



Role of glomalin in soil carbon storage and its variation across land uses in temperate Himalayan regime



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ABSTRACT

Root symbiont arbuscular mycorrhizal fungi (AMF) are ubiquitous in soils of terrestrial ecosystems and play a major role in determining the soil structure dynamics. Glomalin related soil protein (GRSP) produced in the hyphal cell walls is a store house of carbon that influences aggregate formation, stabilization and contributes in soil carbon sequestration. In this work, the variation in the glomalin concentrations was studied across soil of temperate Himalayan regime, its potential role in carbon storage and soil aggregation under different cropping systems. Aggregate stability showed a positive correlation with soil organic carbon ($r = 0.966$; $p < 0.01$), total glomalin (TG) ($r = 0.988$; $p < 0.01$) and easily extractable glomalin (EEG) ($r = 0.967$; $p < 0.01$). TG showed highest value in the forest ecosystem (4.82 mg/g) which is supposed to be an undisturbed site while lowest value was recorded in the wheat field (2.12 mg/g). Positive correlation was observed between glomalin and soil organic carbon ($r = 0.905$, $p < 0.0001$; $r = 0.586$, $p < 0.001$, respectively) for TG and EEG re-iterating its contribution in maintaining the soils carbon pool. Overall, the study highlights the co-relation of glomalin with soil aggregation and land use type and its applicability as a putative indicator of aggregate stability for the hilly terrain.

1. Introduction

Carbon dioxide sequestration from atmosphere using plants is a significant method for lowering CO₂ emissions to mitigate climate change (Powelson et al., 2011). Plants mediate this process through photosynthesis and store the carbon in the form of soil organic carbon (SOC). Of the net photosynthate produced by plant, an estimated 10–20% is allocated to roots in order to support the growth and reproduction of a root dwelling symbiont fungi called arbuscular mycorrhizal fungi (AMF) (Daynes et al., 2013). About 90% of the terrestrial plants have mycorrhizal association which promote plant growth by facilitating plant uptake of soil nutrients in exchange for plant carbohydrates and improving the soil micro-environment (Baumann et al., 2013; Smith et al., 2011; Tardy et al., 2015; Wang et al., 2017a). The hyphae of the AMF produces an abundant amount of glomalin-related soil protein (GRSP) that is released into the soil after decomposition (Treseder and Allen, 2000; Singh et al., 2013). Glomalin is an insoluble, hydrophobic and recalcitrant glycoprotein that is resistant to degradation (Wright

and Upadhyaya, 1996). It forms a lattice-like waxy coating gluing soil particles, organic matter, sand, silt and clay together and initiates the complex process of soil aggregation that can accumulate as much as 5% of soil C and N thus protecting the carbonaceous compounds from degradation and are resistant to erosion by wind and water (Rillig, 2004; Emran et al., 2012). Thus, glomalin assists the soil in maintaining the soil carbon pool, aggregate formation and, holding the organic matter (Plaza et al., 2013; Six and Paustian, 2014). Soil aggregation and soil organic matter (SOM) further upholds nutrient storage capacity, microbial diversity and water-holding ultimately determining the soil fertility and soil health (Lovell et al., 2004; Hallett et al., 2009; Wu et al., 2015; Gupta and Germida, 2015).

Glomalin production by AMF largely depends on the plant productivity and photosynthate allocation. The more dependent a plant is on mycorrhizal symbiosis for nutrient uptake, the more carbon is allotted to AMF by plant in the form of photosynthate making plants a major factor governing glomalin production (Treseder and Allen, 2000). Increase in plant growth rate and nutrient content has shown a positive effect on

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glomalin production (Violi et al., 2007). Influence of plant biomass and litter quality on glomalin concentration has also been reported (Wilson et al., 2009). It has also been reported that cropping systems, and land management practices affect glomalin production significantly (Gispert et al., 2013). Glomalin production is hampered by tillage that destroy microbial habitat and decrease AMF growth (Dai et al., 2015; Wright et al., 1999). Crop rotation and residue management have also significantly increased soil glomalin levels (Singh et al., 2018; Zhao et al., 2015). The present work gives an in-depth detail of the varying glomalin content in soils of temperate Himalayas under different cropping systems and land use types and its effect on the soil aggregation.

