Carbon isotopic ratios of modern C3 and C4 vegetation on the Indian Peninsula and changes along the plant–soil–river continuum; implications for (paleo-)vegetation reconstructions

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Frédérique M.S.A. Kirkels[1], Hugo J. de Boer[2], Paulina Concha Hernández[1], Chris R.T. Martes[1], Marcel T.J. van der Meer[3], Sayak Basu[4,a], Muhammed O. Usman[5,b], Francien Peterse[1]

10   [1]Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, The Netherlands

[2]Department of Environmental Sciences, Copernicus Institute of Sustainable Development, Faculty of Geosciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, The Netherlands

[3]Department of Marine Microbiology and Biogeochemistry, NIOZ Royal Netherlands Institute for Sea

15   Research, PO Box 59, 1790 AB Den Burg, the Netherlands

[4]Department of Earth Sciences, Indian Institute of Science Education and Research Kolkata, Mohanpur 741246, India

[5]Geological Institute, ETH Zürich, Sonneggstrasse 5, 8092 Zürich, Switzerland

20   [a]Present address: Geological Oceanography Department, National Institute of Oceanography, Dona Paula - 403 004, Goa, India

[b]Present address: Department of Physical & Environmental Sciences, University of Toronto Scarborough, Toronto, Ontario M1C1A4, Canada

25   *Correspondence to*: Francien Peterse (f.peterse@uu.nl) and Frédérique Kirkels (f.m.s.a.kirkels@uu.nl)

Abstract

The large difference in the fractionation of stable carbon isotopes between C3 and C4 plants is widely used in vegetation reconstructions, where the predominance of C3 plants suggests wetter and that of C4 plants drier conditions. The isotopic composition of organic carbon (OC) preserved in soils or sediments may be a valuable

30   (paleo-)environmental indicator, based on the assumption that plant-derived material retains the carbon isotopic signature of its photosynthetic pathway during transfer from plant to sediment. In this study, we investigated the carbon isotopic signature of C3 and C4 plants ($\delta^{13}C$) and of organic carbon ($\delta^{13}C_{org}$) in soils, river Suspended Particulate Matter (SPM) and riverbed sediments, to gain insight in the control of precipitation on C3 and C4 plant $\delta^{13}C$ values and to assess changes in $\delta^{13}C_{org}$ values along the plant–soil–river continuum. This information

35   allows us to elucidate the implications of different $\delta^{13}C$ end-members on C3/C4 vegetation reconstructions. Our analysis was performed in the Godavari River basin, which has mixed C3 and C4 vegetation and is situated in the Core Monsoon Zone in peninsular India, a region that integrates the hydroclimatic and vegetation changes caused by variation in monsoonal strength. The Godavari C3 and C4 plants revealed more negative $\delta^{13}C$ values than global average vegetation values, suggesting region-specific plant $\delta^{13}C$ signatures. Godavari C3 plants

40   confirmed a strong control by Mean Annual Precipitation (MAP) on their $\delta^{13}C$ values, with an isotopic enrichment of ~2.2 ‰ for the interval between ~500 and 1500 mm y^{-1}. Tracing $\delta^{13}C_{org}$ values from plant to soils and rivers revealed that soils and riverbed sediments reflected the transition from mixed C3 and C4 vegetation in the dry upper basin to more C3 vegetation in the humid lower basin. Soil degradation and stabilisation processes and hydrodynamic sorting within the river altered the plant-derived $\delta^{13}C$ signal. Phytoplankton dominated the

45   $\delta^{13}C_{org}$ signal carried by SPM in the dry season and year-round in the upper basin. Our analysis revealed that the reconstructed C3/C4 vegetation composition was sensitive to the plant $\delta^{13}C$ end-members used as mixing model input. The %C4 plants in the different subbasins was ~10–19 % higher using Godavari-specific end-members than using global averages, and including a correction for drought enrichment in Godavari C3 plants resulted in a 2–10 % lower estimated C4 plant cover. Hence, incorporating region-specific plant $\delta^{13}C$ end-members and

50   drought correction of the C3 end-member in mixing models need to be considered to determine C3 and C4 distributions of modern- and paleo-vegetation in monsoonal regions.

1. Introduction

Vegetation reconstruction of the coverage of C3 and C4 plants uses the distinct $\delta^{13}C$ composition of both

55   vegetation types with the assumption that Organic Carbon (OC) retains the stable isotopic signature during

transfer from plant to soils and sediments (e.g., Koch, 1998; Dawson et al., 2002; Wynn and Bird, 2007). The C3 and C4 photosynthetic pathways fractionate carbon isotopes to a different extent; this is reflected in $\delta^{13}C$ values of ~-20 to -37 ‰ in C3 and ~-10 to -16 ‰ in C4 plants (e.g., Bender, 1971; Farquhar et al., 1989; Kohn, 2010). C3 plants fix CO_2 using the Calvin–Benson cycle and they are prevalent in relatively cold and humid

60   environments. C4 plants add an initial CO_2 fixation step using PEP carboxylase to concentrate CO_2 via bundle sheath cells inside the leaf. This additional step in the photosynthesis pathway allows C4 plants to maintain relatively high photosynthesis rates under low stomatal conductance with limited water loss, which enables them to thrive in high temperature and (semi-)arid environments (e.g., Farquhar, 1983; Sage and Monson, 1999; Sage, 2004).

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Given the sensitivity of vegetation type to water availability, shifts in the relative contribution of C3 and C4 plants can be used to infer hydroclimatic changes, with a shift to more dominant C4 vegetation in drier periods or areas and more dominant C3 vegetation in wetter conditions (Koch, 1998; Sage, 2004). The carbon isotopic composition of organic matter ($\delta^{13}C_{org}$) preserved in soils or in river-dominated sediments in the marine realm is

70   often used as proxy for (paleo-)vegetation reconstructions as it is considered to represent an integrated signal of the vegetation (e.g., Galy et al., 2007; Sarangi et al., 2021). The monsoon-influenced Indian subcontinent is particularly sensitive to changes in hydroclimate on both short (seasonal) and long (orbital) timescales (Turner and Annamalai, 2012; Sinha et al., 2011, 2015; Banerji et al., 2020; Dutt et al., 2021), resulting in changes in the C3 and C4 vegetation distributions over the Neogene and Quaternary period (e.g., Agrawal et al., 2012; Ghosh

75   et al., 2017; Basu et al., 2018, 2019a; Roy et al., 2020). For example, changes in $\delta^{13}C_{org}$ and leaf wax-specific $\delta^{13}C$ values captured the late Miocene (7.4–7.2 Ma) expansion of C4 plants recorded in Himalayan-derived Indus fan sediments (Feakins et al., 2020) as well as in Gangetic plain alluvial sediments and paleosols (Ghosh et al., 2017; Roy et al., 2020). C4 plants spread southward over the Indian peninsula during the mid-Pliocene to mid-Pleistocene (3.5–1.5 Ma) linked to reduced rainfall (Dunlea et al., 2020), whereas an increase in monsoon

80   strength over the last deglaciation led to a shift to a more C3-dominated ecosystem (e.g. Galy et al., 2008a; Contreras-Rosales et al., 2014). Finally, an increase in C4 plants across India from the mid- to late Holocene, establishing the modern-day vegetation, was linked to aridification (Ponton et al., 2012; Contreras-Rosales et al., 2014; Sarkar et al., 2015; Usman et al., 2018; Basu et al., 2019a). At seasonal to decadal scale, changes in monsoon intensity and distribution can affect plant $\delta^{13}C$ as well as preservation and provenance of the $\delta^{13}C_{org}$

85   signal in soils and sediments (e.g. Ittekkot et al., 1985; Galy et al., 2008b). However, the effect of monsoon

variation on the $\delta^{13}C_{(org)}$ signal along the plant–soil–river continuum has not been thoroughly tested for peninsular India.

The mixing models that are used to reconstruct (paleo-)vegetation require C3 and C4 $\delta^{13}C$ end-members as

90   input. These end-members can be based on averages in global vegetation or be based on modern vegetation samples in a region. For C3 vegetation, a value of ~-27 ‰ is commonly used as global average end-member (Cerling et al., 1997; Koch, 1998; Dawson et al., 2002), although Kohn (2010) reported that this value may be biased towards dry ecosystems. Instead, Kohn (2010) determined a value of ~-28.5 ‰, representing an average of global C3 vegetation including equatorial and mid-latitude biomass. For C4 vegetation, the global average is

95   estimated at ~-12 ‰ e.g. Koch et al., 1998; Dawson et al., 2002). However, meta-analyses of global C3 vegetation revealed that hydroclimatic conditions such as rainfall amount and seasonality affect the plant $\delta^{13}C$ (Diefendorf et al., 2010; Kohn, 2010; Basu et al., 2019b, 2021). In particular drought stress results in a less negative $\delta^{13}C$ in C3 plants, where mean annual precipitation (MAP) has a much stronger control than other environmental factors such as temperature or altitude (Stewart et al., 1995; Diefendorf et al., 2010). Observed

100   changes in C3 plant $\delta^{13}C$ due to drought stress are the result of changes in the ratio of leaf interior to atmospheric CO_2 concentrations, which can be the result of changes in stomatal conductance, photosynthetic capacity and photosynthetic rate, or a combination thereof (Farquhar et al., 1989; Diefendorf et al., 2010; Liu et al., 2013). Carbon fractionation in C4 plants is generally unaffected by drought stress, although a few field and experimental studies have shown that C4 plant $\delta^{13}C$ becomes more negative under water-limiting conditions as a

105   result of a less efficient CO_2 concentrating mechanism referred to as 'bundle sheath leakiness' (e.g., Buchmann et al., 1996; Yoneyama et al., 2010; Basu et al., 2015; Ellsworth and Cousins, 2016). Regardless, drought stress has the largest impact on C3 plants and is recognised to cause high intraspecies variability in water-limited ecosystems (<1000 mm y^{-1}; e.g. Ma et al., 2012; Liu et al., 2013, 2014; Luo et al., 2021). Hence, the existing plant community in a region and the impact of water availability on those plant species may vary locally and

110   result in a C3 plant $\delta^{13}C$ value that differs from the global average (Liu et al., 2014; Basu et al., 2019b).

