Prolonged drought moderates flood effects on soil nutrient pools across a rainfall gradient

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ABSTRACT

Climate change is manifesting through increased intensity and frequency of extreme events such as droughts and floods. Drought causes significant stress by limiting water availability, resulting in reduced plant growth and belowground carbon (C) inputs as well as plant nutrient uptake and microbial activity, thus impacting C and nutrient cycling. Severe floods can increase leaching of nutrients, which affect nutrient availability for plants and microorganisms potentially compounding drought-induced effects on C and nutrient cycles. However, few studies have assessed the interactions between drought and floods, constraining our ability to predict ecosystem-level effects of projected climate shifts toward fewer but larger rainfall events with longer dry spells between events. We conducted a study to assess how long-term drought moderates the effect of flooding on soil C, nitrogen (N) and phosphorus (P) pools across a rainfall gradient in south-eastern Australia. We collected soil monoliths from field rainfall manipulation facilities with a 5–7 years history of simulated reduced rainfall at three sites representing a rainfall gradient (~200–800 mm) and exposed them to a 1-in-100-year flood event under laboratory conditions. We assessed nutrients and C in soil and microbial pools before and after the flood and in flood-induced leachates. The results showed that flooding caused significantly greater losses of N in leachates, with greater effect sizes in the drought treatments compared to ambient rainfall. This response was particularly pronounced for nitrate (152 % increase on average), especially at the site with the highest mean annual precipitation (>25-fold increase). This suggest that drought may significantly reduce the capacity of ecosystems to retain N following flood events, particularly in mesic ecosystems where C and nutrient pools are greater.

1. Introduction

Soils are under constant and increasing pressure from climate change, which can disrupt key soil functions, such as water infiltration and storage, carbon (C) sequestration and nutrient cycling (Höök and Tang, 2013; Barlow et al., 2016). Climatic changes have resulted in significant warming, with current global average temperatures 1.1 °C above pre-industrial (1850–1900) levels (Intergovernmental Panel on Climate Change, 2021). However, warming is not uniform across the globe and observations indicate that the average terrestrial surface air temperature in Australia, a predominantly arid continent, increased by 1.6 °C from 1850 to 1900 to 2011–2020 and modelling suggests that Australia can reach temperature increases of 2.1 °C when the world hits +1.5 °C (Cowtan and Way, 2014; Trewin et al., 2020). These increases in

temperatures have cascading effects on rainfall patterns given the ability of warmer air to retain more moisture. Within Australia, changes in rainfall will vary across the continent with decreases in rainfall predominantly predicted for inland regions (Intergovernmental Panel on Climate Change, 2022). Additionally, models show a high probability of longer periods with reduced rainfall (McLaughlin, 2011; Grillakis, 2019). This, combined with higher temperatures, will contribute to increased aridity and greater frequency of drought events (Calanca, 2007; Nam et al., 2015; Alamgir et al., 2020).

Plants respond to drought-driven water stress mainly by reducing water loss through stomatal regulation and decreasing canopy leaf area, which reduces C uptake and photosynthetic rates. This reduction in photosynthesis negatively impacts C supply into plant organs and belowground soil pools (Ehleringer and Cooper, 1992; Chaves et al.,

2009). This decrease in C supply combined with lower soil water content can negatively impact soil microbial communities that are responsible for multiple key soil processes, including nitrification, denitrification, decomposition, and C and nutrient mineralization (Tate et al., 1988; Arnold et al., 1999; Emmett et al., 2004). For example, reductions in water availability can force microbes to decrease their production of extra-cellular enzymes (e.g., β-Glucosidase, Protease) (Dilly and Munch, 1996; Sardans and Peñuelas, 2005) and shift their nutrient content (Sparling and West, 1989; Wang et al., 2015). These microbial impacts have cascading effects on ecosystem-level element cycling (Borken and Matzner, 2009; Hartmann et al., 2013). Additionally, changes in water availability can also have direct effects on phosphorus (P) pools as its mobilisation from mineral pools and bioavailability is dependent on water availability (Wood et al., 2016; Helfenstein et al., 2018). Hence, drought might cause changes in the balance of C, N and P cycling, potentially decoupling their cycling (Suseela and Tharayil, 2018; Gao et al., 2020).

Chemical and biological changes caused by reduced water availability can also have cascading effects on soil physical properties such as aggregation and aggregate stability that results from shrinking or cracking (Raveh and Avnimelech, 1978; Dinka et al., 2013). Together, drought driven changes in biological, chemical and physical soil properties may increase vulnerability to any further stressors, which in the longer term can lead to plant death, community shifts, reduction of biodiversity and microbial function and overall ecosystem degradation (Scheffer et al., 2001; Yuan and Chen, 2015). Further degradation and extreme water deficits can lead to desertification resulting in irreversible loss of the capability to sustain any plants and microbes (Millennium Ecosystem Assessment, 2005; Valdiya, 2013).

By contrast, climate change driven precipitation fluctuations can also result in larger rainfall events leading to the occurrence of floods (Kundzewicz et al., 2014; Nam et al., 2015; Alamgir et al., 2020). These events can have positive impacts on ecosystems by replenishing soil water reserves but may also have detrimental effects on soil biogeochemical processes, particularly when severe (Stark and Firestone, 1995; Vitousek et al., 1995). For example, prolonged inundation of soil can result in reduced oxygen availability, which negatively affects plant root systems, reducing gas exchange between plants and the atmosphere, and impacts plant nutrient acquisition (Armstrong, 1980; Pezeshki et al., 1999). An anaerobic environment also negatively impacts oxygen dependent microbes, forcing them to shift to alternative electron acceptors for their metabolic needs. This results in reduced forms of oxygen, N, iron or sulphur and changes in nutrient solubility (Richardson and Vepraskas, 2001). Reduced oxygen levels can directly inhibit some oxygen dependent transformations such as nitrification (Ohte et al., 1997; Alaoui-Sossé et al., 2005). Additionally, studies show that anaerobic conditions will disrupt decomposition, which will negatively alter C and nutrient availability (Baker III et al., 2001; Schuur and Matson, 2001). Beyond direct impacts on soil chemical processes, excess water can lead to leaching (Van der Sloot et al., 1996). This will move available nutrients for plants and microbes into deeper soil layers, reducing C, N and P nutrient pools in the topsoil (Maguire and Sims, 2002; Huber et al., 2012). In addition, floods can cause surface runoff, which results in net loss of C and nutrients via movement of soil particles, biomass and soluble forms towards depressions and water bodies (Dilshad et al., 1996; Morgan, 2009). In the longer term, this can result in severe changes in ecosystem structure and function or even ecosystem state changes type (Tockner and Stanford, 2002).

