alfisol	Orchards with banana, arecanut, mango, litchi and jackfruit	Plantation (5 years old)	25°46′1.7″	93°53′8.1″	517.9
EA	Entisol	Rice–rice	Wet rice cultivation (5 years old)	25°49′16.6″	93°39′54.4″	157.0
EF	Entisol	Forest (teak)	Old forests are replaced by teak (>10 years old)	25°49′15.6″	93°39′59.4″	159.0
EO	Entisol	Orchard (banana)	Plantation (2–3 years)	25°49′15.9″	93°40′6.3″	161.0
EP	Entisol	*Cynodon dactylon* (major species)	Non-cultivated pasture land	25°49′19.2″	93°40′19.3″	158.0

Notation	pH	EC (dS m^{-1})	Available N (kg ha^{-1})	Available P (kg ha^{-1})	Available K (kg ha^{-1})	OC (g 100 g^{-1})	TOC (g 100 g^{-1})	LC (g 100 g^{-1})
AF	3.90	0.075	260.9	15.5	114.3	0.65	1.50	0.21
AO	4.15	0.080	160.6	25.7	115.6	0.50	1.60	0.15
EA	5.00	0.110	210.5	24.7	170.8	0.47	1.56	0.17
EF	5.00	0.085	280.0	33.4	170.3	0.78	1.75	0.15
EO	5.04	0.120	215.9	35.2	165.0	0.73	1.79	0.21
EP	5.60	0.129	210.8	29.2	212.7	0.54	1.44	0.21

Notation	DOC (μg g^{-1})	MBC (μg g^{-1})	MBN (μg g^{-1})	DHA (μg TPF g^{-1} h^{-1})	PME (μg *p*-nitrophenol g^{-1})	FDA (μg fluorescein g^{-1} h^{-1})	AS (μg *p*-nitrophenol g^{-1} h^{-1})	BGLU (μg *p*-nitrophenol g^{-1} h^{-1})
AF	2401.7	3005.0	99.5	0.50	75.98	26.74	5.99	35.40
AO	3031.3	3120.0	97.8	0.22	58.89	46.49	3.90	21.36
EA	1243.6	3401.6	80.4	0.43	110.11	25.70	10.01	22.68
EF	1809.2	4370.0	91.8	1.32	103.87	52.44	9.19	22.81
EO	1607.0	3974.5	115.4	0.86	100.90	49.22	15.11	31.11
EP	2799.4	4494.7	130.5	1.11	115.19	44.88	9.77	45.33

EC, Electrical conductivity; OC, Oxidizable organic carbon; TOC, Total organic carbon; LC, Labile carbon; DOC, Dissolved organic carbon; MBC, Microbial biomass carbon; MBN, Microbial biomass nitrogen; DHA, Dehydrogenase activity; PME, Acid phosphomonoesterase activity; FDA, Fluorescein diacetate hydrolase; AS, Aryl sulphatase; BGLU, β-glucosidase.

Oxidizable organic carbon and TOC were determined by wet digestion method[23] and 0.4 N chromic acid oxidation in the presence of external heat supply[24] respectively. LC was estimated by oxidizing with 333 mM $KMnO_4$ (ref. 25). Soil MBC was measured by modified chloroform fumigation–extraction method with fumigation at atmospheric pressure[26]. Dissolved organic carbon (DOC) was determined after 0.5 mol l^{-1} K_2SO_4 solution extraction in unfumigated soil samples[27]. Dehydrogenase (DHA) activity was determined by reduction of 2,3,5-triphenyltetrazolium chloride (TTC)[28]. Fluorescein diacetate (FDA) hydrolysis activity measurements were made following the method of Adam and Duncan[29]. Acid phosphomonoesterase (PME) activity was assessed following Tabatabai[30], with modifications suggested by Schinner *et al.*[31]. Aryl sulphatase (AS) and β-glucosidase (BGLU) activity was assessed following Tabatabai[30], and Eivazi and Tabatabai[32] respectively.

Statistical analysis

Treatments comprised of six types of land-use systems (AF, AO, EA, EF, EO and EP) and four temperature levels (ambient, 36°C, 39°C and 42°C) replicated thrice for the analysis of variance under factorial complete randomized design (CRD) to test differences among the treatment means using MSTATC software. Treatment means were compared at the $P < 0.05$ level using LSD range test for all the parameters and correlation coefficients were computed using SPSS program (SPSS version 16.0).

Results and discussion

Effect of elevated incubation temperature on soil chemical properties and fertility

Wide variability in soil pH existed among the collected soil samples from different land-use systems incubated under elevated temperature treatment. The pH of soil-water suspension ranged from 3.9 to 5.7 at ambient (AM, 27°C), 3.8 to 5.3 at maximum temperature (MT, 36°C), 3.8 to 6.0 at 39°C and 4.2 to 5.8 at 42°C respectively. The highest pH was about 6.0 in EO at 39°C, which is statistically similar ($P < 0.05$) to pH of EP at 39°C, EO at 42°C and EP at 39°C (Figure 1 *a*). No significant difference ($P < 0.05$) in acidity existed among the soil samples