Although it is possible to determine region-specific plant $\delta^{13}C$ end-members, this approach requires detailed knowledge of $\delta^{13}C$ in the regional C3 and C4 vegetation as well as of rainfall distributions. Problematically, such detailed information is often unavailable and yet to be established for Indian plants in the Core Monsoon

115   Zone (CMZ). Alternatively, correction of global average C3 end-member for drought conditions in peninsular

India requires details on regional rainfall distributions and heavily depends on the average $\delta^{13}C$ value (-27 or -28.5 ‰) that is chosen. Recently, a study of $\delta^{13}C$ in modern vegetation on the Gangetic plain has prompted a recalculation of C3/C4 covers in paleo-vegetation, revealing an underestimation of C4 plants (~20 %) and changing the timing of (Miocene) C4 grassland expansion to an earlier date (~11 Ma) (Basu et al., 2015, 2019b).

120 This shift highlights the effect of plant $\delta^{13}C$ end-member values on paleo-vegetation reconstructions.

Next to precipitation controls on vegetation $\delta^{13}C$, the initial plant $\delta^{13}C$ signal may be altered during transit from plant to the sedimentary archive, depending on physical and biogeochemical processes that determine the stability i.e., protection against degradation and transport efficiency of this plant-derived OC (e.g., Battin et al.,

125 2009; Ward et al., 2017). First of all, it is well-established that soil degradation processes enrich OC isotopes, which is usually estimated to be ~1– 3‰ but can be as high as 6 ‰ in tropical and semi-arid regions (e.g., Krull et al., 2005). Possible factors that contribute to this enrichment are preferred uptake and degradation to CO_2 of ^{13}C-depleted OC by microbes, incorporation of ^{13}C-enriched microbial and fungal biomass in the soil and/or preferential adsorption of ^{13}C by fine mineral particles (Krull et al., 2005; Wynn, 2007; Wynn and Bird, 2007).

130 OC comprises a complex mixture of different types of material (e.g., lipids, proteins, carbohydrates etc.), while compound-specific degradation or preservation rates in soils have been reported to affect the $\delta^{13}C$ signatures of long-chain fatty acids, *n*-alkanes and *n*-alkanoic acids derived from Indian vegetation (Sarangi et al., 2021; Roy and Sanyal, 2022) which may challenge their use for vegetation reconstructions. Furthermore, the marked hydrological changes in Indian monsoonal rivers can change the source and thereby the $\delta^{13}C$ value of the OC

135 that it contains at a seasonal scale, from mainly soil-derived OC in the wet season to aquatic produced OC in the dry season, or change its provenance by sourcing from particular parts of the basin with a different vegetation cover in response to the rainfall distribution (Gupta et al., 1997; Balakrishna and Probst, 2005; Aucour et al., 2006; Galy et al., 2008b, 2011; Kirkels et al., 2020a; Menges et al., 2020). For example, Galy et al. (2008b) showed that $\delta^{13}C_{org}$ values of suspended particulate matter (SPM) in the Ganges-Brahmaputra River reflected

140 dominant C3 input in the Himalayan tributaries, but after in-river degradation, this signal was replaced by C4 inputs in the Gangetic plain. Finally, hydrodynamic sorting within the river may result in depth-specific OC distributions and thereby influence the $\delta^{13}C$ signal that is transported downriver (Galy et al., 2008b; Bouchez et al., 2014; Feng et al., 2016; Repasch et al., 2022). Hence, interpretation of $\delta^{13}C$-based vegetation reconstructions needs to consider potential alterations during transit from plant source to sedimentary deposits.

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In this study, we examine the $\delta^{13}C$ of C3 and C4 vegetation in the modern-day Godavari River basin, the largest monsoonal river of peninsular India (Fig. 1a), to examine links between monsoon-driven hydroclimate and plant $\delta^{13}C$ values. In addition, we analyse the $\delta^{13}C_{org}$ values in soils, river SPM and riverbed sediments collected in a wet and dry season to explore the evolution of the initial plant-derived $\delta^{13}C$ signal along the plant–soil–river continuum. Finally, we use our insights in the modern system to assess the influence of drought stress and the use of region-specific plant $\delta^{13}C$ end-members on C3/C4 vegetation mixing model estimates and thus the uncertainty of $\delta^{13}C$-based (paleo-)vegetation reconstructions.
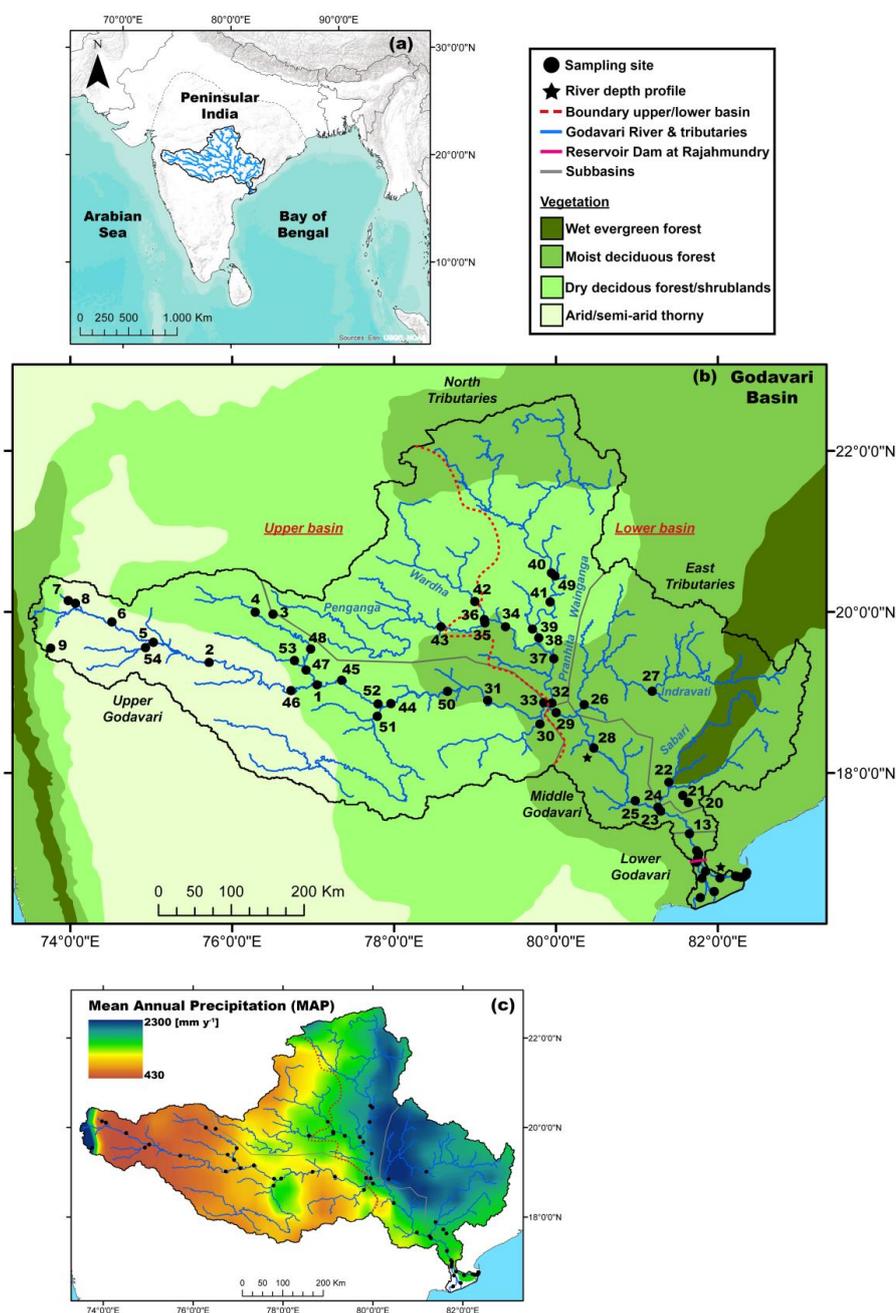
2. Materials and methods

2.1. Regional Setting

The natural vegetation in the Godavari basin varies from (C4) grasses, dry deciduous forests and thorny shrublands in the upper basin to moist and evergreen deciduous forests with mostly C3 flora in the lower basin (Olson et al., 2001; Asouti and Fuller, 2008; Fig. 1b). Agriculture covers ~60 % of the basin with dominant C4 crops (sorghum, millet, maize, sugar cane) in the upper basin and rice fields (C3) in the lower basin (CWC, 2014; Pradhan et al., 2014). The vegetation distribution reflects the precipitation gradient in the basin, ranging from ~430 mm y^{-1} in the interior upper basin that is located in the rain shadow of the Western Ghats mountain range to ~2300 mm y^{-1} in near the Bay of Bengal coast (Fig. 1c).

The passage of the Indian monsoon dictates the seasonality of the Godavari River, with 75–85% of the annual rainfall and 98 % of the sediment transport in the monsoon/wet season between June and September (Biksham and Subramanian, 1988a,b). The Godavari is the largest peninsular river of India (catchment area: $3.1*10^5$ km^2, length: 1465 km) with an annual discharge of 110 km^3 and sediment load of 170 Mt of which ~2.8 Mt of OC (Biksham and Subramanian, 1988a,b; Gupta et al., 1997). The Godavari River starts in the Western Ghats mountains and flows across peninsular India before emptying in the Bay of Bengal, and is situated in the Core Monsoon Zone (Ponton et al., 2012; Sarkar et al., 2015; Giosan et al., 2017) (Fig. 1a). The upper basin developed on Deccan flood basalts and the lower basin on felsic rock formations (Giosan et al., 2017); petrogenic OC is absent in the former (Reddy et al., 2021) and very sporadic (i.e., coal deposits) in the latter (Usman et al., 2018). The Godavari basin is divided in 5 subbasins: the Upper (~37 % of the total basin area), Middle (6 %) and Lower (2 %) Godavari cover the main stem river, and are joined by the North (35 %;

Wainganga, Penganga, Wardha and Pranhita rivers) and East Tributaries (20 %; Indravati and Sabari rivers)
(Babar and Kaplay, 2018) (Fig. 1b, S1). Abundant dams in the upper basin limit the river flow, while a large
dam with reservoir lake at Rajahmundry controls the flow into the tidally influenced delta (Pradhan et al., 2014).