2. Material and methods

2.1. Study site

The study was conducted in the agricultural and horticultural ecosystems of Ranichauri village in Tehri district of Uttarakhand, India (30°18.759'N; 78°24.680'E; 5964 ft above sea level) for two consecutive years (2013–2015). The natural vegetation in the locality is dominated by oaks, pines, cyprus and deodars. Soil is silty loam and rich in organic carbon and nitrogen. Climatically, the area falls under temperate zone with extreme cold winters that even receive snowfall (November–February) and cool summers (April–June). The area receives an average annual rainfall of 1383 mm, ambient temperature varying from -8°C to 33°C with relative humidity varying from 48% to 85%.

2.2. Soil sampling and analytical methods

A common sampling methodology has been followed for all the crop fields and orchards so as to yield a more rapid advancement of the understanding of soil biological processes and improved management. In horticultural fields, soil just below plant canopy was sampled as this would be a true representative of rhizospheric soil. Soil sampling was performed during April and October from 2013 to 2015, which was around 2 years. The samples were collected randomly from fields at two depths: surface (0–15 cm) and subsurface (15–30 cm) of three agricultural crops, viz., finger millet (*Eleusine coracana*), soybean (*Glycine max*) and amaranths (*Amaranthus* spp.) in one season (October) while wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and lentils (*Lens culinaris*) in the other season (April) and three fruit crops viz. apple (*Malus domestica*), plum (*Prunus domestica*) and peach (*Prunus persica*). Sub-samples were bulked to make a composite sample (approximately 500 g). A total of 18 soil samples (3 orchards \times 2 depths \times 3 replications) were collected (from agricultural and horticultural systems), sieved (2 mm mesh) to remove plant tissues and then placed in labelled plastic bags and kept at 4°C until further analysis. The gravimetric moisture content was determined immediately.

The soil was further analyzed for pH (pH meter), moisture (oven dry), texture (international pipette method), bulk density (measuring cylinder), carbon (Walkley and Black titration method), microbial biomass carbon (chloroform-fumigation), microbial population (plate count) and available nitrogen (Kjeldahl's method). The standard protocols for all the parameters were followed as given by Allen et al. (1974); Anderson and Ingram (1993). Dehydrogenase enzyme activity was determined by the method developed by Casida et al. (1964). The extraction of the total protein and easily extractable protein containing glomalin from the medium was carried out as described by Wright and Upadhyaya (1998). 1 g of soil sample was taken and 8 ml of sodium citrate solution was added to it. The mixture was autoclaved at 121°C . Total glomalin (TG) was defined as the maximum amount of glomalin that can be extracted by autoclaving at 121°C in 1 h with 50 mM Sodium citrate buffer while easily extractable glomalin (EEG) was the fraction of glomalin that can be extracted by autoclaving in 30 min with 20 mM sodium citrate buffer. It was then centrifuged at $5000\times g$ for 20 min. Further, the protein concentration was quantified by Bradford total

protein assay as per the standard protocol (Wright and Upadhyaya, 1996). Aggregate stability was determined by the wet sieving method as described by Kemper and Koch (1966).

2.3. Statistical analysis

The software SPSS 16 was used for analyzing the collected data. Pearson's Correlation was applied to check the association of glomalin concentrations (TG and EEG) with soil carbon, nitrogen, microbial biomass carbon and microbial population across each land-use type. Similarly, association of aggregate stability with SOC, TG and EEG were also studied. ANOVA was applied to assess the variance between different parameters.

3. Results

The soil was silty loam in texture and acidic in nature (pH 3.01–6.83), across different land use types. The moisture content varied from 5.74% to 19.80% during the two-year study with water holding capacity (WHC) ranging from 10.62% to 19.68%. The electrical conductivity (EC) varied from 0.28 ds/m to 0.38 ds/m and the cation exchange capacity (CEC) ranged from 12.07 Me/100 g to 16.33 Me/100 g. The bulk density did not vary much seasonally during the study period and remained almost the same ($1.24\text{--}1.41\text{ g/cm}^3$) with a slight change within the cropping systems.

