Phosphorus availability and arbuscular mycorrhizal fungi limit soil C cycling and influence plant responses to elevated CO_2 conditions.

Castañeda-Gómez L.[1*], Powell J.R.[1], Pendall E.[1], Carrillo Y.[1].

[1]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia.

* Corresponding author. Current affiliation: Department of Physical and Environmental Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, ON, M1C 1A4, Canada

Abstract

Enhanced soil organic matter (SOM) decomposition and organic phosphorus (P) cycling may help sustain plant productivity under elevated CO_2 (eCO_2) and P-limiting conditions. P-acquisition by arbuscular mycorrhizal (AM) fungi and their impacts on SOM decomposition may become even more relevant in these conditions. Yet, experimental evidence of the interactive effect of AM fungi and P availability influencing altered SOM cycling under eCO_2 is scarce and the mechanisms of this control are poorly understood. Here, we performed a pot experiment manipulating P availability, AM fungal presence and atmospheric CO_2 levels and assessed their impacts on soil C cycling and plant growth. Plants were grown in chambers with a continuous ^{13}C-input that allowed differentiation between plant- and SOM-derived fractions of respired CO_2 (R), dissolved organic C (DOC) and microbial biomass (MBC) as relevant C pools in the soil C cycle. We hypothesised that under low P availability, increases in SOM cycling may support sustained plant growth under eCO_2 and that AM fungi would intensify this effect. We found the impacts of CO_2 enrichment and P availability on soil C cycling were generally independent of each other with higher root biomass and slight increases in soil C cycling under eCO_2 occurring regardless of the P treatment. Contrary to our hypotheses, soil C cycling was enhanced with P addition suggesting that low P conditions

were limiting soil C cycling. eCO_2 conditions increased the fraction of SOM-derived DOC pointing to increased SOM decomposition with eCO_2. Finally, AM fungi increased microbial biomass under eCO_2 conditions and low-P without enhanced soil C cycling, probably due to competitive interactions with free-living microorganisms over nutrients. Our findings in this plant-soil system suggest that, contrary to what has been reported for N-limited systems, the impacts of eCO_2 and P availability on soil C cycling are independent of each other.

Keywords: Elevated CO_2, Soil organic matter, decomposition, isotopic natural abundance, phosphorus limitation, fertilisation effect, mycorrhizal fungi, carbon pools.

1. Introduction

The effect of increased atmospheric CO_2 concentrations on plant productivity and its potential impacts on soil carbon (C) are regulated by nutrient availability (Ainsworth and Long, 2004; Finzi et al., 2011; Reich et al., 2014; Terrer et al., 2019). Higher plant productivity and increases in soil C with elevated CO_2 (eCO_2) have been observed when combined with nutrient addition (De Graaff et al., 2006; Dieleman et al., 2010; Hungate et al., 2009; Maroco et al., 2002; Piñeiro et al., 2017; van Groenigen et al., 2006). In the absence of external nutrient supplies, higher soil organic matter (SOM) decomposition under eCO_2 contributes to meet plant nutrient demands with negative impacts on soil C (Carrillo et al., 2014; Drake et al., 2011; Finzi et al., 2006; Hoosbeek et al., 2004; Phillips et al., 2012; Reich et al., 2006). However, a pre-existent nutrient limitation may constrain productivity responses to eCO_2 (Ellsworth et al., 2017; Reed et al., 2015; Reich et al., 2006), potentially preventing any changes in soil C. The current understanding about nutrient availability regulating eCO_2 impacts on C cycling has been obtained mainly from northern hemisphere systems, where nitrogen (N) often constrains ecosystem productivity. But the impacts of eCO_2 on soil C may be dependent on what the most limiting nutrient is (Dijkstra et al., 2013). Phosphorus-limited tropical and subtropical ecosystems are relevant C sinks that cover a vast area (Keenan et al., 2015; Pan et al., 2011; Soepadmo, 1993) and although the role of P availability regulating the impact of eCO_2 on soil C storage is broadly recognised (Goll et al., 2012; Reed et al., 2015; Sun et al., 2017; Vitousek et al., 2010), the mechanisms of this control are poorly understood (Ellsworth et al., 2017; Norby et al., 2015; Terrer et al., 2019).

Opposite to N, soil P cycling is less coupled to soil C dynamics because P mobilisation is not necessarily linked with SOM decomposition. P cycling can be divided into inorganic and organic sub-cycles (Liu and Chen, 2008; Mullen, 2005). In the inorganic sub-cycle, mobilisation of inorganic P occurs via biochemical mechanisms without SOM mineralisation

nor CO_2 production, thus C and P cycles are not coupled. In the organic P sub-cycle, C and P cycles are more coupled and P mineralisation occurs via biological mechanisms that lead to SOM decomposition and CO_2 production (McGill and Cole, 1981; Sharma et al., 2013; Tate, 1984). Most P is made available via inorganic P mobilisation, particularly with P sufficiency. But in low-P systems, mineral P sources are depleted and P derived from rock weathering is minimal (Goll et al., 2012; Reed et al., 2011). Therefore, the majority of P acquisition occurs via internal recycling of organic P sources (Fox et al., 2011; Johnson et al., 2003; Reed et al., 2011) involving SOM decomposition and CO_2 production. Most of the research on the effects of eCO_2 on soil P availability are focused on its impacts on inorganic P cycling via biochemical P mobilisation mechanisms. For example, higher microbial P enzymatic activity is reported with eCO_2 (Hasegawa et al., 2016; Kelley et al., 2011; Moorhead and Linkins, 1997; Souza et al., 2017) as well as higher production of organic acids and siderophores involved in P mobilisation (Fransson and Johansson, 2010; Högy et al., 2010; Tarnawski and Aragno, 2006; Watt and Evans, 1999). Moreover, increases in fine root production and changes in pH and soil moisture with eCO_2 can indirectly enhance inorganic P cycling in soils (Dijkstra et al., 2012; Hasegawa et al., 2016; Jin et al., 2015). It is likely that organic P cycling is also affected by eCO_2 due to the influence of eCO_2 on ecosystem stoichiometry (Gifford et al., 2000; Loladze, 2014, 2002) but experimental evidence for this is scarce. A better understanding about how eCO_2 and P availability influence soil C cycling is important to better predict changes in global soil C due to eCO_2 (Finzi et al., 2011; Goll et al., 2012; Yang et al., 2016).

In low-P conditions, organic P cycling may help sustain plant productivity under eCO_2 at the expense of higher SOM decomposition. A study by Jing et al, (2017) demonstrated that inputs of labile C led to higher SOM decomposition in low-P soils mediated by altered microbial community composition and increases in microbial biomass. Thus, as C allocation

belowground increases with eCO_2 (Canadell et al., 1995; Cotrufo and Gorissen, 1997; Pausch and Kuzyakov, 2018), the higher labile C availability, increased microbial biomass and activity and higher SOM decomposition may allow for a sustained nutrient release for plant uptake and growth in low-P soils. However, evidence from field experiments exposed to eCO_2 suggests that under P-limiting conditions, changes in soil C cycling are minor or undetected (Castañeda-Gómez et al., 2020; Dijkstra et al., 2013; Drake et al., 2016) and that the CO_2 fertilization effect is reduced or not observed (Conroy et al., 1992; Deng et al., 2015; Ellsworth et al., 2017; Goll et al., 2012; Peñuelas et al., 2012; Zhang et al., 2014). Thus, if P availability becomes limiting, ecosystem productivity and microbial-mediated SOM decomposition may be hampered, preventing further changes in soil C cycling. Soil microbial communities play a key role in SOM decomposition and both biological and biochemical P mineralisation and mobilisation. Moreover, the responses of SOM decomposition and C stabilisation to P availability have been found to be largely mediated by changes in saprotrophic microbial community composition and activity (Fang et al., 2019; Feng and Zhu, 2019; Liu et al., 2018; Soong et al., 2018; Yuan et al., 2021) and by symbiotic fungi such as arbuscular mycorrhizal (AM) fungi (Xu et al., 2018). Yet the role of saprotrophic and mycorrhizal fungi altering SOM decomposition under eCO_2 conditions and low-P availability is poorly understood.

AM fungi are known to greatly contribute to P mobilisation under eCO_2 conditions, especially in ecosystems with low soil P availability (Delucia et al., 1997; Matamala and Schlesinger, 2000; Terrer et al., 2016) where AM fungi tend to be more abundant (Treseder and Cross, 2006). AM fungi also alleviate P limitation conditions for plants (Soka and Ritchie, 2014; Willis et al., 2013) possibly via excretion of P hydrolytic enzymes (Joner et al., 2000; Sato et al., 2015) and certainly via uptake of inorganic nutrients from the soil solution (Javot et al., 2007; Smith et al., 2011). They have also been linked with increased

SOM decomposition and changes in soil C cycling with climate change (Carrillo et al., 2015; Cheng et al., 2012; Talbot et al., 2008; Wei et al., 2019). Higher C transfer to AM fungi under eCO_2 enhances AM fungi growth and activity (Mohan et al., 2014) and so their contribution to plant P acquisition in P-limited ecosystems may be enhanced with eCO_2 (Cavagnaro et al., 2011). On the other hand, AM fungi can also suppress eCO_2-mediated increases in plant growth due to increased P immobilisation in AM fungal biomass and increased competition over P with saprotrophic communities (Jin et al., 2015) that can simultaneously decrease AM fungi-mediated SOM decomposition (Talbot et al., 2008). If P availability is low, the role of AM fungi mobilising P and promoting plant growth may be constrained due to P-limitation (Treseder and Allen, 2002), which might further regulate impacts of eCO_2 on ecosystem productivity in P-limited ecosystems. Due to the significant role of AM fungi on P and SOM dynamics, predictions of altered soil C stocks under eCO_2 require an understanding how eCO_2 can change AM fungal activity, their impact on saprotrophic communities and plant responses to eCO_2, particularly under P limitation.

In this study, we explored the role of P availability and AM fungi mediating responses of SOM decomposition and plant productivity to eCO_2. We did this by manipulating P availability, AM fungal presence and atmospheric CO_2 levels in a pot experiment. An Australian native grass species (*Microlaena stipoides*) with the ability to grow in a wide range of P availability conditions and forming arbuscular mycorrhizal associations (Clark et al., 2014; Hill et al., 2010) was grown in chambers that allowed the continuous isotopic labelling of plant tissues so we could directly assess changes in SOM-derived C in different C pools: respired CO_2 (R; the product of decomposition), dissolved organic C (DOC; considered an active pool of C) and microbial biomass C (MBC; the agent of SOM decomposition). This approach allowed for a holistic assessment of the impact of eCO_2, P availability and AM fungal presence on soil C cycling and plant growth. Changes in

saprotrophic communities were also measured (using phospholipid fatty acids) in relation to eCO_2 conditions, P treatment and AM fungal presence. These responses, along with nutrient contents in plant tissues and soil extracts (dissolved nutrients), were collected to enhance result interpretations.

We hypothesised that for plants grown under eCO_2 and enhanced P availability – achieved by P addition – a fertilisation effect would be observed as increased plant biomass without changes in SOM decomposition (**Figure 1A**) since P addition will allow for plant requirements to be met under eCO_2. Contrarily, if P is low, an eCO_2 fertilisation effect would only occur with increases in SOM decomposition, evidenced as higher SOM-derived respired CO_2, MB and MB (**Figure 1B**). Alternatively, we hypothesised that no fertilisation effect would be observed if soil C and P cycling are decoupled in this experimental system (**Figure 1C**). The presence of AM fungi would increase SOM decomposition as a mechanism to obtain P from SOM via changes in saprotrophic communities. This effect will be observed in the different C pools, particularly with low P conditions and eCO_2 since both low P availability and eCO_2 promote AM fungal colonisation rates and activity.

