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ORIGINAL PAPER

Residue decomposition and soil carbon priming in three contrasting soils previously exposed to elevated CO_2

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Abstract

The effects of elevated atmospheric carbon dioxide (eCO_2) on belowground processes are known to occur directly and indirectly via plants. However, the long-term impact of eCO_2 on biochemical properties and processes of agricultural soils in the absence of plants is unclear. The current study investigated whether residue decomposition and the subsequent 'priming effect' on soil organic C (SOC) mineralisation were altered in three contrasting soils previously exposed to either ambient CO_2 (aCO_2; 390 ppm) or eCO_2 (550 ppm) using free-air CO_2 enrichment (FACE) for 4 years. Surface soils (0–2 cm) of calcisol, luvisol and vertisol were amended (0.5% *w* w^{-1}) with ^{13}C-labelled field pea (*Pisum sativum* L. cv. PBA; C:N 20) or wheat (*Triticum aestivum* cv. Yitpi; C:N 60) residues, and CO_2 derived from soil ($CO_{2\ soil}$) and residue ($CO_{2\ residue}$) were quantified over the 96-day incubation study. Field pea decomposition was not affected by soil type or CO_2 history, and the decomposition of wheat was similar in all soils previously exposed to aCO_2. However, wheat decomposition was increased in luvisol (14.4%), decreased in vertisol (26.7%) or not affected by eCO_2 in the calcisol. The relative differences between soils were largely driven by labile N content and the potential to replenish inorganic N via mineralisation. Notably, priming was not influenced by residue type, despite their contrasting N content. In the calcisol, lower basal C mineralisation and C priming under eCO_2 were not explained by lower N concentrations. A greater priming effect in field pea–amended vertisol previously exposed to eCO_2 than aCO_2 was likely due to overcoming the N limitation on microbial C mineralisation in this soil. Overall, the study highlighted that C mineralisation was mainly determined by soil N status, less by CO_2 history and least by residue quality (C:N ratio).

Keywords Crop residue · Priming effect · Free-air CO_2 enrichment (FACE) · Carbon and nitrogen cycling

Introduction

Elevated atmospheric carbon dioxide (eCO_2) concentrations resulting from anthropogenic emissions are predicted to rise to 550 ppm in the middle of the current century (IPCC 2014). Plant growth is known to be stimulated under eCO_2 due to enhanced photosynthesis and greater water-use efficiency, which ultimately increases soil organic matter inputs (Ainsworth and Long 2005; Norby and Zak 2011). In general, legumes exhibit greater responses to eCO_2 than non-legumes assuming that N_2-fixation is not constrained by other factors (Ainsworth and Rogers 2007; Butterly et al. 2016a). Elevated CO_2 decreases the N concentration of non-legume plant tissue (Kimball et al. 2002), increases the C:N ratio, and this occurs

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even with added N fertiliser (Butterly et al. 2015). Changes in the amounts and quality of soil organic matter inputs are thought to alter C and N cycling in soils.

The overall impact of eCO_2 on soil C storage and soil fertility will depend on the balance between soil organic matter input and its decomposition. Many studies have shown that eCO_2 does not increase SOC stocks over time (Cheng et al. 2012; van Groenigen et al. 2014). Hence, faster decomposition under eCO_2 limits soil C storage (Carney et al. 2007; van Groenigen et al. 2014). In particular, recently added soil C is likely to have increased turnover under eCO_2 (Cheng et al. 2012) particularly when N abundance is high (van Groenigen et al. 2006). Over time, the net increase in N demand may deplete soil N (de Graaff et al. 2007). If fertiliser N is not increased to meet the demand, this progressive N limitation is expected to exert a negative feedback on soil organic matter inputs and their turnover (Luo et al. 2004).

Most studies which have examined eCO_2 effects on residue decomposition have focussed on two key aspects. Firstly, residues produced under eCO_2 tend to have greater amounts of structural components and for non-legumes a greater C:N ratio (Norby et al. 2001; Yang et al. 2011). Secondly, eCO_2 indirectly alters belowground processes via the plant rhizosphere (Cheng and Johnson 1998). These changes in residue quality and biochemical processes in the rhizosphere are likely to influence residue decomposition. The plant rhizosphere is likely to dominate these processes due to labile C inputs and either providing N to or competing for N against the microbial decomposer community (Butterly et al. 2016c). Although numerous studies have been undertaken, many did not utilise suitable approaches to adequately separate the effects of eCO_2 history on the decomposition of added and existing soil C pools. Faster decomposition of perennial grass (Carrillo et al. 2014) and wheat (Cheng et al. 2012) residues have been observed under eCO_2. In contrast, other studies have shown that residue decomposition is reduced or unaffected by eCO_2 (Marhan et al. 2008; Torbert et al. 2000; Viswanath et al. 2010).

In addition to the decomposition of residues themselves, residues may enhance or decrease the mineralisation of existing soil organic matter, the 'priming effect' (Carrillo et al. 2014; Sulman et al. 2014), although the impact of CO_2 history on soil C priming is not clear (Reinsch et al. 2013). Soil microbes in ecosystems exposed to eCO_2 are thought to have a greater capacity to mineralise more recalcitrant organic materials such as crop residues (Carney et al. 2007; de Graaff et al. 2009). However, conclusive evidence of this has not yet been demonstrated, particularly in the absence of a living plant. Soils in many dryland agricultural systems can remain without plants for considerable time between growing seasons. It is not clear whether eCO_2 history impacts C and N cycling during these periods.

The aim of the current study was to determine whether a 4-year exposure of three contrasting soil types to either ambient CO_2 (aCO_2) or eCO_2 (CO_2 history) altered the decomposition of crop residues and the subsequent mineralisation of soil organic C (SOC) and C priming. Specifically, we aimed to ascertain whether inherent changes in these processes occurred in the absence of a living plant. Few studies have examined more than one soil type (Procter et al. 2014). Importantly, we investigated the effect of CO_2 history in three major soil types of dryland cropping systems from south-eastern Australia that have undergone the same agronomic management and environmental conditions. We hypothesised that (a) residue decomposition and priming effects would be greater for field pea residues (higher N content) and soils with a greater capacity to supply N to the decomposer community, and (b) primed C would be greater in soils previously exposed to eCO_2 than aCO_2 due to greater soil organic matter inputs (18.5, 26.5 and 14.8% more aboveground biomass for Calcarosol, Chromosol and Vertosol, respectively (2009–2012).

