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Lazicki, Patricia
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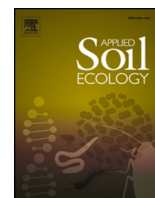
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Acid stress and compost addition decouple carbon and nitrogen cycling in an agricultural soil: An incubation study

Patricia Lazicki^{*}, Jorge L. Mazza Rodrigues, Daniel Geisseler

University of California Davis, Department of Land, Air, and Water Resources, Plant and Environmental Science Building, One Shields Avenue, Davis, CA, USA

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ABSTRACT

Agricultural practices can lead to fluctuations in soil pH and salinity, likely affecting soil nutrient cycling. Compost addition may reduce the impact of these stresses, leading to more stable and resilient systems. We tested nitrogen (N) and carbon (C) cycling responses to the imposition and relief of an acute stress in an agricultural soil, and whether these responses were moderated by compost. In greenhouse pots, we mixed soil with elemental sulfur (S) and compost in a complete 2-way factorial design and incubated at ambient temperatures. Sulfur induced strong acidity and mild salinity stress. After 70 d, stress was partially alleviated by leaching with liquid lime. We took samples 21 and 42 d after S addition and one week after alleviation, measured enzyme activity, microbial biomass, and soluble organic C and N, and performed N and C cycle assays by incubating subsamples with and without ground legume residues to stimulate mineralization and microbial growth. Net N mineralization increased in response to the applied stress, and declined after alleviation. Conversely, stress reduced most C cycling indicators and inhibited nitrification. Stress limited microbial growth more than respiration. Unexpectedly, compost additions to the stressed soils consistently stimulated net N mineralization compared to stressed soils without compost. Compost thus exacerbated rather than buffered the effects of stress on net N mineralization. Compost addition did not affect microbial growth or respiration in any treatment, or how any C cycle parameter responded to stress. The decoupled C and N responses suggest that the localized stresses associated with intensive agriculture may have important implications for C and N turnover in these systems, and warrant further study. Additionally, they demonstrate that biogeochemical processes should be evaluated concurrently when accessing the effect of stressors in soil systems.

1. Introduction

In intensive agriculture, irrigation and fertilization can lead to rapid increases in soil salinity and acidity (Chung and Zasoski, 1993; Hanson and May, 2011; Venterea and Rolston, 2000). Acidity and salinity are known to have profound stressful effects on nutrient cycling (e.g. Aciego Pietri and Brookes, 2008b; Kemmitt et al., 2006; Malik et al., 2018; Rath et al., 2019a, 2019b; Rousk et al., 2009; Silva-Sánchez et al., 2019). Practices such as fertigation through drip systems, which aim to improve input use efficiency by targeting water or nutrients to the plant rooting zone, can exacerbate the magnitude and heterogeneity of acidity or salinity stresses by concentrating them in smaller soil volumes (Hanson and May, 2011; Haynes and Swift, 1987). The use of subsurface drip irrigation (SDI) has expanded very rapidly in recent decades. For example, in California's processing tomato industry, the proportion of growers using drip irrigation rose from 0% in 1987 to 85% in 2011

(Taylor and Zilberman, 2017). While SDI generally increases yields and water use efficiency, it can also cause rapid acidification under intensive processing tomato production (Stork et al., 2003). A preliminary field study suggests that SDI may carry tradeoffs for microbial nutrient cycling in ways that are not yet fully understood (Schmidt et al., 2018). In managed systems, acidity and salinity stresses can generally be corrected rapidly through liming or leaching. However, most work examining the impact of acidity and salinity on nutrient cycling has been done in static systems in which soils and microbial communities have had decades or centuries to adapt. Few studies have tested how acidity and salinity impact nutrient cycling under the fluctuating conditions which characterize intensive agriculture, and the recovery of those processes after the stress is relieved (Yan and Marschner, 2013).

Additionally, while the effects of acid and salinity stress on carbon (C) cycle processes have been well documented, the effects on nitrogen (N) cycling are unclear. Chemical stresses have been shown to reduce

^{*} Corresponding author.

E-mail address: palazicki@ucdavis.edu (P. Lazicki).

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microbial growth, respiration, and C use efficiency (Rousk et al., 2009; Malik et al., 2018). Nitrification is also consistently inhibited (Aciego Pietri and Brookes, 2008b; Xiao et al., 2013). However, the effects of acidity and salinity on N mineralization are mixed. Some have observed that net N mineralization at low pH is reduced (Chen et al., 2013; Kemmitt et al., 2005) and that lime application increases N mineralization, at least temporarily (Curtin et al., 1998; Nyborg and Hoyt, 1978). Conversely, others have found no clear relationship between pH and N mineralization (Xiao et al., 2013), very fast ammonification (Aciego Pietri and Brookes, 2008b), and gross mineralization (Zhu et al., 2019) rates sometimes occur in the most acid soils in a gradient. As coupled cycling of C and N contributes to the efficiency of agricultural systems (Bowles et al., 2015), a better understanding of their joint reaction to chemical stresses is a necessary component of sustainable agricultural intensification.

In an agricultural context, compost is a potential tool for buffering the impacts of chemical stress on microbial functions. Compost has been reported to increase proton consumption capacity and reduce aluminum (Al) toxicity in acid soils, improving crop growth (Mokolobate and Haynes, 2002; Wong and Swift, 2003; Zhang et al., 2017). Additionally, results from pH and salinity gradients in natural studies and long-term agricultural sites suggest that the effects of stress on microbial community structure and function, and the length of their recovery time if the stress is relieved, may be reduced in soils with a higher soil organic matter (SOM) content or where a substrate is added (Aciego Pietri and Brookes, 2009; Rath et al., 2019b; Wichern et al., 2006). It seems possible therefore that compost addition could buffer the effects of a stressful management-induced change on microbial N and C cycling and allow for a faster recovery. Compost use is currently incentivized due to its potential benefits for climate resilience (CDFA, 2016). However, its potential for improving resilience to chemical stresses has yet to be fully explored.

The first objective of this study was to measure how the microbial biomass and several metrics of N and C cycling activity were affected by the imposition, persistence, and partial alleviation of acidity and salinity stresses in combination. The second objective was to test whether compost application at an agronomically realistic rate moderated these effects. To this end we performed a greenhouse experiment in which chemical stress was imposed by mixing powdered elemental sulfur (S) into an agricultural soil with or without compost. Sulfur was chosen as a stressor because it does not add N, has multiple agricultural uses, can be uniformly mixed with soil, and rapidly increases both acidity and salinity (in the absence of leaching; McTee et al., 2017; Wiedenfield, 2011).

We hypothesized that 1) Microbial biomass and metrics of microbial N and C cycling activity would initially be strongly repressed by S-induced stress, 2) All functions and pools would recover (become more similar to the unstressed control) to varying extents following alleviation, and 3) The presence of compost would buffer the stress response result in a faster and more complete recovery. The present study is part of a larger project that investigates the effects of induced stress and soil health promoting practices on soil microorganisms and crops.

2. Methods

2.1. Experimental design

2.1.1. Compost and soil collection

Green waste compost was collected from a local commercial composting facility and used as-is. Compost was thoroughly mixed in a large bin and then stored moist at 4 °C in covered buckets until use. Moisture was measured by drying subsamples at 105 °C for 24 h. Total C and N were measured on dried, ground material by dry combustion (Nelson and Sommers, 1996) on an elemental analyzer (Costech Analytical Technologies, Valencia, California, USA). The compost had a dry matter (DM) concentration of 48%, total N and C content of 15 g kg⁻¹ DM and

250 g kg⁻¹ DM respectively, and a C:N ratio of 17:1. The electrical conductivity (EC) and pH, as determined in a 5:1 (weight: weight) water: compost slurry (Thomas, 1996) were 99 µS cm⁻¹ and 8.5, respectively.

