

RESEARCH ARTICLE

Effects of long-term phosphorus fertilizer inputs and seasonal conditions on organic soil phosphorus cycling under grazed pasture

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Funding information

Mohammed VI Polytechnic University; Office Cherifien des Phosphates (OCP)

Abstract

Soil microbes and phosphatase enzymes play a critical role in organic soil phosphorus (P) cycling. However, how long-term P inputs influence microbial P transformations and phosphatase enzyme activity under grazed pastures remains unclear. We collected top-soil (0–75 mm) from a grazed pasture receiving contrasting P inputs (control, 188 kg ha⁻¹ year⁻¹ of single super phosphate [SSP], and 376 kg ha⁻¹ year⁻¹ of SSP) for more than 65 years. Olsen P, microbial biomass P, and acid and alkaline phosphatase enzyme activities were measured regularly over a 2-year period. Pasture dry matter and soil chemical properties were also investigated. Results showed that long-term P inputs significantly increased pasture dry matter, total N, and the concentrations of NO₃⁻-N but significantly decreased soil pH and the concentrations of NH₄⁺-N. Total C was not affected by P fertilization. Although Olsen P significantly increased with increasing long-term P inputs, microbial biomass P was similar under P fertilized treatments. Long-term P inputs decreased acid phosphatase activity but increased alkaline phosphatase activity. Microbial biomass P was similar across seasons in the control but decreased in spring and autumn while increased in summer and winter under P fertilized treatments. Acid and alkaline phosphatase activities were significantly affected by season and followed similar seasonal trends being maximum in summer and minimum in winter regardless of P treatment. Correlation and principal component analysis revealed that acid and alkaline phosphatase activities were significantly positively correlated with soil temperature and significantly negatively correlated with soil moisture. In contrast, Olsen P and microbial biomass P were weakly correlated with environmental conditions. The findings of this study highlight the intertwined relationship between organic P cycling and the availability of C and N in soil systems and the need to integrate both soil moisture and temperature in models predicting organic P mineralization, especially in the context of global climate change.

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KEYWORDS

long-term experiments, microbial biomass phosphorus, phosphatase enzyme activity, phosphorus fertilization, soil moisture, temperature

1 | INTRODUCTION

Inputs of phosphorus (P) are necessary to increase the productivity of most agroecosystems (Haygarth et al., 2013; Vance et al., 2003). In addition to P removal in produce and drainage, ongoing immobilization of added P via adsorption onto soil mineral surfaces and organic matter means that continued inputs of P in the form of mineral fertilizer and/or manure are required to maintain production at desired levels (Condrón, 2003; Richardson & Simpson, 2011). These fertilization practices have resulted in the accumulation of significant quantities of P in many agroecosystems, which is commonly referred to as “legacy P” (MacDonald et al., 2012; Pavinato et al., 2020). This accumulated P has been shown to increase the risk and occurrence of elevated P loss in drainage which has been linked to enhanced eutrophication (McDowell et al., 2003; Sharpley et al., 2001). Accordingly, to maintain or boost production while minimizing P losses, there is an urgent need to improve P use efficiency, which in turn requires an improved understanding of the impact of P inputs on soil P dynamics and bioavailability in different agroecosystems (Frossard et al., 2000; Haygarth et al., 2013).

Soil microorganisms significantly impact plant P nutrition not only because they compete with plants for P (Marschner et al., 2011), but they also control organic P cycling via an interplay between immobilization and mineralization processes (Richardson, 1994; Richardson & Simpson, 2011). Under pasture systems, management practices such as the quantity of P inputs, plant biomass management, and grazing intensity have been found to have a significant effect on microbial biomass P transformations and consequently P availability (Boitt et al., 2018; Katsalirou et al., 2016; Perrott et al., 1992; Wei et al., 2017). With respect to P fertilization effects on microbial biomass P, contrasting results have been reported under pasture systems. For instance, long-term P applications under a cut and carry system had no impact on soil microbial biomass P (Massey et al., 2016), whereas microbial biomass P increased with increasing P inputs in a grazed pasture system in Ireland (Chen et al., 2014). Ross et al. (1995) noted the inconsistent response of microbial biomass P to rock phosphate applications in a grazed pasture system in New Zealand because of the variability in total carbon (C) and nitrogen (N) concentrations. Changes in microbial biomass P under pasture systems seem to be linked to the availability of soil nutrients (C and N) other than P. A better understanding of the factors governing microbial P cycling in soil systems can offer opportunities