Materials and methods

SoilFACE facility and sampling details

This study utilised soils from the soil free-air carbon dioxide enrichment (SoilFACE) facility at Agriculture Victoria Research, Horsham, in the Victorian Wimmera region of Australia (36°44′ 57″ S, 142° 06′ 50″ E). Intact mesocosms (30 cm wide, 100 cm deep) of three major soil types of dryland cropping systems from south-eastern Australia were exposed to either ambient CO_2 (aCO_2; 390 ppm) or elevated CO_2 (eCO_2; 550 ppm) concentration for 4 years using FACE (Mollah et al. 2009). The annual rainfall during the study period ranged from 288 (2010) to 544 mm (2012) and was mostly lower than expected (~ 440 mm $year^{-1}$) for the Mediterranean climate in this area. A full description of the site is outlined in Butterly et al. (2015). Briefly, calcisol (loam sand), luvisol (silty loam) and vertisol (clay) (WRB 2014) or calcarosol, chromosol and vertosol (Isbell 1996) were managed in an annual cropping rotation (field pea in 2009, wheat in 2010, field pea in 2011, wheat in 2012, except that canola was grown in 2012 in the calcisol).

In February 2013, surface soils of each mesocosm were sampled by taking a single soil core (5 cm diameter × 2 cm long) with a total of 12 samples obtained for each soil type (3 mesocosms × 4 replicates). The soils were kept on ice in the dark until the following day when soils were combined to form a composite sample for each soil type, sieved (≤ 2 mm) and then stored at 4 °C for the incubation experiment. Initial characterisation of the soil chemical properties were

performed using air-dried samples (Table 1). Importantly, carbonates were not detected in any soil, hence the calcisol did not contain carbonates in the soil layer used in this study. Therefore, total C is equivalent to organic C in all soils. Soil texture was characterised by determining the particle-size distribution using a Laser Particle Size Analyser (Malvern Mastersizer 2000, Worcestershire, UK) following dispersion of soil (~ 10 g) with 10 ml of 0.164 M $Na_6P_5O_{18}$ in 800 ml of RO water.

Crop residues

Two ^{13}C-labelled residues were generated under field conditions in 2011 as outlined in Butterly et al. (2015). Field pea (*Pisum sativum* L. cv. PBA Twilight) and wheat (*Triticum aestivum* cv Yitpi) were grown with 40 mg N kg^{-1} (added as $Ca(NO_3)_2$) and pulse-labelled with $^{13}CO_2$ by temporarily placing plants with an airtight chamber seven times during the growing season. The frequency of labelling was increased through time to match the rate of plant growth. Aboveground biomass was collected at physiological maturity, grain removed, and the remaining residues were ground (< 2 mm) using a centrifugal mill (ZM200, Retsch GmbH, Haan, Germany). The residues had C to N ratios of 20 and 60 for field pea and wheat, respectively.

Incubation experiment

Soils were air-dried immediately prior to the start of the incubation experiment to facilitate residue incorporation and accuracy of initial measurements. The gravimetric water contents were determined following oven drying at 105 °C overnight. Soils were amended with field pea or wheat residues at 0.5% *w*/*w* (5 mg g^{-1}) or non-amended (nil). Twenty-five grams of each was lightly packed (1.2 g cm^3) into PVC cores (3.7 cm ID × 5 cm high) fitted with nylon mesh at the base and placed in 1-l glass jars containing a vial with 9 ml H_20 to maintain humidity (Butterly et al. 2009). Soils were wet to 70% field capacity (θ_g) with reverse osmosis (RO) H_2O. The θ_g used for calcisol, luvisol and vertisol were 0.12, 0.46 and 0.44 g g^{-1}, respectively. Then, separate vials containing 15 ml 0.5 M NaOH solution (alkali traps) were immediately added to absorb headspace CO_2; the jars were closed and incubated at 25 °C in the dark. Alkali traps were exchanged with fresh NaOH at 6, 12, 27, 55 and 96 days. All soil cores were destructively sampled at 96 days for chemical and biological measurements. Overall, the study consisted of a completely randomised design with 2 CO_2 concentrations × 3 soil types × 3 residues × 3 replicates ($n = 54$). In addition to experimental cores, 8 g of each soil and residue combination were added to centrifuge tubes (3 cm ID × 11.5 cm high) and placed into individual jars as previously described, except that NaOH traps were not added and these were vented regularly to avoid increases in ambient CO_2 concentration. These soil tubes were used to quantify temporal inorganic N concentrations at 0, 15 and 96 days.

Carbon mineralisation

Carbon mineralisation was quantified using alkali absorption (Zibilske 1994) but with some modification. Briefly, 2 ml of each trap, 2 ml of 1.72 M $BaCl_2$ and two drops of phenolphthalein (1% *w*/*v* in ethanol) were titrated with 0.25 N HCl using a digital burette (Brand Titrette, Germany). Traps from jars without soil or residue were used as blanks. Cumulative CO_2 release (μg CO_2-C g^{-1} soil) was calculated as the sum of C mineralised at 6, 12, 27, 55 and 96 days. A 4-ml aliquot of each trap was neutralised with 0.5 M HCl and 4 ml of 1 M $SrCl_2$ was added to form $SrCO_3$. Solutions were centrifuged at 1100*g* for 2 min, resuspended in 9 ml of RO water before being re-centrifuged. This was repeated four times. Precipitates were oven-dried (75 °C, 48 h), and the ^{13}C abundance ($\delta^{13}C$ Pee Dee Belemnite, PDB) was quantified using isotope ratio mass spectrometry (IRMS) (Hydra 20–22, SerCon, Crewe, UK). The proportion of CO_2 derived from residue ($\propto CO_{2\ residue}$) was calculated using the following equation:

$$\propto CO_{2residue} = \left(\delta^{13}C\ \text{residue–amended soil} - \delta^{13}C\ \text{soil}\right) / \left(\delta^{13}C\ \text{residue} - \delta^{13}C\ soil\right)$$

where $\delta^{13}C$ residue-amended soil and $\delta^{13}C$ soil are the $\delta^{13}C$ of the precipitates formed from residue- and non-amended soil columns, and $\delta^{13}C$ residue is the $\delta^{13}C$ value of the added residue. The amount of CO_2 derived from residue ($CO_{2\ residue}$) was

Table 1 Total C, total N, C to N ratio and ^{13}C abundance of calcisol, luvisol and vertisol soils after 4 years of exposure to ambient CO_2 (aCO_2, 390 ppm) or elevated CO_2 (eCO_2, 550 ppm) concentrations

Soil	Total C[a] (g kg^{-1})		Total N[a] (g kg^{-1})		C:N		$\delta^{13}C$ PDB[a]	
	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2
Calcisol	5.6	7.8	0.6	0.8	10.1	9.8	− 23.3	− 23.1
Luvisol	52.6	48.8	4.8	4.4	11.0	11.1	− 27.8	− 27.8
Vertisol	13.3	11.8	1.3	1.2	10.2	9.8	− 22.7	− 23.0

[a] Quantified by isotope ratio mass spectrometry using Pee Dee Belemnite (PDB) as a reference

calculated by multiplying $\propto CO_{2\ residue}$ by the cumulative CO_2 released at each sampling time. The amount of CO_2 derived from the soil ($CO_{2\ soil}$) was then calculated as the difference between cumulative CO_2 and $CO_{2\ residue}$ at the end of the experiment. The additional CO_2-C released as a result of residue addition, 'primed C', was then calculated as the difference $CO_{2\ soil}$ of residue-amended treatments and the respective non-amended controls. It is acknowledged that the pulse-labelling approach used here may result in a non-uniform distribution of ^{13}C within plant parts, but constant labelling of plants is cost prohibitive. A greater enrichment of more labile residue components may underestimate $CO_{2\ residue}$ during the initial phase of decomposition and this could overestimate $CO_{2\ soil}$ and primed C.