Soil was collected from the top 30 cm of a fallow agricultural field near Davis, California (38°32' N, 121°46' W). The soil was mapped as a Yolo Silt Loam (Fine-silty, mixed, superactive, nonacid, thermic Mollic Xerofluvents). This soil series comprises 148,463 acres in California and is intensively farmed (Soil Survey Staff, 2014). A neutral, non-saline site with minimal recent C or fertilizer inputs was chosen to maximize response to compost and S treatments. Moisture was determined on several subsamples and soils were stored moist in covered bins until use.

2.1.2. Greenhouse experiment

The greenhouse experiment was set up as a randomized complete block design with 2 factors and 5 replicate blocks. All soil for each block was sieved using 12-mm mesh and thoroughly homogenized prior to applying the treatments. For each pot, the moist equivalent of 30 kg dry soil was weighed into a large plastic bin. Compost (290 g moist compost pot⁻¹, equivalent to 1200 mg C kg soil⁻¹ and 70 mg N kg soil⁻¹) and finely powdered elemental S (2 g kg⁻¹ soil) were added in factorial combinations to yield the non-stressed treatments C—S— (no-compost, no-S control) and C + S- (+ compost, no-S), and the stressed treatments C-S+ (no-compost, + S) and C + S+ (+ compost, + S). The compost rate (20 Mg ha⁻¹) was on the high end of the rate incentivized under the California Healthy Soils Act (Graveur, 2016). Although NH₄-based fertilizers are the main cause of acidity in agricultural systems, they were not used in order to better enable the comparison of N cycling between stressed- and non-stressed treatments. The high S rate was chosen to reduce soil pH to a level (4–5) comparable to those reported from California soils under high localized applications of NH₄ fertilizers (e.g. Chung and Zasoski, 1993; Venterea and Rolston, 2000). Amendments were mixed thoroughly by hand with the sieved soil and then packed into nursery pots (35 cm diameter, 30 cm height) to a uniform bulk density of 1.0 g cm⁻³. Control pots without amendments (treatment C—S—) were mixed in a similar manner. Within each block, two pots were prepared for each treatment so that sufficient soil could be obtained at subsequent sampling dates without changing the hydraulic properties by over-sampling a single pot. Pots were randomized within blocks and placed on greenhouse benches. For each treatment, additional material amended at the same rates was prepared and reserved in covered buckets. Unamended soil was similarly reserved.

Two angled drip emitter stakes (2 L hr⁻¹, Netafim Ltd., Israel) were placed in each pot to a depth of about 7 cm. Pots were initially irrigated to saturation and allowed to drain. Subsequently pots were drip-irrigated as needed to maintain an average soil moisture of about 30 to 45% water-holding capacity. Cracking, ponding, and preferential flow leaching were not observed. The greenhouse did not receive artificial lighting or heating. Average air temperature during the trial period was 17 °C. Pots were maintained under these conditions for 70 d, after which a stress alleviation event was implemented to simulate a dynamic system and to test the effects of C and N cycling against multiple phases of management-induced stress. Stress was partly alleviated in the S+ pots by adding 60 mL of liquid lime (CalFlo, 0.64 calcium-carbonate equivalent, density = 1.77 g mL⁻¹) suspended in 3 L of water, followed by leaching with an additional 6 L of water. The S- control pots were also leached with 9 L of water. Three days later, all pots were re-leached with an additional 9 L of water. The total volume of leaching water corresponded to roughly 1.7 pore volumes.

2.2. Soil sampling

For baseline analyses, approximately 1 kg of soil was taken from each block prior to treatment application and immediately placed on ice and kept at 4 °C until further analysis. Soil was sampled at 21 d and 42 d after S and compost application from the top 18 cm of each pot using a 2-cm

diameter soil probe. To ensure consistent moisture and aeration conditions, at each date a single sample was taken from each pot at a distance of 7.6 cm from a drip emitter and at least 7.6 cm from the pot wall. Sampling holes were backfilled with the reserved amended soil and marked to avoid re-sampling. The samples from the two duplicate pots within each block were composited, and samples were put on ice and kept at 4 °C until analysis. At 8 d after the final leaching, a third sampling was performed using the same method.

At each date soils were sieved to 4.75 mm on the day of sampling, and a subsample was dried at 105 °C overnight to determine moisture content. At the “Baseline” sampling only, water holding capacity (WHC) was determined as the gravimetric water content of soil that had been saturated and let to freely drain for 1 h. The soil 60% WHC was calculated using the average WHC from all five blocks and used for all subsequent incubations.

2.3. Soil analyses

2.3.1. Microbial C and N cycling assays on moist soils

A set of assays was performed at each sampling date to assess microbial C and N cycling functions with and without the addition of fresh residues. Measured and calculated parameters are summarized in Supplementary Table S1. Within 1 day of each sampling, 6 subsamples of 6 g of moist sieved soil were weighed into separate 40-mL glass vials (vials A through F). Vial A was extracted immediately with 30 mL 0.5 M K₂SO₄. Vial B was fumigated with chloroform for 24 h, and then similarly extracted. To vials C and D, powdered bell bean residue (*Vicia faba*, L.; 3.9% N, C:N = 10.5) was added at a rate of 2.5 mg g⁻¹ dry soil, corresponding to 1058 mg C kg⁻¹ dry soil and 98 mg N kg⁻¹ dry soil. Residue was mixed thoroughly with the soil, after which vials were adjusted to 60% WHC with deionized water and placed together uncovered into a 907-mL glass jar with an airtight lid fitted with a rubber septum for headspace sampling. Vials E and F were treated similarly, except that no residue was added. Jar headspace CO₂-C was measured after 24 h, 72 h and 7 d using an infrared gas analyzer (Qubit Systems, Canada). Jars were aerated after each sampling event. After 7 d vials C and E were immediately extracted with K₂SO₄ as described above, while vials D and F were fumigated with chloroform and then extracted. Extracts from the unfumigated vials A, C, and E were analyzed for ammonium (NH₄-N) and nitrate (NO₃-N) using the salicylate method (Verdouw et al., 1978; Forster, 1995) and a single reagent method (Doane and Horwath, 2003), respectively. Extracts from all six vials were analyzed for total organic C (TOC) using a TOC Analyzer (Shimadzu Corporation, Japan). Microbial biomass C before incubation (MBC₀), after incubation with residues (MBC-Res), and after incubation without residues (MBC-Soil) was calculated as the difference in TOC between the fumigated and unfumigated extracts of vials A and B, C and D, and E and F respectively, according to Horwath and Paul (1994). Initial mineral N (Mineral N₀) was calculated as the sum of NH₄-N and NO₃-N in non-fumigated non-incubated soil extracts (vial A). Net N mineralization from SOM (Nmin-Soil) was calculated as the difference between mineral N in the vial incubated without residues (Vial E) and Vial A. The C mineralization from SOM (CO₂-Soil) was measured as the cumulative C evolved from the jar containing unamended vials E and F. Apparent C (CO₂-Res) and net N (Nmin-Res) mineralization in response to residue addition was calculated as the difference in cumulative C respiration or mineral N between vials incubated with and without residue additions, while apparent MBC growth in response to residue additions (MBC-Res) was calculated as the MBC difference between vials incubated with and without residue additions. Baseline and unamended mineralization measurements were calculated as mg C or N kg⁻¹ dry soil, while mineralization and growth responses for amended soils were calculated as a percentage of the added residue C or N. The proportion of NH₄-N in the mineral N (NH₄-N plus NO₃-N) measured in vial C after 7 d (NH₄-Res) was used to assess nitrification activity.