3.1. Aggregate stability

The aggregate stability (AS) ranged from 42.67% to 81.33%. The highest value was recorded in forest while lowest in agricultural field with horticultural fields as the intermediate (Fig. 1). Aggregate stability showed a positive correlation with SOC ($r = 0.966$; $p < 0.01$), TG ($r = 0.988$; $p < 0.01$) and EEG ($r = 0.967$; $p < 0.01$) (Table 1).

3.2. Glomalin (glomalin related soil protein, GRSP) across soil profile and land use types

Glomalin showed variation among different cropping systems during the study period ranging from 2.12 mg/g to 4.82 mg/g. Glomalin concentrations across soil profile and different land use types are shown in Tables 2 and 3. TG showed highest value in the forest ecosystem (4.82 mg/g) which is supposed to be an undisturbed site while lowest value was recorded in the wheat field (2.12 mg/g). The horticultural systems showed the intermediate values for glomalin. Similar trend was apparent for EEG i.e. highest in forest (0.53 mg/g) and lowest in agricultural field (0.28 mg/g) with some slight change. Among horticultural systems, plum field showed highest value for TG (3.95 mg/g) and EEG (0.48 mg/g) both. Within agricultural systems, leguminous cropping had comparatively greater values of TG (2.57 mg/g) and EEG (0.42 mg/g) in both the seasons.

The effect of soil depth was not found significant on TG but EEG varied significantly. Among the land uses, TG varied significantly but the difference in EEG was not found to be statistically significant (Table 4). Both the fractions of glomalin (TG and EEG) showed a clear decreasing pattern on moving down the soil profile.

3.3. Relationship between glomalin and soil characteristics

The relationships between glomalin and soil characteristics are shown in Table 4. It was found that glomalin concentrations (TG and EEG) were highly positively correlated with C, N, MBC and microbial population. The correlation matrix showed that there exists a strong positive correlation between glomalin and soil organic carbon ($r = 0.905$, $p < 0.0001$; $r = 0.586$, $p < 0.001$) respectively for TG and EEG. Aggregate stability was also found to be positively correlated to soil organic carbon. Table 4 shows correlation of C, N, FC and MBC with

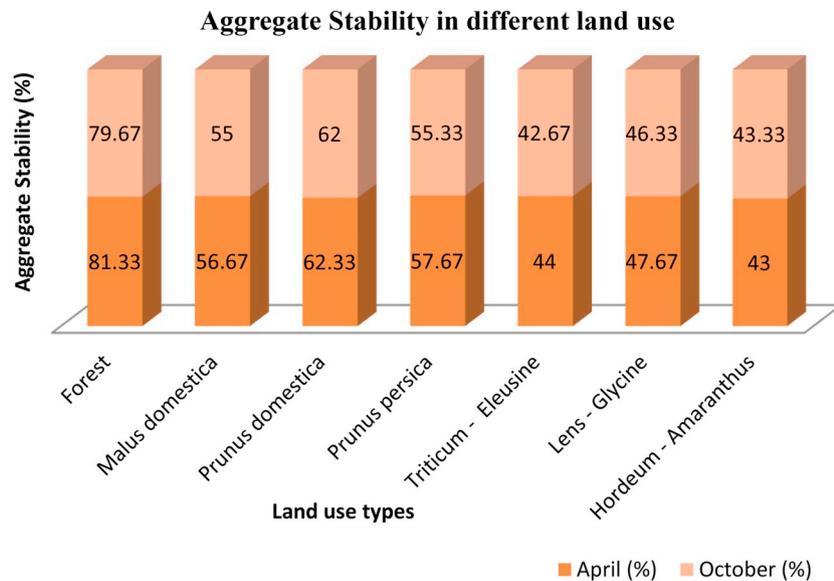


Fig. 1. Aggregate stability (%) in different land use in the study sites.