Extractable organic C and N, microbial biomass C and N

Soil tubes were extracted for extractable organic C (EOC), extractable organic N (EON) and inorganic N as described in the following, stored at − 20 °C and analysed with samples from soil cores at the end of the study.

Microbial biomass C (MBC) and N (MBN) were quantified immediately at sampling (96 days) using 24-h fumigation-extraction according to Vance et al. (1987) using moist soil with the following modifications. Soil (8 g dry wt) was extracted with 32 ml 0.5 M K_2SO_4 by shaking end-over-end for 1 h and centrifuged at 1100*g* for 3 min. Extracts were passed through a Whatman #42 filter and stored at − 20 °C until analysis.

Organic C concentrations in fumigated and non-fumigated extracts were determined using wet oxidation (Vance et al. 1987) as outlined in Heanes (1984). Briefly, 2 ml of extract, 2 ml of 1 N $K_2Cr_2O_7$ and 4 ml of 98% H_2SO_4 were reacted at 135 °C for 30 min, allowed to cool, made up to 50 ml with RO water and the C concentration was determined spectrophotometrically at 600 nm. Two analytical replicates were performed. Sucrose solutions with known concentrations were included as standards. The C contained within digested non-fumigated samples was denoted EOC. Microbial biomass C was estimated as the difference between fumigated and non-fumigated samples using a k_{EC} of 0.37 (Joergensen 1996; Sparling and Zhu 1993).

Total N contained within fumigated and non-fumigated extracts was determined using the wet-oxidation method of Cabrera and Beare (1993). Specifically, 2.5 ml of extract and digestion mix (25 g $K_2S_2O_8$ and 15 g H_3BO_4 in 50 ml of 3.75 M NaOH adjusted to 1 l with H_2O) (1:1) were autoclaved (121 °C) for 30 min and stored at 4 °C until analysis. Solutions with known concentrations of Urea were included as controls. The inorganic N ($NH_4^+ + NO_x^-$) concentration of non-fumigated extracts was determined using a flow injection analyser (Lachat QuickChem 8500 Series II, USA). The N contained within digested non-fumigated samples was denoted AEON. MBN was estimated as the difference between fumigated and non-fumigated samples using a k_{EN} of 0.54 (Brookes et al. 1985).

Statistical analyses

A three-way analysis of variance (ANOVA) in a completely randomised design was used to test the effects of CO_2 history × soil × residue on MBC, MBN, MBC:N, EOC, AEON, $CO_{2\ soil}$, $CO_{2\ residue}$ and primed C. In addition, repeated measures ANOVA was used to test the effects of CO_2 history × soil × residue on total C mineralisation at 6, 12, 27, 55 and 96 days and the concentrations of inorganic N at 0, 15 and 96 days. In each case, differences between means were tested using least significance difference (LSD) test at $P = 0.05$.

Results

Total C mineralisation

The relative differences in basal C mineralisation between the non-amended soils were related to their C and N contents (Fig. S1) (Table 1). The luvisol had between ~ 4 (aCO_2 and eCO_2) times more C than the vertisol and 9.4 (aCO_2) and 6.3 (eCO_2) times more C than the calcisol, respectively. Similarly, N concentrations were 3.7 times greater in the luvisol than in the vertisol and 8–5.5 times greater than in the calcisol, i.e. the C to N ratio of the soils was similar. Consequently, C mineralisation data were normalised for C content (mg CO_2-C g soil C^{-1}) to account for differences in initial soil C contents. All descriptions of soil C mineralisation and parameters calculated using these data (e.g. C priming) hereafter refer to normalised values.

Overall, basal C mineralisation in the non-amended (nil) treatments was similar between vertisol and luvisol and greater in the calcisol (Fig. 1). The higher rates of CO_2 release during the first week of the experiment were expected due to the rewetting effect since soils were not pre-incubated at a stable water content prior to the start of the experiment. For the non-amended soils, CO_2 history had a disparate effect on CO_2 release for each soil. Specifically, eCO_2 significantly ($P = 0.02$, LSD 8.7) decreased total C mineralisation in the non-amended calcisol (− 19.6%, 13.1 mg CO_2-C g soil C) and vertisol (−29.7%, 15.8 mg CO_2-C g soil C) and increased total C mineralisation in the luvisol (28.9%, 9.7 mg CO_2-C g soil C) (two-way ANOVA, CO_2 × soil). However, due to the large effect of residue, CO_2 treatments in the luvisol were not significantly ($P < 0.05$) different when all treatments were included (three-way ANOVA, CO_2 × soil × residue) (data not shown).

A significant ($P = 0.011$) CO_2 × soil × residue interaction on C mineralisation was observed using repeated measures

ANOVA (Fig. 1). Particularly, the relative differences between aCO_2 and eCO_2 treatments were greater for wheat than field pea residue and also greatest for calcisol than vertisol and least for luvisol, although there was no significant ($P < 0.05$) effect of CO_2 on total C mineralisation in the field pea-amended vertisol. Furthermore, total C mineralisation in the calcisol was almost two times than that of the vertisol and four times than that in the luvisol. For all soils, field pea-amended soils had the greatest total C mineralisation at the first three sampling times (6, 12 and 27 days) but wheat-amended soils generally produced similar cumulative CO_2 than field pea–amended soils at the end of the 96-day study.