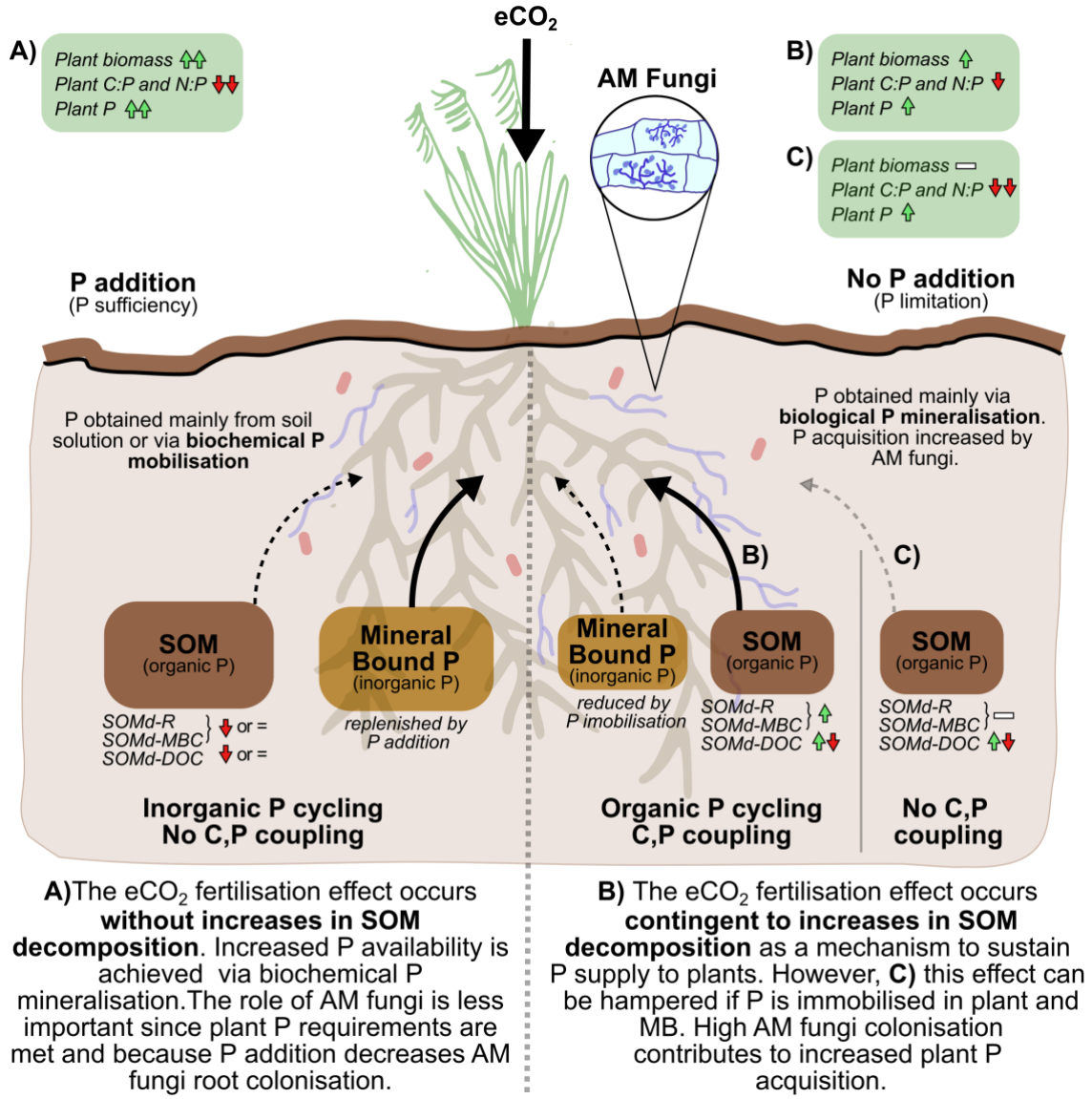


Figure 1 Conceptual framework and expected responses of measured variables in the experiment (green arrow: increase; red arrow: decrease; -: no effect). Increases in plant biomass under eCO_2 conditions are dependent on nutrient availability. In low phosphorus (P) soils, **A)** P addition (left side) will support an increase in plant biomass with eCO_2 (fertilisation effect) without major impacts in soil organic matter-derived (SOMd) C pools: R, respired CO_2; MB, microbial biomass; DOC, dissolved organic C. Without P addition (right side), **B)** P acquisition may be more reliant on organic P cycling (coupled C and P cycles) with enhancements in plant biomass with eCO_2 only observed if SOM decomposition and biological P mineralisation increase. Immobilisation of P by plants, AM fungi and microbial biomass becomes relevant in this scenario further increasing SOM decomposition **C)** If P availability is too low, becoming limiting, increased P immobilisation and higher P competition will decrease the impact on SOM decomposition and plant biomass.

2. Materials and methods

We set up a factorial experiment with three factors: **phosphorus (P) treatment**: P addition (+P)/control; **AM fungi**: Active AM inoculum (AM)/Non-mycorrhizal (Sterile AM

inoculum, NM) and **CO_2**: ambient (400 ppm - aCO_2) and elevated (640 ppm - eCO_2) for a total of 8 treatment combinations with 4 replicates each (+P/AM/aCO_2; +P/AM/eCO_2; +P/NM/aCO_2; +P/NM/eCO_2; control/AM/aCO_2; control /AM/eCO_2; control /NM/aCO_2; control /NM/eCO_2; n=32, **Figure SI 1A**). Plants of *Microlaena stipoides* (Labill.) R.Br., a native Australian C_3 grass with a broad P range, were grown from seed in 125mm pots containing around 500 g of dry soil. Plants were grown in growth chambers for twelve weeks and soil water content was kept between 15 and 20 % gravimetric content by addition of MilliQ water as needed every 2-3 days.

2.1. Soil characteristics and treatment preparation

Soil was collected from a Cumberland plain natural woodland in Western Sydney (33°37'01'' S, 150°44'26'' E, 20 m.a.s.l) near the *Eucalyptus* Free-Air CO_2 experiment (EucFACE). Soil at this site is an aeric podsol, slightly acidic (pH 5.38 ± 0.02 at 0-10 cm) (Ross et al., 2020), with a N content of 677 mg Kg^{-1}, low total C (1.8%, 0-15 cm), and P content (76.28 mg Kg^{-1}) (Hasegawa et al., 2016). Previous studies have demonstrated that both the vegetation (Crous et al., 2015) and soil fauna (Nielsen et al., 2015) are limited by P within this ecosystem. Soil was sieved (to 2 mm) and sterilised (gamma irradiated, 50 kGy) to remove viable AM fungal propagules. To reintroduce a homogenous microbial community to all pots, excluding AM fungi, we prepared a microbial inoculum. For this, approx. 3 Kg of freshly collected soil from a nearby grassland was mixed with water in a 1:3 proportion by volume and the suspension passed through a 20 µm mesh sieve to remove AM fungal spores (Brundett and Australian Centre for International Agricultural Research, 1995). Prior to potting, the filtrate was added to the sterile soil at a rate of 50 mL filtrate per Kg soil. The soil was incubated for a week at room temperature, mixing it daily.

The soil was then divided into four subsets based on whether they were to receive additional P and AM fungal inoculum. For the former, triple super phosphate (Richgro, super

phosphate fertiliser supplement 9.1% P w/w) was added in a rate of 0.4 g/kg dry soil. The triple super phosphate powder was weighed, diluted and sprayed into the soil while low P treatments received MilliQ water only. The soil was then thoroughly mixed and left to settle for a day. Next, AM fungi treatments were created by applying AM fungal inoculum in a 1:10 AM fungi inoculum:soil with non-mycorrhizal controls produced by autoclaving the live AM inoculum (121 ^{o}C, two hours) and applying it to the soil in the same manner (**See supplementary information for AM inoculum production**). Once the four types of soils were prepared, soil was added to pots and five surface sterilised *M. stipoides* seeds (30 % H_2O_2 for 10 minutes followed washing) were sown per pot. Pots were randomly split and placed in aCO_2 and eCO_2 chambers. After two weeks of growth, pots were thinned to one plant per pot. Unplanted pots (n=16) with the different P and CO_2 treatments (+P/NM/aCO_2; +P/NM/eCO_2; control/NM/aCO_2; control/NM/eCO_2 n=4 each), were included to estimate effects on SOM decomposition in the absence of plants and AM fungi (**Figure SI 1A**). Unplanted pots were all prepared using soil with sterile AM inoculum and were kept under the same conditions as the planted pots for the duration of the experiment.

2.2. Growth Chambers set up

The growth chambers (six in total, three per CO_2 treatment) were modified using the approach of Cheng and Dijkstra (2007) to achieve a continuous ^{13}C- labelling of plant tissues in both aCO_2 and eCO_2 treatments. The chambers were adapted to take an influx of naturally ^{13}C-depleted CO_2 ($\delta^{13}C$= -31.7 $^{o}/_{oo}$ ±1.2) delivered during the photoperiod, combined with a scrubbing system made of a soda lime-filled PVC tube (72 L) that allowed continuous supply of CO_2-free air (**Figure SI 1B**). Chambers were adjusted to a 16h/8h photoperiod with 25 ^{o}C/18 ^{o}C, 60 % relative humidity, and light intensity of 900 µmol/m^2s^1. The chamber atmosphere was sampled frequently to confirm depletion in ^{13}C. Air samples from the chambes were extracted via a pump system into a tedlar bag (Tedlar® SCV Gas Sampling

Bag) and analysed for $\delta^{13}C$ in a PICARRO G2201i isotopic CO_2/CH_4 analyser (Picarro Inc., Santa Clara, CA, USA). To avoid plant-uptake of ^{13}C from outside the chambers, watering and all other manipulations were performed during the night period aided by green light.

2.3. Harvest and sample processing

Gas sampling of the plant-soil system

After twelve weeks of growth, we quantified rates of total respired CO_2 (R) and its C isotopic composition as described by Carrillo et al., (2015, 2014). Briefly, pots were placed on an elevated platform inside a water filled tray and covered with a PVC chamber (45 cm H x 15 cm D) adapted with an air-tight rubber stopper for air sampling. Free-CO_2 air was circulated for 2 hours using an aquarium pump connected to a CO_2 scrubber (50 cm H x 4 cm D PVC tubing filled with soda lime). After 2 hours of scrubbing, an air sample was taken to determine baseline CO_2 concentrations using a 7890A gas chromatograph with a G1888 network headspace sampler (Agilent Technologies, USA). Later, the CO_2 scrubbers were removed and the pump reconnected to the PVC chamber to allow for air circulation while pots were incubated. After two to three hours of incubation, a gas sample was collected in an airtight gas collection bag (Tedlar® PVDF, 1L) using an aquarium pump system and analysed for its C isotopic composition.

Plant and soil harvest

One day after gas sampling, pots were destructively harvested. Aboveground biomass was cut and roots separated from the soil and washed. Plant aboveground biomass, roots and a subsample of fresh soil were oven dried at 60 ºC for measurements of dry plant biomass, soil gravimetric water content and total nutrients. A fresh soil subsample was stored at -20 ºC for microbial community analyses and the remaining fresh soil was used for assessments of dissolved nutrients and microbial biomass.

Plant, soil nutrients and microbial biomass C and N

Two sub-samples of soil were weighed. Dissolved nutrients in soil were extracted from the first subsample with a 0.05M K_2SO_4 solution in a 4:1 solution to soil ratio, shaking at 180 rpm for an hour. Samples were filtered through a Whatman # 42 filter paper and frozen (-20ºC) until analyses. The second subsample was fumigated for 5 days with chloroform and then nutrients were extracted as for unfumigated samples. The fumigated and unfumigated extracts were analysed for total dissolved organic C and N (Shimadzu® TN, TOC-L, Japan) and microbial biomass C and N calculated by subtracting fumigated and unfumigated samples (Vance et al., 1987). The volume left of these K_2SO_4 extractions was used to obtain the isotopic composition of DOC and microbial biomass (see section below). Phosphates were extracted following the Bray 1-P method for acidic soils, in a 1:7 solution:soil ratio using a 0.03M NH_4F solution in 0.025 M hydrochloride (HCl) adjusted pH to 2.6 ± 0.05 with HCl (Rayment et al., 2010). Samples were manually shaken for 60s and immediately poured over a Whatman # 42 filter paper. Collected extracts were analysed by colorimetry (AQ2 Discrete Analyser, SEAL Analytical, Mequon, WI, USA).