180 **Fig. 1: (a) Location of the Godavari River basin in peninsular India. (b) Godavari River basin and sampling sites, with the major vegetation zones (Olson et al., 2001; Asouti and Fuller, 2008). Names of the subbasins (grey) and major rivers (blue) are indicated, a zoom for the Godavari delta is available in Fig. S1. (c) Mean Annual Precipitation spatial distribution in the Godavari basin (30-year average, 0.25°, APHRODITE dataset; Yatagai et al., 2009).**

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2.2. Sample collection

Samples of above-ground plant material were collected in February/March 2015 (dry season) across the Godavari basin, selecting the 3–5 most dominant species at each site and spanning the full range of plant lifeforms (i.e., trees, shrubs, herbaceous plants and grasses). Depending on plant size, each sample consisted of

190 approximately 10 to 50 grams of leaves or aboveground plant parts of 3–5 individuals of the same species or multiple 'sun' and 'shade' leaves of the same individual. Dominant agricultural crops (e.g. sorghum, maize, millet, sugarcane) were also sampled. After collection, plant samples were air-dried and subsequently frozen upon arrival in the laboratory. In total, 77 samples of C3 plants and 16 samples of C4 plants were prepared for analysis.

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Topsoils (1–10 cm) were collected during the same campaign (n=47), after removal of the litter layer and by combining 3–5 spatial replicates. This topsoil layer receives most plant input and gets most likely eroded and transported into the river. SPM (n=40) and riverbed sediments (n=37) were collected in a dry (February/March 2015) and wet (July/August 2015) season. For SPM, surface river water (10–80 L) was collected at mid-channel

200 position from a bridge or boat, or 2–3 m out of the riverbank, and filtered on pre-combusted (450 °C, 6 h) GFF filters (0.7 μm, Whatman) using pressurized steel filtration units (after Galy et al., 2007). Additional river depth profiles (2–3 depths, 1–3 sites across river) were sampled in the Godavari delta and in the Middle Godavari (Fig. 1b; site 10 and 28). At these sites, river water was collected at equal increments to the riverbed with a custom-built depth sampler (after Lupker et al., 2011). Riverbed sediments were dredged at each location with a

205 sediment grabber (Van Veen grab 04.30.01, Eijkelkamp) or with a shovel when the water level was low. The fine fraction (≤63 μm) was isolated by sieving for a selection of sites for soils (n=10) and riverbed sediments collected in the wet season (n=25). All samples were frozen upon arrival in the laboratory.

2.3. Elemental and isotopic analysis

210   Prior to analysis, C3 and C4 plants, bulk soils and riverbed sediments were freeze-dried, homogenised and

ground into powder using an agate mortar and pestle or a steel ball-mill. The bulk soils and sediments were

decalcified by overnight treatment with 1 M HCL, then rinsed twice with deionised water and left to dry at 60

°C, following van Helmond et al. (2017). SPM was decalcified by vapour acidification (Komada et al., 2008;

van der Voort et al., 2016). In short, randomly selected, small pieces of GFF filters containing the SPM were

215   placed in pre-combusted (450°C, 6h) Ag capsules and put in a desiccator at 70 °C with 37 % HCl for 72 h and

subsequently dried for minimal 120 h with NaOH. Fine fraction (≤63 μm) soils and sediments were placed in

pre-combusted Ag capsules and decalcified by addition of 100 μL 1 M HCL and then left to dry overnight at 60

°C, following Vonk et al. (2008, 2010).

220   Total Organic Carbon (TOC) content and stable carbon isotopic composition ($\delta^{13}C$) of plants, (bulk) soils,

riverbed sediments and SPM was measured with a Flash 2000 Organic Element Analyser connected to a

Thermo Delta V Advantage isotope ratio mass spectrometer (Thermo Scientific, Italy), at NIOZ (Texel, The

Netherlands). Total Nitrogen (TN) was measured for plants and in non-decalcified bulk soils in the same way.

Integration was performed with Isodat 3.0 software. TN in non-decalcified bulk sediments was measured with a

225   NA 1500 NCS Analyser (Fisons Instruments, United Kingdom), at Utrecht University (Utrecht, The

Netherlands). Fine fraction (≤63 μm) soils and riverbed sediments were analysed with a NC2500 Elemental

Analyser coupled to a Thermo Finnigan DeltaPlus isotope ratio mass spectrometer (ThermoQuest, Germany), at

VU University (Amsterdam, The Netherlands). The results were normalized to certified standards (Acetanilide,

Benzoic acid and Urea at NIOZ and USGS40, USGS41 and IAEA601 at VU University), with an analytical

230   uncertainty <0.1 % for TOC, <0.2 ‰ for $\delta^{13}C$ and <3 % for TN, based on replicate analysis of standards and

samples. The $\delta^{13}C$ values are reported in the standard delta notation, relative to the international Vienna Pee Dee

Belemnite (VPDB) standard for $\delta^{13}C$.

2.4. Precipitation and regression analysis

235   The Mean Annual Precipitation (MAP) in the Godavari basin is used to evaluate the control of drought stress on

plant $\delta^{13}C$ values, as a robust relationship between MAP and $\delta^{13}C$ has been shown to prevail in C3 plants around

the world (Stewart et al., 1995; Diefendorf et al., 2010; Kohn, 2010). We focused on MAP in 2014, the growing

season preceding the sampling campaign in the dry season in early 2015, considering that the majority (>80 %)

of rainfall falls in the wet season and that dry to moist deciduous vegetation is prevalent, which grows new

240 leaves over the wet season and sheds them at the end of the dry period (Kushwaha and Singh, 2005; Elliott et al., 2006). Long-term MAP (1901–2015) was markedly lower in the upper than the lower basin ($p \leq 0.001$) and this contrast became more extreme for the 5-year average and 2014 MAP, which resulted in pronounced drought conditions in the upper basin (Kirkels et al., 2021a) (Fig. S2). The effect of atmospheric CO_2 concentrations on C3 plant $\delta^{13}C$ values is highly debated and may be confounded by changes in MAP, but on geological

245 timescales pCO_2 effects are considered minor or negligible (e.g. Arens et al., 2000; Diefendorf et al., 2015; Kohn, 2016; Schlanser et al., 2020; Stein et al., 2021), so we focused here on MAP. In order to deal with inherent inter- and intraspecies variability in C3 plant $\delta^{13}C$ values in response to MAP, regression analysis was performed on binned C3 plant $\delta^{13}C$ values, rather than on $\delta^{13}C$ values of individual C3 plants.

250 **2.5. Mixing model**

The relative abundance of C3 and C4 plants was estimated using the following linear mass-balance equations (adapted from Philips and Gregg, 2001):

$$\%C3 = [(\delta^{13}C_S - \delta^{13}C_{C4})/(\delta^{13}C_{C3} - \delta^{13}C_{C4})] * 100\% \qquad \text{Eq. (1)}$$

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$$\%C4 = 100 - \%C3 \qquad \text{Eq. (2)}$$

In Eq. (1) $\delta^{13}C_{C3}$ and $\delta^{13}C_{C4}$ represent the $\delta^{13}C$ plant end-member values (‰) and $\delta^{13}C_S$ is the (sub)basin-specific, concentration-weighted $\delta^{13}C$ value (‰) of soil or riverbed sediments.

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To evaluate the impact of C4 and C3 plant end-members on the reconstructed vegetation distribution, we compared four scenarios that included average global and regional vegetation end-members and C3 plant end-members with and without a correction for drought-induced enrichment (i.e., drought correction). This included: (1) Godavari C4 and C3 plant end-members, with drought correction of C3 plant $\delta^{13}C$ (2) Godavari C4 and C3

265 end-members, with no drought correction of C3 plant $\delta^{13}C$ (3) average global C4 (-12 ‰; Koch, 1998; Dawson et al., 2002) and C3 (-28.5 ‰; Kohn, 2010) end-members, and (4) average global C4 (-12 ‰) and the commonly used global C3 (-27 ‰; Cerling et al., 1997; Koch, 1998; Dawson et al., 2002) end-members. Correction of the C3 plant end-member for drought effects was done using the correlation established by regression analysis and the (sub)basin-specific MAP. A $\delta^{13}C$ end-member for Godavari C3 plants with no

270   drought stress was determined using the correlation established by the regression analysis for MAP of 1750 mm

y^{-1}, as above this MAP the C3 plant $\delta^{13}C$ value can be considered constant as there is no water limitation (Kohn,

2010). The plant $\delta^{13}C$ signal is subsequently transferred to soils or sedimentary deposits, where the $\delta^{13}C_{org}$ signal

is assumed to integrate long-term and/or spatial areas and thus incorporate/average the plant $\delta^{13}C$ signal for a

range of precipitation within this period/region.

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2.6. Statistics

Spatial and seasonal differences were evaluated with (Welch's) one and two-way ANOVA, (paired) t-tests and

non-parametric Mann-Whitney and Kruskal-Wallis tests with R software package for statistical computing

(R4.0.4; RStudio, v. 1.2.5033) and SPSS (IBM, v. 27.0.1.0). The level of significance was $p \leq 0.05$. The reported

280   values are the mean ± standard error (SE). Linear regression analysis (Pearson's R) was performed to obtain the

correlation between $\delta^{13}C$ and MAP. Spatial patterns were further investigated with ArcGIS software (ESRI, v.

10.8.1).