Hence, the projected enhanced variation in rainfall will increase the exposure of the soil environment to cycles of drying and rewetting, which have impact on soil microbial communities (Nijs et al., 2019; Leizeaga et al., 2021), and may have detrimental effects on nutrient cycling and other soil processes (Kruse et al., 2004; Wu and Brookes, 2005). The results of drying and rewetting cycles on soil systems vary depending on soil type, rewetting rate, land-use characteristics and C and nutrient status (Falloon et al., 2011; Reichstein et al., 2013).

However, it is not clear how these impacts will differ across precipitation gradients.

To better understand the interactive effects of drought and flooding on soil C and nutrient pools, with a particular focus on flood-induced leaching, we conducted a study on Australian grassland soils. The study was conducted in growth chambers using large monoliths collected from field plots with a 5 to 7-year history of rainfall manipulation (reduced vs ambient rainfall) across a rainfall gradient. The monoliths were maintained in a growth chamber with rainfall regimes simulating field conditions for seven months to standardize rainfall drought treatments before imposing a single flood event equivalent to a 1-in-100-year rainfall event. The study addressed three research questions: 1. How does drought impact soil C and nutrient content? 2. How does drought affect the impact of a flood event on soil C and nutrients, and losses due to leaching? 3. How do nutrient losses vary across the rainfall gradient? We hypothesized that: 1. Drought reduces total and microbial C and nutrient pools, but increases soluble nutrient pools due to lower uptake of nutrients by plants and microbes; 2. Drought enhances the effects of floods resulting in higher nutrient losses through leaching as a result of accumulation of soluble forms; 3. The drought impact on flood-induced losses via leaching will be stronger in areas with lower rainfall where biological uptake of nutrients, especially N, is lower.

2. Materials and methods

2.1. Site characteristics

The study was conducted using soil monoliths (i.e., large intact soil cores) collected from long-term rainfall manipulation facilities at three sites in eastern Australia spanning a substantial rainfall gradient (Table 1). Rainfall manipulations at arid Broken Hill and semi-arid Nyngan were imposed using a standard rainfall shelter design (Yahdjian and Sala, 2002) to exclude approximately 65% of the incoming rain relative to ambient from 3×3 m plots (Fig. S1), with three replicates of each treatment (i.e. reduced rainfall, ambient). Similarly, rainfall shelters were used to exclude approximately 50% of the incoming rain from three 2×2 m plots at the third site, Bringelly, compared with three ambient rainfall plots (Canarini et al., 2016). Rainfall manipulations commenced in 2014 in Bringelly and 2016 at Broken Hill and Nyngan. The soil monoliths were collected in spring 2021, resulting in a history of 5 years reduced rainfall for Broken Hill and Nyngan and 7 years of reduced rainfall for Bringelly. It should be noted that a natural prolonged drought was taking place across all NSW from 2017 to 2019.

2.2. Soil sampling from experimental sites

Soil monoliths measuring 20 cm in diameter and 30 cm in depth were collected in April 2021 from drought and ambient plots by hammering in pre-cut PVC pipes and excavating the intact monoliths. It should be noted that in April 1990, the severe natural flood event was observed in Nyngan and in November 2005 at Broken Hill (Bureau of Meteorology, 2009). We collected the monoliths well within the experimental area but avoided the central 1.5×1.5 m core area in Broken Hill and Nyngan, and the core 1×1 m in Bringelly given the smaller plot size, to minimize disturbance on soil given ongoing experimental work at the sites. Very little vegetation was present in the plots at Broken Hill and Nyngan when the monoliths were collected. Twelve monoliths were collected from each site, with two monoliths collected in each of three drought and ambient treatment plots, resulting in 6 monoliths per treatment per site and 36 monoliths in total for all three sites. Both ends of the soil monoliths were closed with PVC caps in the field, transported to Hawkesbury Campus, and placed in growth chambers for the duration of the study (Fig. S2).

Table 1

List of sites including location names, coordinates and ecosystem characteristics. Soil classification is based on the World Reference Base (WRB) (Nachtergaele, 2007). Mean annual precipitation (MAP, in mm year^{-1}) and temperature (MAT, in °C) are based on 1970–2000 data from WorldClim2 (Fick and Hijmans, 2017).

Site name	Coordinates		Site characteristic				
	Latitude	Longitude	Climate	Soil (WRB)	Ecosystem type	MAP (mm·yr^{-1})	MAT (°C)
Bringelly	33.9 S	150.7 E	Temperate	Luvisols	Grassland	771	16.6
Nyngan	31.7 S	146.6 E	Semi-arid	Yermosols	Grass/shrubland	405	18.5
Broken Hill	32.0 S	141.6 E	Arid	Lithosols	Grass/shrubland	258	18.4

2.3. Growth chamber setup and watering

Monoliths were kept in growth chambers with the temperature set to reflect average annual temperature in Nyngan (Bureau of Meteorology, 2019), with day-time highs of 25 °C (13 h) and night-time lows of 11 °C (11 h). This diurnal temperature variation occurs naturally as part of the seasonal variation at all sites. The CO_2 level was set to a global annual mean concentration of 410 μl/L level in 2019. The volume of water added to the ambient treatments was based on the long-term annual rainfall for each site using the rainfall for the nearest Bureau of Meteorology weather station and recalculated to the monolith surface area (in cm^3). Watering for the drought treatment was reduced by 65 % relative to ambient for all three sites to pre-condition the soils prior to the flood. Watering using tap water was conducted twice per week (Bringelly – 120 mL ambient, 42 mL drought; Nyngan – 72 mL ambient, 25 mL drought; Broken Hill – 42 mL ambient, 15 mL drought). The monoliths were maintained at this temperature and watering regime for seven months prior to the flood event.

2.4. Flood event

Before inducing the flood event, a leachate collection system was installed by drilling a small hole in the bottom of the PVC cap and attaching clear vinyl tubing and 50 mL plastic vials to collect leachate (Fig. S3).

The flood represented a 1-in-100-year event for each separate site relative to historical data, based on the Bureau of Meteorology climate data from the nearest weather stations, with Bringelly receiving the equivalent of a 422 mm event (=1800 mL), Nyngan receiving the equivalent of 365 mm (=1500 mL), and Broken Hill receiving the equivalent of 252 mm (=960 mL). Ambient and drought treatments within sites received the same flood event size. The exact amount of water for each monolith was applied using a graduated cylinder. Water was added slowly enough to avoid water spilling over the edge of the PVC pipes but allowing the water to pool on the surface (30–40 min), as under natural flood conditions.