2.3.2. Chemical and biological measurements on dried soils

On the same day as the incubation setup, the remainder of the soil was air-dried at room temperature by spreading in a single-aggregate layer. Dried soils were then ground to pass through a 2-mm sieve. The EC and pH were measured in a 2:1 water:soil slurry (Thomas, 1996). Potential activities of the enzymes β-glucosidase (BG₀) and N-acetyl-β-glucosaminidase (NAG₀) were measured using p-nitrophenol substrate according to Tabatabai (1994) and Parham and Deng (2000), respectively. Enzyme analyses were performed on air-dried rather than fresh soils, as air-drying allowed for greater uniformity in processing and storage among sampling dates, and for later re-analysis to be performed if necessary (Dick, 2011). While air-drying alters NAG enzyme activity, it is unlikely to alter comparisons between soils of the same type which are processed and stored in a similar way (Bandick and Dick, 1999). Microbially-available pools of C and N were assayed by extracting 6 g of soil with 30 mL 0.01 M CaCl₂ (Self-Davis et al., 2000), using a filter paper with 5 to 10-μm particle retention (Fisherbrand, Q5). Subsamples of filtered dilute salt extracts were analyzed for total organic C (DSOC₀) and mineral N as described above. Total dissolved N in the extracts was analyzed using the persulfate digestion method (Cabrera and Beare, 1993). Organic N in the dilute salt extract (DSO_N₀) was calculated as the difference between the total dissolved and mineral N pools. As an index of Al toxicity, 10 g of soil were extracted with 20 mL 0.01 M CaCl₂ and filtered through paper with a 5 to 10-μm particle retention (Bertsch and Bloom, 1996). Total soluble Al (Al_{tot}) was measured on extracts in 2% nitric acid solution using an inductively coupled plasma optical emission spectrometer (ICP-OES; Thermo Scientific, Waltham, MA) at a wavelength of 167.08 nm (Kerven et al., 1989). Soluble monomeric Al (Al_{mono}) was measured using the pyrocatechol violet method with a read time of 60 s, as described by Kerven et al. (1989). Organically complexed soluble Al was calculated as the difference between Al_{tot} and Al_{mono} (Mokolobate and Haynes, 2002).

Additional physical and chemical analyses were all measured on baseline soil samples (Table 1). These included total C and N by dry combustion (Nelson and Sommers, 1996), texture by the pipet method (Gee and Bauder, 1996), bicarbonate-extractable phosphorus (Watanabe and Olsen, 1965), and extractable base cations by the ammonium acetate method (Helmke and Sparks, 1996; Suarez, 1996).

2.4. Statistical analyses

The main and interactive effects of compost and S treatments and sampling date were analyzed as a three-way ANOVA in a randomized complete block design with compost, S and date as fixed effects and block as random, using PROC GLIMMIX in Statistical Analysis System (SAS Corporation, Cary, NC). Differences between treatments were assessed by Tukey's honestly significant difference (HSD) test for multiple comparisons among treatments (α = 0.05). To interpret

Table 1

Baseline soil properties. Electrical conductivity (EC) and pH were measured in 2:1 water:soil slurry. Mg, Ca, K and Na were determined in ammonium acetate extracts. s.e. = standard error (n = 5).

	Avg	s.e.
Total C (g kg ⁻¹)	8.03	0.13
Total N (g kg ⁻¹)	1.11	0.07
Sand (%)	32.50	0.96
Clay (%)	26.65	2.52
NH ₄ -N (mg kg ⁻¹)	0.68	0.04
NO ₃ -N (mg kg ⁻¹)	12.2	1.28
EC (μS cm ⁻¹)	106	10.5
pH	7.44	0.04
Olsen P (mg kg ⁻¹)	13.6	0.20
Mg (mg kg ⁻¹)	1528	20.3
Ca (mg kg ⁻¹)	1818	13.2
K (mg kg ⁻¹)	349	5.71
Na (mg kg ⁻¹)	14.0	1.35

interactions among fixed effects, SLICE statements were used to partition LSMEANS and significance was assessed using Tukey adjusted *p*-values. The “Baseline” sampling date was not included in the statistical analysis, as the sampling unit was not the same. Time of sampling (date) was considered a repeated measure, indicated using the REPEATED statement in SAS with “pot” as subject. For each parameter the covariance structure which resulted in the lowest Akaike Information Criterion was selected. To test the hypothesis that compost would reduce the effect of stress, the difference between compost treatments for the stressed soils (C-S+ and C + S+) was assessed at each date and across all three sampling dates using contrast statements. Data were log-transformed prior to analysis if necessary to meet the assumptions of normal, independently distributed residuals and equal variance. The linear relationship between MBC and either soil pH or Al_{mono} in stressed soils was assessed using PROC REG in SAS. The residuals were examined visually to determine if assumptions were met.

3. Results

3.1. Effect of sulfur addition on soil pH, salinity, and soluble Al

Sulfur addition decreased pH from a slightly alkaline value of 7.4 to 4.6 ($p < 0.0001$; Fig. 1a), which is considered strongly acidic (Brady and Weil, 2004). The pH in S treated (S+) soils was similar at 21 days and 42 days after incorporation (DAI), but after alleviation increased to approximately 6 ($p < 0.0001$). Additions of compost did not affect the pH for soils with or without S at any date. Sulfur addition increased salinity in 2:1 suspension from a baseline of about $100 \mu S cm^{-1}$ to $1500\text{--}3000 \mu S cm^{-1}$ at 21 and 42 DAI (Fig. 1b). This is equivalent to roughly 4 to 8 dS m^{-1} in a saturated paste extract (Hogg and Henry, 1984). Soils in this range are considered to be slightly to moderately saline (Brady and Weil, 2004). Salinity increased between 21 and 42 DAI for both S+ ($p < 0.0001$) and S- ($P = 0.01$) treatments. After alleviation salinity in the S+ soils returned to the same level as at 21 DAI, while leaching the controls reduced salinity below their level at 21 DAI ($p < 0.0001$). Across all dates and S levels, compost treatments (C+) were slightly but not significantly more saline than non-compost treatments (C-; $p = 0.10$).

Monomeric soluble Al (Al_{mono}) began to increase below pH 5.5 and increased exponentially as pH decreased further (Fig. 2). Total soluble Al (Al_{tot}) generally followed the same pattern. The organically bound soluble Al tended to increase with increasing pH, being on average 20% of Al_{tot} at pH < 5.5 and 60% at pH > 5.5.

3.2. Responses of N parameters to S-induced stress and its alleviation

For the S- control treatments with or without compost addition, most parameters remained constant over the course of the incubation. The only exception was Mineral N_0 , which was lower after leaching than

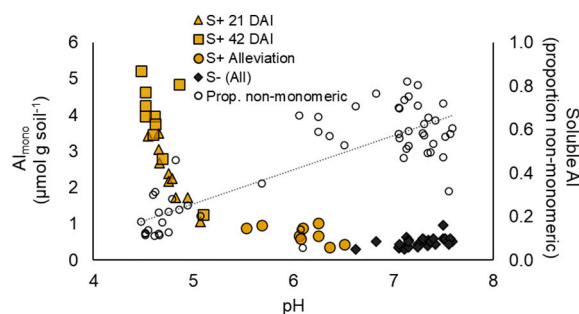


Fig. 2. Relationship between pH in 2:1 water:soil slurry and monomeric Al (Al_{mono}) in 0.01 M $CaCl_2$ extracts as well as the proportion of the soluble Al in the non-monomeric form for sulfur (S+) and non-sulfur (S-) treatments at 21 and 42 days after incorporation (DAI) and at Alleviation.

during the first two sampling dates (Fig. 3).