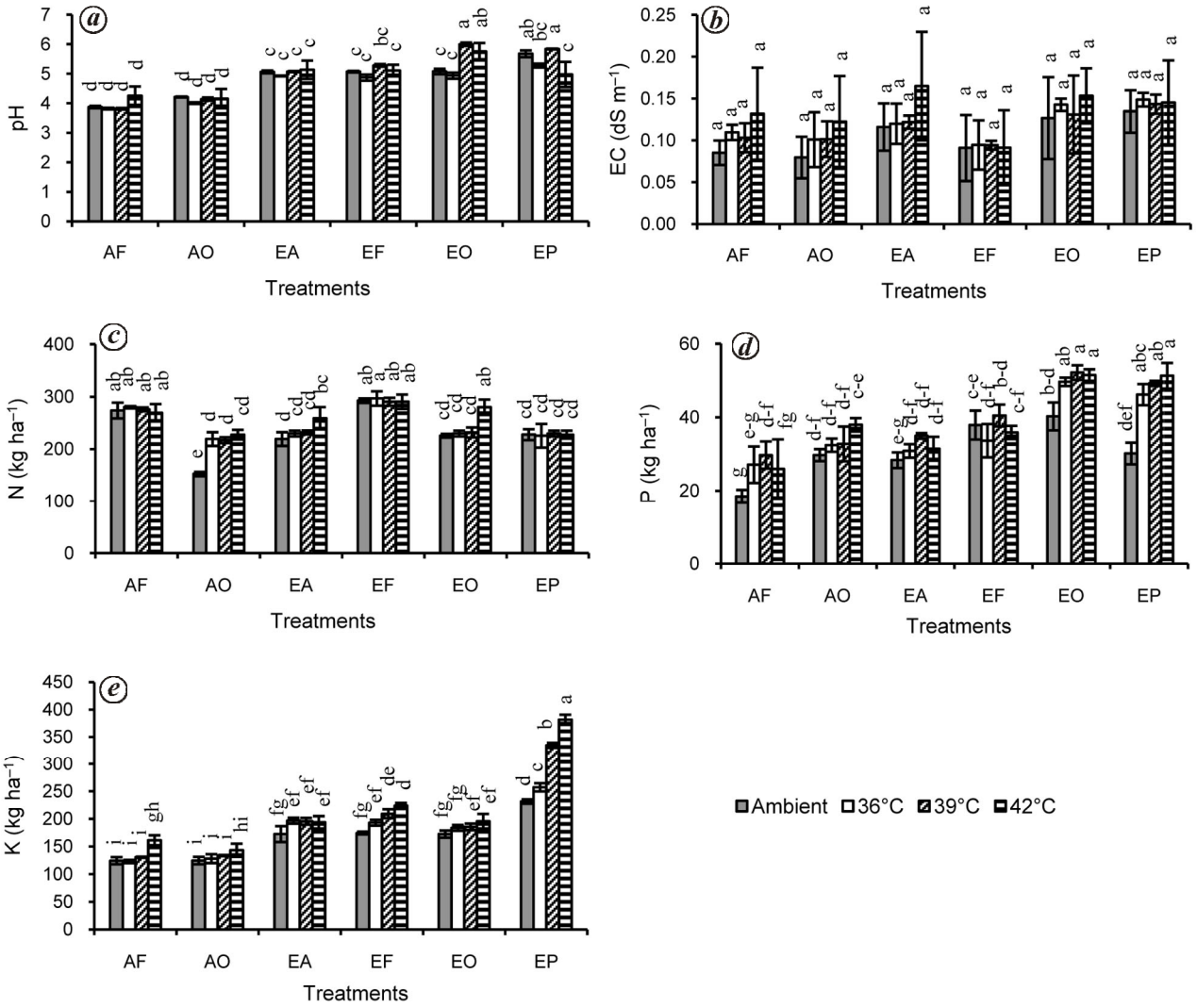

Figure 1. Effect of elevated incubation temperature on (***a***) pH, (***b***) electrical conductivity (EC, dS m^{-1}), (***c***) available nitrogen (N, kg ha^{-1}), (***d***) available phosphorus (P, kg ha^{-1}) and (***e***) available potassium (K, kg ha^{-1}) of soils collected from different land-use systems.

collected from AF, AO and EA systems. By averaging out the effect of temperature, we observed the highest pH (5.44) in EO and EP systems (Table 2). However, Alfisol was more acidic than Entisol for all the elevated temperature treatments. We observed no significant change in soil pH among the treatments with increase in incubation temperature for both the soil groups. EC ranged from 0.080 to 0.135 dS m^{-1} at AM, 0.095 to 0.149 dS m^{-1} at 36°C, 0.094 to 0.143 dS m^{-1} at 39°C and 0.091 to 0.165 dS m^{-1} at 42°C (Figure 1 *b*). We observed no significant difference ($P < 0.05$) in EC values among the treatments, preferably due to their high variation among the treatment replications. However, four land-use systems, namely AF (28.5–54.7%), AO (26.8–54.0%), EA (3.4–42.2%) and EO (3.4–21.2%) showed an increase in EC values with increase in incubation temperature over ambient.