2.5. Soil sampling and analyses

Soil samples were collected using a soil corer to 5 cm depth immediately prior to the flood, during the flood (after water started leaching from the monoliths), and 3 and 7 days after flooding. After water was added, all leached material was collected into vials replaced as necessary. Leachate collection was continued until no additional water was retrieved. Soil samples were prepared for laboratory processing immediately after sampling. Plant biomass was harvested at the end of the experiment (7 days after the flood). Both roots and shoots were collected from monoliths, washed to remove soil particles and weighed after oven drying at 60 °C for 2 days. However, plant growth only occurred in the monoliths from Bringelly, with no biomass recorded in Nyngan or Broken Hill soil monoliths when collection took place for either treatment due to the impact of the ongoing drought at the time of monolith collection, which severely impacted standing biomass and most likely influenced the soil seed bank.

Soil samples were sieved through a 2 mm sieve to remove rocks and plant material. The homogenized soil was then subsampled for

individual analyses. Soil water content was estimated by oven drying ~10 g fresh soil at 105 °C for 2 days. pH was measured on a 1:5 soil: water slurry (S20 SevenEasy Mettler Toledo). Approximately 5 g air dried soil was mixed with 25 mL distilled water and shaken for 1h before measurements were taken. Total C and N content was determined by oxidative combustion based on the Dumas method (Buckee, 1994), using a LECO TruMac CN analyser with a detection limit of 0.1 % and 0.02 % for C and N, respectively (LECO Corporation, 2003) with a combustion temperature of 1350 °C. Total P was determined on pellets made of 1 g air-dried soil mixed with 2.5 g boric acid powder (Krishna et al., 2007), using an Epsilon 4 Benchtop X-ray fluorescence (XRF) analysis spectrometer with detection resolution <145 eV at 5.9 keV cps (Malvern Panalytical, Malvern, UK). Quality control samples were included in both analyses.

Microbial C, N and P, were obtained using the chloroform fumigation extraction. Unfumigated extracts were used to determine soluble C, N and P while microbial biomass C, N and P was estimated from the difference between the unfumigated and fumigated samples. Fumigated and unfumigated 10 g fresh soil subsamples for C and N were extracted using 0.5 M K_2SO_4 solution with 33 mL solution following shaking for 2 h and 4 days of fumigation. Phosphorus was extracted from 4 to 4.05 g fresh soil using reverse osmosis water at a ratio of 1:10 following shaking for 3 h and 1 day of fumigation (Vance et al., 1987). Extracts were filtered using ashless Grade 42 quantitative filter circles (125 mm diameter). Both fumigated and unfumigated samples were then analysed for total C and N using a TOC-L analyser with a detection limit of 0.004 mg/L (Shimadzu, Kyoto, Japan), and for phosphates with a AQ2 analyser with a detection limit of 0.003 mg/L (SEAL Analytical, Maquon WI, USA). Quality control samples were included in the analysis. Unfumigated samples were also analysed for ammonium and nitrate with the AQ2 with a detection limit of 0.0002 mg/L. Data were corrected to account for moisture content. No extraction efficiency correction was used to avoid artifacts due to expected differences in efficiencies of extraction among sites. All data are reported in mg/kg.

2.6. Leachate analyses

Leaching material was collected in separate 50 mL tubes, that were replaced when full. Most leachate was collected immediately following the flood, but soil leaching continued over several days with the last leachate collected prior to harvesting. All leachate from each monolith was collected into one beaker and subsampled for analysis (approximately 70 mL for each monolith). Leachate was filtered using Grade 1 filter paper (125 mm diameter) to remove soil particles. Filtered samples were analysed for total C (TC), total nitrogen (TN), nitrate, ammonium and phosphates as above. Values were converted to total amount C and nutrients lost per monolith and reported in mg/monolith.

2.7. Statistical analyses

All data were analysed to check for normality using the Shapiro-Wilk normality test (Royston, 1982). All data, except total P, showed a non-normal distribution and were square-root transformed for further statistical analysis. Data from each site were analysed separately (Broken Hill, Nyngan and Bringelly) given the different rainfall and flood treatments imposed. Then using linear mixed effect model (LMM)

with analysis of variance (ANOVA) from the "lme4" and "lmerTest" R package, we evaluated the effects of treatment (drought and ambient) as a fixed effect with time as repeated measurement (4-time sampling periods: before flood, during flood, 3 days after flood and 7 days after). Rainout shelter plot from which each monolith was taken was set as random effect given that two monoliths were collected from each plot. Relevant multiple comparison was analysed by Tukey's Honest Significant Different (HSD) test for post-hoc analysis using the "emmeans" R package. Because leachates were collected at one point in time only, leaching material was only assessed for treatment effect. Lastly, linear regressions were produced for leached nutrients significantly affected by treatment to evaluate relationships with C and nutrients pre-flood. All statistics were conducted using R (R Foundation for Statistical Computing) ver. 3.6.1 (2019-07-05) with R-Studio 2022.07.01 Build 554 "Spotted Wakerobin" Release (7872775e, 2022-07-22) for Windows.

3. Results

3.1. Plant biomass and pH

Total biomass (shoot and root) production was observed only in temperate Bringelly where it differed significantly between rainfall treatments ($F_{1,10} = 36.08$, $p < 0.05$) with ambient monoliths containing on average five times more biomass than drought (Table S3). Soil pH was significantly affected by time in arid Broken Hill ($F_{3,40} = 29.07$, $p < 0.05$) and semi-arid Nyngan ($F_{3,40} = 22.98$, $p < 0.05$) with higher pH observed during flood and gradually dropping to pre-flooding levels after the flooding event (Tables S1–2). Bringelly showed lower pH in the drought treatment ($F_{3,40} = 19.34$, $p < 0.05$; Table S3).

3.2. Effects of drought and flood on total and soil C, N and P

In general, no significant effects of drought were observed on total C, N and P. However, in Broken Hill, the driest site, marginally significant interactions of drought by time were driven by reductions in C, N and P with drought pre-flooding. Pools differed through time after flooding. Broken Hill and semi-arid Nyngan showed significant decreases in total C and N after 3 days compared to pre-flood levels (Fig. 1A and B). Significant interactive effects of treatment and time on soluble pools were commonly observed. Soluble C was higher under drought before the flooding, but this difference mostly disappeared during (Broken Hill) or after the flooding (Nyngan and Bringelly) leading to reduction in soluble C after flooding (Fig. 2A). There was no effect of drought on soluble N in the drier sites (Nyngan and Broken Hill), but N decreased immediately following the flooding event, followed by a recovery. In the case of Nyngan recovery was to pre-flood levels (Fig. 2B). In contrast, at the wetter site (Bringelly) soluble N was higher under drought compared with ambient rainfall prior to the flood and drought moderated the effects of the flood. Specifically, soluble N was lowest during the flood for the drought treatment with the highest contents at day 3 and 7, whereas soluble N increased progressively through time in the ambient treatment. Soluble P behaved differently across sites. At Broken Hill there was no effect of drought and P increased after the flood event (Fig. 2C). At Nyngan, P also increased after flooding, but this initial increase was more pronounced under drought. In contrast, at the wetter site (Bringelly) P decreased during flooding under drought but only after 7 days under ambient conditions.