Residue decomposition

Residue decomposition ($CO_{2\ residue}$) expressed per unit of soil (μg CO_2-C g $soil^{-1}$) was not greater for field pea (C:N 20) than wheat (C:N 60) despite it having a higher N content, contrary to our hypothesis (Table 2). A significant ($P = 0.001$) CO_2 × soil × residue interaction on $CO_{2\ residue}$ was observed at the end of the study, whereby there was no effects of CO_2 history or soil type on $CO_{2\ residue}$ in field pea–amended soils. $CO_{2\ residue}$ was greater under eCO_2 than aCO_2 in wheat-amended luvisol (14.4%), lower under eCO_2 than aCO_2 in wheat-amended vertisol (26.7%) and not affected by CO_2 history in the calcisol (Table 2). Interestingly, these differences in $CO_{2\ residue}$ between wheat-amended soils were due to changes in $CO_{2\ residue}$ under eCO_2, as $CO_{2\ residue}$ in wheat-amended soils was not different under aCO_2 (Table 2). Around 2 mg C g $soil^{-1}$ was added as a residue. As mentioned previously, the variation in residue decomposed between treatments was smaller than expected and was only 12.4% (248 μg CO_2-C g $soil^{-1}$). The significant ($P = 0.001$) CO_2 × soil × residue interaction on %residue decomposed occurred with greater decomposition of wheat than field pea, except under eCO_2 in the calcisol

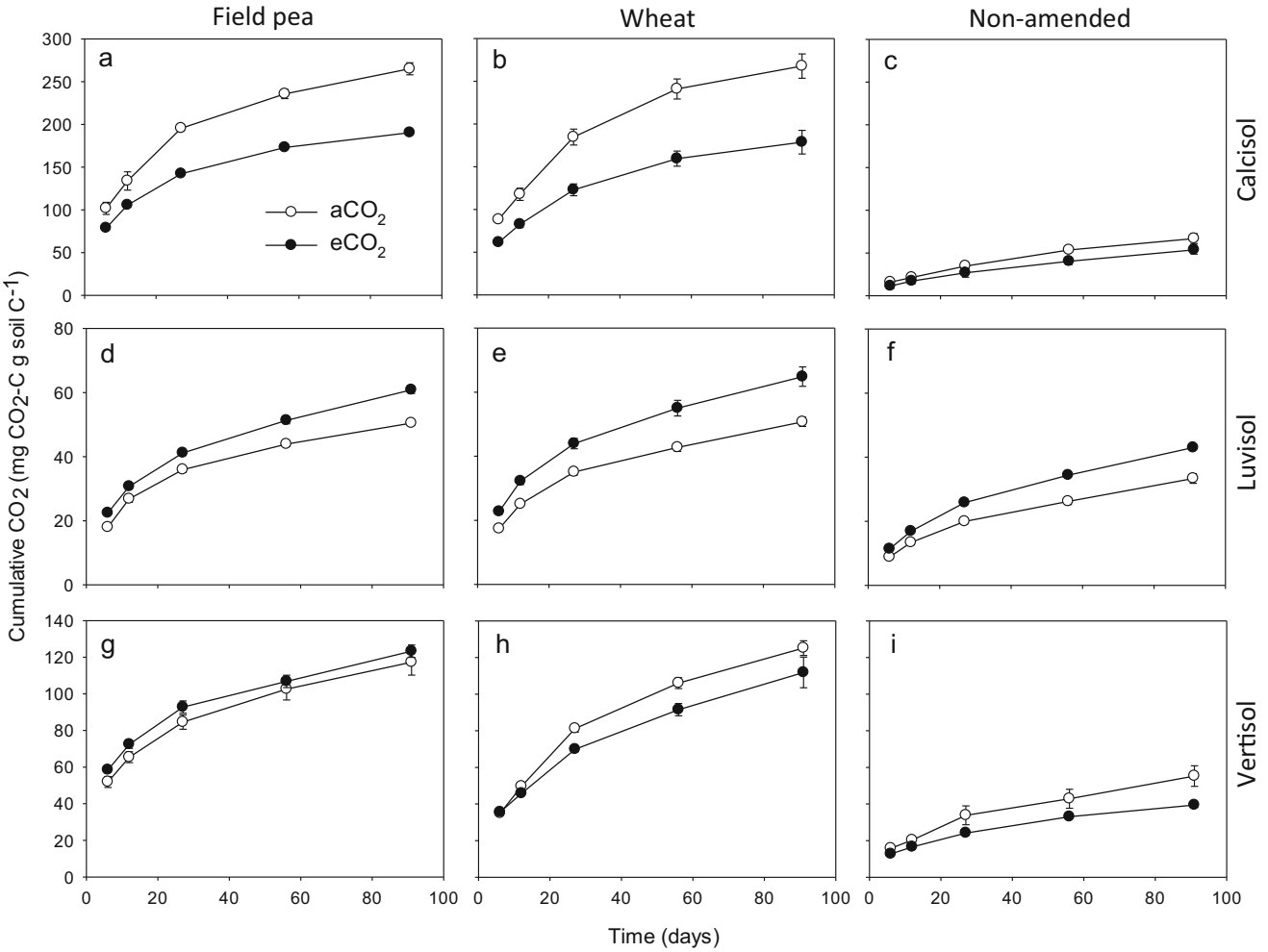

Fig. 1 Cumulative CO_2 (mg CO_2-C g soil C^{-1}) in calcisol (**a**, **b**, **c**), luvisol (**d**, **e**, **f**) and vertisol (**g**, **h**, **i**) soils previously exposed to ambient CO_2 (aCO_2, 390 ppm) (white circles) or elevated CO_2 (eCO_2, 550 ppm) (black circles) concentrations for 4 years and incubated with field pea (**a**, **d**, **g**) or wheat (**b**, **e**, **h**) residues or non-amended (**c**, **f**, **i**). Error bars are the standard error of the mean ($n = 3$) where greater than the symbols

and vertisol. Also, wheat decomposition was 26.7% less under eCO_2 than aCO_2 in the vertisol and 14.4% greater under eCO_2 than aCO_2 in the Luvisol, but not affected by CO_2 in other treatments (Table 2).

Soil C decomposition and priming effects

At the end of the study, $CO_{2\ soil}$ showed a significant ($P < 0.001$) CO_2 × soil × residue interaction (Table 3). Overall, soil type had the greatest impact on $CO_{2\ soil}$ than CO_2 history, with 1.8 and 3.4 times more $CO_{2\ soil}$ in the calcisol than the luvisol and vertisol, respectively. Specifically, $CO_{2\ soil}$ was lower under eCO_2 than aCO_2 in field pea–amended (28.3%) and wheat-amended (33.2%) calcisol and the non-amended vertisol (29.1%), but was not different in other treatments. The significant effect of residue was such that residue-amended soils had significantly greater $CO_{2\ soil}$ than non-amended soils, but there was no significant ($P < 0.05$) difference in $CO_{2\ soil}$ between the field pea and wheat residues (Table 3). Given the large differences in $CO_{2\ soil}$ between soil types, two-way ANOVA (CO_2 × residue) were also performed separately for each soil which highlighted significant effects of CO_2 history with greater $CO_{2\ soil}$ in luvisol and lower $CO_{2\ soil}$ in vertisol and calcisol under eCO_2, except in the field pea–amended vertisol and non-amended calcisol (data not shown).