Increase in incubation temperature increased the release of available nutrients. However the effect was not universal, but depended on the ecosystem health and season[33]. For the three land-use systems, viz. AF, EF and EP, available N content remained unchanged. The increase in soil available N content (by 1.85–49.32%) was significant ($P < 0.05$) with the increase in incubation temperature for soils collected from orchards (AO and EO) and agriculture (EA) land use (Figure 1 *c*). Probably, the addition of external inputs (fertilizers and manures) in soils under orchards and agriculture land use promoted more organic matter decomposition and mineralization of organic nitrogen through rhizosphere priming effect[34]. By averaging the effect of temperature, the highest available N was 292.7 kg ha^{-1} in EF (Table 2). The enzymes controlling N cycle will be more active under elevated temperature[35]. Higher enzyme activities related to N-cycling like urease and protease activity in response to warming could be another reason for obtaining such results[36]. This may increase N mineralization, resulting in an

Table 2. Effect of increase in temperature on soil fertility, carbon fractions and soil enzyme activities (by averaging out the effect of different incubation temperature exposures)

Parameters	Land-use systems						CD ($P < 0.05$)
	AF	AO	EA	EF	EO	EP	
Soil fertility parameters							
pH	3.94^{c}	4.13^{c}	5.05^{b}	5.08^{b}	5.44^{a}	5.44^{a}	0.24
EC (dS m^{-1})	0.108^{a}	0.101^{a}	0.131^{a}	0.093^{a}	0.138^{a}	0.143^{a}	NS
N (kg ha^{-1})	274.9^{b}	204.4^{d}	235.2^{c}	292.7^{a}	242.0^{c}	227.9^{c}	15.88
P (kg ha^{-1})	25.35^{d}	33.28^{bc}	31.45^{c}	37.03^{b}	48.41^{a}	44.25^{a}	4.65
K (kg ha^{-1})	134.8^{d}	132.5^{d}	189.7^{bc}	200.2^{b}	184.3^{c}	301.3^{a}	10.73
Carbon fractions and microbial biomass							
OC (g 100 g^{-1})	0.75^{a}	0.58^{b}	0.60^{b}	0.73^{a}	0.78^{a}	0.59^{b}	0.078
TOC (g 100 g^{-1})	1.17^{a}	1.14^{a}	1.22^{a}	1.18^{a}	1.24^{a}	1.17^{a}	NS
LC (g 100 g^{-1})	0.26^{b}	0.26^{b}	0.27^{ab}	0.26^{b}	0.29^{a}	0.30^{a}	0.026
LT (wt%)	23.18^{b}	24.92^{ab}	25.73^{ab}	24.02^{ab}	25.81^{ab}	26.63^{a}	2.77
DOC (μg g^{-1})	1633^{ab}	1745^{a}	1068^{c}	1331^{bc}	1173^{c}	1499^{ab}	299.3
MBC (μg g^{-1})	4231^{c}	3913^{c}	4784^{b}	5346^{a}	5605^{a}	5572^{a}	494.0
MBN (μg g^{-1})	140.1^{a}	113.3^{b}	141.8^{a}	166.7^{a}	159.5^{a}	140.9^{a}	34.58
Soil enzymes							
DHA (μg TPF g^{-1} h^{-1})	0.793^{d}	0.518^{f}	0.668^{e}	1.799^{a}	1.163^{c}	1.354^{b}	0.058
PME (μg *p*-nitrophenol g^{-1})	74.45^{c}	63.74^{d}	101.8^{ab}	96.45^{ab}	94.83^{b}	103.6^{a}	7.62
FDA (μg fluorescein g^{-1} h^{-1})	57.86^{ab}	58.32^{ab}	50.94^{c}	62.94^{a}	58.82^{ab}	52.57^{bc}	6.31
AS (μg *p*-nitrophenol g^{-1} h^{-1})	4.20^{d}	3.23^{e}	9.35^{b}	6.61^{c}	12.25^{a}	6.17^{c}	0.67
BGLU (μg *p*-nitrophenol g^{-1} h^{-1})	84.35^{a}	73.71^{b}	35.20^{e}	43.88^{d}	61.53^{c}	59.12^{c}	5.86

Note: In any single row, means followed by the same letter are not significantly different at $P < 0.05$ by DMRT.

increase in available N content in the soil with increase in incubation temperature. Phorphorus is the most common limiting nutrient element for plants growing in acid soils. Average available P content over the six land-use systems showed significant increase ($P < 0.05$) with increase in incubation temperature from 30.84 (AM) to 36.68 kg ha^{-1} (36°C); up to 39.96 kg ha^{-1} (39°C), followed by a slight decrease at 42°C (39.06 kg ha^{-1}) (Figure 1 *d*). The available P content was statistically similar in all the elevated incubation temperature treatments (Table 3). By averaging the effect of temperature, available P was highest for soils collected from EO system (48.41 kg ha^{-1}) that was statistically similar ($P < 0.05$) to available P from soils of the EP system (44.25 kg ha^{-1}) (Table 2). The average change in available P content was 28.12% (36°C), 35.78% (39°C) and 34.41% (42°C) for Alfisols under different land-use systems (AF and AO). The enhancement showed similar pattern, viz. 18.50% (36°C), 30.72% (39°C) and 25.91% (42°C) for Entisols under the respective land-use systems, viz. EA, EF, EO and EP. Our results were in contrast to the reported decrease ($P < 0.05$) in soil available P content by 18.8% in the jointing stage of wheat at Taihu Lake region, China, with +2°C temperature elevation over the ambient[37]. At higher temperature (from 39°C to 42°C), available P content was observed to decrease. This may be attributed to the fact that increase in the conversion of weekly bonded P into strongly bonded forms by elevated incubation temperature[38]. Initial increase in P content (ambient to elevated) may be due to higher mineralization of organic P induced by increasing temperature[38]. On the contrary, soil warming by 0.8–1.1°C over the ambient for short-term (2 years) and long-term (10 years) experiments did not affect soil pH, bulk density, total carbon, nitrogen, phosphorus, organic carbon, available phosphorus, NO_3-N, MBC, MBN and MBP, and cellulase, catalase and phosphatase activities significantly in an alpine meadow ecosystem in Qinghai–Tibet Plateau (QTP), China[39].