At the drier sites nitrate was more abundant than ammonium, comprising about two thirds of the soluble N, while at Bringelly both N
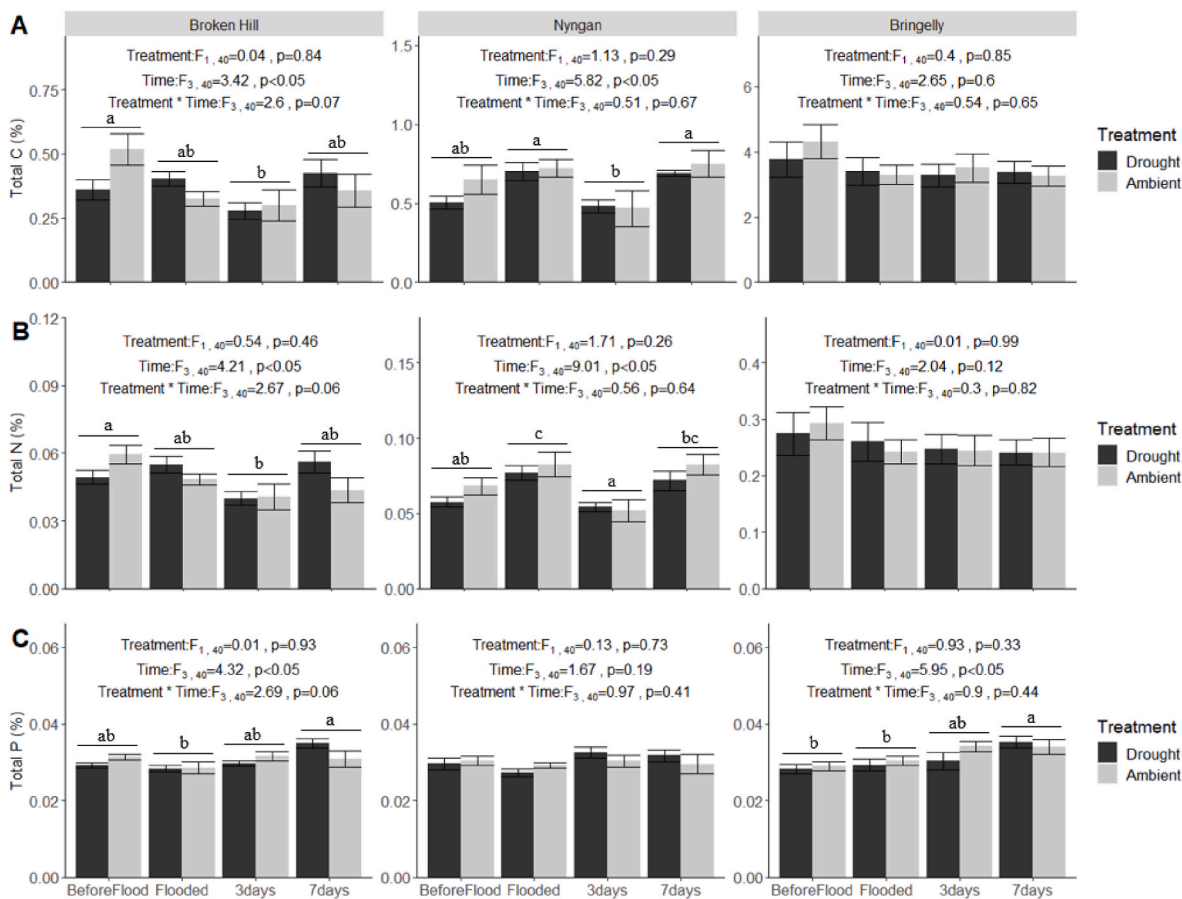

