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Limitations on the climatic and ecological signals provided by the $\delta^{13}C$ values of phytoliths from a C_4 North American prairie grass

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Abstract

Silica phytoliths, which are deposits of opal-A that precipitate in the intra- and intercellular spaces of plant tissues during transpiration, commonly contain small amounts of occluded organic matter. In this paper, we investigate whether the $\delta^{13}C$ values of phytoliths from a C_4 grass, *Calamovilfa longifolia*, vary in response to climatic variables that can affect the carbon-isotope composition of plant tissues. There is no significant correlation ($r^2 < 0.3$) between climate variables and the $\delta^{13}C$ values of *C. longifolia* tissues (average $\delta^{13}C_{tissue} = -13.1 \pm 0.6$ ‰; $n = 70$) across the North American prairies. However, plant tissue $\delta^{13}C$ values are lower for grasses collected in populated areas where the $\delta^{13}C$ value of atmospheric CO_2 is expected to be lower because of fossil fuel burning. Phytolith $\delta^{13}C$ values are more variable ($\delta^{13}C = -27.3$ to -23.0‰; average = -25.1 ± 1.3‰; $n = 34$) and more sensitive to changes in aridity than whole tissue $\delta^{13}C$ values. The strongest correlations are obtained between the $\delta^{13}C$ values of stem or sheath phytoliths and humidity ($r^2 = 0.3$), latitude ($r^2 = 0.4$) and amount of precipitation ($r^2 = 0.5$). However, use of these relationships is limited by the wide spread in $\delta^{13}C$ values of phytoliths from different plant tissues at the same location. We have been unable to infer any relationship between $\delta^{13}C$ values of phytoliths and expected variations in the $\delta^{13}C$ values of atmospheric CO_2. The *C. longifolia* phytoliths are depleted of ^{13}C relative to tissue carbon by 10–14‰. This means that the phytoliths examined in this study have carbon isotopic compositions within the range reported previously for phytoliths from C_3 plants. This observation may further limit the usefulness of soil-phytolith assemblage $\delta^{13}C$ values for identifying shifts in grassland C_3:C_4 ratios.

1. INTRODUCTION

Plants absorb aqueous silicic acid through their roots, and as a result many plants precipitate opal-A within their cells and intercellular spaces. Silica deposition can occur in any tissue of the plant (roots, stems, leaves), but is particularly common in the leaves along the transpiration stream where silica saturation is reached via the removal of water. These discrete silica bodies are called phytoliths. Members of the Gramineae family are particularly abundant phytolith producers and typical dry-land grasses will contain 1–3% wt. silica (Jones and Handreck, 1967). As phytoliths form they occlude some organic plant matrix thought to be the original cytoplasmic material of the silicified cell (Wilding et al., 1967). The organic matter is not bound to the silica structure, but trapped among the pore spaces between the spherules comprising the amorphous opal of the phytolith (Wilding et al., 1967; Carter, 2009). Phytoliths can have carbon contents of 0.09–5.8 wt.% (Jones and Beavers, 1963; Jones and Milne, 1963; Wilding et al., 1967; Kelly et al., 1991; Mulholland and Prior, 1993; Smith and Anderson, 2001; Hodson et al., 2008). The carbon sequestered in this manner is insulated from decay and hence largely retained in the soil even after the rest of the plant material has decomposed. Phytoliths are believed to comprise a significant amount of carbon within the refractory pool stored in soil organic matter (Parr and Sullivan, 2005).

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The protected nature of the carbon in phytoliths makes it a potential archive of information about biochemical and/or environmental conditions during plant growth (e.g. Smith and White, 2004; Carter, 2009). Stable carbon-isotope compositions, in particular, have been used to differentiate between phytoliths produced in C_3 versus C_4 plants (Kelly et al., 1991; Lü et al., 2000; Krull et al., 2003; Smith and White, 2004). Because grasses are the primary producers of phytoliths, the carbon-isotope composition of phytoliths preserved in soils may have the potential to reveal subtle changes in C_3 versus C_4 dominated grasslands over time (McClaran and Umlauf, 2000; Smith and White, 2004).

The C_3:C_4 comparison is complicated by the fact that phytolith carbon-isotope compositions ($\delta^{13}C_{phyt}$) are typically lower than those of the associated plant tissues. The extent of ^{13}C-depletion in phytoliths versus tissues varies between C_3 and C_4 plants with greater shifts occurring for C_4 plants. The average $\delta^{13}C_{phyt}$ value reported for C_3 grasses is −28.5‰, which is on average 1.7‰ lower than typical $\delta^{13}C$ values of whole tissues from the same plants (Table 1; Kelly et al., 1991; Lü et al., 2000; Krull et al., 2003; Smith and White, 2004; Hodson et al., 2008; Carter, 2009). Phytoliths from C_4 grasses have an average $\delta^{13}C$ value of −20.9‰, which is lower than the plant's tissues by 8.7‰ (Table 1; Kelly et al., 1991; Lü et al., 2000; Krull et al., 2003; Smith and White, 2004). As a result, the reported differences between the average $\delta^{13}C$ values of C_3 and C_4 phytoliths from previous studies range from 2.1‰ (Krull et al., 2003) to 9.8‰ (Lü et al., 2000), which is much smaller than the ~13–16‰ spread typically present between C_3 and C_4 plant tissues. This compression is reported to be the product of differential fractionation during lipid formation in these two plant types, which is then reflected in the phytolith carbon-isotope compositions (Smith and White, 2004). That said, the remaining spread between the $\delta^{13}C$ values of C_3 and C_4 phytoliths can still be significant and some researchers have used the carbon isotopic composition of soil-phytolith assemblages to determine the C_3:C_4 balance in an ecosystem (Fredlund, 1993; Kelly et al., 1998; Lü et al., 2000; McClaran and Umlauf, 2000).