Although K is the second most abundant nutrient in plant photosynthetic tissues after N, studies on K availability with modified temperature regime are rarely reported[36]. The available K content showed an increasing trend with rise in incubation temperature for all land-use systems considered in the present study (Figure 1 *e*). However, the average magnitude of increase was significant ($P < 0.05$) for AF (29.7%), EF (28.5%) and EP (64.8%) systems at 42°C over the ambient. The highest increase in available K content was as high as 14.07% at 36°C (EA), 44.68% at 39°C (EP) and 64.84 at 42°C (EP) over the ambient. The average increase ($P < 0.05$) in available K content was 0.75% (36°C), 6.15% (39°C) and 22.35% (42°C) for land use based on Alfisols (AF and AO), whereas it was 10.60% (36°C), 21.45% (39°C) and 29.77% (42°C) for land use based on Entisols (EA, EF, EO and EP). Similarly, the average increase ($P < 0.05$) in available K was 4.75% (36°C), 12.62% (39°C) and 29.10% (42°C) over the ambient for Alfisols and Entisols under the forest land-use system and 4.59% (36°C), 7.38% (39°C) and 14.19% (42°C) for orchard soils under Alfisols and Entisols. Also, 42°C showed the highest available K (216.6 kg ha^{-1}; $P < 0.05$) by averaging the effect of land-use system (Table 3). By averaging the

Table 3. Effect of increase in temperature on soil chemical properties and fertility, carbon fractions and soil enzyme activities (by averaging out the effect of different land uses)

Parameters	Ambient	Temperature (°C)			CD ($P < 0.05$)
		36	39	42	
Soil fertility parameters					
pH	4.83[b]	4.64[b]	5.03[a]	4.90[a]	0.19
EC (dS m^{-1})	0.106[a]	0.119[a]	0.116[a]	0.135[a]	NS
N (kg ha^{-1})	232.1[b]	247.0[a]	246.4[a]	259.2[a]	12.97
P (kg ha^{-1})	30.83[b]	36.68[a]	39.94[a]	39.05[a]	3.79
K (kg ha^{-1})	166.6[d]	180.3[c]	198.3[b]	216.6[a]	8.76
Carbon fractions and microbial biomass					
OC (g 100 g^{-1})	0.62[b]	0.72[a]	0.73[a]	0.62[b]	0.064
TOC (g 100 g^{-1})	1.56[a]	1.25[b]	1.09[c]	0.84[d]	0.070
LC (g 100 g^{-1})	0.20[d]	0.29[b]	0.35[a]	0.26[c]	0.021
LT (wt%)	12.96[c]	23.46[b]	32.57[a]	31.21[a]	2.26
DOC (μg g^{-1})	2098[a]	1397[b]	1137[c]	1000[c]	244.4
MBC (μg g^{-1})	3901[d]	4484[c]	5109[b]	6140[a]	403.3
MBN (μg g^{-1})	107.1[c]	153.3[b]	176.8[a]	137.8[b]	20.3
Soil enzymes					
DHA (μg TPF g^{-1} h^{-1})	0.83[c]	1.01[b]	1.18[a]	1.18[a]	0.05
PME (μg *p*-nitrophenol g^{-1})	92.56[a]	92.14[a]	86.63[ab]	85.25[b]	6.22
FDA (μg fluorescein g^{-1} h^{-1})	43.88[c]	64.64[a]	63.81[a]	55.30[b]	5.15
AS (μg *p*-nitrophenol g^{-1} h^{-1})	8.53[a]	7.97[b]	7.36[c]	4.02[d]	0.52
BGLU (μg *p*-nitrophenol g^{-1} h^{-1})	32.96[d]	50.59[c]	71.96[b]	83.02[a]	4.78

Note: In any single row, means followed by the same letter are not significantly different at $P < 0.05$ by Duncan's multiple range test (DMRT).

effect of incubation temperature, *EP* had the highest available K by 301.3 kg ha^{-1} (Table 2). We did not come across many reports showing how the increase in temperature affects available K dynamics in the soil–plant system. The increase in incubation temperature might have increased the transformation of non-exchangeable K into exchangeable K, and thus available K content (soil solution K + exchangeable K) had increased substantially[40].