Total P and N were determined from ground oven-dried soil and root samples. Total P concentration was analysed by an X-ray fluorescence spectrometer (PANalytical, εpsilon 3. 10Kv, 0.9mA. Lelyweg, Almelo, Netherlands) while total C and N from soil, roots and soil extracts were analysed along their isotopic composition.

2.4. Respired, dissolved organic C (DOC) and microbial biomass isotopic composition and partitioning

Gas samples from plant-soil system incubations were analysed in a PICARRO analyser (G2201i; Picarro, Santa Clara, CA, USA. Precision values below 0.16‰) for the $\delta^{13}C$ and CO_2 concentration of the total respired CO_2 (R). For the isotopic composition of the DOC and microbial biomass C (MBC), fumigated (*f*) and unfumigated (*uf*) soil K_2SO_4 extracts were oven dried at 60ºC. The dried extracts were scraped and weighed for analysis on a Thermo

GC-C-IRMS system (Trace GC Ultra gas chromatograph, Thermo Electron Corp., Milan, Italy; coupled to a Delta V Advantage isotope ratio mass spectrometer through a GC/C-III); University of California, Davis Campus, USA). The $\delta^{13}C$ of unfumigated soil extracts was used as the isotopic composition of the DOC while $\delta^{13}C$ of MBC ($\delta^{13}C_{MBC}$) were calculated from $\delta^{13}C$ values of both fumigated (*f*) and unfumigated (*uf*) extractions (**See supplementary information for calculations of the isotopic composition of the microbial biomass**). Samples of dried soil were also analysed on the Thermo GC-C-IRMS system for C, N and $\delta^{13}C$.

To calculate the fractions of SOM-derived C in the total respired CO_2 (R), dissolved organic C (DOC) and microbial biomass C (MBC) we used isotopic partitioning as: $SOM.C_{R,DOC,MBC} = (\delta^{13}C_{R,DOC,MBC} - \delta^{13}C_p) / (\delta^{13}C_{control} - \delta^{13}C_p)$. Where $\delta^{13}C_{R,DOC,MBC}$ were the $\delta^{13}C$ of either the CO_2 measured in the total respired CO_2 (R), dissolved organic C (DOC) or microbial biomass C (MBC)) from each pot; $\delta^{13}C_p$ is the isotopic ratio of the plant source averaged across P treatments per CO_2 condition (root biomass at aCO_2 $\delta^{13}C$= -40.01±0.08 and eCO_2 $\delta^{13}C$= -43.20±0.04) and $\delta^{13}C_{control}$ is the average $\delta^{13}C$ of the native SOM source obtained from the dried bulk soil across CO_2 and P conditions ($\delta^{13}C$= -25.31±0.02). The fractions of plant-derived C were obtained by subtracting SOM-derived fractions from the unit. Measured total respired CO_2 rates, DOC and MBC were partitioned into SOM-derived and plant-derived, using these fractions to obtain the mass of the SOM derived R, MBC and DOC pools. In this study, we focus only on the SOM-derived C pools and fractions.

2.5. Microbial community analysis: Phospholipid-derived fatty acids (PLFA) and Neutral lipid-derived fatty acids (NLFA)

Soil PLFAs were extracted to assess the overall microbial communities while the 16:1ω5c NLFA was used as an indicator of arbuscular mycorrhizal (AM) fungi presence and

289 abundance (Olsson, 1999). Freeze-dried soil from planted pots (n=32) were extracted
290 following the protocol by Buyer & Sasser (2012) with modifications by Castañeda-Gómez et
291 al. (2020) (**See supplementary information for PLFA and NLFA analyses**). Functional
292 groups were defined as shown in **Table SI 1**. Fungal to bacterial ratio (F:B) was calculated
293 by dividing fungal PLFAs (not including AM fungi) by the sum of bacterial PLFAs. The sum
294 of individual lipids was used as an indicator of the size of the community (µg PLFA g^{-1} dry
295 soil).

296 **2.6. Statistical analyses**

297 The effect of CO_2 condition, AM fungi treatment and P addition and their interactions on
298 the response variables was analysed with a linear model fitted with the function "lm" from
299 the stats package in R version 3.3.2 (R Core Team 2016). This approach was used instead of
300 a mixed effects modelling approach since pots were moved among chambers with the same
301 CO_2 treatment so it was not possible to estimate a random effect associated with each
302 chamber. The normality of the residuals of each model was inspected to check the
303 appropriateness of the fit and transformations were performed when needed. Statistical
304 significance was determined performing an ANOVA (Analyses of variance) with the
305 "Anova" function ("car" package, Fox et al. 2017). Multiple mean comparisons were
306 performed using the Tukey test using the "glht" function ("multcomp" package, Hothorn et
307 al. 2017). As soil moisture can affect soil respiration measurements, we tested for
308 correlations between soil moisture and the total respired CO_2, SOMd- respired CO_2 fraction
309 and total mass of SOMd- respired CO_2. For response variables with a significant correlation
310 with moisture, a 3-way ANCOVA was performed with soil moisture as covariate, to account
311 for the variability brought by the slightly different moisture contents at the time of CO_2
312 sampling. The homogeneity of the regression slopes, normality of residuals and homogeneity

of variances was tested when performing the ANCOVA. Significance levels were: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤ 0.001(***).

Microbial communities were analysed as the PLFA-based total microbial biomass (sum of all individual lipids, in µg PLFA g^{-1} dry soil), as absolute microbial abundance (reflecting the size or biomass of the community, in µg PLFA g^{-1} dry soil) and as relative abundance (in percentage, reflecting microbial community composition) of the different microbial groups and as individual lipids. To visualise significant three-way interactions of experimental factors in the abundance of microbial groups from the ANOVA, the "emmip" function from the "emmeans" package (Lenth et al., 2020) was used to show the estimated marginal means from the fitted linear model.

3. Results

3.1. *Influence of elevated CO_2, P availability and AM fungi on SOM decomposition and C pools*

Higher SOM-C losses under eCO_2 were expected for control P conditions (low P) and particularly when AM fungi were inoculated **(Figure 1)**. However, we found that in general, there was not a significant interactive impact of the three experimental factors on the respired CO_2, microbial biomass C (MBC) and dissolved organic C (DOC) as initially expected. Instead, we found that the interaction of AM and P treatments was relevant determining the fate of these soil C pools, regardless of eCO_2. AM and P treatments significantly affected the total respired CO_2 (**Figure 2**), which decreased with P addition but only for the NM treatment ($P<0.05$, Tukey's multiple comparison). However, we did not find any significant effects of CO_2 conditions, AM or P treatments on the SOM-derived respired CO_2 **(Figure 2)**. On the other hand, most of the microbial biomass C (MBC) was derived from SOM (above 80%, **Table SI 2**) and while neither the total microbial biomass C nor the SOM-derived MBC (**Figure 2**) were affected by the experimental factors, the C sources used by the microbial

338 biomass were affected by the interaction between AM and P treatment (**Table SI 2**). The
339 fraction of MBC derived from SOM marginally increased by 6% with P addition in NM
340 treatments (P=0.1, Tukey's multiple comparison. **Table SI 2**). Similar to the MBC pool, most
341 of the DOC was derived from SOM (above 80%, **Table SI 2**) and both the total DOC and
342 SOM-derived DOC were affected by the interaction between AM and P treatments (**Figure**
343 **2**) with P addition significantly increasing the SOM-derived DOC in NM treatment (P=0.001,
344 Tukey's multiple comparison). Finally, although not evidenced in the total DOC or SOM-
345 derived DOC, the fraction of DOM-derived DOC significantly increased with eCO_2 (**Table**
346 **SI 2**).
347

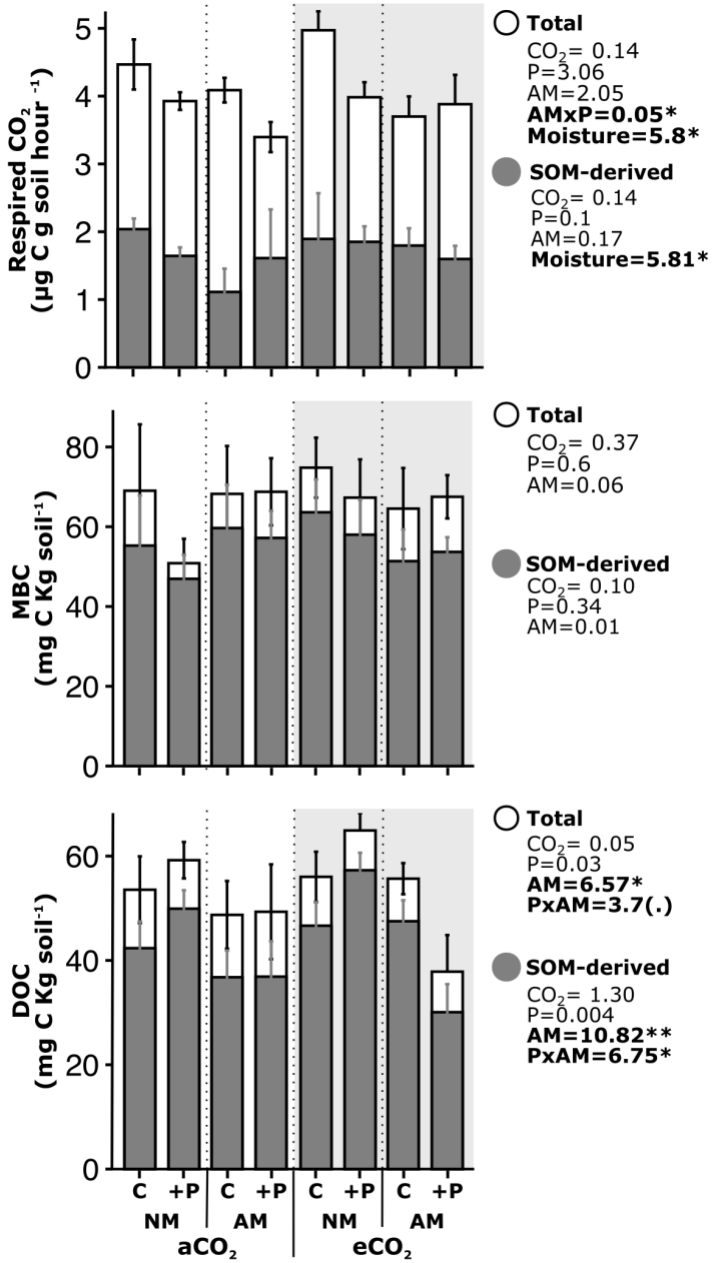


Figure 2. Mean values (± standard error, n=4) of the total(white) and SOM-derived (grey) respired CO_2, microbial biomass C (MBC) and dissolved organic C (DOC) per CO_2 condition, AM fungi and P addition treatment (C: control and +P: P addition). CO_2 conditions are shown on light grey (elevated) and white (ambient) backgrounds. $F_{(1,24)}$ values of ANCOVAs (for respired CO_2) and ANOVAs from linear model for response variables displayed on the right. Significance levels: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤ 0.001(***). Only significant interactions of the treatments displayed.

3.2. Soil nutrient responses to elevated CO_2, P availability and AM fungi

We expected eCO_2 to increase C and nutrient availability, P addition to increase soil P, and AM fungi to decrease soil P and N due to higher nutrient acquisition and immobilisation by the fungal biomass. These expectations were partially supported with our observations. eCO_2 increased total soil N, but only for control P pots while dissolved N marginally decreased with eCO_2 for AM pots (**Table 1**). Total soil P was unaffected by eCO_2 conditions while soil dissolved P significantly decreased with eCO_2 conditions, particularly for control P

and AM pots (**Table 1**). P addition increased total soil P while AM decreased total P and dissolved N (**Table 1**). Finally, we detected lower dissolved C:N with P addition for AM pots but higher dissolved C:N for AM pots with eCO_2 (**Figure 3**). Dissolved C:P decreased with P addition for pots under eCO_2 conditions while it increased with eCO_2 for AM pots (**Figure 3**).