3. Results and Discussion

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3.1. Modern C3 and C4 plants in the Godavari basin and control by MAP

The Godavari plants (n=96) showed two distinct groups, with $\delta^{13}C$ values that ranged from -24.3 to -33.2 ‰ for

C3 plants (n=77, 38 different species) and from -12.7 to -15.1 ‰ for C4 plants (n=16, 9 different species)

(Kirkels et al., 2021a) (Fig. 2a,b, 3a). The sampled Godavari plants fell within, but at the lower end of the

290   typical ranges of ~-20 to -37 ‰ and -10 to -16 ‰ for global C3 and C4 plants, respectively (e.g. Cerling et al.,
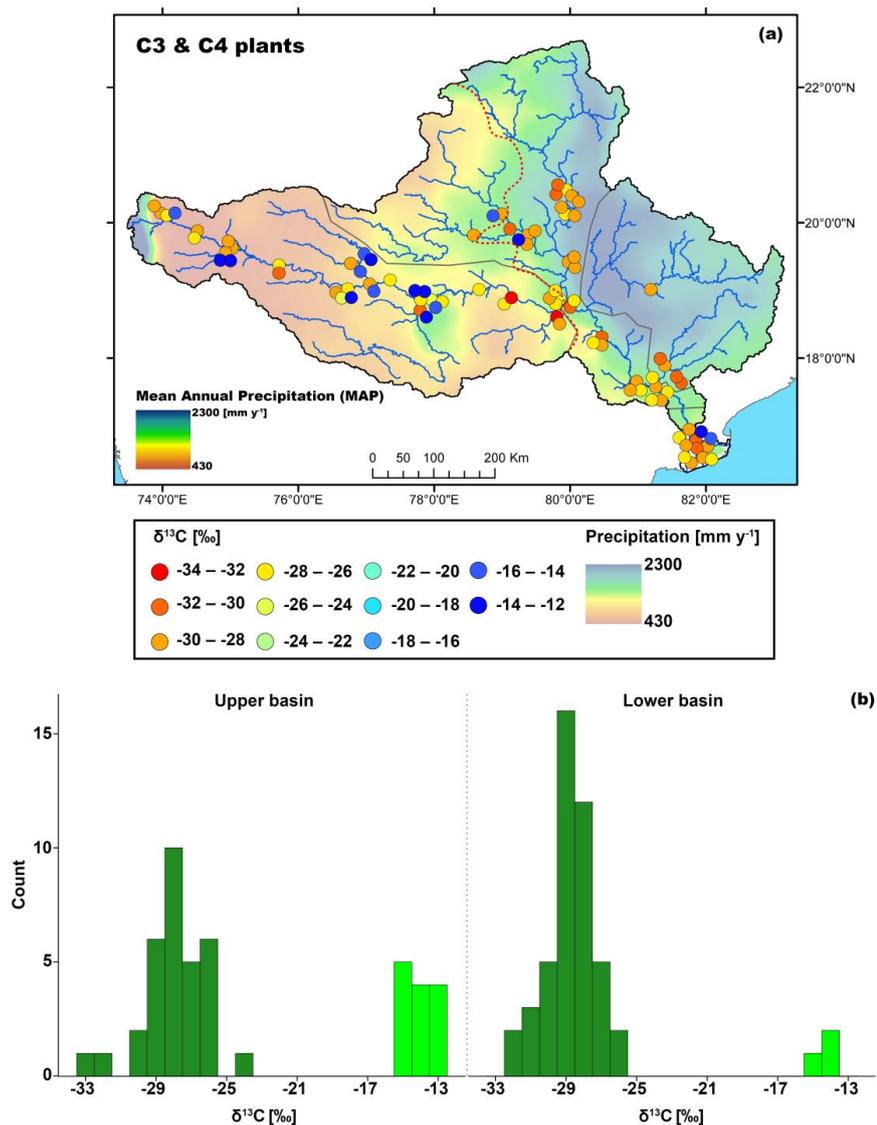
1997; Dawson et al., 2002; Kohn, 2010).

Fig. 2: (a) Map showing the spatial distribution of C3 and C4 plant δ^{13}C values in the Godavari basin. The red dashed line indicates the upper/lower basin boundary. The coloured points refer to the δ^{13}C values and the 30-year average rainfall distribution is shown on the background. (b) Histogram of δ^{13}C values of C3 and C4 plants in the upper and lower Godavari basin.

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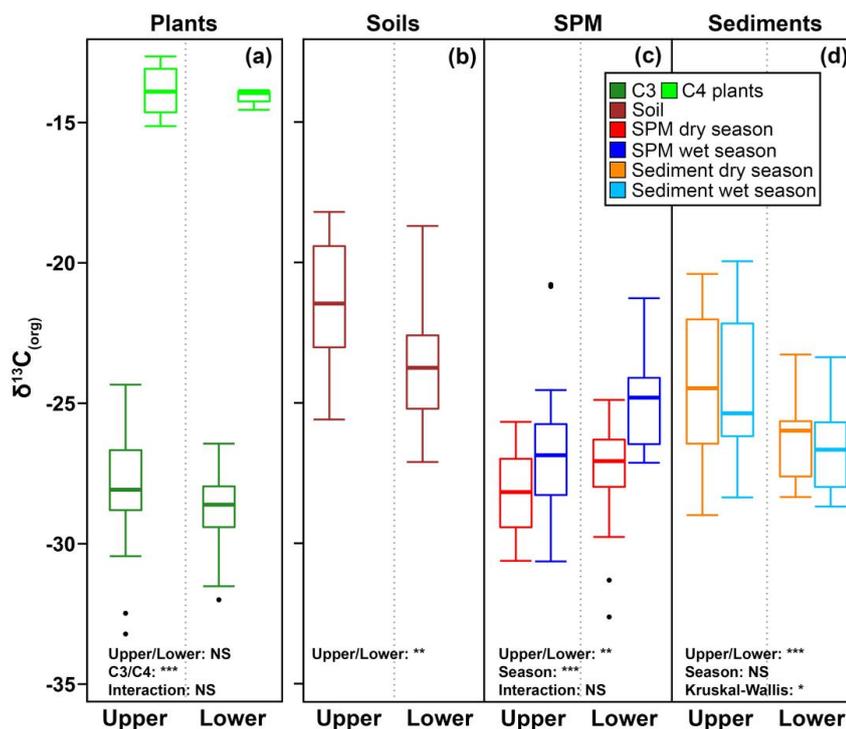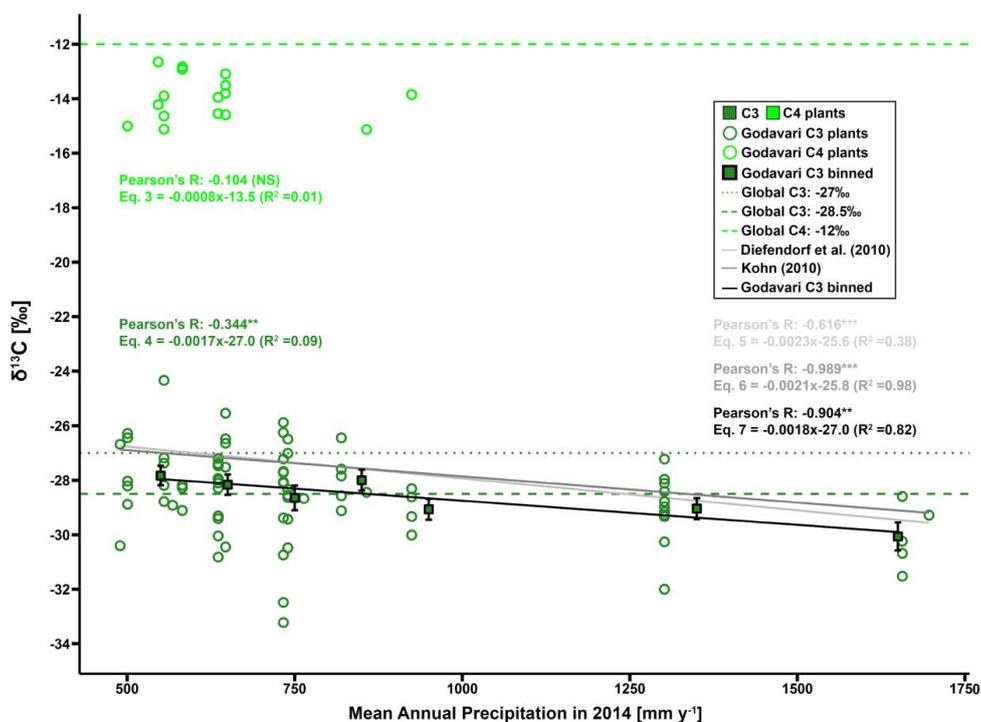**Fig. 3:** Box-and-whisker plot of $\delta^{13}C_{(org)}$ values in C3 and C4 plants, soils, SPM and riverbed sediments
300   collected in the dry and wet season in the upper and lower Godavari basin. The box represents the first
(Q1) and third (Q3) quartiles, and the line in the box represents the median value, the whiskers extent to
1.5*(Q3–Q1) values and outliers are shown as points. Outcomes of the two-way ANOVA are indicated for
plants, soils and SPM, and of non-parametric tests (Mann-Whitney and Kruskal-Wallis) for the
sediments. The level of significance is: (NS) not significant, * $p \leq 0.05$, ** $p \leq 0.01$ and *** $p \leq 0.001$.

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For C4 plants, the plants collected in the Godavari basin had significantly more negative $\delta^{13}C$ values than the
global average estimate (-14.0±0.2 ‰ (±standard error: SE) vs -12.0 ‰; $p \leq 0.001$), revealing a difference
between the local and global average C4 end-members (Eq. 3; Fig. 4). Notably, the C4 crops *Z. mays, S. vulgare*
and *S. officinarum* had similar $\delta^{13}C$ values as a few earlier samples taken in the Godavari basin (Pradhan et al.,
310   2014; Krishna et al., 2015). The Godavari C4 plants showed no significant correlation with MAP (Eq. 3;
Pearson's R = -0.10; p=0.70) (Fig. 4), in contrast to Indian C4 plants from the Gangetic plain which revealed a
positive relation (Basu et al., 2015). Similarly to the Godavari C4 plants, earlier studies found mostly no trend of
C4 plant $\delta^{13}C$ values in response to MAP in dry ecosystems around the globe (<800 mm y^{-1}; Schulze et al.,

1996; Swap et al., 2004), as a result of the CO_2 concentrating mechanism in C4 plants. This adaption to water

315 loss due to evaporation in warm and dry climates may be influenced by leaking of CO_2 from bundle sheath cells

during extreme drought, but functions relatively robustly for a wide range of environmental conditions,

including drought stress (Murphy and Bowman, 2009). Thus, our findings on Godavari C4 plants warrant no

correction of the $\delta^{13}C$ C4 end-member in response to MAP.

Fig. 4: Regression analysis of $\delta^{13}C$ values against MAP (2014, previous growing season) for C3 and C4

plants in the Godavari basin and estimates based on global C3 vegetation models by Diefendorf et al.