Effect of elevated incubation temperature on carbon fractions and microbial biomass

Planting trees or perennial crops is an effective option to increase SOC of surface soils[41]. This study evaluated the sensitivity of accumulated organic C fractions for different land use systems. The SOC content of surface soils was highest for forest lands (Entisols and Alfisols) followed by orchards and pasture land-use system under Entisols. Our results contradict the findings of higher SOC stock for pasture lands followed by forests of northwest India[11]. The increase in incubation temperature increased the organic C steadily under EA (Figure 2 *a*). The highest magnitude was 50.75% ($P < 0.05$) for initial +3°C increase over the maximum in incubation temperature that gradually narrowed down with further increase in incubation temperature level from 45.5% (36°C) to 6.5% (39°C). For forest soils, incubation at 36°C and 39°C significantly increased ($P < 0.05$) the organic C availability, but the trend reversed for +6°C increase over MT (42°C). In forest soil, about 12–18.3% increase ($P < 0.05$) in organic C content was recorded for Alfisols, while 6.5–6.8% increase ($P < 0.05$) in organic C content was recorded for Entisols. Further +3°C rise (i.e. 42°C) in incubation temperature significantly decreased the organic C availability, even up to the tune of 5.3–15% for forest soils. However, the net effect was not statistically significant. Irrespective of soil type, orchard soils showed greater stability against the rise in incubation temperature with no significant change in organic C availability. Our results confirmed the potential of soils to act as a stable sink organic C under the orchard system[42,43].

The steady decrease in TOC level with rise in incubation temperature (Figure 2 *b*) that ranged from 4.1% to 31.4% ($P < 0.05$) across soil types and land-use systems (except EA), with a concomitant rise in LC fractions that ranged from 21.8% to 75% ($P < 0.05$) (Figure 2 *c*). A net increase in +3°C incubation temperature over MT (39°C) enhanced the magnitude of LC by 33.2–96.6% ($P < 0.05$), with a significant reduction in soil TOC by 14.6–42.6% ($P < 0.05$). However, further increase of +3°C incubation temperature (42°C) reduced LC content by 34.4–83.5% and accelerated the loss of soil TOC by 39.4–52.4% ($P < 0.05$) for different soil type and land-cover system combinations. As a result, the net LC : TOC ratio increased from 29.4% to 227% ($P < 0.05$) (Figure 2 *d*) that was significant while eliminating the effect of land use (Table 3), preferably due to higher temperature sensitivity of stable SOC pool in comparison to LC[44]. Our results