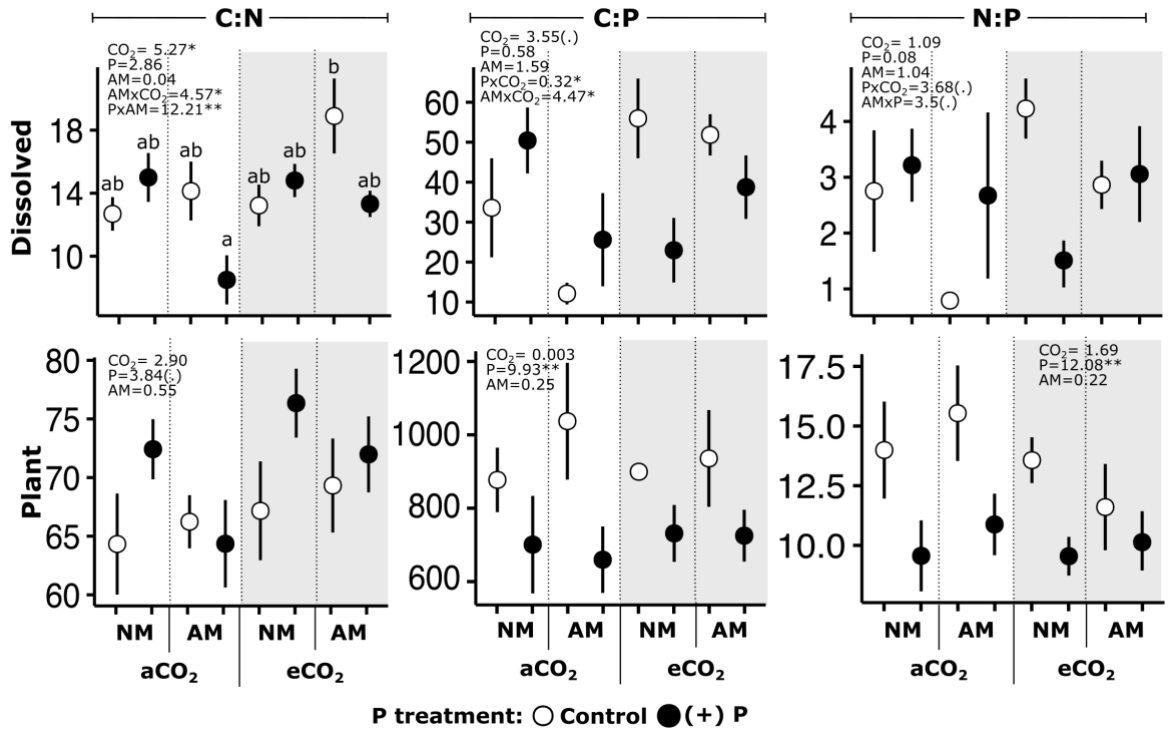
Table 1 Soil nutrients (total and dissolved (ppm)) per CO_2 condition, AM fungi and P addition treatment. Dissolved nutrients as: DOC – total dissolved organic Carbon, TN – total nitrogen and phosphates (PO_4). Mean values (± standard error, n=4) followed by the same letter are not significantly different ($p \leq 0.05$, Tukey multiple comparison test), no letters indicate non-significant effect of the treatments. AM: Arbuscular mycorrhizal and NM: non-mycorrhizal. Below, ANOVA results from linear model (lm) for response variables (¤ natural log transformed). $F_{(1,24)}$ values displayed with significance levels: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤ 0.001(***).

			Total		Dissolved	
			Soil N	**Soil P**	**TN¤**	**PO_4¤**
		control	347.2(9.5)a	166(20)a	4.2(0.4)	2.49(0.8)ab
	NM	**+P**	558.2(39.7)ab	268(10)b	4.2(0.5)	1.25(0.1)ab
		control	472.9(23.5)a	167(12)a	3.6(0.6)	3.86(0.3)b
aCO_2	**AM**	**+P**	526.1(60.7)ab	207(32)a	4.8(1.0)	2.75(0.6)ab
		control	665.0(116.4)b	155(26)a	4.4(0.1)	1.08(0.1)a
	NM	**+P**	425.1(63.0)ab	238(21)b	4.5(0.5)	3.40(0.8)ab
		control	633.7(103.9)b	132(10)a	3.7(0.2)	1.09(0.1)a
eCO_2	**AM**	**+P**	643.0(70.3)ab	195(11)a	3.0(0.8)	1.00(0.1)a
		CO_2	**5.46***	2.52	1.74	**8.84****
		P	0.03	**28.01*****	0.16	0.0001
		AM	2.00	**5.41***	**6.58***	0.08
		CO_2xP	**6.25***	0.003	0.60	**7.64***
		CO_2xAM	0.22	0.02	3.64(.)	**11.45****
		AMxP	0.21	2.30	0.15	3.46
		PxAMxCO_2	4.23(.)	0.56	1.22	2.90

3.3. Plant responses to elevated CO_2, P availability and AM fungi

We expected that plant biomass would increase with eCO_2 when P availability was high, and be unresponsive to eCO_2 when P availability was low unless AM fungi were present, supporting further plant growth by increasing SOM decomposition and P uptake (**Figure 1**). We did not observe a significant impact of eCO_2 on aboveground plant biomass regardless of the P and AM treatments. However, eCO_2 effects increased root biomass when AM fungi were present, regardless of the P treatment (**Table 2**). Increases in plant biomass with P addition were not observed either, but we expected to see increases in plant P concentrations in response to P addition and decreases in plant C-to-nutrient ratios with eCO_2 as an

411 indication of nutrient resorption and higher nutrient immobilisation, which would be
412 particularly important in low P conditions. Supporting our predictions, we observed
413 increases in plant P concentration as well as the plant P pool in both shoot and roots with P
414 addition (**Table 2**). As a consequence, plant C:P and N:P significantly decreased with P
415 addition (**Figure 3**). However, C-to-nutrient ratios in plant tissues were not strongly affected
416 by eCO_2 and no clear evidence for increased P immobilisation under eCO_2 was found. On the
417 other hand, plant N increased with AM presence but only under eCO_2 (**Table 2**). Finally,
418 higher plant C:N was observed with eCO_2, whereas plant C:N increased with P addition for
419 NM pots (**Figure 3**).
420



421

422 **Figure 3**. Mean values (± standard error, n=4) of mass nutrient ratios (columns) in plant and soil
423 solution (dissolved) per treatment. eCO_2 conditions shown as grey areas and P treatment as
424 white(control) or black (+P) circles. NM (non-mycorrhizal). $F_{(1,24)}$ values of ANOVAs from linear
425 model for response variables displayed. Significance levels: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤
426 0.001(***); only significant interactions of the treatments displayed. Treatments with different letters
427 are significantly different (p≤ 0.05, Tukey multiple comparison test).
428
429
430

Table 2 Plant biomass (shoot and roots), nutrient contents and plant P and N pools (plant P and N content per unit of shoot and root biomass) per CO_2 condition, AM fungi and P addition treatment. NM (non-mycorrhizal). Mean values (± standard error, n=4) followed by the same letter are not significantly different ($p \leq 0.05$, Tukey multiple comparison test), no letters indicate non-significant effect of the treatments. Below, results of the ANOVA from linear model (lm) for response variables (✖ log transformed). $F_{(1,24)}$ values displayed with significance levels: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤ 0.001(***).

			Biomass		Nutrient Concentration		
			Shoot	Root	Plant C	Plant N✖	Plant P
			g		g/Kg		
		control	2.7(0.2)	2.1(0.08)ab	356.9(30.2)	5.5(0.2)	0.45(0.07) a
	NM	+P	2.8(0.3)	2.0(0.3)ab	380.6(14.6)	5.3(0.1)	0.59(0.09) b
		control	2.8(0.1)	1.7(0.3)a	395.0(11.5)	6.0(0.4)	0.41(0.07) a
aCO₂	AM	+P	4.3(1.2)	1.8(0.3)a	400.8(6.4)	6.2(0.4)	0.64(0.08) b
		control	3.2(0.5)	1.7(0.2)ab	391.6(8.9)	5.9(0.3)	0.44(0.01) a
	NM	+P	3.2(0.4)	2.1(0.2)ab	390.1(8.5)	5.1(0.2)	0.55(0.06) b
		control	3.4(0.3)	2.4(0.4)b	376.1(16.1)	5.5(0.2)	0.44(0.09) a
eCO₂	AM	+P	3.6(0.3)	2.4(0.3)b	382.7(14.8)	5.3(0.2)	0.55(0.09) b
		CO₂	0.3516	2.1	0.03	2.48	0.19
		P	1.0574	0.2835	0.65	2.52	**8.87****
		AM	2.1422	0.1943	0.61	2.35	0.03
		CO₂xP	0.9543	0.4923	0.29	1.13	0.54
		CO₂xAM	0.4513	**5.1081***	**3.49(.)**	**5.22***	0.03
		AMxP	1.241	0.4535	0.06	2.81	0.08
		PxAMxCO₂	0.758	1.0528	0.33	0.04	0.08

			P pool		N pool	
			Shoot P	Root P	Shoot N✖	Root N
			mg			
		control	1.2(0.2) a	0.89(0.14) a	15.14(0.87)	11.64(0.65)
	NM	+P	1.6(0.2) b	1.25(0.35) b	14.46(1.48)	10.52(1.34)
		control	1.2(0.2) a	0.66(0.04) a	16.75(1.13)	10.09(0.99)
aCO₂	AM	+P	3.0(1.1) b	1.06(0.06) b	19.38(2.22)	13.84(2.15)
		control	1.4(0.2) a	0.72(0.06) a	19.29(3.75)	9.85(1.44)
	NM	+P	1.8(0.3) b	1.23(0.22) b	16.59(3.05)	11.25(1.37)
		control	1.5(0.3) a	0.99(0.10) a	18.97(2.59)	13.27(2.04)
eCO₂	AM	+P	2.0(0.3) b	1.22(0.03) b	18.89(1.23)	12.46(1.68)
		CO₂	0.03	0.40	1.65	0.03
		P	**5.62***	**10.98****	0.08	0.55
		AM	1.50	0.11	2.60	2.19
		CO₂xP	1.08	0.002	0.32	0.22
		CO₂xAM	0.67	2.25	0.35	0.43
		AMxP	1.24	0.28	1.10	0.38
		PxAMxCO₂	0.91	0.49	0.01	2.67

3.4. Microbial communities including AM

AM fungi presence and abundance was assessed with the 16:1ω5c neutral lipid, which was high in AM-inoculated pots lacking additional P. However, P addition reduced the concentration of the AM fungal lipid in soil to a level approaching the uninoculated pots (AMxP: $F_{(1,24)}$= 6.28, $P < 0.001$ **Table SI 2**). We assessed the biomass and composition of

the microbial community as we expected that AM fungi would alter soil saprotrophic communities as a mechanisms to enhance SOM decomposition under low P conditions. We observed a significant increase in microbial biomass with AM fungi in low P (control pots) and eCO_2 conditions. The increase in microbial biomass in these conditions was particularly due to the response of Gram positive bacteria and Actinobacteria (**Figure 4**). Gram negative bacteria and fungi significantly increased with eCO_2 while protozoa increased with eCO_2 only for NM pots (**Figure SI 2).**