The $\delta^{13}C$ values of plant tissue vary in response to changes in temperature, relative humidity, precipitation, altitude, nutrient availability, light levels, canopy density and the $\delta^{13}C$ values of atmospheric CO_2 (Tieszen, 1991; Arens et al., 2000). Hence, plant tissues and their phytoliths display some degree of variation in their $\delta^{13}C$ values at one site and among different locations. In some cases individual variability may be large enough to hinder identification of phytoliths from C_3 versus C_4 plants based solely on $\delta^{13}C$ values. Kelly et al. (1991), for example, reported one $\delta^{13}C$ value for C_4 phytoliths as low as −27.7‰ – identical to the $\delta^{13}C_{phyt}$ value of a C_3 plant at the same site (Oberlin, Kansas). Other studies of C_3 grasses and trees have reported $\delta^{13}C_{phyt}$ values that are higher than the associated tissue – closer to those of phytoliths from C_4 vegetation (Krull et al., 2003; Hodson et al., 2008; Carter, 2009).

Farquhar (1983) has shown that the $\delta^{13}C$ values of tissues from C_4 plants should vary in response to the $\delta^{13}C$ values of atmospheric CO_2 ($\delta^{13}C_{atm}$), the ratio of intercellular

Table 1
Summary of the range of $\delta^{13}C$ values (‰, VPDB) for grass tissues and corresponding phytoliths reported in the literature for samples grown under natural conditions.

Plant type	Study	Location	Number of samples[a]	$\delta^{13}C_{tissue}$ (‰)			$\delta^{13}C_{phyt}$ (‰)			$\Delta^{13}C_{tissue-phytolith}$ (‰)		
				Min	Max	Avg. ± SD	Min	Max	Avg. ± SD	Min	Max	Avg. ± SD
C3 grasses	Kelly et al. (1991)	North America	5	−26.8	−24.2	−25.4 ± 1.2	−30.0	−26.6	−28.4 ± 1.3	2.3	3.7	3.1 ± 0.6
	Lü et al. (2000)	China	6	–	–	–	−28.5	−24.8	−27.3 ± 1.7	–	–	–
	Krull et al. (2003)	Australia	1	–	–	−27.6	–	–	−24.8	–	–	−2.8
	Smith and White (2004)[b]	North America	10	−28.1	−25.5	−27.1 ± 0.7	−34.4	−27.0	−30.4 ± 2.3	1.2	10.9	5.3 ± 2.9
	Hodson et al. (2008)	United Kingdom	5	−29.0	−27.3	−28.3 ± 0.8	−28.7	−27.1	−28.2 ± 0.7	−0.9	1.4	−0.2 ± 1.1
	Carter (2009)	New Zealand	9	−30.0	−26.8	−28.5 ± 1.2	−34.0	−30.0	−31.6 ± 1.4	1.0	5.6	3.1 ± 1.3
	Average of above:			−28.5	−26.0	−27.4 ± 1.0	−31.1	−27.1	−28.5 ± 1.5	0.9	5.4	1.7 ± 1.5
C_4 grasses	Kelly et al. (1991)	North America	14	−16.8	−12.0	−14.0 ± 1.6	−27.7	−19.9	−22.3 ± 1.8	5.6	15.7	8.3 ± 2.5
	Lü et al. (2000)	China	5	–	–	–	−20.1	−15.1	−17.5 ± 2.0	–	–	–
	Krull et al. (2003)	Australia	2	−14.2	−13.1	−13.7 ± 0.8	−23.0	−22.3	−22.7 ± 0.5	8.8	9.2	9.0 ± 0.3
	Smith and White (2004)[b]	North America	7	−15.5	−12.6	−14.2 ± 1.2	−25.7	−17.2	−21.2 ± 2.9	5.6	12.2	8.9 ± 2.6
	Average of above:			−15.5	−12.6	−14.0 ± 1.2	−24.1	−18.6	−20.9 ± 1.8	6.7	12.4	8.7 ± 1.8
C_4 grass	This study	North America	70 (tissue) 34 (phytoliths)	−15.2	−11.3	−13.1 ± 0.3	−27.4	−23.0	−25.4 ± 1.3	9.6	14.1	12.2 ± 1.4

[a] For all studies except the current one, the number of tissue samples is the same as the number of phytolith samples.
[b] The $\delta^{13}C$ values listed for whole tissues from Smith and White (2004) were adjusted from the reported $\delta^{13}C$ cellulose values by subtracting 2‰; see Benner et al. (1987).