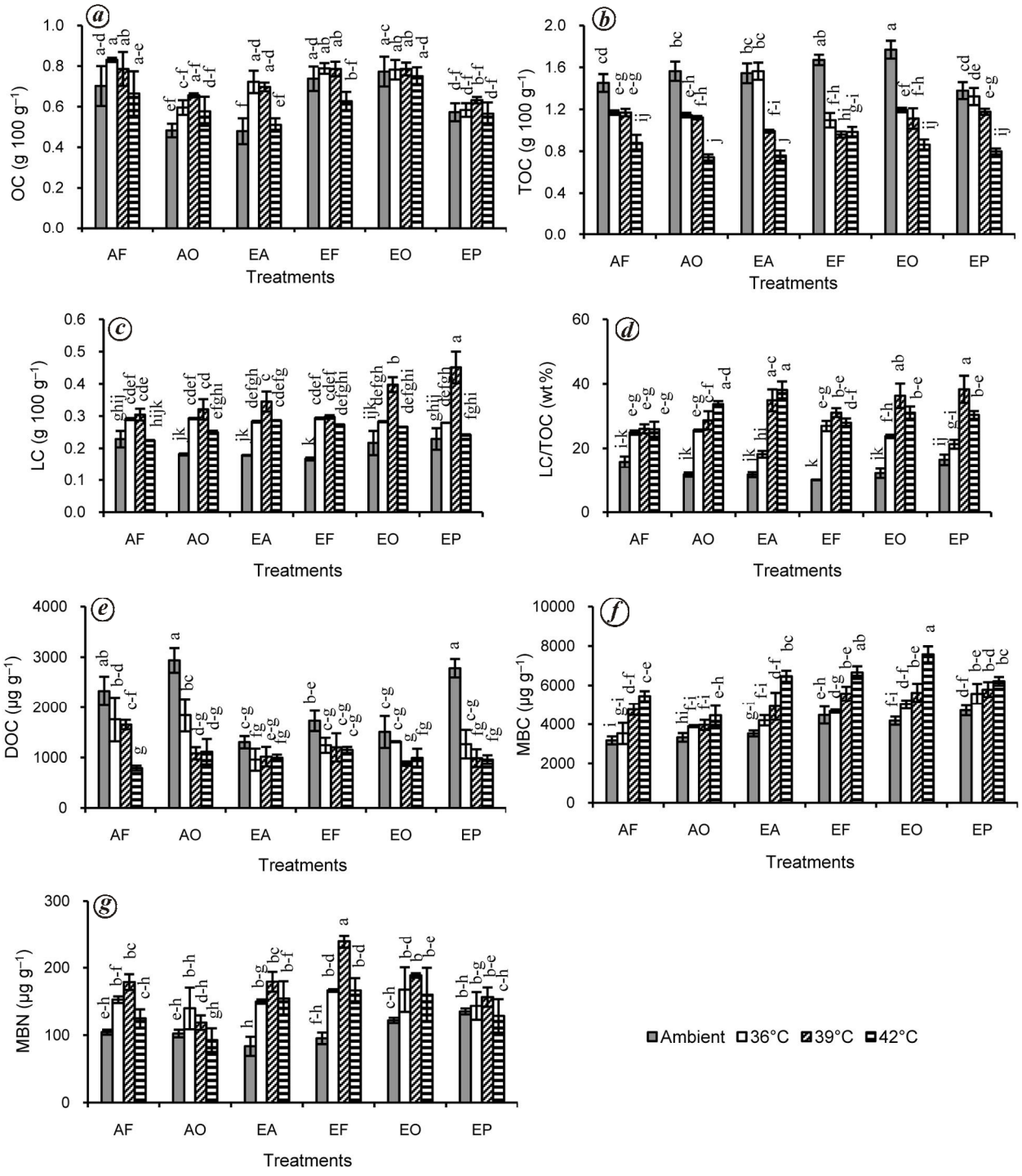

Figure 2. Effect of elevated incubation temperature on (***a***) oxidizable organic carbon (OC, g 100 g^{-1}), (***b***) total organic carbon (TOC, g 100 g^{-1}), (***c***) labile carbon (LC, g 100 g^{-1}), (***d***) labile carbon/total organic carbon (LC/TOC, wt%), (***e***) dissolved organic carbon (DOC, µg g^{-1}), (***f***) microbial biomass carbon (MBC, µg g^{-1}), and (***g***) microbial biomass nitrogen (MBN, µg g^{-1}) of soils collected from different land-use systems.

suggest that the decomposition of resistant organic pool is more temperature-sensitive than labile organic matter[45,46].

With an increase in incubation temperature, a sharp decrease in DOC content was evident for all the land-use system soil samples, considered in the present laboratory incubation study (Figure 2 *e* and Table 3). For MT, the magnitude varied from 12.8% to 54.5% ($P < 0.05$) that increased irreversibly with further +3°C and +6°C rise in incubation temperature over MT (21.8%–66%; $P < 0.05$). The maximum reduction in soil DOC with increasing incubation temperature was evident for EP (54.5% for

36°C; 64.5% for 39°C and 65.5% for 42°C; significant at $P < 0.05$ level) that was preferably due to reduced substrate availability in all the soil samples collected from different land-use systems[47].

We observed no significant difference between the surface soils of forest and pasture systems. However, significant rise in MBC was evident in the majority, with elevation of ambient incubation temperature (Figure 2 *f*). The increase was least for forest soils (EF and AF) with rise in incubation temperature up to 36°C (4.43–11.3%; $P < 0.05$). The magnitude of amplification varied by 19.7–50% ($P < 0.05$) and 31.7–83% ($P < 0.05$) for the respective rise in incubation temperature by 3° and 6°C over MT. The significant rise in MBN varied with increase in incubation temperature over the ambient (Figure 2 *g*). The pasture soil showed least response (increased by 6.1%; $P < 0.05$) towards rise in incubation temperature at 36°C. The trend was maintained for further elevation in incubation temperature level (39°C and 42°C). The highest level of enhanced soil MBN was maintained for EF (~100% increase over the ambient) followed by EA (~93.2% increase over the ambient; $P < 0.05$). Increase in MBC and MBN at higher temperatures may be due to higher rate of release of substrate from microbes and plant roots[48]. Decrease in MBN at 42°C may be attributed to the death of mesophylls due to thermal denaturation[48].

Effect of elevated incubation temperature on enzyme activities

Rise in temperature is generally known to increase enzyme activities[49], as was the case in this study. Increase in incubation temperature may affect the overall and relative rate of enzyme production due to effects on enzyme efficiency, substrate availability and microbial efficiency. Thus, changes in soil environment will affect the enzyme pool size. In response to the increased activity of existing enzyme pools as soil temperature increases with given available substrate, microbes may allocate fewer resources to enzyme production if microbial biomass remains unchanged[50]. In our experiment, dehydrogenase activity increased significantly with increase in incubation temperature from AM (0.83 μg TPF g^{-1} h^{-1}) to 36°C (1.01 μg TPF g^{-1} h^{-1}), 39°C (1.18 μg TPF g^{-1} h^{-1}) and 42°C (1.18 μg TPF g^{-1} h^{-1}) (Figure 3 *a*). However, dehydrogenase activities at 39ºC and 42ºC were statistically similar (Table 3). The average dehydrogenase activity in Alfisols increased by 35.92% at 36°C, 113.06% at 39°C and 118.96% at 42°C over the ambient ($P < 0.05$), whereas the extent of increase in dehydrogenase activity was much less in Entisols, viz. 27.50% at 36°C, 41.12% at 39°C and 32.89% at 42°C over the ambient ($P < 0.05$). The highest dehydrogenase was observed in EF (1.799 μg TPF g^{-1} h^{-1}) which was significantly superior over rest of the land-use systems (Table 3). In accordance with our results, Bhattacharyya *et al*.[51] observed significantly high dehydrogenase activity exposed to elevated temperature environment (+2°C higher compared to the ambient chamber).