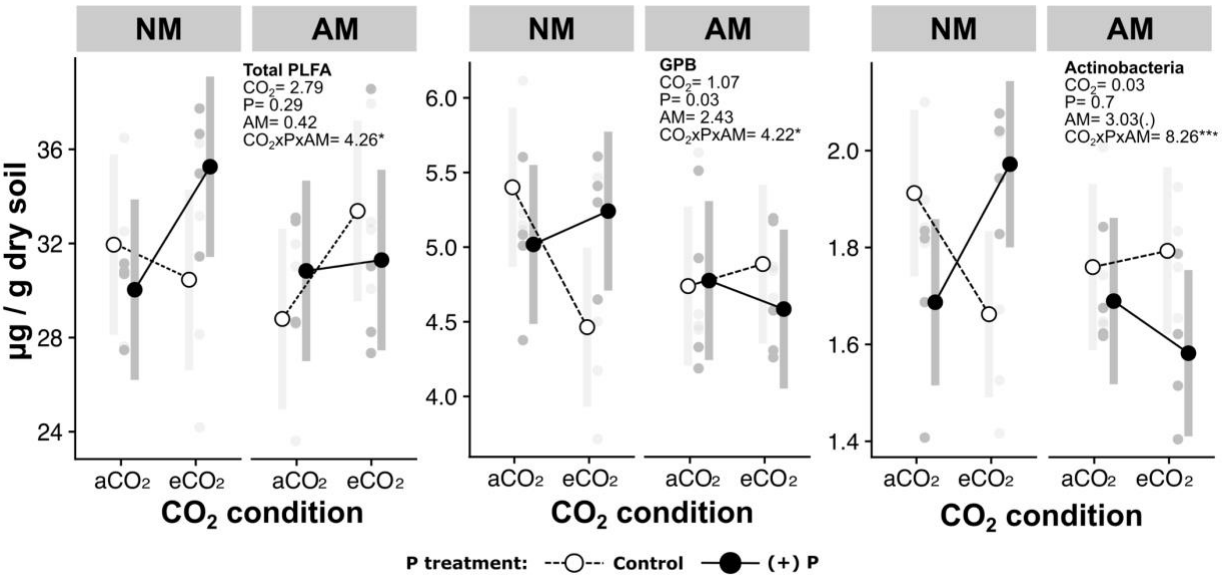


Figure 4. Estimated marginal means with original data (grey circles) and confidence intervals (grey bars) of the total microbial biomass, GPB (Gram positive bacteria) and actinobacteria (µg /g dry soil) from fitted lineal models per experimental treatments. P treatment as white circles and dashed lines (control) or black circles and solid lines (+P) for estimated means, and as light grey (control) and dark grey (+P) for original data. NM: non-mycorrhizal. ANOVA results displayed with significance levels: ≤ 0.1(.), ≤ 0.05(*), ≤0.01 (**), ≤ 0.001(***); only significant interactions of the treatments displayed. Grey circles are the original data input for the models.

4. Discussion

Our experiment investigated whether, under low P conditions, increased SOM decomposition and organic P cycling would allow for a sustained plant fertilisation effect with eCO_2. We expected to observe increases in plant biomass under eCO_2 conditions and low P availability paired with higher SOM derived C pools (SOM derived respired CO_2,

MBC, DOC), with further enhancements of SOM decomposition when AM fungi were inoculated due to the role of this symbiotic fungi on P acquisition. We did not find strong evidence suggesting that increases in soil C cycling with low P availability supported plant growth under eCO_2. Instead, we found that the impacts of CO_2 enrichment and P availability on plant growth and soil C cycling were generally independent of each other with increases in root biomass and soil C cycling under eCO_2 occurring regardless of the P treatment. Contrary to our hypotheses (**Figure 1**), soil C cycling was enhanced with P addition, suggesting that low P conditions were limiting soil C cycling. On the other hand, root biomass increased with eCO_2 conditions and AM presence, while microbial biomass increased with eCO_2 in AM-inoculated pots and control P conditions mainly due to the response of Gram positive bacteria and Actinobacteria. Taken together, our findings in this plant-soil system demonstrate that C and P biogeochemical cycles may not become coupled to sustain an eCO_2 fertilisation effect but instead, that low soil P will limit C cycling responses to eCO_2 with AM potentially outcompeting saprotrophic communities for nutrients and hampering SOM decomposition.

The CO_2 fertilization effect is modulated by the interaction of mycorrhizal associations and nutrient availability (Terrer et al., 2019, 2016; Treseder, 2004). In this study, although the increases in root biomass under eCO_2 conditions occurred when AM fungi were present, this effect occurred regardless of P availability. The CO_2 fertilization effect is a product of higher plant photosynthetic activity leading to excess C in plant tissues leading to increased growth. In this study, we observed a marginally higher plant C:N ratio with eCO_2 (**Figure 3**) but no significant increases in plant biomass. The observed additional assimilated C was potentially allocated belowground, driving the detected increases in root biomass and AM fungi growth and activity (Cheng and Johnson, 1998; Mohan et al., 2014; Treseder, 2004). The presence of AM fungi has been previously reported to increase root biomass with eCO_2 (Baslam et al., 2012; Dong et al., 2018; Zhu et al., 2016) and root biomass responses to eCO_2

may not be necessarily affected by low P conditions (Jiang et al., 2020). It is hypothesised that the positive feedback of eCO_2 and AM fungi on plant growth is mediated by the nutrient uptake role of these symbiotic fungi (Alberton et al., 2005). While P availability has been found to drive the CO_2 fertilization effect on ectomycorrhizal plants, the response of arbuscular mycorrhizal plants to eCO_2 seems to be more dependent on soil N availability (Terrer et al., 2019). Although we did not find that P availability mediated increases in root biomass with eCO_2 and AM fungal presence, we observed that AM fungi marginally increased plant N contents in the aboveground biomass (**Table 2**), as well as decreased dissolved N and P in soil with eCO_2 (**Table 1**) and plant C:N with P addition (**Figure 3**), all of this indicating that AM fungi might have promoted N uptake when P was added and facilitated the observed increases in root biomass.

We hypothesised that higher SOM decomposition would occur with low P availability as organic P cycling and biological P mobilisation mechanisms are crucial when mineral P sources are depleted (Reed et al., 2011). Contrary to our expectations, we found that P addition enhanced soil C cycling. Increases in SOM decomposition with P addition in P-limited systems have been previously reported (Cleveland et al., 2006) and can be explained by the higher affinity of P to mineral surfaces and the consequent release of labile C that promotes microbial activity (Mori et al., 2018). We expected that AM fungi presence would further enhance SOM decomposition in low P conditions (**Figure 1**). Labile C funnelled via AM fungi to the saprotrophic community may enhance soil microbial community activity and promote SOM decomposition (Frey, 2019). Although we observed higher microbial biomass under eCO_2 and AM presence in control P conditions, we suggest that the lack of significant increases in SOM decomposition in these conditions may be due to higher competition between AM fungi and saprotrophic communities that might have limited enhanced soil C cycling (Zhou et al., 2019). The changes in plant C:N, soil dissolved C:N, total soil C:N with

AM fungi explained above further support the idea that AM fungi might outcompete saprotrophic microbes in N and P uptake. Finally, we detected a decrease in SOM decomposition with P addition and AM-inoculated pots (**Figure 2**), but caution must be taken when interpreting this result since P addition also significantly reduced AM fungi presence and thus, it cannot be claimed that the reduction in SOM decomposition with P addition in AM pots is due to AM fungi presence.

We expected that SOM decomposition and, thus, organic P cycling would increase with eCO_2 particularly under low P conditions as a mechanism to sustain plant nutrient demands (**Figure 1**). Our results show evidence for increased C cycling with CO_2 enrichment, particularly for the fraction of SOM-derived DOC, but this effect was not dependent on P availability. Increases in DOC with eCO_2 have been previously attributed to increases in C allocation belowground and higher rhizodeposition (Drake et al., 2011; Freeman et al., 2004; Lukac et al., 2003; Phillips et al., 2011) but it can also be due to increased SOM decomposition (Hagedorn et al., 2008, 2002). Our isotopic analyses allowed us to detect that increases in DOC under eCO_2 in this system were due to enhanced SOM decomposition given the observed increase in SOM-derived DOC fraction (**Table SI 2**). The DOC made available via SOM decomposition can be either incorporated in the microbial biomass or lost via leaching. We did not observed changes in the SOM-derived MBC with eCO_2 and thus the extra DOC was likely not incorporated in the microbial biomass but rather lost via leaching (Kindler et al., 2011). On the other hand, only marginally higher soil respiration with eCO_2 was found in the present study which can be due to the low diffusivity of CO_2 from soils, particularly with high soil moisture (Davidson et al., 2000; Hashimoto and Komatsu, 2006; Maier and Schack-Kirchner, 2014). In our experiment, volumetric soil water content was on average 23% for planted pots, which is slightly above the expected (12-21%) soil water

539 holding capacity for a soil with sandy to loamy texture as the one used for this experiment
540 (Datta et al., 2017; Easton and Bock, 2016).

541 We observed higher P concentrations in plant tissues but this was not accompanied by
542 increases in biomass under any CO_2 condition. Higher P concentration in plant tissues
543 without increases in biomass can occur due to a P luxury consumption of plants, where
544 higher P immobilisation is not necessarily related to increases in growth (Brar and Tolleson,
545 1975). Lack of responses to P addition in biomass (Nie et al., 2009) and abundance
546 (Robinson et al., 1993) for *Microlaena stipoides* have been observed before and attributed to
547 a nutrient accumulation strategy of this grass species, the time and frequency of fertilizer
548 additions and the low response that Australian native grasses typically have to fertilizer
549 application. In this study, only one addition of P as triple superphosphate was done at the
550 start of this experiment. Australian native grasses are less responsive to fertilizer addition
551 during establishment (Nie et al., 2009), which explains the lack of biomass effects of *M.*
552 *stipoides* in this experiment. Also, triple superphosphate is highly soluble in water and
553 becomes rapidly available for plant uptake (Mullins et al., 1995) by the first week of
554 application (Ghosal and Chakraborty, 2012). Hence, increases in P concentrations in plant
555 tissues occurred at the beginning of the experiment when AM fungi had not fully colonised
556 the roots and so, their role in soil C transformations and plant P uptake were less relevant.

557 Current understanding of the impacts of eCO_2 on plant productivity with low nutrient
558 conditions have focused on N-limited ecosystems. Higher SOM decomposition under eCO_2
559 when N availability is low occurs as a mechanism to sustain nutrient supply and plant
560 growth, with mycorrhizal fungi aiding to deliver the mined nutrients to the plants. For P-
561 limited ecosystems however, low P availability generally constrains ecosystem responses to
562 CO_2 enrichment (Ellsworth et al., 2017; Jiang et al., 2020; Reed et al., 2015; Reich et al.,
563 2006) and the role of AM fungi mediating plant and soil C responses to eCO_2 with low P

availability is not fully clear. Thanks to the detailed measurement of soil C cycling as changes in total C pools, SOM-derived fractions and total mass of SOM-derived C pools, we show that the impacts of CO_2 enrichment and P availability on plant growth and soil C cycling were independent of each other and are not likely to become coupled with eCO_2 conditions. We also demonstrate that although AM fungi may contribute to increases in microbial biomass with eCO_2 and low-P conditions, this effect may not translate into enhanced SOM decomposition due to increased nutrient competition that may limit saprotrophic communities. Our findings highlight that ecosystem responses to eCO_2 with P limitation are different from those reported for N-limited systems and therefore, inferences of the behaviour of P-limited ecosystems based on current knowledge about N-limited ecosystems are not ideal. Moreover, our results also contribute to the current gap in knowledge regarding the impacts of soil C cycling with low P availability exposed to eCO_2 conditions.

5. Acknowledgements

We thank Gavin McKenzie and Goran Lopaticki for their help with the chamber set up, maintenance and troubleshooting for the duration of this experiment. Thanks to Pushpinder Matta and Christopher Mitchell for their help with nutrient analyses and to Johanna Pihlblad and Johanna Wong- Bajracharya for their assistance during the harvest of this experiment and sample processing.