Fig. 1. Soil total C (A), N (B) and P (C) content across sites, treatments and time. Bars represent standard error. Note that the scale of the y-axes differs among sites given the large variation in contents. Test statistics are shown for significant differences among treatments and through time based on a linear mixed effect model. Letters above horizontal lines above pairs of bars indicate statistically significant differences among time periods when no significant interaction effects were present.
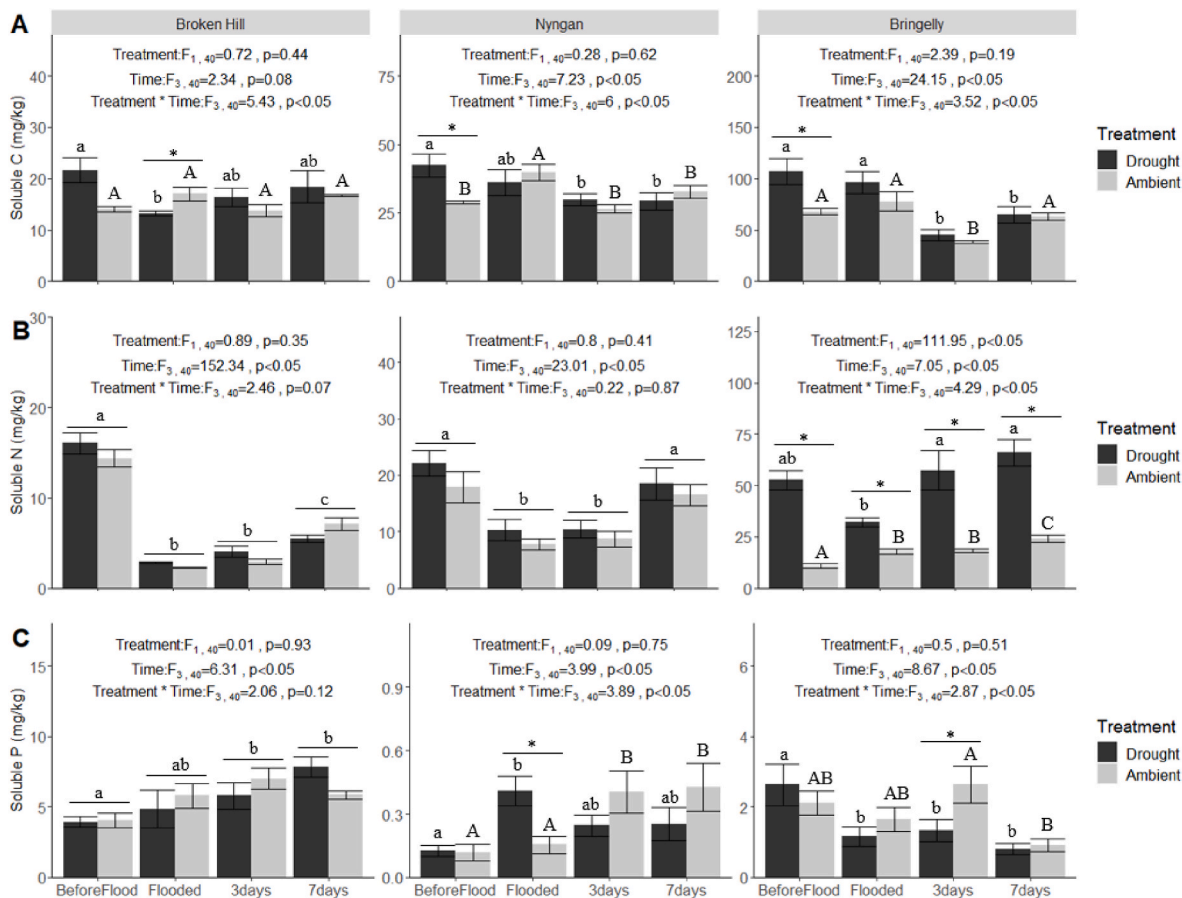
Fig. 2. Soil C (A), N (B) and P (C) soluble content across sites, treatments and time. Bars represent standard error. Note that the scale of the y-axes differs among sites given the large variation in contents. Test statistics are shown for significant differences among treatments and through time based on a linear mixed effect model. Letters above lines indicate statistically significant differences among time periods; letters above bars indicate significant differences among times for each treatment (lower case for drought, upper case for ambient); asterisks indicate significant differences between treatments at one time point. Letters above horizontal lines above pairs of bars indicate statistically significant differences among time periods when no significant interaction effects were present.
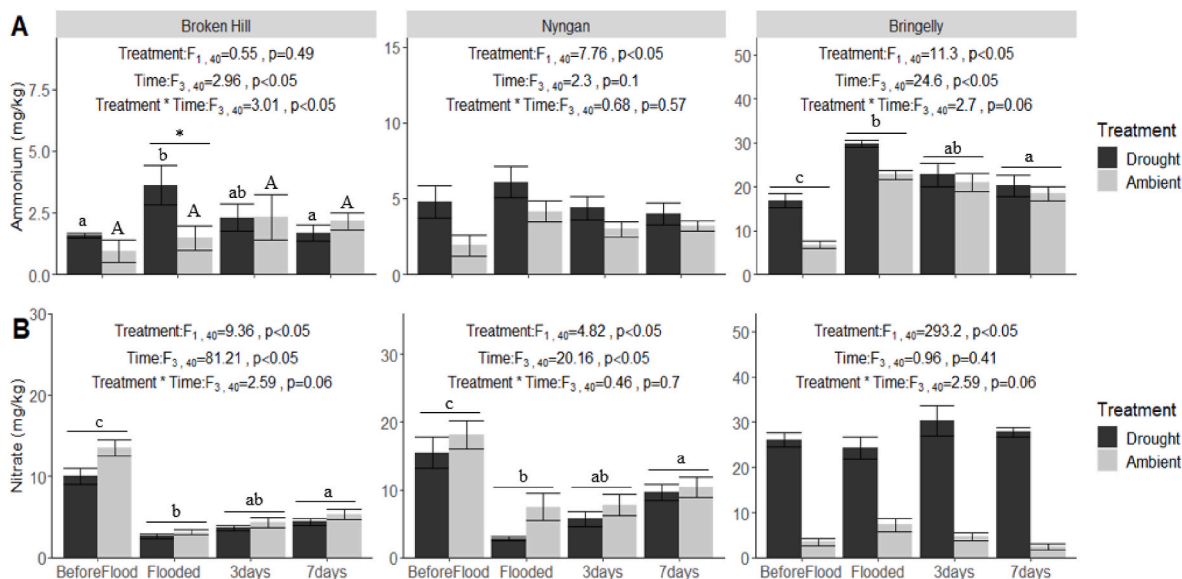

Fig. 3. Soil ammonium (A) and nitrate (B) content across sites, treatments and time. Bars represent standard error. Note that the scale of the y-axes differs among sites given the large variation in contents. Test statistics are shown for significant differences among treatments and through time based on a linear mixed effect model. Letters above lines indicate statistically significant differences among time periods; letters above bars indicate significant differences among times for each treatment (lower case for drought, upper case for ambient); asterisks indicate significant differences between treatments at one time point. Letters above horizontal lines above pairs of bars indicate statistically significant differences among time periods when no significant interaction effects were present.

forms occurred in similar proportions. Ammonium was generally higher under drought but for Broken Hill this only occurred after its increase with flooding. Ammonium increased after the flood event in Bringelly. Soil nitrate content was higher in the ambient treatments for Nyngan and Broken Hill. In contrast, at Bringelly, nitrate was higher with drought (Fig. 3A and B). Nitrate content in Broken Hill and Nyngan decreased following the flood with no recovery. By contrast, nitrate remained stable.

3.3. Microbial C and nutrient content across treatments and through time

Drought had a significant effect on microbial N across all sites, with drought treatments generally containing lower microbial N both pre- and post-flood. Microbial C was lower under drought, but this was only significant at semi-arid Nyngan. After the flooding event, microbial C increased across all sites with arid Broken Hill and mesic Bringelly presenting a drop after 7 days (Fig. 4A). The negative effect of drought on microbial N and P was stronger than that for Microbial C. Microbial N increased in Broken Hill and Nyngan following the flood event, while Bringelly showed a peak in microbial N content during the flood and a drop after it (Fig. 4B). Microbial P was lower under drought across sites, although not significantly for Bringelly. Microbial P showed an increase following the flooding for Broken Hill only under the ambient treatment, but for both rainfall treatments at Nyngan (Fig. 4C).

3.4. Flood-induced leaching of C and nutrients

Drought affected the impact of flooding on leaching of soluble C and N (specifically nitrate), but this effect differed among sites. Drought increased the loss of C in semi-arid Nyngan (Fig. 5A) and of total N in arid Broken Hill and mesic Bringelly (Fig. 5B) which, in turn, was driven by increased loss of nitrates with drought across all sites (Fig. 5D). No significant treatment effect was observed for ammonium or phosphates (Fig. 5C–E).

4. Discussion

4.1. Drought induced shifts in soil soluble and microbial C, N and P nutrient pools

Our results showed that drought had no impact on total soil C, N or P content prior to flooding, indicating that the soils were highly resistant to reductions in rainfall. As such, our results differ from several previous studies that have found drought-induced decreases in soil C and nutrient content (Sardans et al., 2006, 2008).