On the contrary, acid phosphomonoesterase activity was 92.56 μg *p*-nitrophenol g^{-1} h^{-1} at AM, 92.14 μg *p*-nitrophenol g^{-1} h^{-1} at 36°C, 86.63 μg *p*-nitrophenol g^{-1} h^{-1} at 39°C, and 85.25 μg *p*-nitrophenol g^{-1} h^{-1} at 42°C. Our results clearly showed the reduction of acid phosphomonoesterase activity with increase in incubation temperature (Table 3). However, the decrease was significant ($P < 0.05$) at 42°C over AM. Such significant decrease in acid phosphomonoesterase activity at 42°C may be due to the increase in kinetic energy of molecules and breaking of the bonds, holding the active amino group under elevated temperatures. Thus the denaturation of enzyme results in loss of enzyme activity. Our results contradict the reported increase in mineralization of organic-P with increase in temperature, which is facilitated by enhanced activities of phosphatase enzymes in wheat rhizosphere [52]. However, the activities of acid phosphomonoesterase were reported to increase with increasing temperature at 0–5 cm soil depth[6]. The temperature regime selected in the present experiment was much higher than that in previously reported experiments. Average acid phosphomonoesterase activity in Alfisols was reduced by 2.63% at 39°C and 3.03% at 42°C over the ambient ($P < 0.05$), except in MT that showed significant increase ($P < 0.05$) in acid phosphomonoesterase activity by 20.80% over the ambient (Figure 3 *b*). Average acid phosphomonoesterase activity in Entisols was lower than the ambient in all treatment combinations (6.94% at 36°C, 7.41% at 39°C and 9.17% at 42°C). The highest acid phosphomonoesterase activity was observed in EP (103.6 μg *p*-nitrophenol g^{-1} h^{-1}) followed by EA (101.8 μg *p*-nitrophenol g^{-1} h^{-1}) after averaging out the net effect of elevation in incubation temperature (Table 3).

Fluorescein diacetate hydrolase activity in soils collected from all land-use systems showed a significant increase ($P < 0.05$) from 43.88 μg fluorescein g^{-1} h^{-1} under AM to 64.64 μg fluorescein g^{-1} h^{-1} at 36°C, that was slightly reduced further to 63.80 μg fluorescein g^{-1} h^{-1} at 39°C and 55.30 μg fluorescein g^{-1} h^{-1} at 42ºC (Table 3). The effect was statistically non-significant between 36°C and 39°C. The highest increase in fluorescein diacetate hydrolase activity was observed in AF land use, which was 158.24% at 36°C, 143.74% at 39°C and 78.69% at 42°C over AM (Figure 3 *c*). By averaging the effect of elevation in incubation temperature, the highest fluorescein diacetate hydrolase activity was observed as 62.94 μg fluorescein g^{-1} h^{-1} under EF that was statistically similar with fluorescein diacetate hydrolase activity under AF, AO and EO systems (Table 3).

Arylsulphatase activity indicates the ability of the soil to degrade sulphur compounds, particularly aromatic sulphur. Like acid phosphomonoesterase activity, the