When averaged across compost treatments, all measured N pools and processes were strongly affected by S addition at 21 DAI (Table 2; Fig. 3a-f). Mineral N_0 in the S+ treatments was less than half of that in the S- treatments (Fig. 3a). More than 90% of the mineral N ($NO_3\text{-N} + NH_4\text{-N}$) in the residue-added incubated soils was in the form of NH_4^+ in the S+ treatments, compared with 2% in the S- treatments (Fig. 3b). $N_{min}\text{-Soil}$ was lower in S+ than S- treatments on average, although the differences between individual treatments were not significant, and showed slight immobilization over the 7-d incubation (Fig. 3c). Potential NAG_0 activity was reduced by about 30% (Fig. 3f). In contrast to these decreases in N cycling activity, $N_{min}\text{-Res}$ was more than doubled on average in the S+ compared to S- treatments (Fig. 3d), although there was a significant interaction with compost (Table 3; discussed below). The DSO_{N_0} was on average 75% higher in the S+ treatments than the S- treatments (Fig. 3e).

Between 21 and 42 DAI in the S+ treatments, $N_{min}\text{-Soil}$ in the S+ treatments increased significantly, and at 42 DAI $N_{min}\text{-soil}$ in the S+ treatments was approximately double that of the S- treatments (Fig. 3c). Mineral N_0 also significantly increased in S+ treatments between 21 and 42 DAI (Fig. 3a; $p = 0.0094$) but not in the S- treatments, such that the difference between them became non-significant ($p > 0.05$) on average. The $N_{min}\text{-Res}$ did not change between 21 and 42 DAI, and continued to be significantly elevated in the S+ compared to S- treatments (Fig. 3d). The DSO_{N_0} decreased significantly between 21 and 42 DAI (Fig. 3e; $p = 0.0004$), but remained significantly higher in the S+ than S- treatments ($p = 0.0001$). Potential NAG_0 activity also decreased between 21 and 42 DAI (Fig. 3f; $p < 0.0001$) and was significantly lower in S+ than S- treatments ($p = 0.0003$).

Between 42 DAI and alleviation, the N cycling parameters in the S+ treatments either increased ($N_{min}\text{-Soil}$, NAG_0 ; Fig. 3c,f), decreased (Mineral N_0 , $N_{min}\text{-Res}$; Fig. 3a,d), or remained stable ($NH_4\text{-Res}$, DSO_{N_0} ; Fig. 3b,e). In S+ treatments $N_{min}\text{-Soil}$ and $N_{min}\text{-Res}$ showed reversed

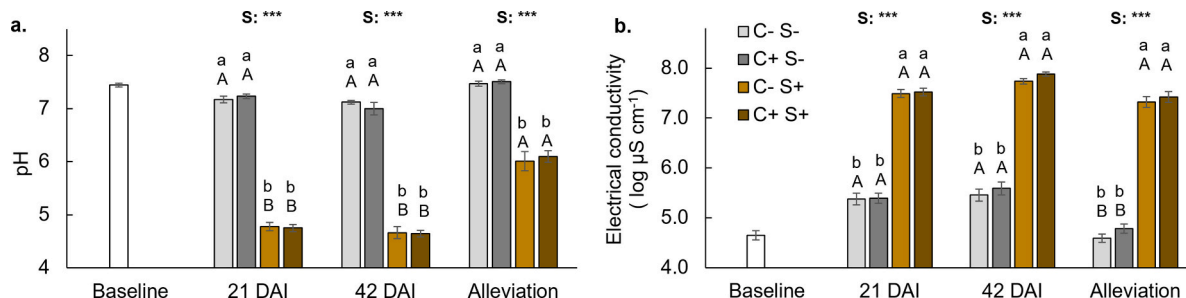


Fig. 1. Soil a) pH and b) salinity for soils with and without compost (C+ and C-) and sulfur (S+ and S-) incorporated prior to incorporation (Baseline), 21 and 42 d after incorporation (DAI), and 7 d after leaching with liquid lime (Alleviation). Different lower-case letters denote significant ($p < 0.05$) differences among treatments at each sampling date, and different uppercase letters denote significant differences for a single treatment among sampling dates. Asterisks *** denote Tukey-adjusted *p*-values of $p < 0.001$ for the main effect of sulfur for each date. Error bars denote the standard error of the mean.