Table 1

Relation of aggregate stability (AS) to soil organic carbon (SOC); total glomalin (TG); easily extractable glomalin (EEG) in the study sites ($p < 0.01$).

Aggregate Stability	Total Glomalin	Easily Extractable Glomalin	Soil Organic Carbon
	$Y = 0.068x - 0.597$	$Y = 0.003x + 0.227$	$Y = 0.044x - 0.027$
	$R^2 = 0.977$	$R^2 = 0.937$	$R^2 = 0.935$

glomalin pools for each land-use type individually (across all horizons).

3.4. Percent contribution of glomalin and MBC to SOC

Tables 2 and 3 illustrate the percent contribution of MBC and glomalin to SOC, respectively. Among all the systems, the percent contribution of MBC to SOC was found to be maximum in the field cultivated with *Prunus domestica* whereas both the fractions of glomalin (TG and EEG) followed a slightly different pattern with maximum contribution to SOC in the field cultivated with *Amaranthus* spp.

Table 2

SOC, MBC, TG, EEG and % contribution to SOC in the two soil depths of the three land use types (standard error of the mean in brackets).

Soil Depth	Land Use	Systems	SOC (mg/g)	MBC (mg/g)	% MBC to SOC	TG (mg/g)	% TG to SOC	EEG (mg/g)	% EEG to SOC	
0–15 cm	Forest	Forest	36.2 (0.03)	0.82 (0.04)	2.28	4.79 (0.01)	13.23	0.51 (0.03)	1.43	
		Agriculture	<i>Eleusine coracana</i>	19.1 (0.00)	0.19 (0.02)	1.00	2.32 (0.02)	12.15	0.38 (0.03)	1.99
			<i>Glycine max</i>	22.5 (0.02)	0.26 (0.05)	1.19	2.57 (0.03)	11.42	0.41 (0.02)	1.84
	<i>Amaranthus</i> spp.		16.4 (0.08)	0.12 (0.05)	0.79	2.38 (0.02)	14.56	0.37 (0.03)	2.28	
	Horticulture	<i>Malus domestica</i>	24.9 (0.00)	0.63 (0.03)	2.53	3.14 (0.01)	12.61	0.43 (0.05)	1.75	
		<i>Prunus domestica</i>	26.4 (0.03)	0.78 (0.08)	2.98	3.95 (0.01)	14.92	0.47 (0.02)	1.79	
		<i>Prunus persica</i>	24.2 (0.04)	0.59 (0.09)	2.45	3.16 (0.05)	13.08	0.45 (0.01)	1.84	
	15–30 cm	Forest	Forest	35.4 (0.03)	0.81 (0.02)	2.29	4.24 (0.01)	11.98	0.35 (0.04)	0.99
			Agriculture	<i>Eleusine coracana</i>	16.5 (0.05)	0.16 (0.03)	0.97	2.12 (0.02)	12.81	0.28 (0.02)
<i>Glycine max</i>				20.0 (0.03)	0.19 (0.07)	0.94	2.47 (0.03)	11.94	0.29 (0.01)	1.42
<i>Amaranthus</i> spp.		16.1 (0.17)		0.11 (0.06)	0.69	2.18 (0.02)	13.57	0.28 (0.03)	1.78	
Horticulture		<i>Malus domestica</i>	25.0 (0.00)	0.59 (0.09)	2.37	3.01 (0.29)	12.03	0.31 (0.03)	1.26	
		<i>Prunus domestica</i>	26.5 (0.03)	0.80 (0.08)	3.02	3.63 (0.01)	13.70	0.34 (0.03)	1.29	
		<i>Prunus persica</i>	24.2 (0.04)	0.57 (0.04)	2.37	3.02 (0.05)	12.45	0.32 (0.04)	1.34	

Note: Values are the means of the data collected during October 2013–October 2014.

SOC = soil organic carbon; MBC = microbial biomass carbon; TG = total glomalin; EEG = easily extractable glomalin.