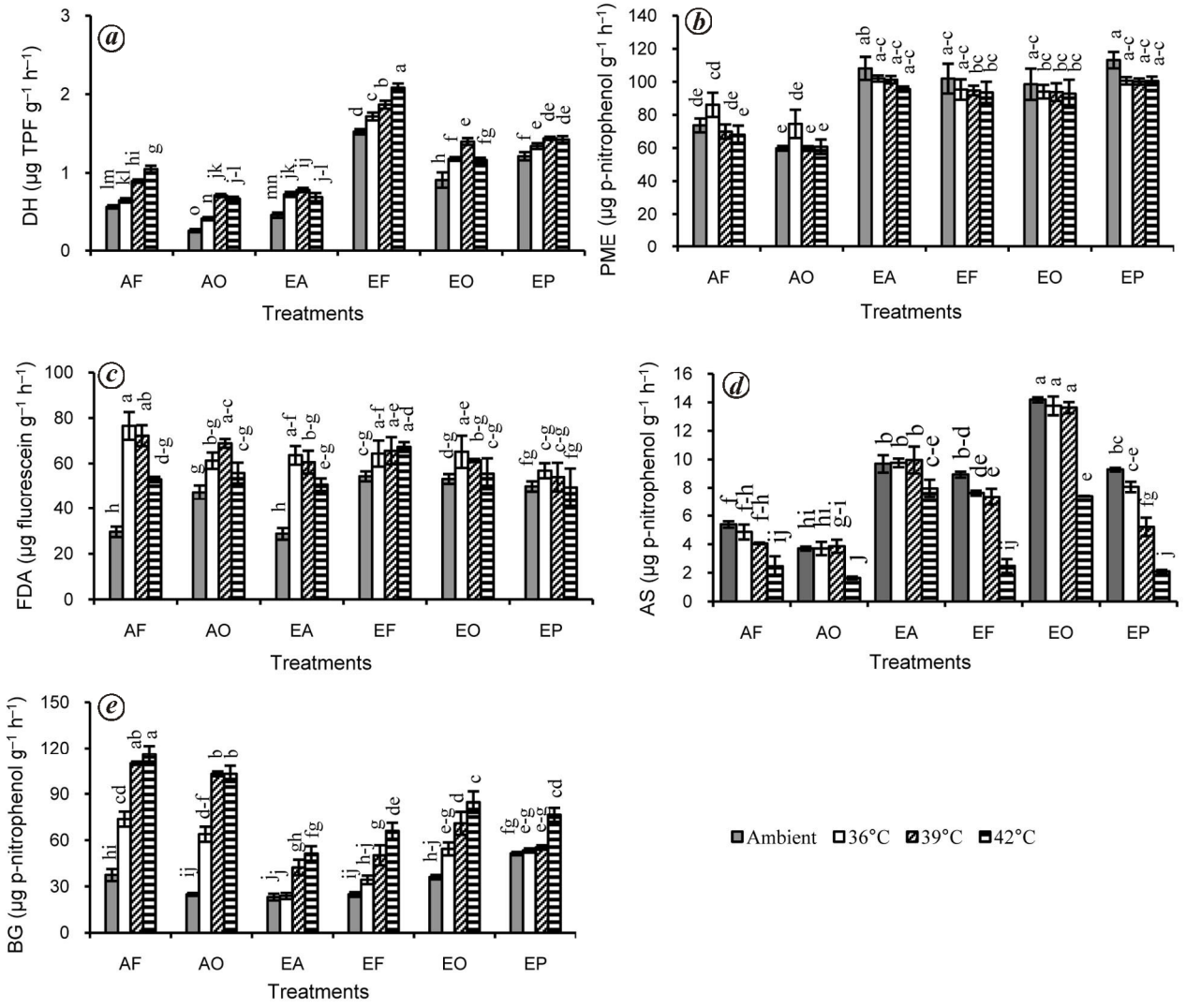

Figure 3. Effect of elevated incubation temperature on (***a***) dehydrogenase (DH, µg TPF g^{-1} h^{-1}), (***b***) acid phosphomoesterase (PME, µg *p*-nitrophenol g^{-1}), (***c***) fluorescein diacetate hydrolase (FDA, µg fluorescein g^{-1} h^{-1}), (***d***) arylsulphatase (AS, µg *p*-nitrophenol g^{-1} h^{-1}), (***e***) *β*-glucosidase (BG, µg *p*-nitrophenol g^{-1} h^{-1}) activity of soils collected from different land-use systems.

decreasing trend was observed for arylsulphatase activity (Figure 3 *d*). Average arylsulphatase activity of all land-use systems under study varied, viz. 8.53 µg *p*-nitrophenol g^{-1} h^{-1} in AM, 7.97 µg *p*-nitrophenol g^{-1} h^{-1} at 36°C, 7.35 µg *p*-nitrophenol g^{-1} h^{-1} at 39°C and 4.02 µg *p*-nitrophenol g^{-1} h^{-1} at 42°C (Table 3). There was a significant decrease ($P < 0.05$) in arylsulphatase activity by 4.83% and 7.48% at 36°C; 10.02% and 15.61% at 39°C and 54.76% and 53.72% at 42°C over AM for Alfisols and Entisols respectively (Figure 3 *d*). By averaging the net effect of elevation in incubation temperature, the highest arylsulphatase activity was recorded as 12.25 µg *p*-nitrophenol g^{-1} h^{-1} in EO, which was significantly superior over arylsulphatase activity in other land-use systems (Table 3).

The *β*-glucosidase activity increased significantly ($P < 0.05$) from 32.9 µg *p*-nitrophenol g^{-1} h^{-1} in AM to 50.59 µg *p*-nitrophenol g^{-1} h^{-1} at 36°C, 71.9 µg *p*-nitrophenol g^{-1} h^{-1} at 39°C, and 83.02 µg *p*-nitrophenol g^{-1} h^{-1} at 42°C (Table 3). By averaging the temperature, we observed highest *β*-glucosidase activity under in AF system (84.35 µg *p*-nitrophenol g^{-1} h^{-1}) that was significantly superior over rest of the treatment combinations (Table 2). The average *β*-glucosidase activity in Alfisols increased by 126.93% at 36°C, 254.12% at 39°C and 262.65% at 42°C over the ambient ($P < 0.05$), whereas the extent of increase in *β*-glucosidase activity was much less in Entisol; 23.95% at 36°C, 72.23% at 39°C and 117.93% at 42°C ($P < 0.05$) over the ambient (Figure 3 *e*). The rate of *in situ* enzyme activity is directly responsive to temperature and moisture[6]. Since we maintained soil moisture at field capacity, hence the increasing effect may be due to the influence of an increase in incubation temperature. Fluorescein diacetate hydrolase and

β-glucosidase are two important enzymes that play a major role in catalysing the hydrolysis of cellobiose, and thus are involved in the decomposition of organic C compounds[53]. The concurrent increase in fluorescein diacetate hydrolase (Figure 3 *c*) and β-glucosidase (Figure 3 *e*) activities in the present study was in better agreement with the observed decrease in TOC level (Figure 2 *b*).

In general, we observed an increase in dehydrogenase, fluorescein diacetate hydrolase and β-glucosidase activities with increase in incubation temperature. Dehydrogenase and fluorescein diacetate hydrolase represent microbial activities in general, while β-glucosidase is a carbon-degrading enzyme involved in carbon depolymerization. The probable reason for the increase in enzyme activities may be due to increase in the substrate (e.g. microbial biomass) availability at elevated temperatures[48]. On the contrary, decrease in acid phosphomonoesterase and aryl sulphatase activities may be due to their denaturation at higher temperature. The present study for assessing temperature sensitivity of microbial enzyme activity and associated nutrient dynamics is less biased as the external factors other than temperature influencing SOC decomposition are cut-off. Therefore, the present research findings will provide new insights regarding temperature control on soil C dynamics and nutrient availability in terms of modified soil enzyme activity. Our results will be useful to model the dynamics of SOM and associated nutrient availability for different existing land-use systems prevailing under the widespread acidic soils in subtropical humid regions of NE India.

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