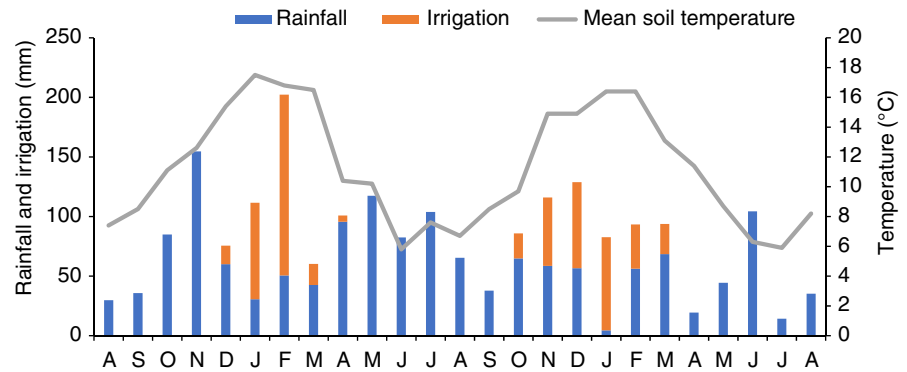
to enhance P fertilizer use efficiency and P availability to plants (Richardson, 2001; Richardson et al., 2011).

Acid and alkaline phosphatase enzymes play a pivotal role in plant nutrition by cleaving organically P-bound to release free orthophosphates for plant roots, especially under P deficient conditions (Nannipieri et al., 2011). It is widely acknowledged that soil organic P mineralization is inhibited under high P; nevertheless, phosphatase enzyme activity has shown opposing responses to P inputs in pasture soils (Ikoyi et al., 2018; Randall et al., 2019; Shi et al., 2020). Furthermore, past investigations under pasture systems have evaluated acid and alkaline phosphatase activities under short-term P fertilization (Ikoyi et al., 2018), while long-term P addition experiments investigated either acid or alkaline phosphatase activity (Randall et al., 2019; Tan et al., 2013). Therefore, our understanding of how both acid and alkaline phosphatase activities are influenced by long-term P under pasture systems remains evasive.

A growing body of literature has shown that acid phosphatase enzymes are released by plant roots (Colvan et al., 2001; Speir & Cowling, 1991), whereas alkaline phosphatases are mainly ascribed to the activity of soil microorganisms (Sakurai et al., 2008; Spohn & Kuzyakov, 2013a). Additionally, it has been found that acid and alkaline phosphatase activities are driven by different nutrient demands (Spohn et al., 2015; Spohn & Kuzyakov, 2013b). While evidence of this differentiation in origin and nutrient demand between acid and alkaline phosphatase enzymes has been shown under pot experiments, little proof has been driven from field studies.

Environmental conditions such as soil moisture and temperature can influence P immobilization and mineralization processes via their impact on soil microbial biomass and activity and plant growth (Chen et al., 2008; Dalal, 1977; Margalef et al., 2021; Shi et al., 2013). In general, P mineralization increases with increasing soil temperatures, whereas P immobilization occurs at low temperatures (Arenberg & Arai, 2019). However, authors have reached inconclusive results when studying the relationships between environmental conditions, microbial biomass P, and phosphatase enzyme activity under different P regimes and experiment designs. Perrott et al. (1992) found that microbial biomass P increased with increasing soil moisture in a low P grassland soil, whereas He et al. (1997) described no clear relationship between microbial biomass P and air temperature in both unfertilized and P fertilized pasture systems in the United Kingdom. On the other hand, Randall et al. (2020) pointed out a significant response of acid phosphatase

FIGURE 1 Monthly mean soil temperature, rainfall, and irrigation by a pivot at the Winchmore fertilizer trial from August 2018 to August 2020



activity to historical soil P status but not of water availability in soils taken from a long-term P fertilization experiment under pastures. A more refined understanding of P immobilization and mineralization processes as affected by soil moisture, temperature, and P availability is needed to better predict organic P cycling, especially under future scenarios of climate change.

Although past research has demonstrated that long-term P inputs and seasons significantly affected microbial biomass P dynamics under pasture systems (Chen et al., 2014), scarce information is available on how acid and alkaline phosphatase enzyme activities seasonally fluctuate under pasture systems subjected to long-term P. Furthermore, little attention has been given to link changes in environmental conditions and soil P availability to both microbial biomass P transformations and phosphatase enzyme activities in pasture soils receiving long-term P fertilization. Bering in mind the socio-economic benefits of pasture systems (Hynd, 2019; Phelps & Kaplan, 2017) and the critical role of P in pasture production (McDowell & Condron, 2012; Simpson et al., 2014), identifying key factors controlling organic P cycling under pastures is a prerequisite to efficiently manage these important ecosystems in a context of global climate change and declining rock phosphate reserves.