Table 3

SOC, MBC, TG, EEG and % contribution to SOC in the two soil depths of the three land use types (standard error of the mean in brackets).

Soil Depth	Land Use	Systems	SOC (mg/g)	MBC (mg/g)	% MBC to SOC	TG (mg/g)	% TG to SOC	EEG (mg/g)	% EEG to SOC	
0–15 cm	Forest	Forest	36.8 (0.02)	0.81 (0.02)	2.22	4.82 (0.06)	13.10	0.53 (0.05)	1.44	
		Agriculture	<i>Triticum aestivum</i>	2.06 (0.04)	0.14 (0.02)	0.73	2.33 (0.09)	11.32	0.39 (0.09)	1.89
			<i>Lens culinaris</i>	2.36 (0.01)	0.24 (0.03)	1.03	2.56 (0.02)	10.82	0.42 (0.03)	1.79
	Horticulture	<i>Hordeum vulgare</i>	1.83 (0.03)	0.13 (0.02)	0.74	2.34 (0.03)	12.73	0.38 (0.03)	2.09	
		<i>Malus domestica</i>	2.45 (0.06)	0.50 (0.03)	2.08	3.19 (0.04)	13.01	0.44 (0.04)	1.79	
		<i>Prunus domestica</i>	2.56 (0.02)	0.70 (0.08)	2.73	3.91 (0.01)	15.24	0.48 (0.04)	1.89	
	15–30 cm	Forest	<i>Prunus persica</i>	2.42 (0.09)	0.56 (0.09)	2.34	3.19 (0.02)	13.16	0.46 (0.05)	1.90
			Forest	3.62 (0.02)	0.81 (0.02)	2.24	4.47 (0.04)	12.36	0.35 (0.03)	0.96
			Agriculture	<i>Triticum aestivum</i>	1.87 (0.04)	0.12 (0.01)	0.69	2.12 (0.02)	11.33	0.29 (0.05)
Agriculture		<i>Lens culinaris</i>	2.18 (0.01)	0.18 (0.01)	0.83	2.42 (0.02)	11.13	0.30 (0.04)	1.40	
		<i>Hordeum vulgare</i>	1.64 (0.05)	0.11 (0.02)	0.70	2.16 (0.02)	13.10	0.29 (0.01)	1.80	
		Horticulture	<i>Malus domestica</i>	2.45 (0.06)	0.54 (0.08)	2.20	3.03 (0.01)	12.36	0.31 (0.03)	1.28
<i>Prunus domestica</i>			2.57 (0.02)	0.67 (0.08)	2.64	3.62 (0.01)	14.09	0.34 (0.02)	1.34	
<i>Prunus persica</i>			2.42 (0.09)	0.55 (0.04)	2.28	3.02 (0.02)	12.44	0.32 (0.01)	1.34	

Note: Values are the means of the data collected during April 2014–April 2015.

SOC = soil organic carbon; MBC = microbial biomass carbon; TG = total glomalin; EEG = easily extractable glomalin.

Table 4

Relationship (r, p) of TG and EEG with soil characteristics across all sites and both the soil depths (N = 28) and effect of land use and soil depth on glomalin.

Soil Parameters	TG		EEG	
	r	p	r	P
SOC	0.905**	<0.0001	0.586**	0.001
TC	0.744**	<0.0001	0.617**	<0.0001
MBC	0.921**	<0.0001	0.377*	0.048
DHA	0.926**	<0.0001	0.503**	0.006
FC	0.881**	<0.0001	0.701**	<0.0001
BC	0.924**	<0.0001	0.513**	0.005
AN	0.791**	<0.0001	0.522**	0.004
	F	p	F	p
Land use	77.92**	<0.0001	0.619	0.765
Soil depth	0.506	0.482	69.39**	<0.0001

TG = total glomalin; EEG = easily extractable glomalin; SOC = soil organic carbon; TC = total carbon; MBC = microbial biomass carbon; DHA = dehydrogenase activity; FC = fungal count; BC = bacterial count; AN = available nitrogen.