References

Ainsworth, E.A., Long, S.P., 2004. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2: Tansley review. New Phytologist 165, 351–372. doi:10.1111/j.1469-8137.2004.01224.x

Alberton, O., Kuyper, T.W., Gorissen, A., 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. New Phytologist 167, 859–868. doi:10.1111/j.1469-8137.2005.01458.x

Baslam, M., Erice, G., Goicoechea, N., 2012. Impact of arbuscular mycorrhizal fungi (AMF) and atmospheric CO_2 concentration on the biomass production and partitioning in the forage legume alfalfa. Symbiosis 58, 171–181. doi:10.1007/s13199-012-0199-6

593 Brar, G.S., Tolleson, E.L., 1975. The luxury uptake phenomenon for removal of phosphates
594 from municipal wastewater. Water Research 9, 71–77. doi:10.1016/0043-
595 1354(75)90154-2
596 Brundett, M., Australian Centre for International Agricultural Research (Eds.), 1995.
597 Mycorrhizas for plantation forestry in Asia: proceedings of an international
598 symposium and workshop, Kaiping, Guangdong Province, P.R. China 7 - 11
599 November, 1994, ACIAR proceedings. Canberra.
600 Buyer, J.S., Sasser, M., 2012. High throughput phospholipid fatty acid analysis of soils.
601 Applied Soil Ecology, Microorganisms and the Sustainable Management of Soil 61,
602 127–130. doi:10.1016/j.apsoil.2012.06.005
603 Canadell, J.G., Pitelka, L.F., Ingram, J.S.I., 1995. The effects of elevated [CO_2] on plant-soil
604 carbon below-ground: A summary and synthesis. Plant and Soil 187, 391–400.
605 doi:10.1007/BF00017102
606 Carrillo, Y., Dijkstra, F.A., LeCain, D., Pendall, E., 2015. Mediation of soil C decomposition
607 by arbuscular mycorrizhal fungi in grass rhizospheres under elevated CO_2.
608 Biogeochemistry. doi:10.1007/s10533-015-0159-3
609 Carrillo, Y., Dijkstra, F.A., Pendall, E., LeCain, D., Tucker, C., 2014. Plant rhizosphere
610 influence on microbial C metabolism: the role of elevated CO2, N availability and
611 root stoichiometry. Biogeochemistry 117, 229–240. doi:10.1007/s10533-014-9954-5
612 Castañeda-Gómez, L., Walker, J.K.M., Powell, J.R., Ellsworth, D.S., Pendall, E., Carrillo, Y.,
613 2020. Impacts of elevated carbon dioxide on carbon gains and losses from soil and
614 associated microbes in a Eucalyptus woodland. Soil Biology and Biochemistry 143,
615 107734. doi:10.1016/j.soilbio.2020.107734
616 Cavagnaro, T.R., Gleadow, R.M., Miller, R.E., 2011. Plant nutrient acquisition and utilisation
617 in a high carbon dioxide world. Functional Plant Biology 38, 87–96.
618 doi:10.1071/FP10124
619 Cheng, L., Booker, F.L., Tu, C., Burkey, K.O., Zhou, L., Shew, H.D., Rufty, T.W., Hu, S.,
620 2012. Arbuscular Mycorrhizal Fungi Increase Organic Carbon Decomposition Under
621 Elevated CO_2. Science 337, 1084–1087. doi:10.1126/science.1224304
622 Cheng, W., Dijkstra, F.A., 2007. Theoretical Proof and Empirical Confirmation of a
623 Continuous Labeling Method Using Naturally ^{13}C-Depleted Carbon Dioxide. Journal
624 of Integrative Plant Biology 49, 401–407.
625 Cheng, W., Johnson, D.W., 1998. Elevated CO_2, rhizosphere processes, and soil organic
626 matter decomposition 202, 167–174.
627 Clark, C.E.F., Mitchell, M.L., Islam, M.R., Jacobs, B., 2014. Phosphorus content of the soil
628 influences the growth and productivity of Themeda triandra Forssk. and Microlaena
629 stipoides (Labill.) R.Br. The Rangeland Journal 36, 233–237. doi:10.1071/RJ13108
630 Cleveland, C.C., Reed, S.C., Townsend, A.R., 2006. Nutrient Regulation of Organic Matter
631 Decomposition in a Tropical Rain Forest. Ecology 87, 492–503. doi:10.1890/05-0525
632 Conroy, J.P., Milham, P.J., Barlow, E.W.R., 1992. Effect of nitrogen and phosphorus
633 availability on the growth response of Eucalyptus grandis to high CO_2. Plant, Cell &
634 Environment 15, 843–847. doi:10.1111/j.1365-3040.1992.tb02152.x
635 Cotrufo, M.F., Gorissen, A., 1997. Elevated CO_2 enhances below-ground C allocation in
636 three perennial grass species at different levels of N availability. New Phytologist
637 137, 421–431. doi:10.1046/j.1469-8137.1997.00839.x
638 Crous, K.Y., Ósvaldsson, A., Ellsworth, D.S., 2015. Is phosphorus limiting in a mature
639 Eucalyptus woodland? Phosphorus fertilisation stimulates stem growth. Plant and Soil
640 391, 293–305. doi:10.1007/s11104-015-2426-4
641 Datta, S., Taghvaeian, S., Stivers, J., 2017. Understanding Soil Water Content and
642 Thresholds for Irrigation Management (No. BAE-1537).

643 Davidson, E.A., Verchot, L.V., Cattânio, J.H., Ackerman, I.L., Carvalho, J.E.M., 2000.
644 Effects of soil water content on soil respiration in forests and cattle pastures of eastern
645 Amazonia. Biogeochemistry 48, 53–69. doi:10.1023/A:1006204113917
646 De Graaff, M.-A., Groenigen, K.-J.V., Six, J., Hungate, B., Kessel, C.V., 2006. Interactions
647 between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis.
648 Global Change Biology 12, 2077–2091. doi:10.1111/j.1365-2486.2006.01240.x
649 Delucia, E.H., Callaway, R.M., Thomas, E.M., Schlesinger, W.H., 1997. Mechanisms of
650 Phosphorus Acquisition for Ponderosa Pine Seedlings under High CO_2 and
651 Temperature. Annals of Botany 79, 111–120. doi:10.1006/anbo.1996.0320
652 Deng, Q., Hui, D., Luo, Y., Elser, J., Wang, Y.-P., Loladze, I., Zhang, Q., Dennis, S., 2015.
653 Down-regulation of tissue N:P ratios in terrestrial plants by elevated CO2. Ecology
654 96, 3354–3362. doi:10.1890/15-0217.1
655 Dieleman, W.I.J., Luyssaert, S., Rey, A., Angelis, P.D., Barton, C.V.M., Broadmeadow,
656 M.S.J., Broadmeadow, S.B., Chigwerewe, K.S., Crookshanks, M., Dufrêne, E., Jarvis,
657 P.G., Kasurinen, A., Kellomäki, S., Dantec, V.L., Liberloo, M., Marek, M., Medlyn,
658 B., Pokorný, R., Scarascia-Mugnozza, G., Temperton, V.M., Tingey, D., Urban, O.,
659 Ceulemans, R., Janssens, I.A., 2010. Soil [N] modulates soil C cycling in CO2-
660 fumigated tree stands: a meta-analysis. Plant, Cell & Environment 33, 2001–2011.
661 doi:10.1111/j.1365-3040.2010.02201.x
662 Dijkstra, F.A., Carrillo, Y., Pendall, E., Morgan, J.A., 2013. Rhizosphere priming: a nutrient
663 perspective. Frontiers in Microbiology 4. doi:10.3389/fmicb.2013.00216
664 Dijkstra, F.A., Pendall, E., Morgan, J.A., Blumenthal, D.M., Carrillo, Y., LeCain, D.R.,
665 Follett, R.F., Williams, D.G., 2012. Climate change alters stoichiometry of
666 phosphorus and nitrogen in a semiarid grassland. New Phytologist 196, 807–815.
667 doi:10.1111/j.1469-8137.2012.04349.x
668 Dong, Y., Wang, Z., Sun, H., Yang, W., Xu, H., 2018. The Response Patterns of Arbuscular
669 Mycorrhizal and Ectomycorrhizal Symbionts Under Elevated CO_2: A Meta-Analysis.
670 Frontiers in Microbiology 9, 1248. doi:10.3389/fmicb.2018.01248
671 Drake, J.E., Gallet-Budynek, A., Hofmockel, K.S., Bernhardt, E.S., Billings, S.A., Jackson,
672 R.B., Johnsen, K.S., Lichter, J., McCarthy, H.R., McCormack, M.L., Moore, D.J.P.,
673 Oren, R., Palmroth, S., Phillips, R.P., Pippen, J.S., Pritchard, S.G., Treseder, K.K.,
674 Schlesinger, W.H., DeLucia, E.H., Finzi, A.C., 2011. Increases in the flux of carbon
675 belowground stimulate nitrogen uptake and sustain the long-term enhancement of
676 forest productivity under elevated CO_2. Ecology Letters 14, 349–357.
677 doi:10.1111/j.1461-0248.2011.01593.x
678 Drake, J.E., Macdonald, C.A., Tjoelker, M.G., Crous, K.Y., Gimeno, T.E., Singh, B.K.,
679 Reich, P.B., Anderson, I.C., Ellsworth, D.S., 2016. Short-term carbon cycling
680 responses of a mature eucalypt woodland to gradual stepwise enrichment of
681 atmospheric CO_2 concentration. Global Change Biology 22, 380–390.
682 doi:10.1111/gcb.13109
683 Easton, Z.M., Bock, E., 2016. Soil and Soil Water Relationships (No. BSE-194P).
684 Ellsworth, D.S., Anderson, I.C., Crous, K.Y., Cooke, J., Drake, J.E., Gherlenda, A.N.,
685 Gimeno, T.E., Macdonald, C.A., Medlyn, B.E., Powell, J.R., Tjoelker, M.G., Reich,
686 P.B., 2017. Elevated CO_2 does not increase eucalypt forest productivity on a low-
687 phosphorus soil. Nature Climate Change 7, 279–282. doi:10.1038/nclimate3235
688 Fang, X.-M., Zhang, X.-L., Chen, F.-S., Zong, Y.-Y., Bu, W.-S., Wan, S.-Z., Luo, Y., Wang,
689 H., 2019. Phosphorus addition alters the response of soil organic carbon
690 decomposition to nitrogen deposition in a subtropical forest. Soil Biology and
691 Biochemistry 133, 119–128. doi:10.1016/j.soilbio.2019.03.005

692 Feng, J., Zhu, B., 2019. A global meta-analysis of soil respiration and its components in
693 response to phosphorus addition. Soil Biology and Biochemistry 135, 38–47.
694 doi:10.1016/j.soilbio.2019.04.008
695 Finzi, A.C., Austin, A.T., Cleland, E.E., Frey, S.D., Houlton, B.Z., Wallenstein, M.D., 2011.
696 Responses and feedbacks of coupled biogeochemical cycles to climate change:
697 examples from terrestrial ecosystems. Frontiers in Ecology and the Environment 9,
698 61–67. doi:10.1890/100001
699 Finzi, A.C., Sinsabaugh, R.L., Long, T.M., Osgood, M.P., 2006. Microbial Community
700 Responses to Atmospheric Carbon Dioxide Enrichment in a Warm-Temperate Forest.
701 Ecosystems 9, 215–226. doi:10.1007/s10021-005-0078-6
702 Fox, T.R., Miller, B.W., Rubilar, R., Stape, J.L., Albaugh, T.J., 2011. Phosphorus Nutrition
703 of Forest Plantations: The Role of Inorganic and Organic Phosphorus, in: Bünemann,
704 E., Oberson, A., Frossard, E. (Eds.), Phosphorus in Action: Biological Processes in
705 Soil Phosphorus Cycling, Soil Biology. Springer Berlin Heidelberg, Berlin,
706 Heidelberg, pp. 317–338. doi:10.1007/978-3-642-15271-9_13
707 Fransson, P.M.A., Johansson, E.M., 2010. Elevated CO_2 and nitrogen influence exudation of
708 soluble organic compounds by ectomycorrhizal root systems. FEMS Microbiology
709 Ecology 71, 186–196. doi:10.1111/j.1574-6941.2009.00795.x
710 Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A.,
711 Sleep, D., Hughes, S., Hudson, J., 2004. Export of dissolved organic carbon from
712 peatlands under elevated carbon dioxide levels. Nature 430, 195–198.
713 doi:10.1038/nature02707
714 Frey, S.D., 2019. Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics. Annual
715 Review of Ecology, Evolution, and Systematics 50, 237–259. doi:10.1146/annurev-
716 ecolsys-110617-062331
717 Ghosal, P., Chakraborty, T., 2012. Comparative Solubility Study of Four Phosphatic
718 Fertilizers in Different Solvents and the Effect of Soil. Resources and Environment 2,
719 175–179. doi:10.5923/j.re.20120204.07
720 Gifford, R.M., Barrett, D.J., Lutze, J.L., 2000. The effects of elevated [CO_2] on the C:N and
721 C:P mass ratios of plant tissues. Plant and Soil 224, 1–14.
722 doi:10.1023/A:1004790612630
723 Goll, D.S., Brovkin, V., Parida, B.R., Reick, C.H., Kattge, J., Reich, P.B., van Bodegom,
724 P.M., Niinemets, ü., 2012. Nutrient limitation reduces land carbon uptake in
725 simulations with a model of combined carbon, nitrogen and phosphorus cycling.
726 Biogeosciences 9, 3547–3569. doi:10.5194/bg-9-3547-2012
727 Hagedorn, F., Blaser, P., Siegwolf, R., 2002. Elevated atmospheric CO_2 and increased N
728 deposition effects on dissolved organic carbon—clues from $\delta^{13}C$ signature. Soil
729 Biology and Biochemistry 34, 355–366. doi:10.1016/S0038-0717(01)00191-2
730 Hagedorn, F., Hees, P.A.W. van, Handa, I.T., Hättenschwiler, S., 2008. Elevated atmospheric
731 CO_2 fuels leaching of old dissolved organic matter at the alpine treeline. Global
732 Biogeochemical Cycles 22. doi:10.1029/2007GB003026
733 Hasegawa, S., Macdonald, C.A., Power, S.A., 2016. Elevated carbon dioxide increases soil
734 nitrogen and phosphorus availability in a phosphorus-limited Eucalyptus woodland.
735 Global Change Biology 22, 1628–1643.
736 Hashimoto, S., Komatsu, H., 2006. Relationships between soil CO_2 concentration and CO_2
737 production, temperature, water content, and gas diffusivity: implications for field
738 studies through sensitivity analyses. Journal of Forest Research 11, 41–50.
739 doi:10.1007/s10310-005-0185-4