(2010) and Kohn et al (2010). For Godavari C3 plants, $\delta^{13}C$ values are also binned per MAP of 100 mm y^{-1},

and the mean ± standard error (SE; whiskers) is presented. The bin of 500–600 mm y^{-1} includes two

samples with a MAP of 489 mm. The solid lines denote the linear fit for the Diefendorf et al. (2010), Kohn

325 (2010) and C3 binned correlation. The Pearson's R, equation and R^2 are given for each correlation.

Global averages for C4 plant $\delta^{13}C$ (-12 ‰) (green dashed) and for C3 plant $\delta^{13}C$ are given. The latter is

represented by a commonly used $\delta^{13}C$ value of -27 ‰ (dark green dotted) that is potentially biased

toward dry ecosystems and a $\delta^{13}C$ value of -28.5 ‰ (Kohn, 2010) (dark green dashed) that includes more

equatorial and mid-latitude C3 biomass.

330

For C3 plants, the Godavari C3 plants differed not significantly from the global average $\delta^{13}C$ value determined

by Kohn (2010) (-28.5±0.2 ‰ vs -28.5 ‰; p=0.90). However, the Godavari C3 plants were significantly more

negative than the average global estimate of -27 ‰ (p≤0.001) (e.g. Cerling et al., 1997; Koch et al., 1998;

Dawson et al., 2002). This difference suggests that the latter value, which is reportedly strongly biased towards

335   dry ecosystems, is not representative of Indian C3 vegetation (Fig. 4). For Godavari C3 plants, the average $\delta^{13}C$

value was significantly less negative in the upper basin (-28.0±0.3 ‰, n=32) than in the lower basin (-28.8±0.2

‰, n=45; p≤0.05) (Fig. 3a), reflecting the gradient in MAP. The most negative subbasin-averaged $\delta^{13}C$ value

for C3 plants was found in the East Tributaries subbasin that received most precipitation ($\delta^{13}C$: -30.1±0.5 ‰,

n=5; MAP: 1530±142 mm y^{-1}), compared to the least negative value in the Upper Godavari that received

340   significantly less precipitation ($\delta^{13}C$: -28.0±0.3 ‰, n=30; p≤0.05; MAP: 593±18 mm y^{-1}; p≤0.01) (Fig. 2a, S2).

Indeed, the individual Godavari C3 plants revealed a significant effect by MAP on their $\delta^{13}C$ values (Eq. 4;

Pearson's R = -0.34; p≤0.0.1) (Fig. 4). This finding supports earlier studies by Diefendorf et al. (2010) and

Kohn (2010) that found a strong control by MAP on C3 plant $\delta^{13}C$ on a global scale and established quantified

relationships between the fractionation of carbon and environmental conditions, including MAP. Application of

345   these established relations for the Godavari basin revealed very similar trends as the Godavari C3 plants (Eq. 5

and Eq. 6, respectively; Fig. 4), although the Kohn (2010) relation was most similar in terms of slope and with a

smaller offset and a higher R^2 than the Diefendorf et al. (2010) correlation. For the Godavari C3 plants, we

noted considerable variation in $\delta^{13}C$ values for any certain amount of precipitation, in line with earlier studies

that found high inter- and intraspecies variation in C3 plant $\delta^{13}C$ values in response to MAP (Ma et al., 2012;

350   Liu et al., 2013, 2014; Basu et al., 2021; Luo et al., 2021). Moreover, the Godavari C3 plants were not evenly

distributed over the entire precipitation range. Together, this resulted in a relatively weak linear correlation with

MAP for the individually measured C3 plants (Eq. 4; R^2 = 0.09).

Subsequent binning of C3 plant $\delta^{13}C$ values revealed a strong and significant correlation with MAP (Eq. 7;

355   Pearson's R = -0.90; p≤0.0.1) (Fig. 4). The slope of this binned C3 plant correlation (i.e., -0.18 ‰ per 100 mm

MAP) could be used to estimate the offset of measured plant $\delta^{13}C$ values to those expected as a function of

MAP. This linear relation applied to the interval of ~500 to 1750 mm y^{-1} precipitation, above which the C3 plant

$\delta^{13}C$ value is assumed to be constant as there is no water limitation (Kohn, 2010). For very dry ecosystems with

MAP <500 mm y^{-1}, non-linear effects on C3 plant $\delta^{13}C$ values need to be considered due to extreme drought

360   stress (Kohn, 2010, 2011; Freeman et al., 2011). Similar to the Godavari C3 plants, a meta-analysis for low

latitude regions (11–30°N) showed that the average C3 plant $\delta^{13}C$ value would change by ~-0.2 ‰ for every 100

mm increase in MAP for the interval of 500–1500 mm y^{-1} (Basu et al., 2019b). We note that although the slope

of the binned Godavari C3 plants was similar to that of the Kohn (2010) correlation, the ~1.5 ‰ offset in

intercept suggests consistently more negative $\delta^{13}C$ signatures for Indian peninsular than average global C3

365   vegetation. Interestingly, within the MAP interval of ~1000–1500 mm y^{-1}, Godavari C3 plants had similar $\delta^{13}C$

values (-29.0±0.4 ‰, n=11; p>0.20) as those collected on the Gangetic plain situated in the Himalayan foreland

(-29.6±0.2‰, n=76; Basu et al., 2015). This similarity corroborates that Indian C3 plants have typically more

negative $\delta^{13}C$ signatures than average global vegetation, with a strong control by MAP, suggesting that these

factors need to be considered for (paleo-)vegetation reconstructions in regions influenced by the Indian

370   monsoon.

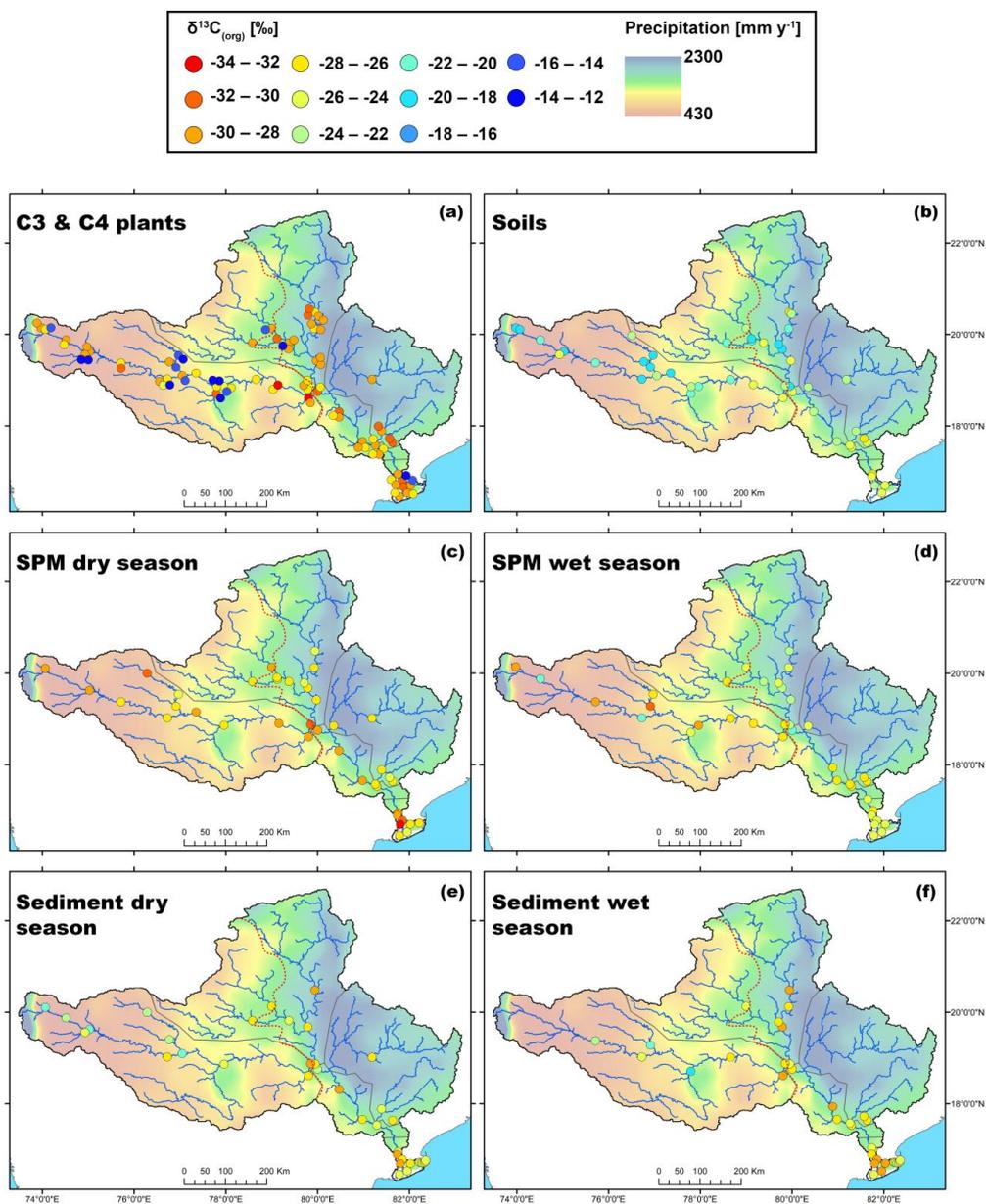### 3.2.   Tracing the plant $\delta^{13}C$ signal along the plant–soil–river continuum

The $\delta^{13}C_{org}$ signal preserved in soil or sedimentary archives depends on the input and integration of the of C3

and C4 plant-derived $\delta^{13}C$ signal, but may also be influenced by hydroclimatic controls on OC degradation and

375   stabilisation mechanisms in soils and in the river (e.g., Carvalhais et al., 2014; Ward et al., 2017; Hein et al.,

2020; Eglinton et al., 2021). The river-transported OC, in the form of suspended (SPM) or riverbed sediments,

may be a complex mixture depending on soil- and plant/litter-derived OC sourcing from particular parts of the

basin following rainfall distributions, soil mobilisation, aquatic primary production and hydrodynamic sorting

processes within the river. This complexity warrants further exploration of the evolution and provenance of the

380    $\delta^{13}C_{org}$ signal along the plant–soil–river continuum in the Godavari basin.