The primary objective of this study was to use the Winchmore P fertilizer trial, considered the longest-running replicated grazed pasture experiment in the world (McDowell et al., 2021), to assess and quantify the cumulative impacts of long-term inputs of different rates of P fertilizer on key soil parameters linked to organic soil P cycling, including Olsen P, microbial biomass P, and phosphatase enzyme activities. A second objective was to investigate the impact of differences in soil P status from previous P inputs on short-term seasonal changes in these parameters. We hypothesized that while Olsen P and microbial biomass P would increase with increasing P fertilization, phosphatase enzyme activities would decrease. We also hypothesized that seasonal changes in soil biology (microbial biomass P) and biochemistry (phosphatase enzyme activities) related to soil organic P cycling would be

influenced by changes in environmental conditions irrespective of P status.

2 | MATERIALS AND METHODS

2.1 | Description of the trial

The field study is situated at Winchmore, New Zealand (latitude: 43.787°S, longitude: 171.795°E, and altitude: 160 m). Full details of the trial and associated physical and chemical data are given in McDowell et al. (2021). Briefly, the mean air temperature in this area is 11.1°C, while the average rainfall is 730 mm, with January being the warmest month and July the month with the most rainfall. The soil is a Lismore stony silt loam (Orthic Brown, New Zealand; Dystric Cambisols, World Reference Base for Soils Resources). In 1949, the site was sown with a pasture mixture dominated by ryegrass and white clover, and in 1952, five P fertilizer treatments were imposed and replicated four times in a randomized block design. Each replicate plot (≈ 0.09 ha) was fenced and grazed by a separate flock of sheep in spring, summer, and autumn (no grazing during the winter period) to avoid the nutrient transfer. The number of sheep per plot was rationalized based on pasture production and pasture utilization (80%) for each treatment. Lime was added on three occasions (1949, 1950 [both 2.5 t ha⁻¹], and 1972 [4.4 t ha⁻¹]) to maintain soil pH at or above six. The average soil pH over the last 30 years was 5.6. For the present study, we focused on three P treatments, namely control (no fertilizer), 188P (188 kg ha⁻¹ year⁻¹ of single super phosphate [SSP]), and 376P (376 kg ha⁻¹ year⁻¹ of SSP), which have been under consistent fertilization management for the last 65 years. The fertilizer was applied by top dressing in August–September each year (late winter). Between 1952 and 2018, the trial was irrigated by a border-dyke system, whereby 100 mm was applied to each replicate plot when soil moisture reached 15%–20% (0–100 mm). In 2018, the system was converted to an overhead spray irrigation system, and an average of 10 mm was applied every 3–5 days

to ensure that ≈ 90 mm of rain and irrigation water was available monthly for pasture growth.

2.2 | Meteorological data

Meteorological data (monthly rainfall and mean soil temperature) for the period of the study have been retrieved from the National Institute of Water and Atmospheric Research (NIWA) website <https://cliflo.niwa.co.nz> for the Winchmore weather station (Number: 6476, latitude: 43.79346°S, longitude: 171.79512°E). The quantities of water supplied to the trial site via central pivot have been provided by The Fertiliser Association of New Zealand. Soil temperature for 1 week before the sampling date was used for calculations. Meteorological data are presented in Figure 1.

2.3 | Plant sampling and plant community composition assessment

Pasture production was measured using two exclusion cages per plot (Lynch, 1966). The exclusion cage dimensions were 3100 × 900 mm. Herbage was cut at 25 mm above ground level with a mower from an area of 3100 × 500 mm. An average of eight harvests (interval of 1–2 months) were collected during the main growing season starting from early September to late May (Nguyen et al., 1989). The first harvest of September each year was assimilated to the winter season. To determine the dry matter, a composite subsample was oven-dried at 70–80°C until a constant weight was achieved. Plant community composition was determined at a mid-point during each season except for winter the sample for which was taken at the first cut in spring in early September. Plant samples were taken from within the exclusion cages, cut at 25 mm above ground level, and dissected into grass, clover, and weeds.

2.4 | Soil sampling

The Winchmore fertilizer trial was sampled in October (spring), January (summer), March (autumn), and July (winter) over 2 years, starting from October 2018 till July 2020. Plots were sampled by taking 20 soil cores from the top 0–75 mm with a 25 mm diameter corer in a zigzag pattern. Care was taken to sample the same part of the plot each time while avoiding sheep camps (Nguyen & Goh, 1992a). Stones and coarse plant materials were removed from the soil samples, and the soil was sieved <2 mm. Soil samples were then kept in the fridge at 4°C for 48 h to allow for microbial activity to stabilize. Soil biological and biochemical properties as well as available N were analysed within a

week from sampling. A subsample was taken to determine the gravimetric soil moisture by oven drying the soil at 105°C until constant weight. The remaining soil was air-dried at room temperature and used for the determination of soil chemical properties.