By contrast, the soil soluble C, N and P pools were more responsive than total pools, indicative of drought-induced shifts in biochemical cycling consistent with previous work. In general, drought increased soluble C and N pools prior to the flood, with the soluble N pool responses being more site dependent than C or P pools. This result thus partially supports our first hypothesis with the drought treatment moderating soluble pools. The observed increase in soluble C under
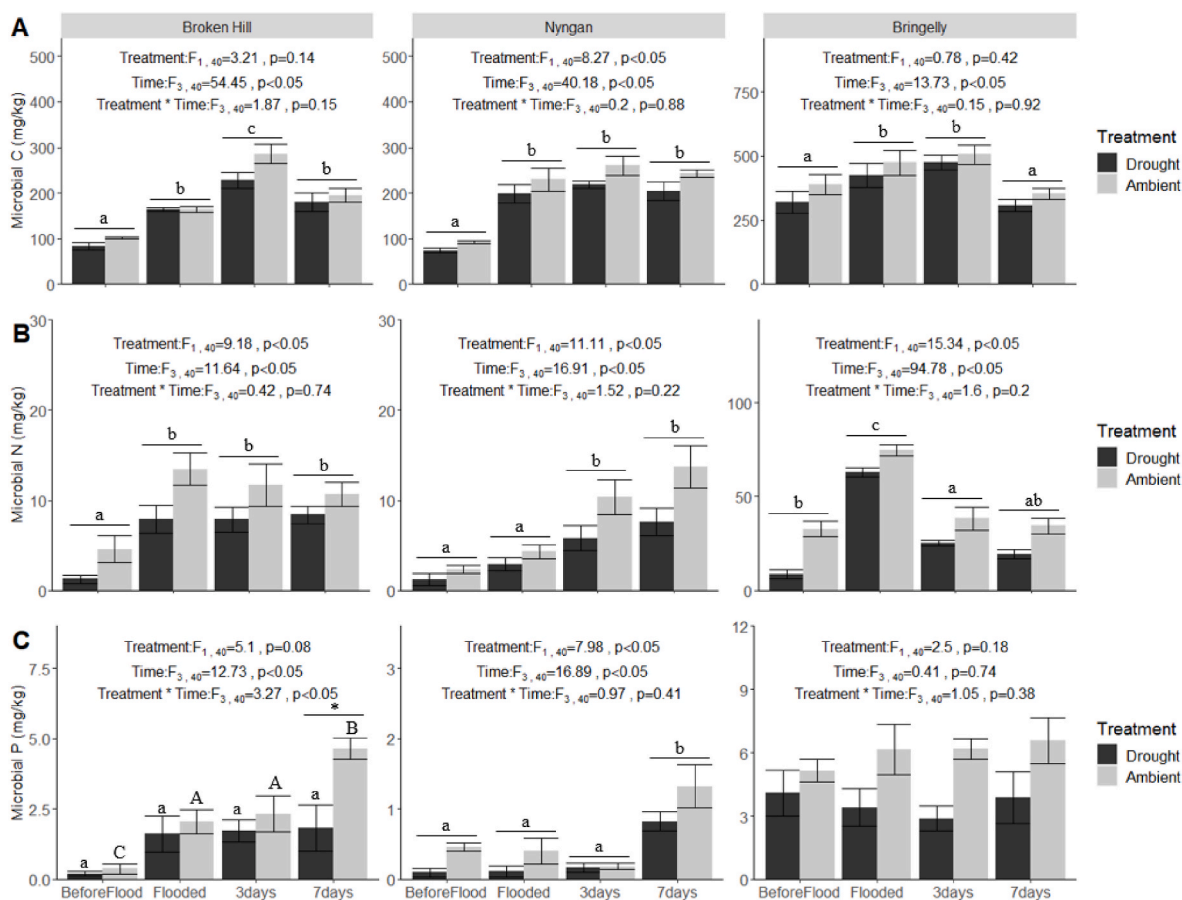

Fig. 4. Soil C (A), N (B) and P (C) microbial content across sites, treatments, and time. Bars represent standard error. Note that the scale of the y-axes differs among sites given the large variation in contents. Test statistics are shown for significant differences among treatments and through time based on a linear mixed effect model. Letters above lines indicate statistically significant differences among time periods; letters above bars indicate significant differences among times for each treatment (lower case for drought, upper case for ambient); asterisks indicate significant differences between treatments at one time point. Letters above horizontal lines above pairs of bars indicate statistically significant differences among time periods when no significant interaction effects were present.
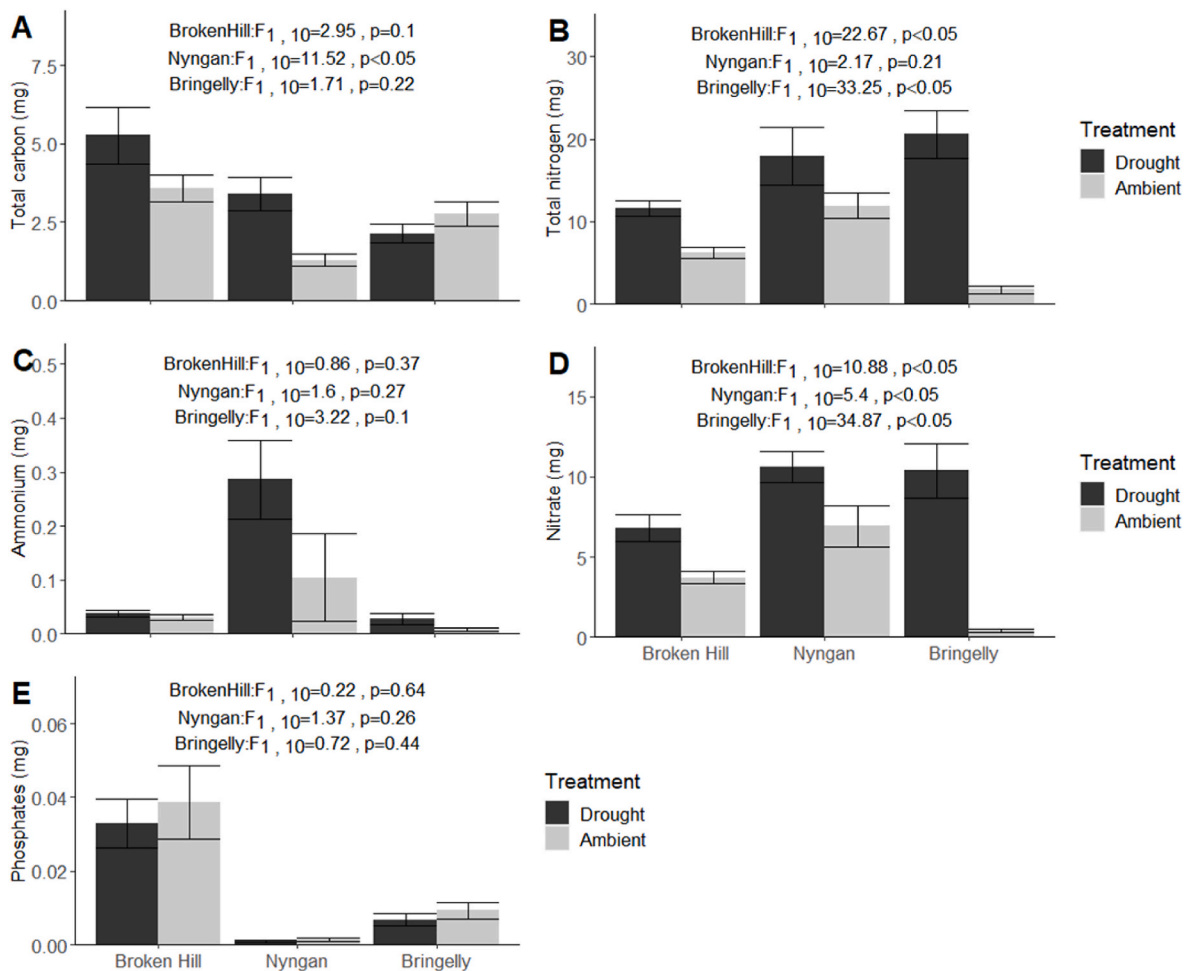
Fig. 5. Total Carbon (A), Total nitrogen (B), ammonium (C), nitrate (D) and phosphates (E) content in analysed leaching material. Bars represent standard error. Note that the scale of the y-axes differs among sites given the large variation in contents. Test statistics are shown for significant differences among treatments based on a linear mixed effect model.