3.2.1. Soils

The Godavari (bulk) soils had on average less negative $\delta^{13}C_{org}$ values in the upper than in the lower basin (-

21.4±0.5 ‰, n=22 vs -23.5±0.5 ‰, n=25; p≤0.01) (Kirkels et al., 2021a) (Fig. 3b, 5b). This isotopic contrast

385   corresponds with the vegetation distribution in the basin, with mixed C3 and C4 vegetation in the upper basin

and more C3 plants in the lower basin (Fig. 1b, 2). The least negative $\delta^{13}C_{org}$ values were found in soils in the

Upper Godavari and North Tributaries (-21.3±0.5 ‰, n=20 and -22.0±0.7 ‰, n=12, respectively) covered by

thorny shrublands, dry deciduous forest and predominantly C4 crops, followed by the Middle Godavari (-

23.5±0.5 ‰, n=4) in a transition zone, and most negative $\delta^{13}C_{org}$ values were found in soils in the East

390   Tributaries and Lower Godavari that were covered by moist/evergreen forests and C3 crops (-24.7±0.6 ‰, n=6

and -25.1±0.6 ‰, n=5, respectively) (Fig. 1b, 5a,b, S3). The $\delta^{13}C_{org}$ values in Godavari soils can thus be

interpreted as a time-averaged signal on decadal to centennial scale that reflects the long-term hydrological

conditions that underlie this vegetation distribution.

395 **Fig. 5: Maps showing the spatial distribution of (bulk) $\delta^{13}C_{(org)}$ values in the Godavari basin for (a) C3 and C4 plants, (b) (bulk) soils, SPM collected in the (c) dry and (d) wet season, and (bulk) riverbed sediments collected in the (e) dry and (f) wet season. The coloured points refer to the $\delta^{13}C_{(org)}$ values and the 30-year average rainfall distribution is shown on the background.**

400 A potential degradation-related enrichment of the plant-derived $\delta^{13}C$ signal in soils may be suggested by the ~5 ‰ difference between C3 plant $\delta^{13}C$ and soil $\delta^{13}C_{org}$ values found in the C3-domianted lower basin (Fig. 3a,b). This offset is relatively large compared to typical 1–3 ‰ enrichment due to soil OC degradation (e.g., Krull et al., 2005; Sreemany and Bera, 2020). Instead of a degradation-induced shift, deforestation since the late 19th century and agricultural expansion with predominantly drought-adapted C4 crops (Ponton et al., 2012; CWC,

405 2014; Pradhan et al., 2014) may have contributed to more C4 input and thus enrichment of topsoil $\delta^{13}C_{org}$ values. Regardless, soil OC degradation and stabilisation processes in tropical to subtropical biomes may have an opposite effect on soil $\delta^{13}C_{org}$ signals. In mixed C3/C4 ecosystems, C4 plant-derived OC has been shown to degrade more rapidly than C3 plant-derived OC (Wynn, 2007; Wynn and Bird, 2007). However, C4-derived OC has also been shown to be preferentially incorporated into fine fractions where it is better protected against

410 degradation, whereas C3-derived OC is preferentially added to the coarse fraction thus leaving it less protected (Bird and Pousai, 1997; Wynn and Bird, 2007). In the Godavari basin, Usman et al. (2018) reported similar ^{14}C ages for soil OC in the upper and lower basin that have different C3 and C4 plant covers, suggesting that the nett effect of preferential degradation (more young OC) and stabilisation (more old OC) is minor. Indeed, extensive degradation of C4 plant-derived OC is unlikely, given that the upper basin with most C4 plants contains clay-

415 rich, fine particles from weathering of the Deccan basalts (Giosan et al., 2017; Usman et al., 2018; Kirkels et al., 2021b), which would contribute to stabilise the C4-derived OC. Fine soils (≤63 µm) sampled in the upper basin had on average slightly less negative $\delta^{13}C_{org}$ values than the bulk soils (-19.7±1.0 ‰, n=8 vs -21.1±0.7 ‰, n=8; p≤0.09), pointing towards preferential stabilisation of C4-derived OC in the fine fraction (Fig. S4). This result highlights that differences between bulk and fine size fractions need to be considered for the $\delta^{13}C_{org}$ signal

420 preserved in soils.

3.2.2. Suspended particulate matter

For SPM collected in the Godavari River, $\delta^{13}C_{org}$ values were consistently more negative in the dry than in the wet season, and more negative in the upper than the lower basin, but there was no significant interaction

425   between the seasonal and upper/lower basin effects (Fig. 3c). In the dry season, SPM $\delta^{13}C_{org}$ values were

significantly more negative than in Godavari soils (-27.8±0.3 ‰, n=40 vs -22.5±0.4 ‰, n=47; p≤0.001), making

predominant soil–to–river input in this season unlikely (Fig. 3b,c, 5b,c). Instead, the quiescent waters behind

dams and very low river discharge favour aquatic primary production (Pradhan et al., 2014). Freshwater

phytoplanktonic matter usually has negative $\delta^{13}C_{org}$ values. The isotopic fractionation between phytoplankton

430   and dissolved inorganic carbon (DIC) has been estimated at ~-23 ‰, resulting in typical phytoplankton-derived

$\delta^{13}C_{org}$ values between -31 and -35 ‰ in the Ganges-Brahmaputra as well as at the start of the dry season in the

Godavari River (e.g., Aucour et al., 2006; Galy et al., 2008b; Krishna et al., 2015). The observation of slightly

less negative $\delta^{13}C_{org}$ values in our SPM collected at the end of the dry season may be explained by eutrophic

conditions due to agricultural/wastewater inputs which fuelled intense aquatic production in the Godavari River

435   (Balakrishna and Probst, 2005; Pradhan et al., 2014). During periods of high aquatic productivity, the

fractionation factor becomes smaller (up to 0‰; Torres et al., 2012) and more ^{13}C gets incorporated into the

phytoplanktonic biomass. Aquatic primary production is also supported by the strong increase in %OC from

soils to dry season SPM (0.8±0.1 %, n=47 vs 11.4±1.1 %, n=39; p≤0.001), since phytoplankton-derived SPM is

typically high in %OC (Aucour et al., 2006; Galy et al., 2008b). Interestingly, $\delta^{13}C_{org}$ values of dry season SPM

440   became less negative near the Godavari's outflows into the Bay of Bengal (Fig. 5c, S3), suggesting mixing of

freshwater and estuarine/marine phytoplankton in the delta, where the latter has typically less negative $\delta^{13}C_{org}$

values (i.e., -22.8 to -24.4 ‰; Dehairs et al., 2000; Krishna et al., 2015; Gawade et al., 2018). This result is also

consistent with changes in electrical conductivity and water isotopic signature ($\delta^{18}O$) that showed seawater

intrusion in the delta in the dry season (Kirkels et al., 2020b).

445

In the wet season, there was a strong isotopic contrast between SPM in the upper and lower basin (-26.4±0.8 ‰,

n=14 vs -25.0±0.3 ‰, n=26; p≤0.001) (Fig. 3c). The negative $\delta^{13}C_{org}$ values in the upper basin suggest

continuous aquatic production, allowed by the limited rainfall and abundant dams in this region that created

standing waters and facilitated year-round aquatic productivity (Pradhan et al., 2014; Kirkels et al., 2020b). A

450   few sites in the upper basin had remarkably less negative $\delta^{13}C_{org}$ values, suggesting that some local soil or C4

plant input occurred at locations where agricultural fields with exposed topsoils were situated next to the river

(Fig. 5d). In the lower basin, wet season SPM $\delta^{13}C_{org}$ values varied from -21.3 to -27.1 ‰ and fell within the

range of bulk soils in this region (-18.7 to -27.1 ‰). This resemblance suggests contribution of soil-derived OC

to wet season SPM in the lower basin. Water isotopic signatures and rainfall distributions confirmed substantial

455   discharge in the wet season and identified the Weiganga/Pranhita rivers in the North Tributaries and the

Indravati River in the East Tributaries subbasin as major source areas (Kirkels et al., 2020b). It is generally

assumed that the high flow velocity and turbidity in the wet season would limit aquatic production as well as

OC degradation during fluvial transport (Balakrishna and Probst, 2005; Acharyya et al., 2012). In contrast, Galy

et al. (2008b) showed for the Ganges-Brahmaputra that ~50 % of the wet season SPM derived from the upper

460   reaches of the basin was degraded during river transit and replaced by local input from the plains. Quantifying

the extent of OC degradation during fluvial transport is thus not straightforward as it depends on the stability of

OC in the river e.g., protected by mineral-associations or unbound and on its residence time in a specific basin

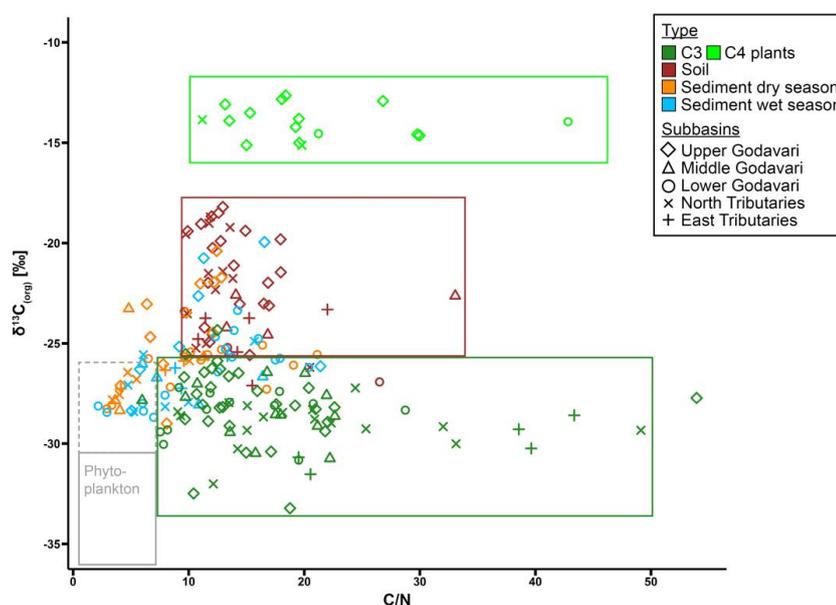(e.g., Ward et al., 2017; Eglinton et al., 2021).