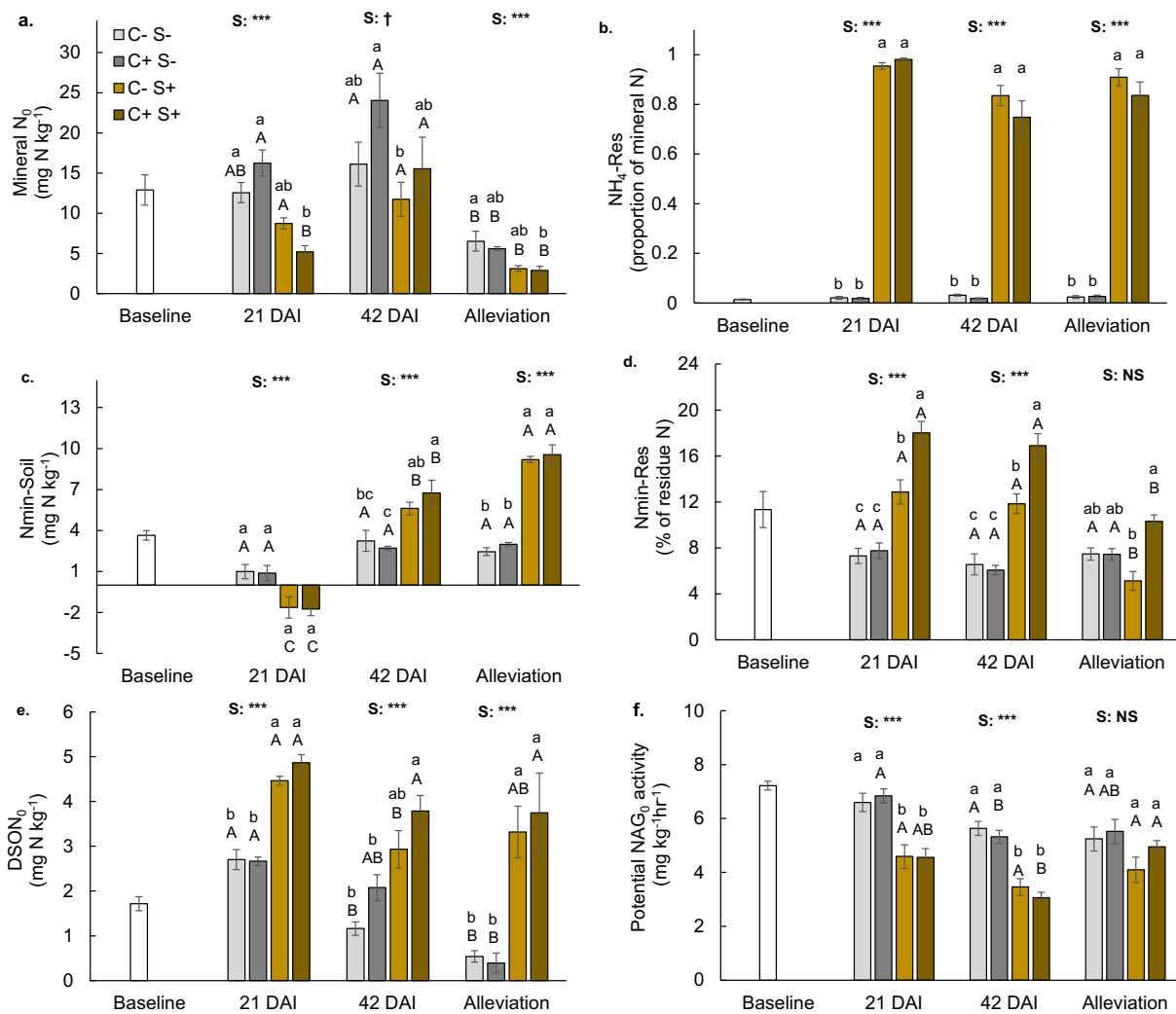


Fig. 3. Nitrogen cycle indicators prior to compost (C+ or C-) and sulfur (S+ or S-) incorporation (Baseline), 21 and 42 days after incorporation (DAI), and 1 week after leaching with liquid lime (Alleviation). Dagger† and asterisks*** denote Tukey-adjusted *p*-values of <0.1 and < 0.001 for the main effect of S, respectively. Different lower-case letters denote significant (*p* < 0.05) differences among treatments at each sampling date, and different uppercase letters denote significant (*p* < 0.05) differences for a single treatment among sampling dates. Mineral N₀ = Initial mineral N. Nmin-Soil = Net N mineralization from soils incubated without residue additions for 7 d at 25 °C. Nmin-Res = additional N measured after incubation when residues were added, compared to Nmin-Soil. NH₄-Res = proportion of mineral N in soil incubated with residues for 7 d measured as NH₄-N. DSON₀ = initial dilute-salt extractable organic N. NAG₀ = *N*-acetyl-β-glucosaminidase activity.

Table 2

Fixed effects of Compost, Sulfur, Date, and their interactions (Tukey-adjusted *p*-values). DSON₀ = Initial dilute-salt extractable organic C. BG₀ = initial β-glucosidase activity. MBC₀ = initial microbial biomass C. MBC-Res = MBC increase during an incubation with residues compared to a no-residue control. CO₂-Soil and CO₂-Res = CO₂-C respired during an incubation without and with residue additions, respectively. DSON₀ = initial dilute-salt extractable organic N. NAG₀ = initial *N*-acetyl-β-glucosaminidase activity. Mineral N₀ = Initial mineral N. Nmin-Soil and Nmin-Res = Net N mineralization from soils incubated without and with residue additions. NH₄-Res = proportion of mineral N in soil incubated with residues for measured as NH₄-N. Samples were incubated for 7 d at 25 °C.

Effect	Carbon cycle indicators					Nitrogen cycle indicators						
	MBC ₀	CO ₂ -Soil	MBC-Res	CO ₂ -Res	BG	DSON	Mineral N ₀	Nmin-Soil	Nmin-Res	NH ₄ -Res	NAG	DSON
Compost	0.353	0.637	0.520	0.214	0.242	0.036	0.749	0.654	<0.0001	0.171	0.615	0.021
Sulfur	<0.0001	0.020	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Compost*Sulfur	0.212	0.845	0.990	0.114	0.889	0.491	0.030	0.423	<0.0001	0.496	0.870	0.676
Date	<0.0001	<0.0001	<0.0001	0.940	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.284	<0.0001	<0.0001
Compost*Date	0.996	0.788	0.296	0.468	0.296	0.080	0.113	0.797	0.906	0.132	0.030	0.175
Sulfur*Date	0.144	<0.0001	0.001	0.006	0.199	0.368	0.337	<0.0001	<0.0001	0.038	0.001	0.259
Compost*Sulfur*Date	0.956	0.236	0.898	0.199	0.379	0.716	0.141	0.483	0.943	0.271	0.531	0.773

trends across the experiment, with Nmin-Soil lowest at 21 DAI and steadily increasing until after alleviation, and Nmin-Res high during stress but significantly lower after alleviation. After alleviation, Nmin-Soil in S+ was on average more than three times higher than in S-

(Fig. 3c), while on average for Nmin-Res the two did not differ (Fig. 3d). As with the other dates, Nmin-Res response was different for the C + S+ treatment (discussed below).

Out of all the measured variables, compost increased only DSON₀ for

Table 3

Comparison of compost treatments for the sulfur-stressed soils at 21 and 42 days after incorporation (DAI) Alleviation, and across all three dates (p-values for estimate statements, using Tukey's adjustments for multiple comparisons). DSO_{C0} = Initial dilute-salt extractable organic C. BG₀ = Initial β-glucosidase activity. MBC₀ = initial microbial biomass C. MBC-Res = MBC increase during an incubation with residues compared to a no-residue control. CO₂-Soil and CO₂-Res = CO₂-C respired during an incubation without and with residue additions, respectively. DSON₀ = initial dilute-salt extractable organic N. NAG₀ = initial N-acetyl-β-glucosaminidase activity. Mineral N₀ = Initial mineral N. Nmin-Soil and Nmin-Res = Net N mineralization from soils incubated without and with residue additions. NH₄-Res = proportion of mineral N in soil incubated with residues measured as NH₄-N. Samples were incubated for 7 d at 25 °C.

Date	Carbon cycle indicators						Nitrogen cycle indicators					
	MBC ₀	CO ₂ -Soil	MBC-Res	CO ₂ -Res	BG	DSOC	Mineral N ₀	Nmin-Soil	Nmin-Res	NH ₄ -Res	NAG	DSON
21 DAI	0.765	0.488	0.424	0.901	0.488	0.944	0.014	0.884	<0.0001	0.915	0.940	0.050
42 DAI	0.717	0.104	0.413	0.336	0.317	0.059	0.290	0.169	<0.0001	0.402	0.354	0.072
Alleviation	0.890	0.609	0.419	0.062	0.030	0.287	0.631	0.655	<0.0001	0.599	0.050	0.609
Overall	0.831	0.849	0.648	0.047	0.440	0.099	0.181	0.393	<0.0001	0.529	0.639	0.055

all treatments and at all dates (i.e., compost had a significant main effect with no interactions; Table 2). Compost had a highly significant effect on Nmin-Res ($p < 0.0001$); however, there was a strong compost by S interaction (Table 2). The compost treatment strongly increased Nmin-Res in the S+ soil at all dates (Table 3), with C + S+ being 40%, 42%, and 100% higher than C-S+ at 21 DAI, 42 DAI, and after alleviation, respectively ($p < 0.0001$; Fig. 3d; Table 3). No corresponding difference was observed in the S- control treatments. Mineral N₀ was significantly lower in C + S+ than C-S+ at 21 DAI (Fig. 4a; Table 3), but the effect was

slight and temporary (Table 3).

3.3. Responses of C parameters to S-induced stress and its alleviation

For the S- control treatments, the only indicators which did not remain constant over the course of the incubation were DSO_{C0} and BG₀, both of which were lower after leaching than during the first two sampling dates (Fig. 4).