740 Hill, J.O., Simpson, R.J., Ryan, M.H., Chapman, D.F., 2010. Root hair morphology and
741 mycorrhizal colonisation of pasture species in response to phosphorus and nitrogen
742 nutrition. Crop and Pasture Science 61, 122. doi:10.1071/CP09217
743 Högy, P., Keck, M., Niehaus, K., Franzaring, J., Fangmeier, A., 2010. Effects of atmospheric
744 CO_2 enrichment on biomass, yield and low molecular weight metabolites in wheat
745 grain. Journal of Cereal Science 52, 215–220. doi:10.1016/j.jcs.2010.05.009
746 Hoosbeek, M.R., Lukac, M., Dam, D. van, Godbold, D.L., Velthorst, E.J., Biondi, F.A.,
747 Peressotti, A., Cotrufo, M.F., Angelis, P. de, Scarascia-Mugnozza, G., 2004. More
748 new carbon in the mineral soil of a poplar plantation under Free Air Carbon
749 Enrichment (POPFACE): Cause of increased priming effect? Global Biogeochemical
750 Cycles 18. doi:10.1029/2003GB002127
751 Hungate, B.A., Groenigen, K.-J.V., Six, J., Jastrow, J.D., Luo, Y., Graaff, M.-A.D., Kessel,
752 C.V., Osenberg, C.W., 2009. Assessing the effect of elevated carbon dioxide on soil
753 carbon: a comparison of four meta-analyses. Global Change Biology 15, 2020–2034.
754 doi:10.1111/j.1365-2486.2009.01866.x
755 Javot, H., Pumplin, N., Harrison, M.J., 2007. Phosphate in the arbuscular mycorrhizal
756 symbiosis: transport properties and regulatory roles: Phosphate transport in the AM
757 symbiosis. Plant, Cell & Environment 30, 310–322. doi:10.1111/j.1365-
758 3040.2006.01617.x
759 Jiang, M., Caldararu, S., Zhang, H., Fleischer, K., Crous, K.Y., Yang, J., Kauwe, M.G.D.,
760 Ellsworth, D.S., Reich, P.B., Tissue, D.T., Zaehle, S., Medlyn, B.E., 2020. Low
761 phosphorus supply constrains plant responses to elevated CO_2: A meta-analysis.
762 Global Change Biology 26, 5856–5873. doi:https://doi.org/10.1111/gcb.15277
763 Jin, J., Tang, C., Sale, P., 2015. The impact of elevated carbon dioxide on the phosphorus
764 nutrition of plants: a review. Annals of Botany 116, 987–999.
765 doi:10.1093/aob/mcv088
766 Jing, Z., Chen, R., Wei, S., Feng, Y., Zhang, J., Lin, X., 2017. Response and feedback of C
767 mineralization to P availability driven by soil microorganisms. Soil Biology and
768 Biochemistry 105, 111–120. doi:10.1016/j.soilbio.2016.11.014
769 Johnson, A.H., Frizano, J., Vann, D.R., 2003. Biogeochemical implications of labile
770 phosphorus in forest soils determined by the Hedley fractionation procedure.
771 Oecologia 135, 487–499. doi:10.1007/s00442-002-1164-5
772 Joner, E.J., van Aarle, I.M., Vosatka, M., 2000. Phosphatase activity of extra-radical
773 arbuscular mycorrhizal hyphae: A review. Plant and Soil 226, 12.
774 Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015.
775 Dynamics of global forest area: Results from the FAO Global Forest Resources
776 Assessment 2015. Forest Ecology and Management, Changes in Global Forest
777 Resources from 1990 to 2015 352, 9–20. doi:10.1016/j.foreco.2015.06.014
778 Kelley, A.M., Fay, P.A., Polley, H.W., Gill, R.A., Jackson, R.B., 2011. Atmospheric CO_2 and
779 soil extracellular enzyme activity: a meta-analysis and CO_2 gradient experiment.
780 Ecosphere 2, art96. doi:10.1890/ES11-00117.1
781 Kindler, R., Siemens, J., Kaiser, K., Walmsley, D.C., Bernhofer, C., Buchmann, N., Cellier,
782 P., Eugster, W., Gleixner, G., Grũnwald, T., Heim, A., Ibrom, A., Jones, S.K., Jones,
783 M., Klumpp, K., Kutsch, W., Larsen, K.S., Lehuger, S., Loubet, B., Mckenzie, R.,
784 Moors, E., Osborne, B., Pilegaard, K., Rebmann, C., Saunders, M., Schmidt, M.W.I.,
785 Schrumpf, M., Seyfferth, J., Skiba, U., Soussana, J.-F., Sutton, M.A., Tefs, C.,
786 Vowinckel, B., Zeeman, M.J., Kaupenjohann, M., 2011. Dissolved carbon leaching
787 from soil is a crucial component of the net ecosystem carbon balance. Global Change
788 Biology 17, 1167–1185. doi:10.1111/j.1365-2486.2010.02282.x

789 Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2020. emmeans: Estimated
790 Marginal Means, aka Least-Squares Means.
791 Liu, Y., Chen, J., 2008. Phosphorus Cycle, in: Jørgensen, S.E., Fath, B.D. (Eds.),
792 Encyclopedia of Ecology. Academic Press, Oxford, pp. 2715–2724.
793 doi:10.1016/B978-008045405-4.00754-0
794 Liu, Y., Zang, H., Ge, T., Bai, J., Lu, S., Zhou, P., Peng, P., Shibistova, O., Zhu, Z., Wu, J.,
795 Guggenberger, G., 2018. Intensive fertilization (N, P, K, Ca, and S) decreases organic
796 matter decomposition in paddy soil. Applied Soil Ecology 127, 51–57.
797 doi:10.1016/j.apsoil.2018.02.012
798 Loladze, I., 2014. Hidden shift of the ionome of plants exposed to elevated CO_2 depletes
799 minerals at the base of human nutrition. ELife 3. doi:10.7554/eLife.02245
800 Loladze, I., 2002. Rising atmospheric CO_2 and human nutrition: toward globally imbalanced
801 plant stoichiometry? Trends in Ecology & Evolution 17, 457–461.
802 doi:10.1016/S0169-5347(02)02587-9
803 Lukac, M., Calfapietra, C., Godbold, D.L., 2003. Production, turnover and mycorrhizal
804 colonization of root systems of three Populus species grown under elevated CO_2
805 (POPFACE). Global Change Biology 9, 838–848. doi:10.1046/j.1365-
806 2486.2003.00582.x
807 Maier, M., Schack-Kirchner, H., 2014. Using the gradient method to determine soil gas flux:
808 A review. Agricultural and Forest Meteorology 192–193, 78–95.
809 doi:10.1016/j.agrformet.2014.03.006
810 Maroco, J.P., Breia, E., Faria, T., Pereira, J.S., Chaves, M.M., 2002. Effects of long-term
811 exposure to elevated CO_2 and N fertilization on the development of photosynthetic
812 capacity and biomass accumulation in Quercus suber L. Plant, Cell & Environment
813 25, 105–113. doi:10.1046/j.0016-8025.2001.00800.x
814 Matamala, R., Schlesinger, W.H., 2000. Effects of elevated atmospheric CO_2 on fine root
815 production and activity in an intact temperate forest ecosystem. Global Change
816 Biology 6, 967–979. doi:10.1046/j.1365-2486.2000.00374.x
817 McGill, W.B., Cole, C.V., 1981. Comparative aspects of cycling of organic C, N, S and P
818 through soil organic matter. Geoderma 26, 267–286. doi:10.1016/0016-
819 7061(81)90024-0
820 Mohan, J.E., Cowden, C.C., Baas, P., Dawadi, A., Frankson, P.T., Helmick, K., Hughes, E.,
821 Khan, S., Lang, A., Machmuller, M., Taylor, M., Witt, C.A., 2014. Mycorrhizal fungi
822 mediation of terrestrial ecosystem responses to global change: mini-review. Fungal
823 Ecology 10, 3–19. doi:10.1016/j.funeco.2014.01.005
824 Moorhead, D.L., Linkins, A.E., 1997. Elevated CO_2 alters belowground exoenzyme activities
825 in tussock tundra. Plant and Soil 189, 321–329. doi:10.1023/A:1004246720186
826 Mori, T., Lu, X., Aoyagi, R., Mo, J., 2018. Reconsidering the phosphorus limitation of soil
827 microbial activity in tropical forests. Functional Ecology 32, 1145–1154.
828 doi:10.1111/1365-2435.13043
829 Mullen, M.D., 2005. PHOSPHORUS IN SOILS | Biological Interactions, in: Hillel, D. (Ed.),
830 Encyclopedia of Soils in the Environment. Elsevier, Oxford, pp. 210–216.
831 doi:10.1016/B0-12-348530-4/00161-2
832 Mullins, G.L., Sikora, F.J., Williams, J.C., 1995. Effect of Water-Soluble Phosphorus on the
833 Effectiveness of Triple Superphosphate Fertilizers. Soil Science Society of America
834 Journal 59, 256–260. doi:10.2136/sssaj1995.03615995005900010040x
835 Nie, Z.N., Zollinger, R.P., Jacobs, J.L., 2009. Performance of 7 Australian native grasses
836 from the temperate zone under a range of cutting and fertiliser regimes. Crop and
837 Pasture Science 60, 943. doi:10.1071/CP09067