4.2. Glomalin in different land uses

The study revealed significant differences in glomalin concentrations among land-use types as shown in Table 4. Glomalin concentration was found to be highest in native forest, followed by the tree dominated sites (though cultivated) as compared to the purely cultivated agricultural fields. This can be attributed to the greater root network in the soils dominated by trees contributing to higher AMF and glomalin concentration as compared to the agricultural soil where roots are smaller and short-lived. This could be one of the possible reasons for the higher glomalin concentrations in the hilly terrain having forest cover. This corroborates with the results of Rillig et al. (2003) who found that the GRSP concentrations were lower in agricultural soils than in native forest and afforested soils. A comparison of glomalin levels between primary forest and farmland revealed that the primary forest had a 2.35–2.56 fold higher GRSP amount than those in the plantation forest and farmland (Wang et al., 2015). Moreover, the forest soils are largely undisturbed as compared to agricultural soils which are often subjected to practices of ploughing and tilling that might have reduced their glomalin content. Similar results were also observed in a previous study where comparison of soils collected from undisturbed and disturbed land use showed that soils with disturbed land use dramatically depleted in SOC and GRSP (Singh et al., 2016). Another study that compared three land use systems revealed that soils from the forest had the highest TG content, followed by the fallow (17% less) and the cultivated fields systems (46% less) highlighting the effect of agricultural practice on the glomalin content (Fokom et al., 2012). Similar trend was also observed in study of *Posidonia oceanica* seagrass mat sediment core from the

Western Mediterranean where agrarian activities had negative affect on AMF communities and the production of GRSP in soils (López-Merino et al., 2015).

4.3. Relation between glomalin, aggregate stability and soil organic carbon and its role in maintaining soil fertility

Among all the parameters studied SOC, N and MBC could explain glomalin the best across both the soil depths and within each land-use type. In the present study also, the TG was highly correlated with SOC and N. The relation between glomalin and MBC was found to be highly positively correlated. Similar relation was observed between glomalin and FC (Table 4). Similar study showing positive association of easily extractable GRSP and total GRSP with soil organic carbon (SOC) and soil organic nitrogen (SON) was done by Zhong et al. (2017). Investigation of glomalin structure through NMR showed that the recalcitrant carbon components in glomalin-related soil protein facilitate soil organic carbon preservation in tropical forests (Zhang et al., 2017).

Further, soil aggregate stability is also found to be correlated with SOC and a strong and positive correlation of aggregate stability was observed with glomalin (Table 1). Earlier, a positive correlation between GRSP and soil aggregate water stability across a variety of soil under different cropping systems and management practices has also been reported (Wright and Anderson, 2000). Structural stability of aggregates investigated in two aggregate fractions indicated the beneficial effect of glomalin on aggregation and carbon storage potential (Emran et al., 2012). Rapid decomposition of SOC was shown to be physically prevented by stable aggregates formation (Zhao et al., 2018). Additionally, absence of mechanized farming in the hills (study site) also helps in maintaining soil aggregates resulting in organic carbon accumulation. This is in support with the study which revealed that tillage treatment affected soil organic matter, mycorrhizal parameters and glomalin concentrations (Curaqueo et al., 2010; Lu et al., 2018). Similar results were also observed in study conducted in the black soil of Northeast China illustrated that while microbial biomass and glomalin were more important driving factors for aggregate stability; conservation tillage practices also promote the aggregation processes positively impacting the soil structure (Zhang et al., 2012).

5. Conclusion

The results from the present study reflect the role of glomalin in maintaining soil aggregation in the temperate Himalayan soils under different cropping systems. Aggregate formation is found to be positively co-related with the soil organic carbon that not only increases the carbon pool, but also binds the organic matter preventing soil erosion further enhancing soil aggregation. Thus, with abilities to improve the

bioavailability of nutrients and enhance aggregate formation, glomalin concentrations in soil can be an effective indicator of soil health and fertility. The study also shows that apart from the plant, glomalin concentration in soil is highly dependent on the land use and management practices.

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Appendix A. Supplementary data

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