All C parameters were significantly reduced by S at 21 DAI (Fig. 4a-

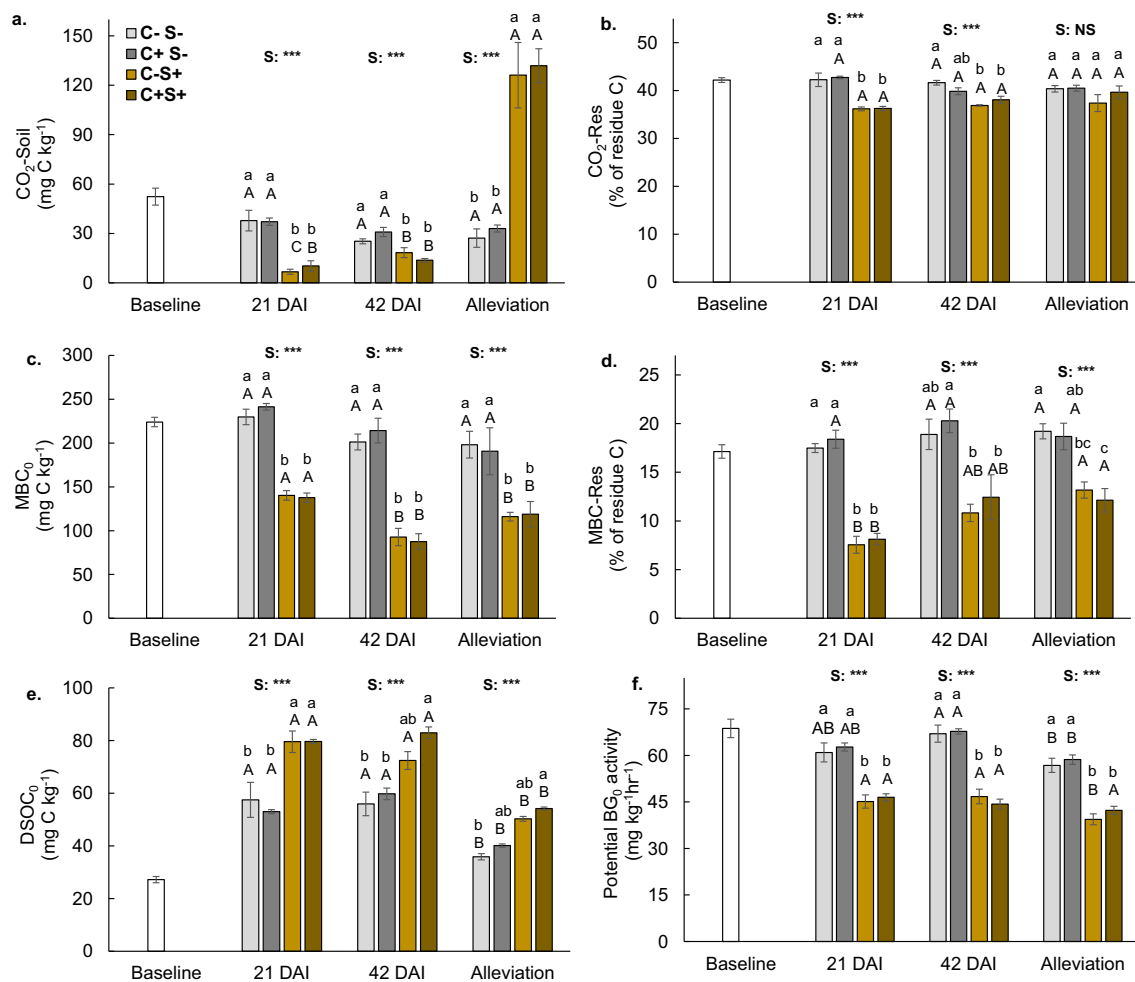


Fig. 4. Carbon parameters prior to compost (C+ or C-) and sulfur (S+ or S-) incorporation (Baseline), 21 and 42 days after incorporation (DAI), and 7 d after leaching with liquid lime (Alleviation). Asterisks *** denote Tukey-adjusted p-values of <0.001 for the main effect of S at each date. Different lower-case letters denote significant ($p < 0.05$) differences among treatments at each sampling date, and different uppercase letters denote significant ($p < 0.05$) differences for a single treatment among sampling dates. CO₂-Soil = CO₂-C respired during a 7-d incubation at 25 °C without residue addition, and CO₂-Res = additional respiration with residue addition, compared to CO₂-Soil. MBC₀ = initial MBC. MBC-Res = MBC increase during a 7-d incubation with residues at 25 °C compared to a no-residue control. DSO_{C0} = initial dilute-salt extractable organic C. BG₀ = initial β-glucosidase activity.

f), with the exception of DSOC₀, which was on average 44% higher in the S+ treatments than the S- treatments (Fig. 4e). The most affected parameter was CO₂-Soil, which was reduced by 75% in S+ compared with S- treatments (Fig. 4a). The least affected parameter was CO₂-Res, which was only reduced by 15% (Fig. 4b). The MBC₀ was reduced by 41% and the MBC-Res by 56% in the S+ compared to the S- treatments, while potential BG₀ activity was reduced by 25% (Fig. 4c,d,f).

Averaged across the compost treatments, all C indicators remained significantly lower in the S+ than the S- treatments after 42 days of stress, except DSOC₀, which remained higher (Fig. 4a-f). However, CO₂-Soil significantly increased in the S+ treatments over time, on average doubling between 21 and 42 DAI (Fig. 4a; $p < 0.0001$). But in contrast to Nmin-Soil, Cmin-Soil in the S+ treatments remained lower than in the S- treatments. The increase was only significant in the absence of compost (C-S+ treatment). Mean MBC-Res in the S+ treatments increased by 48% ($p = 0.0008$), although the difference was not significant for the individual treatments (Fig. 4d). Conversely, the MBC₀ declined by about 35% between 21 and 42 DAI in the S+ treatments (Fig. 4c; $p < 0.0001$). All other parameters remained unchanged or had non-significant increases between the two dates. Across both stress dates in the S+ treatments, MBC₀ had strong (adjusted $r^2 = 0.47$, $p = 0.0007$) and weak (adjusted $r^2 = 0.17$, $p = 0.04$) negative correlations with Al_{mono} and pH, respectively (data not shown).

Microbial biomass, respiration, and the DSOC₀ pools had different responses to leaching with lime (Fig. 4a-f). Despite the increase in pH and decrease in Al_{mono}, the MBC₀ and BG₀ showed no increase after alleviation for S+ treatments (Fig. 4c,f). After alleviation, these parameters were respectively on average 40% and 30% lower in S+ than S- treatments, and the difference between S+ and S- across the whole experiment did not significantly interact with date (Table 2). MBC-Res also did not increase between 42 DAI and after alleviation, where it was still 44% lower in the S+ than S- treatments (Fig. 4d). However, unlike MBC₀ and BG₀, MBC-Res gradually increased over the course of the experiment, and was 60% higher after alleviation than at 21 DAI ($p < 0.0001$). In contrast, CO₂-Soil for S+ soils was dramatically higher after alleviation, compared both to S- soils after alleviation and to S+ soils during stress (Fig. 4a). CO₂-Res differed neither between S+ and S- soils after alleviation, nor between 42 DAI and alleviation for any of the treatments (Fig. 4b). DSOC₀ remained significantly higher in S+ than S- treatments after alleviation. After leaching the DSOC₀ was significantly ($p < 0.0001$) lower in all soils regardless of S addition, such that the differences between S+ and S- treatments were consistent across all sampling dates (Fig. 4e; Table 2).

Compost consistently increased only DSOC₀ at all dates for all treatments (Table 2). CO₂-Res was significantly higher in the C + S+ than C-S+ treatment averaged over all the dates but was not significant at any individual date (Fig. 4b; Table 3).

4. Discussion

We aimed to measure how several N and C cycle pools and processes changed under a strong, short-term stress, how functions could recover after partial stress alleviation, and how those stress response dynamics were moderated by compost addition. We observed that patterns of initial response, adaptation, and recovery differed strongly between different N and C cycling functions. Four clear responses to S-induced stress were observed: an almost complete inhibition of nitrifier activity, a long-lasting increase in DSOC₀ and DSON₀ pools, an apparent decoupling of C and net N mineralization responses, and a pronounced, consistent increase in net N mineralization from a labile residue addition in the compost-amended stressed soils. A summary comparison of the effects of stress on selected C and N cycle processes is given in Fig. 5.