465   **3.2.3. Riverbed sediments**

For riverbed sediments collected in the Godavari River, $\delta^{13}C_{org}$ values were consistently less negative in the

upper than in the lower basin (-24.4±0.6 ‰, n=21 vs -26.6±0.2 ‰, n=53; p≤0.001), but there was no significant

seasonal effect (Fig. 3d, 5e,f). The latter suggests that riverbed sediments represented a season-integrated $\delta^{13}C_{org}$

signal, versus SPM that showed more seasonal variation. A Kruskal-Wallis test revealed that sediments

470   collected in the upper basin in the dry season and those collected in the lower basin in the wet season were

significantly different (-24.4±0.7 ‰, n=13 vs -26.6±0.3 ‰, n=29; (Bonferroni-corrected) p≤0.05) (Fig. 3d).

However, riverbed sediments showed a high spatial variation in $\delta^{13}C_{org}$ values, which ranged from -20.0 to -29.0

‰ in the upper and -23.3 to -28.7 ‰ in the lower basin (Fig. 5e,f). The strong control by upper/lower basin

location on sediment $\delta^{13}C_{org}$ values corresponds to the vegetation distribution with more C4 plants and drought-

475   stressed C3 plants in the upper basin, leading to less negative plant $\delta^{13}C$ and soil $\delta^{13}C_{org}$ values to be transferred

to the riverbed sediments. Riverbed sediment $\delta^{13}C_{org}$ values were consistently more negative than soil $\delta^{13}C_{org}$

values in the upper and lower basin (Fig. 3b,d), suggesting input from an additional, depleted source, likely

phytoplankton- or C3 plant-derived OC.

480   Possible contributions of additional sources can be further explored using a source diagram, where the relation

between $\delta^{13}C_{org}$ values and C/N ratios reveals source-specific distributions which help to identify the

provenance of OC sources in aquatic ecosystems (e.g., Lamb et al., 2006). For the Godavari basin, riverbed

sediments plotted close to Godavari C3 plants, albeit at lower C/N ratios (Fig. 6). This may suggest that slightly

degraded C3 plant-derived OC is selectively transported by/stored in the lower basin sediments. The lower C/N

485   ratios suggest slight degradation of this OC, although there could also be a small contribution of phytoplankton-derived OC that settled onto the riverbed. Notably, the upper basin sediments plotted generally closer to the upper basin soils, suggesting an inherited soil $\delta^{13}C_{org}$ signal in these sediments, as soil input was diminished by limited rainfall in this region during our sampling campaigns.

Fig. 6: Source plot with relation between $\delta^{13}C_{org}$ values and C/N ratios for C3 and C4 plants, (bulk) soils and riverbed sediments collected in the dry and wet season in the Godavari basin. C/N ratios are retrieved from Kirkels et al. (2021c). Freshwater phytoplankton is defined for Indian monsoonal rivers in the dry season (solid line) (C/N: 1–8; data from Balakrishna and Probst, 2005; $\delta^{13}C_{org}$: -31 – -35 ‰; data

495   **from Aucour et al., 2006; Galy et al., 2008b; Krishna et al., 2015), and based on SPM collected at the end of the dry season in this study (dashed line).**

3.2.4. Hydrodynamic sorting

Fluvial transport of fine particles is of particular interest as they are generally enriched in OC and their size

500   facilitates effective offshore transport to sedimentary deposits (e.g. Bianchi et al., 2018). At the same time, coarse- and fine-grained particles have been shown to be sensitive to hydrodynamic sorting effects within the river, resulting in depth-specific OC distributions and/or preferential transport of certain OC components (Galy

et al., 2008b; Bouchez et al., 2014; Feng et al., 2016; Repasch et al., 2022). Similar to the Godavari soils, riverbed sediments collected in the wet season revealed distinctly less negative $\delta^{13}C_{org}$ values for the fine

505   fractions than the corresponding bulk sediments (-24.4±0.3 ‰, n=25 vs -25.7±0.4 ‰, n=25; p≤0.001) (Fig. 5f, S4). This difference corresponds to previous findings that C4 plant-derived OC is preferentially associated with finer fractions whereas C3 plant-derived OC is contained in the coarser fraction of soils (Bird and Pousai, 1997; Wynn and Bird, 2007) and river(-dominated) sediments (e.g., France-Lanord and Derry, 1994; Bianchi et al., 2002). This finding suggests differential transport of C3- and C4-derived OC in the fine and bulk Godavari

510   riverbed sediments.

Furthermore, wet season SPM collected along river depth profiles in the Middle and Lower Godavari showed in general more negative $\delta^{13}C_{org}$ values with depth (Fig. S5). Also, the riverbed sediments dredged at each location had more negative $\delta^{13}C_{org}$ values than the SPM in the water column above. This trend in $\delta^{13}C_{org}$ values suggests

515   that more negative, C3-derived OC was transported in coarse-grained sediments and SPM near the riverbed, similar to findings at peak discharge for the Himalayan-derived Ganges-Brahmaputra (Galy et al., 2008b) and the Rio Bermejo draining the central Andes (Repasch et al., 2022). Alternatively, a depleted phytoplankton source was unlikely given that the high flow velocity and turbidity in the monsoon season prevent light penetration and generally limit algae production (Balakrishna and Probst, 2005; Acharyya et al., 2012). Indeed,

520   analysis of lignin, a macromolecule that is exclusively produced by plants, revealed a C3-derived 'woody undercurrent' in Godavari riverbed sediments collected in the wet season in the lower basin (Pradhan et al., 2014), similar to earlier findings in the Madre de Dios and Mississippi rivers with strong seasonal variability in their hydrology (Bianchi et al., 2002; Feng et al., 2016). This information corroborates differential transport of fine and coarse-grained particles and their associated OC sources in the Godavari basin. This insight has

525   important implications for the $\delta^{13}C_{org}$ signal that is finally exported to sedimentary deposits in the marine realm, where C4-derived OC with less negative $\delta^{13}C_{org}$ values may be overrepresented, as fine fractions are transported farther offshore and in greater quantities than coarse-grained particles (Goñi et al., 1997, 1998; Bianchi et al., 2002).

530   ### 3.3. C3/C4 vegetation reconstruction and end-member analysis

Mixing model estimates based on the $\delta^{13}C_{org}$ signal in Godavari soils revealed a high %C4 plants in the Upper Godavari subbasin (45±4 %; scenario 1) and in general in the upper basin (45±3 %), that decreased toward the

lower basin (32±3 %), from the North Tributaries (42±5 %), Middle Godavari (33±4 %) and East Tributaries (30±4 %) to the lowest %C4 plants in the Lower Godavari subbasin (20±4 %) (Fig. 7a). This result is consistent

535 with the vegetation structure in the Godavari basin, with a mixed C3/C4 vegetation in the dry upper basin and dominant C3 vegetation in the lower basin (Fig. 1b,c, 2) (Giosan et al., 2017; Usman et al., 2018). Pollen assemblages of the modern vegetation corroborate these findings, as they found ~50% *Poaceae* (here C4 grasses) in the upper basin based on surface sediments of the Lonar crater lake (Prasad et al., 2014; Riedel et al., 2015), and ~30 % *Poaceae* for the whole Godavari basin based on marine surface sediments in front of the

540 Godavari mouth in the Bay of Bengal (Zorzi et al., 2015), which was close to our estimate of 39±3 % C4 plants for the whole basin. Notably, the estimated %C4 plants in the C3-dominated lower basin was relatively high (32±3 %), and may have been influenced by degradation-related enrichment of the soil $\delta^{13}C_{org}$ signal leading to a potential overestimation of the %C4 plants. The C3/C4 abundances based on the $\delta^{13}C_{org}$ signal of riverbed sediments collected in the wet season also reflected the vegetation gradient (Fig. 7b, 1b,c, 2). The estimated

545 %C4 plants was consistently lower for riverbed sediments than for soils (-1 to -22 %; scenario 1), particularly in the North Tributaries (-20 %) and the Middle Godavari (-22 %) subbasins. Hydrodynamic sorting and preferential transport of C3 plant-derived OC in the coarse-grained riverbed sediments may have influenced the C3/C4 plant estimates, resulting in a potential underestimation of the %C4 plants in these basins.

550 In order to assess the influence of drought stress and the use of region-specific plant $\delta^{13}C$ end-members on C3/C4 vegetation mixing model estimates, we compared four scenarios (Fig. 7). Comparing Godavari-specific end-members with and without drought correction of the C3 plant $\delta^{13}C$ end-member (scenario 1 and 2, respectively) revealed that the estimated %C4 plants was 2–10 % higher without this correction for MAP, suggesting a potential overestimation of the %C4 plants. Notably, drought correction of the C3 plant $\delta^{13}C$ end-

