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Rise in carbon dioxide changes soil structure

Carbon in soil affects the formation and stabilization of aggregates (groups of primary particles that adhere to each other more strongly than to surrounding soil particles)[1]. Soil aggregation is important for preventing soil loss through wind and water erosion, and the size distribution and abundance of water-stable aggregates influences a range of physical, chemical, biological and agricultural properties of soil[2]. The effects on soil biota and nutrient cycling of increases in soil carbon availability, brought about by increased CO_2, are well studied, but the consequences for soil aggregation and structure have not been examined. Here we show for three ecosystems that the water stability and size distribution of aggregates is affected by long-term CO_2 fumigation, and we propose a mechanism for this that involves the production by fungi of the glycoprotein glomalin.

The Jasper Ridge CO_2 experiment in northern California[3] exposed two natural annual grassland ecosystems (sandstone and serpentine) to increased atmospheric CO_2 for six growing seasons by using cylindrical, open-top chambers (1 m tall, 0.33 m^2, $n=10$). In both grasslands, a higher proportion of soil was found in aggregates 1–2 mm across in elevated CO_2, and the proportion of aggregates of 0.25–1 mm was significantly increased in the sandstone grassland (Table 1). The water stability of both size classes followed a pattern similar to the mass of aggregates. This suggested that the higher mass of aggregates could be explained by an increase in the water stability of aggregates (Table 1).

Although soil aggregation is a complex hierarchical process[4], the soil concentration of the glycoprotein glomalin[5] is tightly correlated with aggregate stability across many soils[6]. Glomalin is produced mainly by hyphae of arbuscular mycorrhizal fungi[5], which form symbiotic associations with plant roots. The length of the hyphae in these fungi increases with elevated CO_2 in the sandstone grassland, but not in the serpentine grassland, with root biomass and length showing the opposite pattern[7]. Total glomalin and immunoreactive glomalin concentrations in soil increased in both grasslands with elevated CO_2 (Table 1). Glomalin concentration in aggregates (from a separate extraction) increased under elevated CO_2 for aggregates of 0.25–1 mm in both communities, but this was not the case for those of 1–2 mm (Table 1). The water stability of that fraction may be under different control.

The Sky Oaks CO_2 study in southern California used 12 greenhouses ($2\times2\times2$ m) with controlled CO_2, ambient lighting and controlled temperature at six CO_2 concentrations from a pre-industrial level of 250 $\mu l\,l^{-1}$ to 750 $\mu l\,l^{-1}$ at intervals of 100 $\mu l\,l^{-1}$ ($n=2$). The chambers were built around *Adenostoma fasciculatum* (chamise) shrubs in chaparral vegetation recovering from an experimental burn. Soil samples were taken after three years of treatment and analysed for soil aggregation and glomalin concentration to see whether the patterns in the grasslands also existed in a different vegetation type. The proportion of soil mass in aggregates of 0.25–1 mm showed a linear increase (linear regression, $P=0.03$, $r^2=0.74$) along the CO_2 gradient, but the 1–2 mm aggregate mass did not ($P=0.68$, $r^2=0.04$). Glomalin concentrations followed a pattern similar to that of the small aggregate size class ($P=0.03$, $r^2=0.71$).

The carbon sink represented by glomalin over the experimental period for Jasper Ridge was 8.29 g C m^{-2} in the serpentine and 4.25 g C m^{-2} in the sandstone grassland. These are very small amounts compared with the large organic carbon stocks in these soils, and are on the order of 5% of the total calculated litter and soil accumulation under elevated CO_2 on an annual basis[8]. Glomalin therefore seems to be more important in carbon sequestration by virtue of its function in soil aggregation (which has been linked with carbon stabilization) than by acting as a carbon sink itself.

Our results indicate that changes in soil structure in response to CO_2 enrichment should be incorporated into global research because soil structure has a strong effect on soil processes and organisms. On a global scale, the extent of soil degradation and erosion is severe[9] and is accelerated by changes in many global factors, including climate and land use[10]. Our finding that an increase in soil aggregation could be brought about by atmospheric change may have implications for studies of soil stabilization in ecosystems.

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Table 1 **Effects of increased CO_2 on aggregates and glomalin in two annual grasslands**

	Sandstone		Serpentine		*P*-values (ANOVA)		
	Ambient CO_2	Increased CO_2	Ambient CO_2	Increased CO_2	CO_2	Grassland	$CO_2\times$grassland
Aggregates 1–2 mm (% of soil)	14.43 (0.54)	15.14 (0.33)	16.70 (0.56)	18.08 (0.50)	**0.04**	**<0.0001**	0.50
Aggregates 0.25–1 mm (% of soil)	17.06 (0.58)	20.04 (0.82)	26.93 (1.62)	25.61 (1.09)	0.46	**<0.0001**	**0.05**
Water stable 1–2 mm (%)	86.70 (1.58)	90.10 (1.27)	76.15 (1.47)	81.02 (1.26)	**0.002**	**<0.0001**	0.06
Water stable 0.25–1 mm (%)	88.87 (0.90)	92.77 (0.63)	84.27 (0.85)	85.32 (0.49)	**0.006**	**<0.0001**	0.87
Total glomalin (mg g^{-1})	2.09 (0.04)	2.17 (0.03)	2.60 (0.05)	2.79 (0.06)	**0.01**	**<0.0001**	0.26
Immunoreactive glomalin (mg g^{-1})	0.67 (0.04)	0.75 (0.02)	0.97 (0.02)	1.06 (0.04)	**0.01**	**<0.0001**	0.97
Glomalin, 1–2 mm (mg g^{-1} ag)	1.83 (0.04)	1.85 (0.05)	2.40 (0.05)	2.36 (0.14)	0.93	**<0.0001**	0.71
Glomalin, 0.25–1 mm (mg g^{-1} ag)	2.08 (0.04)	2.32 (0.05)	2.50 (0.09)	2.62 (0.09)	**0.02**	**<0.0001**	0.34

Values in brackets are standard error of the mean ($n=10$). *P* values (obtained by analysis of variance (ANOVA); suitable transformations were used as necessary) of less than 0.05 are in bold. Water stability of aggregates (expressed as the percentage of stable aggregates) was measured using a wet-sieving method following capillary rewetting of soil samples. Glomalin was extracted by repeated autoclaving in a citrate extraction buffer. Glomalin concentrations were measured by immunoreactivity assay using an enzyme-linked immunosorbent assay with monoclonal antibody 32B11 against glomalin isolated from arbuscular mycorrhizal fungal hyphae. Total glomalin concentration in extracts was measured using a Bradford protein assay. Glomalin concentrations are expressed per gram of soil or aggregate (ag). Further details are available from the authors.