2.5 | Soil analyses

Soil pH was determined in soil-to-water solution ratio of 1:2.5. Total C and N were measured after combustion of air-dried soil in an Elementar Vario Max CN analyser. Available N (NH_4^+ -N and NO_3^- -N) was determined using a total N analyser after extracting field-moist soil with 2 M KCl solution (Blakemore et al., 1987). Bioavailable P was determined by measuring Olsen P according to Watanabe and Olsen (1965), and inorganic P was analysed following the molybdenum blue method (Murphy & Riley, 1962). Microbial biomass P was determined according to the fumigation-extraction method of Brookes et al. (1982) with the recommendations of Morel et al. (1996). A coefficient of recovery (40%) was used to calculate microbial biomass P. Acid and alkaline phosphatase enzyme activities were assessed following the procedure of Tabatabai (1994) and reported as $\mu\text{mol } p\text{-nitrophenol produced g}^{-1} \text{ h}^{-1}$ of fresh soil. Acid and alkaline phosphatase enzyme activities were considered potential enzyme activities (Margenot et al., 2018).

2.6 | Statistical analysis

Acid and alkaline phosphatase activities and soil moisture were subjected to two-way repeated-measures analysis of variance (ANOVA) to test the effects of P treatment, season, and their interaction. Olsen P and microbial biomass P did not meet the assumption of data normality to carry out the two-way ANOVA, even after transformation; therefore, a non-parametric test (Friedman's test) was performed instead. In the presence of a significant effect, one-way ANOVA was used to test the effect of P treatment and season separately. The post-hoc Tukey test was performed to separate group means. For non-normal data, Dunn-Bonferroni post-hoc test was used to separate treatment means. The level of significance was set at 5% probability. Pearson's correlation analysis and principal component analysis (PCA) were carried out to determine relationships between soil biological and biochemical properties and environmental conditions (soil moisture and soil temperature). Spearman's correlation was performed whenever non-normal variables (Olsen P and microbial biomass P) were involved. All the above analyses were performed using SPSS version 25.0 (SPSS), while the data were plotted using Microsoft Excel and SigmaPlot software version 14.0 (Systat Software).

3 | RESULTS

3.1 | Environmental conditions

Between August 2018 to July 2019, the trial received a total of 1159 mm of water (888 mm rainfall and 271 mm irrigation) compared with 921 mm (630 mm rainfall and 291 mm irrigation) between August 2019 and July 2020 (Figure 1). Higher soil temperatures were recorded in summer (January–February), whereas lower soil temperatures were noted in winter (June–July) in both 2019 and 2020 (Figure 1). Soil moisture ranged from 24% to 47% and exhibited higher values during winter (Table 1; Figure 3a). Moreover, throughout the study period, soil water content was lower under the 188P and 376P treatments compared with the control, especially in spring and summer.

3.2 | Dry matter and plant community composition

Dry matter significantly increased in response to long-term P inputs. This increase was 1.7- and 1.8-fold under 188P and 376P treatments compared with the control, respectively (Figure 2). Dry matter in the 188P and 376P treatments was similar over the study period (Figure 2). Regardless of P treatment, the dry matter was highest in summer and lowest in winter (Figure S1). Regardless of P treatment, plant community composition was grass-dominant over the study period (Table S1). More plant species pertaining to the weed family were found under the control compared with 188P and 376P treatments.

The historical average of plant composition over the last 13 years showed a 1.8-fold higher content of clover in the P fertilized treatments compared with the control (Table S1).

3.3 | Soil chemical properties

Long-term P applications significantly decreased soil pH compared with the control in both July 2019 and 2020, though differences were small (Tables 1 and 2). Total C was similar across P treatments and seasons, whereas total N significantly increased by an average of 13% under P fertilized treatments (188P and 376P) compared with the control (Tables 1 and 2). Irrespective of the growing season, available N was significantly affected by long-term P inputs. Specifically, under P fertilized treatments, the concentrations of NO_3^- -N increased by 4-fold, whereas the concentrations of NH_4^+ -N decreased by 26% compared with the control (Tables 1 and 2). No significant differences were observed between 188P and 376P treatments for all soil chemical properties, except total C (Table 2).