555 member became increasing important with decreasing MAP, from a minor (≤2 %) difference in the estimated %C4 plants above 1500 mm y^{-1}, to 4–6 % for the interval of ~1000–1500 mm y^{-1} and up to 6–10 % for ~500–1000 mm y^{-1} (Fig. 7).
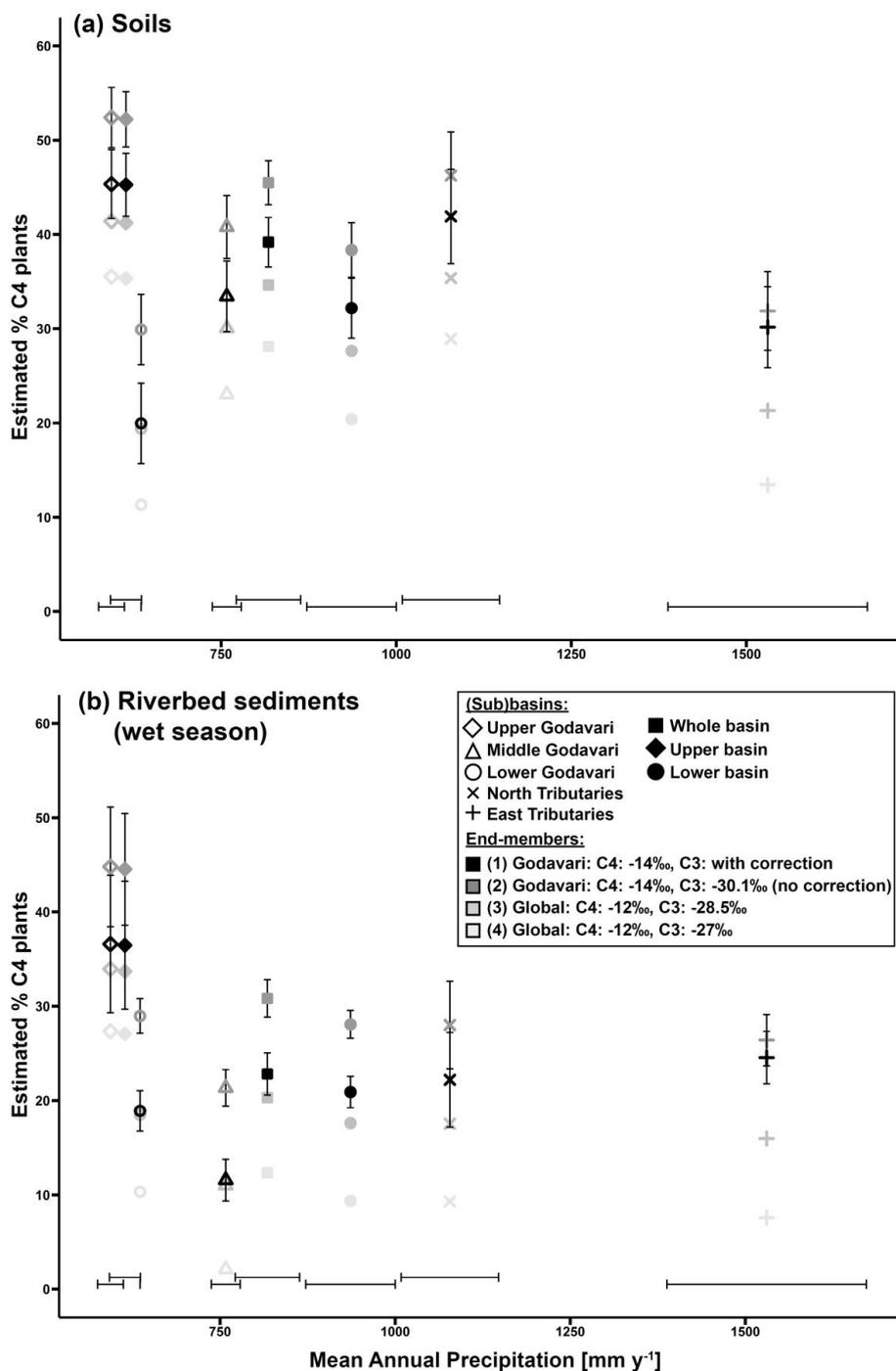
Fig. 7: The estimated proportion (%) of C4 plants determined by a linear mixing model versus MAP for
560   **different (sub)basins, based the OC-weighted $\delta^{13}C_{org}$ signal in (a) soils and (b) riverbed sediments**
collected in the wet season. The whiskers represent ± standard error (SE). Four scenarios are included:
(1) Godavari C4 and C3 plant end-members, with drought correction of C3 plant $\delta^{13}C$ (2) Godavari C4
and C3 end-members, with no drought correction of C3 plant $\delta^{13}C$ (3) average global C4 (-12 ‰; Koch,
1998; Dawson et al., 2002) and C3 (-28.5 ‰; Kohn, 2010) end-members, and (4) average global C4 (-12
565   **‰) and the commonly used C3 (-27 ‰; Cerling et al., 1997; Koch, 1998; Dawson et al., 2002) end-**
members. For scenario (2) the mean $\delta^{13}C$ value for Godavari C3 plants with no drought stress (i.e., -30.1
‰) was determined at MAP of 1750 mm y^{-1} using Eq. 7 (see Fig. 4).

Comparing mixing model results for Godavari-specific end-members with drought correction and global
570   average end-members for C4 plants (-12‰) and C3 plants (-28.5 ‰; based on Kohn, 2010) (scenario 1 and 3,
respectively) revealed that the estimated %C4 plants was 0–9 % lower for the latter, suggesting a potential,
minor underestimation. The estimated %C4 plants was 5–9 % lower for the wetter North and East Tributaries,
while the difference was minor (≤5 % lower) for the other subbasins as well as for the whole, upper and lower
basin. Interestingly, comparing Godavari-specific end-members with drought correction and global average end-
575   members for C4 plants (-12 ‰) and the commonly used estimate of -27 ‰ for C3 plants (Cerling et al., 1997;
Koch, 1998; Dawson et al., 2002) (scenario 1 and 4, respectively), showed that the estimated %C4 plants was 9–
17 % lower for the latter, suggesting a substantial underestimation when using these global end-members. This
would result in a %C4 plants of only 35±3 % for the upper basin, where C4 grasses and crops are most abundant
(Pradhan et al., 2014; Prasad et al., 2014; Riedel et al., 2015; Giosan et al., 2017) and only 20±3 % C4 plants in
580   the C3-dominated lower basin. Finally, the underestimation of %C4 plants was even larger (17–19 %) for all
(sub)basins when comparing the latter global end-members with Godavari-specific end-members without
drought correction (scenario 4 and 2, respectively). Together, these different estimates highlight the importance
of prior knowledge of the plant $\delta^{13}C$ signal in regional C3 and C4 vegetation to select those end-member values
that are best representative of the region-specific vegetation. Our results from the Godavari basin suggest that
585   the use of region-specific plant $\delta^{13}C$ end-members and drought correction of the C3 end-member in mixing
models need to be considered for the interpretation of $\delta^{13}C_{org}$-based (paleo-)vegetation reconstructions in
monsoonal regions.

4. Conclusion – Implications for (paleo-)vegetation reconstructions

590   Our analysis of contemporary C3 and C4 plants, soils and sediments from the Godavari basin has resulted in

three clear recommendations for the reconstruction of vegetation composition using δ^{13}C. Firstly, C3 and C4

plants sampled in the Godavari basin in the CMZ in peninsular India had more negative δ^{13}C signatures than

average global vegetation. Rather, our samples closely resembled observations of other plants on the Indian

subcontinent and thus represented a region-specific plant δ^{13}C signature. In particular in tropical to subtropical

595   regions with generally high vegetation biomass and more negative δ^{13}C C3 plant end-members, the use of

regional plant end-members would yield a higher %C4 plants compared to global average end-members. For the

Godavari basin, using region-specific plant end-members resulted in a ~0–9 % higher estimated %C4 plants

compared to a global average C3 end-member (i.e., -28.5 ‰) that roughly approximated the Godavari C3

vegetation (Table 1). However, the estimated %C4 plants was ~9–19 % higher using regional plant end-

600   members compared to global average end-members that had an offset from the Godavari end-members of ~2 ‰

for C4 and ~3 ‰ for C3 plants (i.e., -12 and -27 ‰, respectively). It is therefore recommended to evaluate a

potential offset between the average δ^{13}C value of the regional and global vegetation, to accurately establish

δ^{13}C plant end-members.

605   **Table 1: Summary of processes/factors influencing the C3/C4 mixing model estimates**

Mixing model parameters	Compared to	Estimated %C4 plants
Regional plant end-members	Global C4 (-12‰) and C3 (-28.5‰)	≈ / ↑[1]
	Global C4 (-12‰) and C3 (-27‰)	↑
Drought correction	Godavari C3 plants without correction	↓
	Godavari C4 plants without correction	–
Soil-river continuum	**Specification**	
Soil degradation	More degradation C3-derived OC	↑
	More degradation C4-derived OC	↓
In-river OC processing	More phytoplankton production	↓
	More riverine OC degradation	↑
Hydrodynamic sorting	More coarse particles	↓
	More fine particles	↑

[1] With/without drought correction of the regional end-member

Secondly, it is well-known that C3 plant δ^{13}C values become less negative with decreasing amounts of

precipitation, which may result in an underestimation of the %C4 plants. Incorporating a drought correction for

610   the C3 plant end-member resulted in a 2–10 % lower %C4 plants for the different Godavari subbasins, but the

extent of this effect will be most pronounced in C3-dominated ecosystems with low MAP. For the Godavari

basin, we established that the impact of drought correction on the estimated %C4 plants was relatively minor

(<6 %) for C3-domianted areas that received 1000–1500 mm y^{-1} but that this effect became larger (6–10 %) for areas with ~500–1000 mm y^{-1} rainfall and mixed C3 and C4 vegetation.

615

Thirdly, C3/C4 vegetation reconstructions based on the $\delta^{13}C_{org}$ signal preserved in soils, riverine and/or marine sediments should take potential alterations in this signal along the plant–soil–river continuum into account. Differential degradation and stabilisation of C3- and C4-derived OC in soils and sediments, as well as phytoplankton contributions in the river and hydrodynamic sorting effects that separate coarse and fine fractions and their associated OC may result in a complex interplay affecting the mixing model estimates (Table 1). For the Godavari basin, our results suggest that the $\delta^{13}C$ signatures of C3 and C4 plants are relatively well-maintained throughout the transport chain, so $\delta^{13}C_{org}$ values of soils and riverbed sediments can be used as proxy for C3/C4 vegetation distributions.

625 Finally, our results in the Godavari basin highlight that precipitation plays a crucial role in the reconstruction of (paleo-)vegetation by influencing plant $\delta^{13}C$ end-members, OC decomposition rates and driving OC transport by rivers. Our results thereby support the assumption that in monsoon-influenced regions, wetter conditions/periods require no drought correction of the C3 plant end-member and generate more erosion and rapid transport downstream, which generally limits degradation during river transit. This implies that the $\delta^{13}C_{org}$ signal exported 630 to sedimentary deposits would reflect the C3/C4 vegetation distribution in the basin.

Data availability

Research data associated with this article are available in the open access Pangaea Data Repository (Kirkels et al., 2022; accessible via: https://doi.pangaea.de/10.1594/PANGAEA.940189). Background geochemical data on 635 the Godavari basin and TN data (Kirkels et al., 2021; accessible via: https://doi.pangaea.de/10.1594/PANGAEA.937965) are also available in the Pangaea Data Repository.

Author contributions

FMSAK, HJB, SB and FP conceptualised this research. FMSAK, MOU and FP planned the fieldwork and 640 carried it out with help from CRTM and SB. FMSAK, PCH, CRTM and MTJM performed laboratory analyses. FMSAK prepared the manuscript, HJB and FP revised and edited the draft with contributions from the other co-authors.

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