In contrast to other parameters, a significant ($P < 0.001$) CO_2 × soil interaction on primed C was observed, without any effect of residue (Table 3). This was not expected and the two residues with contrasting C:N ratios were included in the study to test this effect. Overall, primed C was greatest in calcisol, followed by vertisol and least in luvisol consistent with $CO_{2\ soil}$. Primed C was lower under eCO_2 than aCO_2 in field pea–amended (30.8%) and wheat-amended calcisol (37.7%) and not affected by CO_2 history in the chromosol. In contrast, primed C was greater under eCO_2 than aCO_2 in the field pea–amended vertisol (35.5%).

Inorganic N

Inorganic N concentrations were approximately doubled in the luvisol than in the vertisol and calcisol at the beginning of the study (0 days) (Table 4). In addition, significant

Table 2 CO_2 derived from residue ($CO_{2\ residue}$) and residue decomposed (%) in calcisol, luvisol and vertisol soils previously exposed to ambient CO_2 (aCO_2, 390 ppm) or elevated CO_2 (eCO_2, 550 ppm) concentrations for 4 years and incubated with field pea or wheat residues or non-amended (nil). Not significant (n.s.), *, ** and *** indicate $P > 0.05$, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ for three-way repeated measures analyses of variance (CO_2 × soil × residue)

Soil	Residue	$CO_{2\ residue}$ (μg CO_2-C g^{-1})		Residue decomposed (%)	
		aCO_2	eCO_2	aCO_2	eCO_2
Calcisol	Field pea	514	519	25.7	26.0
	Wheat	607	572	30.4	28.6
Luvisol	Field pea	502	499	25.1	25.0
	Wheat	593	678	29.7	33.9
Vertisol	Field pea	445	466	22.3	23.3
	Wheat	587	430	29.3	21.5
	LSD	66		3.3	
Significance level					
	CO_2	n.s.		n.s.	
	Soil	***		***	
	Residue	***		***	
	CO_2 × soil	**		**	
	CO_2 × residue	n.s.		n.s.	
	Soil × residue	*		*	
	CO_2 × soil × residue	**		**	

Least significant difference (LSD) ($P < 0.05$)

Table 3 CO_2 derived from soil ($CO_{2\ soil}$) and soil C priming (primed C) in calcisol, luvisol and vertisol soils previously exposed to ambient CO_2 (aCO_2, 390 ppm) or elevated CO_2 (eCO_2, 550 ppm) concentrations for 4 years and incubated with field pea or wheat residues or non-amended (nil). Not significant (n.s.), * and *** indicate $P > 0.05$, $P \leq 0.05$ and $P \leq 0.001$ for three-way repeated measures analyses of variance (CO_2 × soil × residue)

Soil	Residue	$CO_{2\ soil}$ (mg CO_2-C g C^{-1})		Primed C (mg CO_2-C g C^{-1})	
		aCO_2	eCO_2	aCO_2	eCO_2
Calcisol	Field pea	265	190	198	137
	Wheat	268	179	201	125
	Nil	67	54	–	–
Luvisol	Field pea	51	61	17	18
	Wheat	51	65	17	22
	Nil	33	43	–	–
Vertisol	Field pea	117	123	62	84
	Wheat	125	112	70	73
	Nil	55	39	–	–
	LSD	18		21	
Significance level					
	CO_2	***		***	
	Soil	***		***	
	Residue	***		n.s.	
	CO_2 × soil	***		***	
	CO_2 × residue	*		n.s.	
	Soil × residue	***		n.s.	
	CO_2 × soil × residue	***		n.s.	

Least significant difference (LSD) ($P < 0.05$)

Table 4 Inorganic N (N_i) concentrations (mg kg^{-1}) at 0, 15 and 96 days in calcisol, luvisol and vertisol soils previously exposed to ambient CO_2 (aCO_2, 390 ppm) or elevated CO_2 (eCO_2, 550 ppm) concentrations for 4 years and incubated with field pea or wheat residues or non-amended (nil). Not significant (n.s.), * and *** indicate $P > 0.05$, $P \leq 0.05$ and $P \leq 0.001$ for three-way repeated measures analyses of variance (CO_2 × soil × residue)

Soil	Residue	0 days		15 days		96 days	
		aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2
Calcisol	Field pea	8	11	12	17	30	33
	Wheat	7	9	5	5	23	18
	Nil	6	8	24	28	30	30
Luvisol	Field pea	43	17	59	32	63	46
	Wheat	44	16	41	13	50	40
	Nil	45	14	70	28	56	46
Vertisol	Field pea	8	6	14	9	26	19
	Wheat	8	5	6	5	15	6
	Nil	7	4	16	10	25	15
	LSD			6			
Significance level							
	CO_2			*			
	Soil			***			
	Residue			***			
	CO_2 × soil			***			
	CO_2 × residue			n.s.			
	Soil × residue			***			
	CO_2 × soil × residue			n.s.			

Least significant difference (LSD) ($P < 0.05$)

($P < 0.001$) CO_2 × soil as well as soil × residue interactions were observed. In particular, luvisol and vertisol previously exposed to eCO_2 had lower inorganic N concentrations than aCO_2 soils, and there was no effect of CO_2 on inorganic N in the calcisol (Table 4). Lower inorganic N concentrations were expected due to greater crop growth and N-uptake under eCO_2. Wheat-amended soils showed a considerable reduction in inorganic N concentration from 0 to 15 days likely due to microbial N immobilisation. Except for vertisol under eCO_2, inorganic N concentrations increased during subsequent incubation (15–96 days); however, they remained significantly lower than field pea–amended and non-amended soils at the end of the study. In contrast, inorganic N concentrations in field pea–amended and non-amended soil increased with incubation time. At the end of the study, luvisol and vertisol exposed to eCO_2 had 22 and 42% less inorganic N than aCO_2 soils, respectively. Furthermore, wheat-amended calcisol, luvisol and vertisol had 33, 15 and 52% less inorganic N than field pea–amended or non-amended soils, which were not different from each other at the end of the study.

Microbial biomass C and N

Microbial biomass C was 6.5 and 6 times greater in the luvisol and vertisol than the calcisol, respectively (Table 5). A significant ($P = 0.003$) CO_2 × soil × residue interaction on MBC was observed, whereby MBC was 201% greater in non-amended calcisol and 37% lower in the non-amended vertisol under eCO_2 than aCO_2. Compared with respective non-amended controls, MBC was significantly greater in wheat-amended calcisol (166%) previously exposed to aCO_2 and in wheat-amended luvisol (26%) and field pea–amended (57%) and wheat-amended (47%) vertisol previously exposed to eCO_2 (Table 5).

Microbial biomass N was 3 and 2.8 times greater in the luvisol and vertisol than the calcisol, respectively (Table 5). Generally, changes in MBN were proportional to MBC and as such MBC:N was not effected by any treatment (Table 5). A significant ($P = 0.039$) CO_2 × soil × residue interaction on MBN was observed, in which MBN was increased in field pea–amended soils, except for eCO_2 calcisol and aCO_2 vertisol and also increased for wheat-amended eCO_2 luvisol. Except for field pea–amended chromosol, MBN was lower under eCO_2 than aCO_2, although this was only significant for non-amended luvisol (52%) and vertisol (30%).