The minimum pH reached in the acidified soil (4.6) was similar to minimum pH observed in soils from this region following the application of high rates of NH₄ fertilizers (Chung and Zasoski, 1993; Venterea and Rolston, 2000). Below pH 4.5, all bacterial and fungal growth were

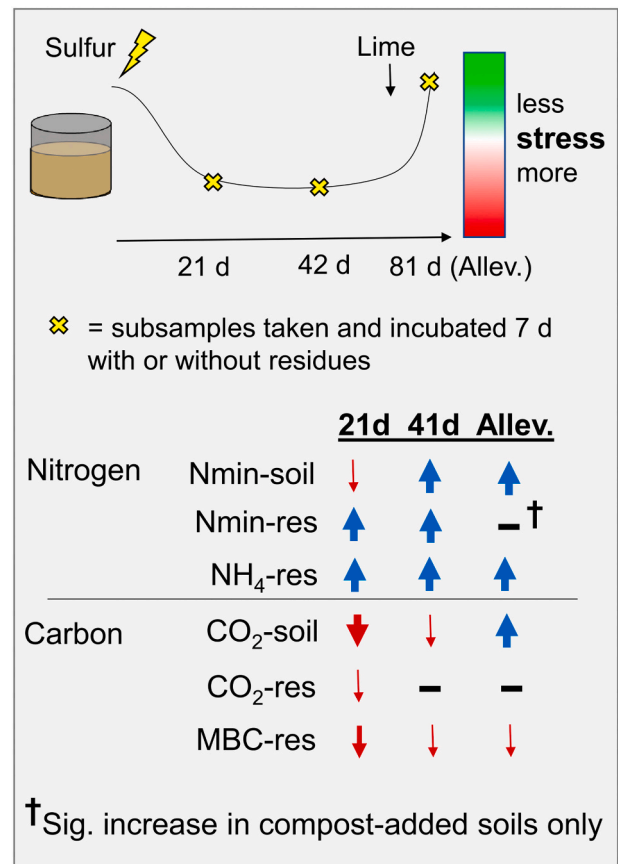


Fig. 5. Summary of the effects of acidification on C and N cycling pools and processes measured 21 and 42 d after a S stress was applied, and after alleviation. The direction and width of the arrows indicates the magnitude of each parameter's increase or reduction in the stressed soils relative to the non-stressed soils. Nmin-Soil and Nmin-Res = Net N mineralization from soils incubated for 7 d without and with residue additions. NH₄-Res = proportion of mineral N in soil incubated with residues measured as NH₄-N. CO₂-Soil and CO₂-Res = CO₂-C respired during incubation without and with residues. MBC-Res = MBC increase during incubation with residues, compared to a no-residue control.

observed to be heavily impacted in a long-term agricultural pH gradient, even when stimulated with substrate additions (Aciego Pietri and Brookes, 2009; Rousk et al., 2010). The authors attributed this inhibition to the high levels of available Al observed at this pH. In our study, soluble Al began to increase exponentially below pH 5.5. While the Al_{mono} concentrations were low, the significant negative correlation with MBC during the period of pH stress suggests Al toxicity may have been a stressor (Chen et al., 2013; Jones et al., 2019). While inter-study salinity comparisons are difficult due to strong effects of moisture, texture, and the method used to measure electrical conductivity, our salinity values are at the lower end of those observed to impact microbial growth and activity (Pathak and Rao, 1998; Rath et al., 2019a; Yan and Marschner, 2013). Therefore, soil pH was likely a stronger stress than salinity in our study.

Although humic substances extracted from composts have been observed to reduce free Al (Winarso et al., 2018) and green waste composts can consume protons in acid soils (Mokolobate and Haynes, 2002; Naramabuye and Haynes, 2006), our green waste compost did not have any discernible effect on Al or pH during the time scale of this experiment. Similarly, McTee et al. (2017) found that compost did not raise pH or improve plant growth in soil from a skeet shooting range heavily contaminated with S.

4.1. Inhibition of nitrifying activity under stress

The strongest functional change due to S addition was an almost complete absence of nitrification from added residues. This is in line with several long-term studies which consistently observed lower nitrification in both acid and saline soils (e.g. Aciego Pietri and Brookes, 2008a; Cheng et al., 2013; Kemmitt et al., 2006). Nitrification has also been observed to be limited by free Al (Kraal et al., 2009). At low pHs, the direct mechanism is thought to be a lack of NH₃ substrate for ammonia monooxygenase, the main enzyme responsible for NH₃ oxidation (Li et al., 2018). However, the fact that liming did not rapidly increase nitrification capacity suggests that the inhibition at this point was due more to the loss or slow recovery of nitrifier community members than the lack of substrate or acid cation toxicity. Nitrification is a multistep process, carried out by different groups of rather specialized organisms, and successful nitrification depends on their coupled function (Norton and Stark, 2011; Li et al., 2018).

4.2. Increase in extractable organic matter under stress

When naturally acid soils are limed, organic matter in the soil solution usually increases as organic matter functional groups are deprotonated and become less attracted to negatively charged mineral surfaces (Andersson et al., 1994; Curtin et al., 1998; Evans et al., 2012). The high DSOC₀ and DSON₀ in the S+ treatments show that the reverse does not necessarily hold when neutral soils are acidified. Our findings parallel those of Kemmitt et al. (2006) for long-term agricultural pH gradients. These authors also observed that dissolved organic C and N were negatively correlated with microbial biomass and activity and closely positively correlated with acidity and exchangeable Al. Decreased microbial metabolic capacity due to acid cation toxicity could help explain the high DSOC₀ and DSON₀ in the acidified soils (Li et al., 2017). Complexation with Al may also reduce organic matter's susceptibility to microbial attack (Álvarez et al., 2012; Haynes and Mokolobate, 2001); however, the very low proportion of complexed soluble Al at low pH suggests this mechanism was not relevant. It is also possible that the acid stress increased soluble organic matter supply through the activity of soil enzymes. While we observed that potential enzyme activities were reduced in the S+ treatments compared to the S- treatments under standardized analytical conditions, actual activity may have been higher due to the low pH optima of both BG₀ and NAG₀ (Parham and Deng, 2000; Turner, 2010).

4.3. Microbial nutrient cycling during stress and after liming

As predicted in our first hypothesis, stress initially strongly reduced microbial biomass, respiration, and N mineralization. However, the more marked decline in respiration than biomass at 21 DAI was unexpected, as stress generally increases the respiration per unit biomass (Anderson and Domsch, 1993; Draghi et al., 2016). A joint inhibition of respiration and growth such as was observed at 21 DAI may be a sign of a poorly adapted community dealing with a specific toxicity which induces widespread death or dormancy (Rath et al., 2016). The low N mineralization which was also observed at this date is consistent with a community undergoing severe metabolic limitation (Yang et al., 2021). Indeed, the slightly but consistently negative values for Nmin-Soil in the S+ treatments and reduced Mineral N₀ at 21 DAI suggest the small microbial community may have been immobilizing N, as significant losses by denitrification and volatilization are unlikely in acidic, low organic matter, aerobic soils (Bremner and Shaw, 1958). Our finding that microorganisms initially depleted the mineral N pool while the DSON₀ pool increased suggests preferential uptake of mineral N.

However, after a longer time of equilibration with the stress, with no change in pH or DSON₀ and an actual decrease in NAG₀ activity, Nmin-Soil increased in the S+ treatments to the point that it exceeded that of the S- treatments. As attested by the reduced MBC₀ but increased Cmin-

Soil observed at 42 DAI, the community at this point appeared to be slower growing but better able to metabolize organic matter in an acid environment (Cruz-Paredes et al., 2017; Rath et al., 2019a). A high rate of respiration to growth is a well-documented characteristic of stress-adapted microbial communities (Anderson and Domsch, 1993). Stoichiometrically, a lower community metabolic efficiency could also help explain the observed increase in Nmin-Soil (Silva-Sánchez et al., 2019). Significant shifts in community tolerance to acidity have been observed within 36 d (Cruz-Paredes et al., 2017), making it plausible that some shift in acid tolerance could be observable within the 42 d under strong acid stress.