drought conditions is in alignment to previous studies where similar increases in soluble C under drought conditions were reported, despite a reduction in photosynthetically assimilated C (Hagedorn et al., 2016; Fekete et al., 2021). This increase of soluble C forms is most likely related to a decrease of microbial activity associated with C turnover in soil in response to reduced water availability (Su et al., 2020). Similarly, we observed increased soluble N under drought treatments; however, in contrast to our expectation, the effect was significant only in Bringelly, the wettest site. Similar increases in soluble N under drought linked to decreased microbial activity and N turnover has been shown previously (Jensen et al., 2003; Deng et al., 2021). Further, we found that in our study the drought effect on mineral N pools (ammonium and nitrate) differed across sites. We observed higher ammonium pools under drought in most cases while drought effects on nitrate differed between sites. The increased ammonium content observed under drought is probably because nitrification, the reduction of ammonium and sequentially oxidation of it to nitrate, is sensitive to fluctuations in water availability (Siebielec et al., 2020), as the reduction in soil moisture can result in a decrease of ammonium-oxidizing bacteria (Stark and Firestone, 1995). This is also consistent with the larger nitrate pools observed under ambient treatments at the drier sites, Broken Hill and Nyngan. In contrast, larger nitrate contents were observed under drought in Bringelly, likely associated with lower plant N acquisition/demand under drought conditions (Blom-Zandstra and Lampe, 1985; Vieira et al., 1998). Thus, the impacts of drought on soluble N varied with sites due to contrasting balances between contributing

processes. Soluble P was not affected by drought (prior to flooding), which contrasts with some studies where an increase of phosphorus solubility under drought conditions was observed (Delgado-Baquerizo et al., 2013; Yue et al., 2018). The lack of a response in soluble P to drought in our study could be linked to a general low P content in Australian soils (Vitousek et al., 2010; Eldridge et al., 2018), and suggest that a longer time frame study may be required for a drought effect to materialize.

Rainfall manipulation also impacted microbial biomass C, N and P, with microbial biomass N being particularly responsive, but the responses differed among sites. Microbial biomass C was significantly lower in the drought treatment at Nyngan ($p = 0.02$) and marginally significantly lower at Broken Hill ($p = 0.09$) prior to the flood. Such reductions in microbial C pools are likely linked to suppression of microbial activity and growth with moisture limitation, which would have been stronger in the drier sites (Hueso et al., 2011). In turn, the lack of a response in Bringelly is linked to its mesic condition so that drought imposed a lower level of moisture limitation allowing microbial C to sustain allowing (Zhang and Sun, 2019; Lane et al., 2023). In contrast, microbial N showed a more consistent and stronger negative response to drought compared to microbial C across all sites. This suggests that drought imposed a stronger limitation on microbial access to N compared to C. A negative effect of drought on microbial P biomass was only significant in Nyngan and was less marked than that of N. This is consistent with the lack of a drought effect on soluble P and suggests that under moisture limitation microbes were better able to access P than N

and in turn had a smaller effect on soluble P pools. These differential responses of microbial biomass C, N and P, with much stronger drought-induced reductions in microbial biomass N, suggest decoupling of biogeochemical cycles (Delgado-Baquerizo et al., 2013; Yuan and Chen, 2015).

4.2. Flood-induced shifts in soil C, N and P pools are moderated by drought, but effects are context dependent

In general, the impacts of flooding on soil soluble C, N and P were moderated by drought, but the effect differed among sites. Thus, this finding partially supports our second hypothesis with drought moderating the outcome of flooding, specifically for soluble C and nutrient pools. Across sites, soluble C decreased with flooding under drought but was rather stable under ambient conditions. This observation aligns with the fact that soluble C content was greater pre-flooding under drought and thus, this extra C was available for loss.

In contrast, the effects of flooding on soluble N and P were site specific. Soluble N was reduced by flooding in the drier sites, particularly due to a reduction in nitrate content. This finding aligns with previous studies showing losses of soluble N after large rainfall (Borchard et al., 2012; Nikiéma et al., 2013). Nitrate could have been lost due to leaching (Nissen and Wander, 2003; Davis, 2014) but also to denitrification, which the flooded conditions would have favored (Pinay et al., 2000; Ranatunga et al., 2018). Bringelly, the wetter site, showed contrasting effects where soluble N was substantially higher under drought with flooding leading to a slight albeit not significant decrease in soluble N under drought but increased soluble N under ambient conditions. Thus, it appears that different processes were at play. At the drier sites under drought the water influx led to similar, although weaker effects(more leaching and/or more denitrification). However, under ambient moisture conditions, it led to increases due to ammonium suggesting an increase in mineralization or a decrease in nitrification under flooding conditions, given that nitrification is an aerobic process (Yamane, 1957; Belder et al., 2005). Soluble P content increased after the flood in Broken Hill and Nyngan, the drier sites, independent of drought. Increased soluble P was most likely related to increased solubility of P and stimulation of microbial mineralization as observed in previous studies (Olsen and Court, 1982; Chepkwony et al., 2001). In contrast, in Bringelly, the wettest site, drought conditions led to decreased soluble P after flooding, which could have been due to enhanced plant uptake after relief of moisture stress.