Extractable organic C and N

Extractable organic C concentrations were similar between the calcisol and vertisol and two times greater in the luvisol (Table 5). Furthermore, EOC decreased during the study except in the non-amended calcisol and field pea-amended and non-amended vertisol (data not shown). At the end of the study, EOC was 1.5 times greater in the luvisol than the other two soils (Table 5). A significant ($P = 0.003$) CO_2 × soil × residue interaction whereby differences in EOC concentrations were much greater eCO_2 than aCO_2, and the effects of the residue amendments depended on the soil. EOC concentrations were greater under eCO_2 than aCO_2 in wheat-amended calcisol (47%) and lower in non-amended calcisol (62%) and wheat-amended luvisol (26%). The lower EOC under eCO_2 in non-amended calcisol resulted in large differences in EOC in this treatment compared to the residue-amended soils (~ 66%). Wheat-amended luvisol previously exposed to eCO_2 had 26% less EOC than the other residue and CO_2 treatments.

Extractable organic N concentrations were similar between the calcisol and vertisol and 3.9 times greater in the luvisol (Table 5). The significant ($P = 0.002$) CO_2 × soil × residue interaction on AEON was such that AEON was increased by field pea residue, decreased by wheat residue in all soils and lower under eCO_2 than aCO_2 in the luvisol (17%) and vertisol (30%). Specifically, AEON concentrations were 21, 10 and 34% lower in wheat-amended calcisol,

Table 5 Microbial biomass C (MBC) and N (MBN), MBC to MBN ratio (MBC:MBN), extractable organic C (EOC) and N (AEON) in calcisol, luvisol and vertisol soils previously exposed to ambient CO_2 (aCO_2, 390 ppm) or elevated CO_2 (eCO_2, 550 ppm) concentrations for 4 years and incubated with field pea, wheat residues or non-amended (nil). Not significant (n.s.), *, ** and *** indicate $P > 0.05$, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ for three-way repeated measures analyses of variance (CO_2 × soil × residue)

Soil	Residue	MBC (mg kg^{-1})		MBN (mg kg^{-1})		MBC:MBN		EOC (mg kg^{-1})		AEON (mg kg^{-1})	
		aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2	aCO_2	eCO_2
Calcisol	Field pea	87	116	51	31	1.7	3.9	112	126	87	99
	Wheat	171	112	32	24	5.4	7.4	90	132	67	63
	Nil	64	193	26	15	2.5	11.5	115	44	81	85
Luvisol	Field pea	386	463	54	72	11.1	6.6	189	183	329	255
	Wheat	465	475	77	70	6.1	6.8	190	139	262	226
	Nil	418	365	77	37	5.4	11.3	172	187	290	250
Vertisol	Field pea	409	469	83	76	4.9	6.2	117	91	76	55
	Wheat	480	430	85	66	5.7	6.5	111	91	50	30
	Nil	390	244	73	51	5.3	4.8	111	104	70	50
	LSD	93		21		–		43		13	
Significance level											
	CO_2	n.s.		***		n.s.		n.s.		***	
	Soil	***		***		n.s.		***		***	
	Residue	**		**		n.s.		n.s.		***	
	CO_2 × soil	n.s.		n.s.		n.s.		n.s.		***	
	CO_2 × residue	*		*		n.s.		n.s.		n.s.	
	Soil × residue	*		n.s.		n.s.		n.s.		*	
CO_2 × soil × residue		**		*		n.s.		**		**	

Least significant difference (LSD) ($P < 0.05$)

luvisol and vertisol, respectively compared with respective non-amended soils. However, AEON was 23% greater in field pea–amended calcisol previously exposed to eCO_2 and 16% greater in field pea–amended luvisol previously exposed to aCO_2. Notably, AEON was 14% greater in field pea–amended eCO_2 than aCO_2 calcisol but was not significantly ($P < 0.05$) affected by CO_2 history for the other residue treatments.

Discussion

This study provides fundamental data on the effects of CO_2 history on residue decomposition and soil C priming in the absence of a living plant, hence without confounding effects of other CO_2-induced impacts on C mineralisation such as differences in plant root biomass, root activity and soil moisture often encountered by other studies. In dryland cropping systems, soils can be plant-free (fallow) for substantial periods, especially during the summer (3–4 months). Residue decomposition and soil C priming in three contrasting cropping soils with either an aCO_2 history or exposed to eCO_2 (FACE) for 4 years were mainly controlled by soil N status, less by CO_2 history and least by residue quality (C:N ratio).

Effect of eCO_2 on C mineralisation

Absolute differences in C mineralisation were largely due to differences in total C, and relative differences between treatments were highlighted by normalising the CO_2 data for C content. This showed that basal C mineralisation was similar for luvisol and vertisol and greatest for the calcisol. Hence, C mineralisation per unit of soil C, often referred to as C turnover, was much faster in the calcisol likely due to its coarse texture. The clay content of the calcisol was 5.5% compared with 18.3 and 51.1% for the luvisol and vertisol, respectively. It is well known that soils with low clay content, such as the calcisol, lack the ability to retain soil C and this is consistent with its low total C (0.56%) content (Sanderman et al. 2014; Six et al. 2000).

The study showed that eCO_2 increased C mineralisation in the non-residue-amended luvisol (28.9%) but reduced C mineralisation in the vertisol (28.8%) and calcisol (19.6%) relative to soils previously exposed to aCO_2. Greater release of CO_2 from the plant-soil systems under eCO_2 is commonly observed due to greater labile C inputs via stimulated photosynthesis (Kou et al. 2007; Pendall et al. 2001). This root-derived organic matter, referred to as rhizodeposits, includes exudation of compounds from living roots, as well as cellular material generated through root growth and root turnover

(Allard et al. 2006). In the current study, most of this labile organic material may have already been mineralised since soils were collected during the summer period between annual cropping rotations. Nevertheless, the relative differences in C mineralisation observed may reflect disparate chemical composition of SOC but are most likely due to differences in the ability of soil microbial community to mineralise SOC.