The tendency towards higher net N mineralization in the S+ soils than the S- soils was much more pronounced with the addition of legume residues. The fact that both C and N mineralization responded so much more strongly to residue additions in the S+ than S- soils despite the former's higher levels of soluble organic matter suggests that the mineralization pulses were not due to relief of substrate limitation. Since legume residues can complex with Al and reduce its activity (Hue, 2011; Xiao et al., 2014), as well as temporarily consume protons through decarboxylation and ammonification of soluble organic acid anions (Dilworth and Glenn, 1999; Xiao et al., 2014; Xu et al., 2006), it is possible that the residues stimulated activity by relieving acid cation toxicity which had been limiting metabolism (Chen et al., 2015). As decarboxylation and ammonification produce CO₂ and NH₄⁺, respectively (Gale, 1946; Haynes and Mokolobate, 2001; Xu et al., 2006), such detoxification products could also have contributed to the observed mineralization pulses.

Liming produced mixed effects on C and N cycling processes. The most obvious effect of liming was a very large CO₂ pulse from the unamended soil, far exceeding the DSOC₀ pool. It is likely that at least part of this was abiotic, issuing from the decomposition of carbonic acid from the liming reaction to CO₂ (Bertrand et al., 2007). While it is not possible to separate biotically and abiotically generated CO₂, the fact that additional respiration due to residues (CO₂-Res) was remarkably similar before and after leaching suggests that liming did not increase the capacity for respiration when adequate substrate was present. Contrary to our hypothesis, MBC₀ and potential BG₀ activity showed no signs of recovering after alleviation. However, the tendency towards higher MBC-Res with equivalent CO₂-Res suggests that the community that grew in response to residue additions after liming was more efficient than that which responded at 42 DAI.

The high Nmin-Res during stress and decline after liming suggests that high net N mineralization in response to substrate addition was caused by an inefficient community whose growth was limited by the adaptations required to survive in a stressful environment. Our results are in line with several studies which found that net N mineralization was not inhibited by salinity and acidity to the same extent as C mineralization and nitrification (Aciego Pietri and Brookes, 2008a, 2008b; Cheng et al., 2013; Kemmitt et al., 2006; Laura, 1974; Pathak and Rao, 1998). Indeed, both net and gross N mineralization have sometimes been observed to be highest in the most acid soils within an experimental gradient (Aciego Pietri and Brookes, 2008b; Zhu et al., 2019; Xiao et al., 2013). Similarly, a 400% increase in net N mineralization from vetch residues was measured in response to Al additions, despite reductions in C mineralization and MBC (Kraal et al., 2009). The most direct explanation for this effect is that immobilization is slower than mineralization at low pH (Xiao et al., 2013); however, this does not always seem to be the case (Zhu et al., 2019). The fact that the increase in MBC-Res after liming was not proportional to the decline in Nmin-Res suggests that reduced immobilization did not entirely explain the mineralization pulse. Other hypothesized mechanisms include increased losses by denitrification or volatilization as pH increases (Aciego Pietri and Brookes, 2008a; Xiao et al., 2013).

Contrary to our hypothesis, compost had no effect on stress response and did not affect most indicators, regardless of S treatment. Compost is generally a stable, microbially processed product, rich in condensed,

high molecular weight compounds, phenols and lignin and depleted in energetic compounds such as sugars (Lerch et al., 2019; Said-Pullicino et al., 2007). This may explain why it did not have a measurable effect on microbial growth or most activity within our experimental time-frame. Transient responses to bioavailable fractions may have occurred prior to our first measurement.

Conversely, compost strongly and consistently increased Nmin-Res across all three sampling dates. As an increased Nmin-Res was likely a stress response, compost appears to have exacerbated the effects of stress, rather than buffering it as hypothesized. This paradoxical result could be explained if the increased net N mineralization under stress was partly due to a community shift towards one with less need for N relative to C. Fungi tend to have a higher C:N ratio than bacteria and are thought to generally be more acid tolerant (Strickland and Rousk, 2010). Rapid fungal but not bacterial growth rates have been observed within days of a labile residue addition to acid soils (Rousk et al., 2010; Silva-Sánchez et al., 2019), and high fungal: bacterial ratios have been observed in experimentally acidified grassland soils (Chen et al., 2013). Since fungi generally have a wider C:N ratio than bacteria, they immobilize less N per unit C fixed. A faster fungal than bacterial growth response to residue additions could help explain why Nmin-Res values in the S+ treatments were on average more than double those in the S- treatments. The presence of a carbon source such as higher SOM or crop inputs often improves community stress adaptation (Rath et al., 2019b). Adding compost could have facilitated that stress-induced community shift, such that the organisms which responded to residue additions in the C + S+ soil needed less N than their counterparts in the C-S+ soil (Silva-Sánchez et al., 2019). Strong community shifts are not necessarily evident in respiration measurements due to functional redundancy. For example, at the Hoosfield acid strip, fungal growth rates increased 30-fold as pH declined from 8.3 to 4.5, while respiration changed by less than one third (Rousk et al., 2009). A compost-facilitated shift towards a less N-retentive community would be in line with two recent studies which observed that soils which were fungally dominated due to acid stress tended to use substrate less efficiently (Soares and Rousk, 2019; Silva-Sánchez et al., 2019).

This work presents the first data on the ability of a compost to moderate the effects of acid stress on nutrient cycling. Green waste compost was chosen for this experiment, as it is typical of the type of compost the production and use of which is predicted to rapidly expand in California (Coker and Ziegenbein, 2018). It is important to note that these results may not be typical of all compost types. For example, a strong liming effect has been observed when poultry manure from layer hens was applied to an acid soil, likely due to the calcium carbonate in the feed (Mokolobate and Haynes, 2002; Naramabuye and Haynes, 2006). However, the strong and unexplained effect on N cycling suggests that further investigation with additional soil and compost types should be pursued. In particular, compost effect on microbial community structure under chemical stress should be investigated further. Additionally, the use of isotopically labeled residues would allow for mechanistic exploration of mineralization and immobilization dynamics.

5. Conclusion

Intensive agricultural methods may cause degradation of soil processes. The goals of this study were a) to demonstrate in a controlled environment the potential effects of a strong, sudden chemical stress and its alleviation on microbial nutrient cycling function and b) to test whether compost would make those functions more resilient to the stress. Our results suggest that like more long-term stresses observed in natural systems, the fluctuating stresses which occur in intensively managed systems could have important implications for C and N availability and retention. Systems subjected to periodic intense chemical changes could experience both reduced N availability when metabolic inhibition is widespread and sudden flushes of mineralization in response to fresh inputs like crop residues. The high concentrations of

soluble organic matter in the acidified soils, and longer recovery time of microbial biomass than respiration after liming, suggest that large fluctuations in acidity may represent a risk for organic matter loss through leaching or mineralization. However, the very pronounced inhibition of nitrification, which also was not directly increased by liming, suggests a reduced potential for nitrate leaching to the groundwater. Surprisingly, amendment with compost strongly stimulated N mineralization from labile residue additions in the stressed soils, while having little effect on C pools and processes. The magnitude and duration of the decoupled C and N cycling responses to acid stress suggest that, as agriculture moves towards methods which target inputs to small volumes of soil, this effect warrants further study.

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CRedit authorship contribution statement

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Patricia Lazicki. The first draft of the manuscript was written by Patricia Lazicki and all authors commented on previous versions of the manuscript.

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Availability of data and material

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability

Code for statistical modeling is available upon request from the authors.

Declaration of competing interest

The authors declare no conflict of interest.

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