Microbial C, N and P pools generally responded positively to flooding, and the effects were not commonly moderated by drought. The
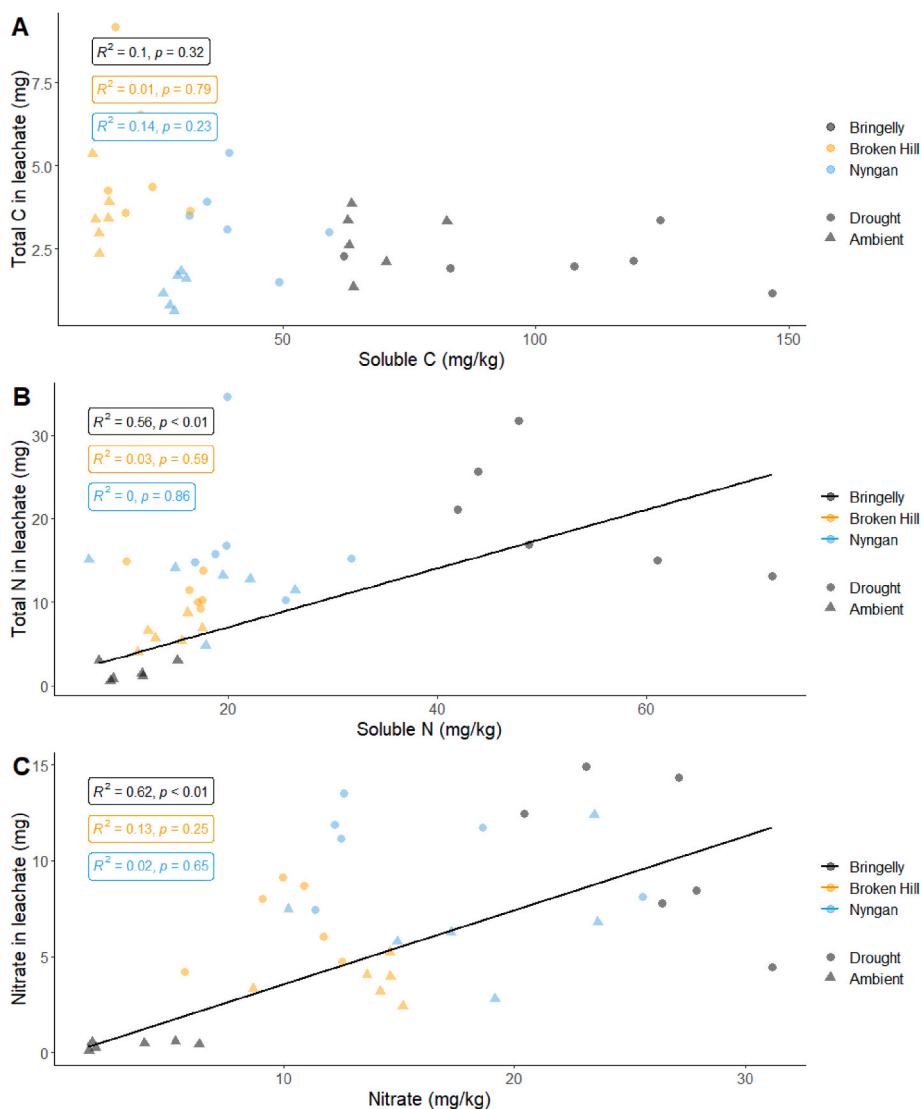

Fig. 6. Relationship between total C (A), total N (B) and nitrate (C) in leachates, and soluble C, soluble N and nitrate, respectively, prior to flooding across all sites and treatments.

observed increase in microbial C, N and P content after flooding in Nyngan and Broken Hill, and microbial C and N in Bringelly, is consistent with findings from other arid and semi-arid systems where large rainfall events were shown to stimulate microbial activity (Schwinning and Ehleringer, 2001; Austin et al., 2004).

4.3. Nutrient loss in leaching material moderated by drought

The flood resulted in substantial leaching of C and N but there was considerable variation among sites and with drought legacies. Despite large losses in the arid sites, the highest loss of nutrients (particularly N) was observed in the wetter site, Bringelly.

Substantial C leaching was observed in the drier sites, with similar C losses through leaching observed in arid and semi-arid grasslands previously (Liu et al., 2018). Higher flood-induced leaching of C under drought is consistent with greater soluble C concentrations pre-flooding that can potentially be leached down the soil profile. However, while in Bringelly, the wetter site, drought also led to higher C pre-flooding, this was not reflected in the amount of leached C (Fig. 6A), indicating that after flooding this C could have quickly been taken up by microbes and/or potentially lost through microbial respiration.

The greatest impact of flooding on leaching was observed for N. In Broken Hill and Nyngan, the drier sites, N loss, mostly as nitrate, was higher in the drought treatment, even though drought had not caused greater solubility of nitrate at these sites prior to flooding. This may indicate a rapid response to water influx of nitrification or potentially a rapid release of soluble N from organic matter which would then render it available to be leached. Moreover, while the amount of leached N was high for the soils from the drier sites, the greatest loss was observed in Bringelly. This is opposite to our third hypothesis where we predicted lower nutrient loss for sites with greater rainfall. The higher loss can be explained by greater solubility of nitrate under drought prior to flooding (Fig. 6B and C). This suggests a greater potential for N loss in higher rainfall areas; however, these losses would be lower with an active plant community where plants could have the ability to quickly acquire N post flooding (Benoit et al., 2014; Abdalla et al., 2019).

Leaching of phosphate in considerable amounts was only observed in Broken Hill, the driest site, but this was not influenced by drought. This is consistent with the lack of impact of drought on soluble P pre-flooding. This site-specific response is likely linked to higher presence of soluble P compared to wetter sites, with microbes not fully utilizing soluble P due to lower activity (Margalef et al., 2017). This resulted in the presence of mobile P forms which under large water influx were removed from top soil as previously observed in another grassland study (Sinaj et al., 2002).

5. Conclusions

This study showed that a legacy of reduced rainfall had significant impacts on soil soluble C and N, and microbial C, N and P pools, and combined with flooding this can lead to greater losses of N, particularly as nitrate. Nitrogen, particularly the nitrate pool, was the least resilient to combined drought and floods suggesting their combination may promote irreversible loss of soluble N. Our study demonstrated a high dependency of impacts of historic drought and flooding on aridity level and sheds some light on potential mechanisms for this dependency. Future studies assessing potential strategies to counteract effects caused by drought and flood combined are needed to prevent nutrient losses and increase soil resilience in dry conditions.

CRediT authorship contribution statement

Jerzy Szejgis: Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Uffe N. Nielsen:** Writing – review & editing, Supervision, Methodology. **Feike A. Dijkstra:** Writing – review & editing,

Methodology. **Yolima Carrillo:** Writing – review & editing, Validation, Supervision, Methodology, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109404.

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