The finding that eCO_2 history increased MBC in the calcisol but decreased it in the luvisol and vertisol is consistent with previous studies using similar soils (Butterly et al. 2016b; Jin et al. 2013). Greater MBC under eCO_2 was expected and consequently lead to greater decomposition of both SOC and residues (de Graaff et al. 2006; Drissner et al. 2007). Many studies have shown that eCO_2 does not increase SOC stocks over time (Cheng et al. 2012; van Groenigen et al. 2014). Hence, the greater C inputs under eCO_2 are offset by increases in C mineralisation (Carney et al. 2007). In the current study, differences in MBC were poorly related to basal SOC mineralisation. In calcisol, MBC in non-residue-amended aCO_2 soils was extremely low and was three times greater in soils exposed to eCO_2. Greater biomass with increased MBC:MBN under eCO_2 indicated that microbes were C-limited under aCO_2 and lower C mineralisation could have been due to preferential C assimilation (into biomass) rather than its utilisation for energy production (released as CO_2). In the vertisol, the reduction in MBC under eCO_2 and lower SOC mineralisation could be explained by greater competition between soil microbes for N. Microbial growth is known to be inhibited under N-limited conditions (Blagodatskaya et al. 2010). In the luvisol however, extractable organic N and inorganic N concentrations were double than that of the vertisol, and greater SOC mineralisation under eCO_2 occurred despite reduced MBC. A large proportion of soil microbial populations may be inactive or functionally redundant (Allison and Martiny 2008). It is possible that the stimulation of active decomposer community under eCO_2 via greater labile C inputs reduced the inactive or dormant soil microbial population.

Changes in microbial biomass and MBC/MBN relative to C mineralisation could indicate changes in the microbial community composition, although differences between CO_2 treatments were not detectable in our previous study using automated ribosomal intergenic spacer analysis (ARISA), a DNA fingerprinting technique (Butterly et al. 2016b). More powerful DNA- and RNA-sequencing approaches are likely to have greater success (Drigo et al. 2013; Fang et al. 2015; Hayden et al. 2012; He et al. 2014; Liu et al. 2017). Perhaps, more important though is to link these subtle changes in soil microbial community composition with key biochemical processes. Butterly et al. (2016b) showed that the abundance of many key C and N cycle functional genes in these soils were reduced under eCO_2 and that their abundance was correlated with total C and N, i.e. substrate availability. Both increases (Fang et al. 2015; He et al. 2010; Xu et al. 2013) and no change in functional gene abundance (Guenet et al. 2012; He et al. 2014) and the effects of CO_2 history on soil microbes and the C and N cycle functions they perform are highly system specific (Procter et al. 2014).

Effect of eCO_2 on residue decomposition

Total C mineralisation was greater in residue-amended soils as expected. Decomposition of field pea residue was generally faster during the initial stages (6 and 12 days), but wheat mineralisation was more sustained over the study, resulting in greater decomposition of wheat than field pea residue in half of the treatments (aCO_2 calcisol, aCO_2 and eCO_2 luvisol). However, the total decomposition of field pea and wheat residues only differed by ~4.3% over the 96-day study, much smaller than anticipated (20–40%) given the contrasting C:N ratios of 60 and 20, respectively. Interestingly, decomposition of field pea residue was not affected by soil type or CO_2 history and decomposition of wheat residue was not different between the soils under aCO_2. Hence, the relative effect of CO_2 history on wheat residue decomposition was soil type specific, either increased in luvisol (14.4%), decreased in vertisol (26.7%) or not affected by eCO_2 in the calcisol.

The impact of CO_2 history on wheat residue decomposition appeared to be related to N cycling rather than differences in the capability of microbes to mineralise the wheat residue per se. Biological capability refers to the inherent potential of the decomposer community to mineralise SOC given the intrinsic constraints of its chemical composition and physical protection (Baldock et al. 2012). Soil microbial communities exposed to aCO_2 decomposed the same amount of wheat residue (~29.8%). However, under eCO_2, soil N status and the soils potential to supply inorganic N to microbes altered the biological capacity for wheat decomposition in these cropping soils. Decomposition of plant residues is known to be differentially affected by CO_2 depending on the soil N status (Pendall et al. 2004). Residues have been shown to decompose faster (Carrillo et al. 2014; Cheng et al. 2012), slower or not be affected by eCO_2 (Torbert et al. 2000; Viswanath et al. 2010). Under eCO_2, decomposition of residues may not be affected if changes in C:N are subtle, the values do not exceed a critical level (24–27) or the soil N status is high (de Graaff et al. 2004; Lam et al. 2014). The luvisol had 3.7 times greater total N concentration than vertisol and 8–5.5 times greater than the calcisol. Greater wheat decomposition under eCO_2 than aCO_2 (14%) in the luvisol would have been due to its ability to supply inorganic N via N mineralisation, consistent with higher inorganic N concentrations. For the vertisol, wheat decomposition was lower under eCO_2 than aCO_2 (27%), most likely due to microbial N limitation. Compared to the other soils, the wheat-amended vertisol had a relatively large microbial biomass, low-extractable organic N and the lowest inorganic N concentrations of any treatment.

The study highlighted that the decomposition of field pea residue was not affected by soil type or CO_2 history. The C:N ratio of the field pea was 20 and below, of which is generally considered the critical point (C:N ~25) at which soil microorganisms start to require additional N to mineralise residues (Jensen 1997). The fact that field pea decomposed at the same rate irrespective of CO_2 history again indicates that the capability of soil microbial community to utilise crop residues was not altered under eCO_2. This is consistent with the previous finding that substrate-induced C mineralisation was not different between eCO_2 and aCO_2 in these soils (Butterly et al. 2016b). However, since field pea decomposition was not limited by N, it is not clear why it decomposed slower than wheat under aCO_2. Wheat grown under FACE showed that 50% of field pea and 27% of wheat residues were decomposed over the 134-day period (Lam et al. 2014). Thus, faster and slower decomposition of field pea and wheat residues, respectively under field conditions was likely exacerbated in part by the uptake of N by wheat. In contrast, decomposition of field pea residue was reduced in the rhizosphere of legume growing under eCO_2 (Butterly et al. 2016c) and this preferential mineralisation of soil organic matter and labile root-derived compounds rather than added residue is commonly observed under eCO_2 (de Graaff et al. 2010). These studies highlight that eCO_2-induced effects on belowground processes via living plants are likely to have a stronger influence on residue decomposition than CO_2 history and residue N content. Nevertheless, residue C:N ratio is generally a good indicator of potential decomposition (Abiven et al. 2005), and the reason for the differences in field pea decomposition in the current study are likely to be due to the availability of other nutrients, particularly phosphorus.

Effect of eCO_2 on priming effect of added residues

The current study showed that C priming was influenced by soil properties (soil type and CO_2 history) but not residue. As previously mentioned, the residues were selected based on their contrasting C:N ratio and were expected to induce either net N mineralisation (field pea) or net N immobilisation (wheat) and subsequently have disparate effects on C priming. This highlights a critical aspect of residue decomposition and consequently soil C priming, in that residue quality had a secondary influence on these parameters which was primarily governed by the availability of other labile substrates and nutrients which provide the capacity of the soil microbial community to initiate residue decomposition.