838 Nielsen, U.N., Prior, S., Delroy, B., Walker, J.K.M., Ellsworth, D.S., Powell, J.R., 2015.
839 Response of belowground communities to short-term phosphorus addition in a
840 phosphorus-limited woodland. Plant and Soil 391, 321–331. doi:10.1007/s11104-015-
841 2432-6
842 Norby, R.J., Kauwe, M.G.D., Domingues, T.F., Duursma, R.A., Ellsworth, D.S., Goll, D.S.,
843 Lapola, D.M., Luus, K.A., MacKenzie, A.R., Medlyn, B.E., Pavlick, R., Rammig, A.,
844 Smith, B., Thomas, R., Thonicke, K., Walker, A.P., Yang, X., Zaehle, S., 2015.
845 Model–data synthesis for the next generation of forest free-air CO_2 enrichment
846 (FACE) experiments. New Phytologist 209, 17–28. doi:10.1111/nph.13593
847 Olsson, P.A., 1999. Signature fatty acids provide tools for determination of the distribution
848 and interactions of mycorrhizal fungi in soil. FEMS Microbiology Ecology 29, 303–
849 310.
850 Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L.,
851 Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W.,
852 McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and
853 Persistent Carbon Sink in the World's Forests. Science 333, 988–993.
854 doi:10.1126/science.1201609
855 Pausch, J., Kuzyakov, Y., 2018. Carbon input by roots into the soil: Quantification of
856 rhizodeposition from root to ecosystem scale. Global Change Biology 24, 1–12.
857 doi:10.1111/gcb.13850
858 Peñuelas, J., Sardans, J., Rivas-ubach, A., Janssens, I.A., 2012. The human-induced
859 imbalance between C, N and P in Earth's life system. Global Change Biology 18, 3–
860 6. doi:10.1111/j.1365-2486.2011.02568.x
861 Phillips, R.P., Finzi, A.C., Bernhardt, E.S., 2011. Enhanced root exudation induces microbial
862 feedbacks to N cycling in a pine forest under long-term CO_2 fumigation. Ecology
863 Letters 14, 187–194. doi:10.1111/j.1461-0248.2010.01570.x
864 Phillips, R.P., Meier, I.C., Bernhardt, E.S., Grandy, A.S., Wickings, K., Finzi, A.C., 2012.
865 Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated
866 CO_2. Ecology Letters 15, 1042–1049. doi:10.1111/j.1461-0248.2012.01827.x
867 Piñeiro, J., Ochoa-Hueso, R., Delgado-Baquerizo, M., Dobrick, S., Reich, P.B., Pendall, E.,
868 Power, S.A., 2017. Effects of elevated CO_2 on fine root biomass are reduced by
869 aridity but enhanced by soil nitrogen: A global assessment. Scientific Reports 7.
870 doi:10.1038/s41598-017-15728-4
871 Rayment, G.E., Lyons, D.J., Shelley, B., 2010. Soil Chemical Methods: Australasia. CSIRO
872 PUBLISHING, Victoria, AUSTRALIA.
873 Reed, S.C., Townsend, A.R., Taylor, P.G., Cleveland, C.C., 2011. Phosphorus Cycling in
874 Tropical Forests Growing on Highly Weathered Soils, in: Bünemann, E., Oberson, A.,
875 Frossard, E. (Eds.), Phosphorus in Action: Biological Processes in Soil Phosphorus
876 Cycling, Soil Biology. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 339–369.
877 doi:10.1007/978-3-642-15271-9_14
878 Reed, S.C., Yang, X., Thornton, P.E., 2015. Incorporating phosphorus cycling into global
879 modeling efforts: a worthwhile, tractable endeavor. New Phytologist 208, 324–329.
880 doi:10.1111/nph.13521
881 Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D., Knops, J.M.H.,
882 Naeem, S., Trost, J., 2006. Nitrogen limitation constrains sustainability of ecosystem
883 response to CO_2. Nature 440, 922–925. doi:10.1038/nature04486
884 Reich, P.B., Hobbie, S.E., Lee, T.D., 2014. Plant growth enhancement by elevated CO_2
885 eliminated by joint water and nitrogen limitation. Nature Geoscience 7, 920–924.
886 doi:10.1038/ngeo2284

887 Robinson, J., Munnich, D., Simpson, P., Orchard, P., 1993. Pasture Associations and Their
888 Relation to Environment and Agronomy in the Goulburn District. Australian Journal
889 of Botany 41, 627. doi:10.1071/BT9930627
890 Ross, G.M., Horn, S., Macdonald, C.A., Powell, J.R., Reynolds, J.K., Ryan, M.M., Cook,
891 J.M., Nielsen, U.N., 2020. Metabarcoding mites: Three years of elevated CO_2 has no
892 effect on oribatid assemblages in a Eucalyptus woodland. Pedobiologia (in press).
893 Sato, T., Ezawa, T., Cheng, W., Tawaraya, K., 2015. Release of acid phosphatase from
894 extraradical hyphae of arbuscular mycorrhizal fungus *Rhizophagus clarus*. Soil
895 Science and Plant Nutrition 61, 269–274. doi:10.1080/00380768.2014.993298
896 Sharma, S.B., Sayyed, R.Z., Trivedi, M.H., Gobi, T.A., 2013. Phosphate solubilizing
897 microbes: sustainable approach for managing phosphorus deficiency in agricultural
898 soils. SpringerPlus 2. doi:10.1186/2193-1801-2-587
899 Smith, S.E., Jakobsen, I., Grønlund, M., Smith, F.A., 2011. Roles of Arbuscular Mycorrhizas
900 in Plant Phosphorus Nutrition: Interactions between Pathways of Phosphorus Uptake
901 in Arbuscular Mycorrhizal Roots Have Important Implications for Understanding and
902 Manipulating Plant Phosphorus Acquisition1. Plant Physiology 156, 1050–1057.
903 doi:10.1104/pp.111.174581
904 Soepadmo, E., 1993. Tropical rain forests as carbon sinks. Chemosphere 27, 1025–1039.
905 doi:10.1016/0045-6535(93)90066-E
906 Soka, G., Ritchie, M., 2014. Arbuscular mycorrhizal symbiosis and ecosystem processes:
907 Prospects for future research in tropical soils. Open Journal of Ecology 04, 11–22.
908 doi:10.4236/oje.2014.41002
909 Soong, J.L., Marañon-Jimenez, S., Cotrufo, M.F., Boeckx, P., Bodé, S., Guenet, B., Peñuelas,
910 J., Richter, A., Stahl, C., Verbruggen, E., Janssens, I.A., 2018. Soil microbial CNP
911 and respiration responses to organic matter and nutrient additions: Evidence from a
912 tropical soil incubation. Soil Biology and Biochemistry 122, 141–149.
913 doi:10.1016/j.soilbio.2018.04.011
914 Souza, R.C., Solly, E.F., Dawes, M.A., Graf, F., Hagedorn, F., Egli, S., Clement, C.R., Nagy,
915 L., Rixen, C., Peter, M., 2017. Responses of soil extracellular enzyme activities to
916 experimental warming and CO_2 enrichment at the alpine treeline. Plant and Soil 416,
917 527–537. doi:10.1007/s11104-017-3235-8
918 Sun, Y., Peng, S., Goll, D.S., Ciais, P., Guenet, B., Guimberteau, M., Hinsinger, P., Janssens,
919 I.A., Peñuelas, J., Piao, S., Poulter, B., Violette, A., Yang, X., Yin, Y., Zeng, H.,
920 2017. Diagnosing phosphorus limitations in natural terrestrial ecosystems in carbon
921 cycle models. Earth's Future 5, 730–749. doi:10.1002/2016EF000472
922 Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal
923 fungi as regulators of soil C dynamics in ecosystems under global change. Functional
924 Ecology 22, 955–963. doi:10.1111/j.1365-2435.2008.01402.x
925 Tarnawski, S., Aragno, M., 2006. The Influence of Elevated [CO_2] on Diversity, Activity and
926 Biogeochemical Functions of Rhizosphere and Soil Bacterial Communities, in:
927 Nösberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.),
928 Managed Ecosystems and CO2. Springer-Verlag, Berlin/Heidelberg, pp. 393–412.
929 doi:10.1007/3-540-31237-4_22
930 Tate, K.R., 1984. The biological transformation of P in soil. Plant and Soil 76, 245–256.
931 doi:10.1007/BF02205584
932 Terrer, C., Jackson, R.B., Prentice, I.C., Keenan, T.F., Kaiser, C., Vicca, S., Fisher, J.B.,
933 Reich, P.B., Stocker, B.D., Hungate, B.A., Peñuelas, J., McCallum, I.,
934 Soudzilovskaia, N.A., Cernusak, L.A., Talhelm, A.F., Sundert, K.V., Piao, S.,
935 Newton, P.C.D., Hovenden, M.J., Blumenthal, D.M., Liu, Y.Y., Müller, C., Winter,
936 K., Field, C.B., Viechtbauer, W., Lissa, C.J.V., Hoosbeek, M.R., Watanabe, M.,

Koike, T., Leshyk, V.O., Polley, H.W., Franklin, O., 2019. Nitrogen and phosphorus constrain the CO 2 fertilization of global plant biomass. Nature Climate Change 9, 684–689. doi:10.1038/s41558-019-0545-2

Terrer, C., Vicca, S., Hungate, B.A., Phillips, R.P., Prentice, I.C., 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353, 72–74. doi:10.1126/science.aaf4610

Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytologist 164, 347–355. doi:10.1111/j.1469-8137.2004.01159.x

Treseder, K.K., Allen, M.F., 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. New Phytologist 155, 507–515. doi:10.1046/j.1469-8137.2002.00470.x

Treseder, K.K., Cross, A., 2006. Global Distributions of Arbuscular Mycorrhizal Fungi. Ecosystems 9, 305–316.

van Groenigen, K.J., De Graaff, M.-A., Six, J., Harris, D., Kuikman, P., Van Kessel, C., 2006. The impact of elevated atmospheric [CO_2] on soil C and N dynamics: a meta-analysis, in: Managed Ecosystems and CO_2. Springer, pp. 373–391.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology & Biochemistry 19, 703–707.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecological Applications 20, 5–15. doi:10.1890/08-0127.1

Watt, M., Evans, J.R., 1999. Linking Development and Determinacy with Organic Acid Efflux from Proteoid Roots of White Lupin Grown with Low Phosphorus and Ambient or Elevated Atmospheric CO_2 Concentration. Plant Physiology 120, 705–716.

Wei, L., Vosátka, M., Cai, B., Ding, J., Lu, C., Xu, J., Yan, W., Li, Y., Liu, C., 2019. The Role of Arbuscular Mycorrhiza Fungi in the Decomposition of Fresh Residue and Soil Organic Carbon: A Mini-Review. Soil Science Society of America Journal 83, 511–517. doi:10.2136/sssaj2018.05.0205

Willis, A., Rodrigues, B.F., Harris, P.J.C., 2013. The Ecology of Arbuscular Mycorrhizal Fungi. Critical Reviews in Plant Sciences 32, 1–20. doi:10.1080/07352689.2012.683375

Xu, J., Liu, S., Song, S., Guo, H., Tang, J., Yong, J.W.H., Ma, Y., Chen, X., 2018. Arbuscular mycorrhizal fungi influence decomposition and the associated soil microbial community under different soil phosphorus availability. Soil Biology and Biochemistry 120, 181–190. doi:10.1016/j.soilbio.2018.02.010

Yang, X., Thornton, P.E., Ricciuto, D.M., Hoffman, F.M., 2016. Phosphorus feedbacks constraining tropical ecosystem responses to changes in atmospheric CO_2 and climate. Geophysical Research Letters 43, 7205–7214. doi:10.1002/2016GL069241

Yuan, Y., Li, Y., Mou, Z., Kuang, L., Wu, W., Zhang, J., Wang, F., Hui, D., Peñuelas, J., Sardans, J., Lambers, H., Wang, J., Kuang, Y., Li, Z., Liu, Z., 2021. Phosphorus addition decreases microbial residual contribution to soil organic carbon pool in a tropical coastal forest. Global Change Biology 27, 454–466. doi:10.1111/gcb.15407

Zhang, Q., Wang, Y.P., Matear, R.J., Pitman, A.J., Dai, Y.J., 2014. Nitrogen and phosphorous limitations significantly reduce future allowable CO_2 emissions. Geophysical Research Letters 41, 632–637. doi:10.1002/2013GL058352

Zhou, J., Zang, H., Loeppmann, S., Gube, M., Kuzyakov, Y., Pausch, J., 2019. Arbuscular mycorrhiza enhances rhizodeposition and reduces the rhizosphere priming effect on

986 the decomposition of soil organic matter. Soil Biology and Biochemistry 107641.
987 doi:10.1016/j.soilbio.2019.107641
988 Zhu, X., Song, F., Liu, S., Liu, F., 2016. Arbuscular mycorrhiza improve growth, nitrogen
989 uptake, and nitrogen use efficiency in wheat grown under elevated CO_2. Mycorrhiza
990 26, 133–140. doi:10.1007/s00572-015-0654-3
991