CO_2 history did not have any effect on C priming in the luvisol. The initial SOC content of this soil was relatively high (50 mg C g $soil^{-1}$) and substantially more than the 2 mg C g $soil^{-1}$ that was added as residue. Hence in this soil, neither residue accelerated the SOC mineralisation despite the fact that wheat residues decomposed faster under eCO_2 than aCO_2. However, labile N (AEON and inorganic N) concentrations were lower in wheat-amended than field pea–amended soils indicating that microbes utilised these N pools during the decomposition of the wheat residue. Furthermore, soil previously exposed to eCO_2 had less labile N than aCO_2 soil. Since more than 70% of the wheat residue remained undecomposed, it is possible that significant effects of CO_2 history and residue on C priming may manifest in the longer term if these labile N pools are exhausted. Notably, absolute priming effects were quite similar between the three soils and the lower relative PE in the luvisol reflects its much higher total C content.

In the calcisol previously exposed to eCO_2, the priming effect induced by field pea and wheat residues was 30.8 and 37.7% lower than aCO_2 soils, respectively. Reduced SOC priming under eCO_2 is commonly observed in the rhizosphere of plants due to greater availability and mineralisation of labile substrate (Martens et al. 2009; Reinsch et al. 2013). This mechanism is referred to as 'preferential substrate mineralisation' (Cheng 1999). However, preferential mineralisation of added residues under eCO_2 did not occur in this study. Decreased C priming under eCO_2 has been attributed to enhanced C-use efficiency of soil-microbial communities (Carrillo et al. 2014). Greater MBC with reduced CO_2 release in the calcisol amended with field pea and wheat residues under eCO_2 indicate a greater utilisation of C for cellular growth rather than energy production than under aCO_2. However, since less than 2% of the microbial biomass is likely to be active (Blagodatskaya and Kuzyakov 2013), we did not express C mineralisation or C priming per unit of MBC, acknowledging that a more detailed quantification of the active decomposer community is necessary to properly define C-use efficiency (Shahbaz et al. 2017). For example, a positive linear relationship was found between soil C qCO_2 (soil C-derived CO_2 per unit of soil C-derived MBC) and soil C priming (Carrillo et al. 2014).

There are two reasons why lower C priming did not appear to be due to low N availability despite the calcisol having the lowest total N of the three soils. Firstly, inorganic N concentrations increased through the study. Secondly, vastly different amounts of N were contained in the wheat and field pea residues and this did not influence C priming. Generally, added residues and low soil N availability enhance C priming as soil microorganisms utilise labile substrates to mineralise soil organic matter to obtain N, the 'N mining' theory (Craine et al. 2007; Fontaine et al. 2004). Although the potential of microbes to mine N in this soil may be limited. Nevertheless, differences in the chemical composition of SOC between aCO_2 and eCO_2 soils as well as the availability of other nutrients, such as phosphorus, may have contributed to the slower C turnover and decreased priming in the calcisol under eCO_2 and require further investigation.

In contrast to the luvisol and calcisol, vertisol previously exposed to either aCO_2 or eCO_2 showed different patterns of C priming through time. In the wheat-amended vertisol, rates of

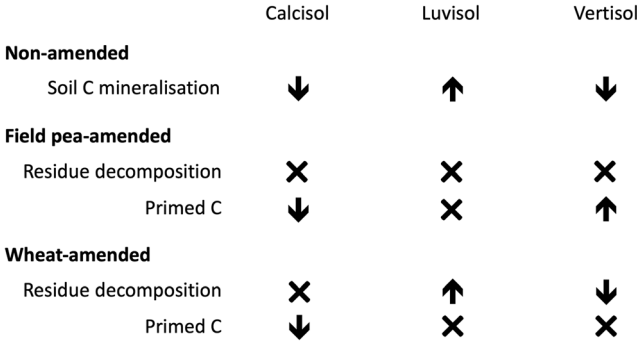

Fig. 2 A summary of the effects of elevated CO_2 (eCO_2) on soil C mineralisation, field pea and wheat residue decomposition, and their effects on primed C in calcisol, luvisol and vertisol. ↑, ↓ and × indicate increased, decreased or no effect of eCO_2 on these processes compared with ambient CO_2, respectively

C priming were almost identical between CO_2 histories throughout the study. Field pea residues induced greater C priming during the initial stage (0–40 days) in both aCO_2 and eCO_2 soils. However, after this time, C priming was slower in the field pea–amended vertisol previously exposed to aCO_2 than both wheat-amended vertisol treatments (Fig. S2). Hence, primed C was greater under eCO_2 than aCO_2 in the field pea–amended vertisol (35.5%) at the end of the study. This finding may indicate that microbial mineralisation of SOC was N limited and this was alleviated following the addition of field pea residue, albeit temporarily in the aCO_2 soil. Labile N (AEON and inorganic N) in the residue-amended vertisol was the lowest of all treatments and proportionally low given that total N was 2.2 (aCO_2) and 1.5 (aCO_2) times that in the calcisol. The fundamental principle of 'stoichiometric decomposition' theory is that soil organic matter decomposition is greatest when the C and N content of the available substrate is equivalent to that required by the decomposer community (Chen et al. 2014). This supports that mineralisation of soil organic matter pools (existing or added) would diminish with decreasing N availability and that N-rich residues would have a greater priming effect. In contrast, other studies have shown that perennial grass residues with higher N content (lower C:N ratio) had lower C priming (Carrillo et al. 2014), and the relative differences between studies are likely due to the overall soil N status and the N mineralisation potential. Greater priming effects under eCO_2 have been suggested via the enhancement of arbuscular mycorrhizal fungi (Cheng et al. 2012). Notably, the increase in C priming observed in the field pea–amended vertisol was not sufficient to change the overall C mineralisation in this soil during the study (Fig. 2).

Conclusion

Carbon mineralisation in three contrasting soil types after a 4-year exposure to eCO_2 and aCO_2 but identical management and climatic conditions, was mainly determined by soil N status, less by CO_2 history and least by residue quality (C:N ratio). The differences in decomposition of wheat and field pea residues were smaller than expected given their C:N ratios of 60 and 20, respectively. Faster (14.4%) decomposition of wheat in luvisol but slower (26.7%) in vertisol soils previously exposed to eCO_2 appeared to be a function of initial N status and either the ability (luvisol) or inability (vertisol) to supply additional N via N mineralisation, since field pea decomposition was not affected. Interestingly, significant effects of CO_2 history on soil C priming and residue decomposition did not occur together. Reduced soil C priming in the calcisol previously exposed to eCO_2 was not explained by N status. In contrast, in the N-poor vertisol, field pea residues induced faster C priming during the initial 30 days than wheat residues, but sustained rates of C mineralisation in the wheat-amended soils resulted in similar priming effects than the aCO_2 field pea–amended vertisol at the end of the study. The study highlighted that C priming was not affected by either residue or CO_2 history in the relatively fertile luvisol. Differences in residue decomposition and C priming in three soils with different CO_2 histories appeared to be controlled by the capacity of the microbial decomposer communities to perform these functions and this requires further examination.

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