3.4 | Olsen P, microbial biomass P, and phosphatase enzyme activities

Long-term P applications significantly increased Olsen P concentrations compared with the unfertilized control. Differences in Olsen P concentrations between 376P and 188P treatments were also significant (Figure 3b). Concentrations of Olsen P averaged 63.1, 17.2, and

TABLE 1 Range and means of soil pH, total C (g kg^{-1}), total N (g kg^{-1}), NH_4^+ -N (mg kg^{-1}), NO_3^- -N (mg kg^{-1}), Olsen P (mg kg^{-1}), microbial biomass P (MBP) (mg kg^{-1}), acid phosphatase (acid P) ($\mu\text{mol g}^{-1} \text{h}^{-1}$), alkaline phosphatase (alkaline P) ($\mu\text{mol g}^{-1} \text{h}^{-1}$), and soil moisture (%) measured in the control, 188P (188 $\text{kg ha}^{-1} \text{ year}^{-1}$ of SSP), and 376P (376 $\text{kg ha}^{-1} \text{ year}^{-1}$ of SSP) treatments over the study period. Soil samples were taken from 0 to 75 mm of the Winchmore fertilizer trial

	Control		188P		376P	
	Range	Mean	Range	Mean	Range	Mean
Soil pH	5.80–6.20	6.04 ^a	5.56–6.11	5.88 ^a	5.62–6.12	5.85 ^a
Total C	37.0–45.7	41.1 ^a	37.5–45.9	41.8 ^a	36.3–46.2	41.1 ^a
Total N	3.5–3.7	3.5 ^a	3.8–4.4	4.0 ^a	3.8–4.3	4.0 ^a
NH_4^+ -N	16.10–35.93	27.23 ^a	11.13–20.22	16.14 ^a	9.53–24.3	16.32 ^a
NO_3^- -N	2.94–8.00	5.52 ^a	19.51–50.34	34.41 ^a	21.04–68.71	36.72 ^a
Olsen P	3.26–5.80	4.46 ^b	13.60–23.39	17.15 ^b	50.63–76.52	63.09 ^b
MBP	25.51–58.84	39.32 ^b	22.27–83.30	50.57 ^b	20.72–86.58	50.51 ^b
Acid P	9.46–13.87	11.56 ^b	8.29–12.64	10.19 ^b	7.86–11.96	10.10 ^b
Alkaline P	3.32–6.27	4.69 ^b	3.70–7.60	5.34 ^b	3.91–7.66	5.71 ^b
Soil moisture	26–47	36 ^b	24–46	33.5 ^b	24–43	33 ^b

^aValues are means of 8 replicates.

^bValues are means of 32 replicates.

4.5 mg kg⁻¹ under 376P, 188P, and the control, respectively (Table 1). Over the study period, Olsen P fluctuated in the fertilized treatments, especially 376P, while no significant differences between seasons were noted for the control treatment (Figure 3b).

Microbial biomass P was significantly higher under 188P and 376P compared with the control treatment, especially in summer and winter (Figure 3c). Differences in microbial biomass P were not significant between 188P and 376P treatments during the study period. Overall averages of microbial biomass P throughout the study period were 50.5, 50.6, and 39.3 mg kg⁻¹ for 376P, 188P, and the control, respectively (Table 1). Significant seasonal variations in microbial biomass P were observed under 188P and 376P, whereas the control treatment showed minor but not significant seasonal variations (Figure 3c). In the 376P and 188P treatments, maximum concentrations of microbial biomass P were recorded in summer and winter

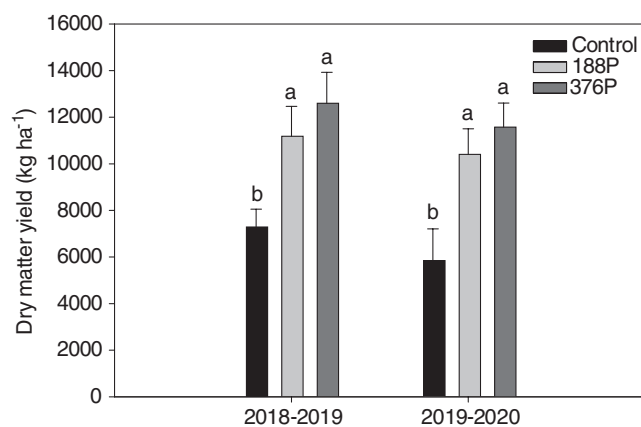


FIGURE 2 Dry matter for the growing seasons 2018–2019 and 2019–2020 in the control, 188P (188 kg ha⁻¹ year⁻¹ of SSP) and 376P (376 kg ha⁻¹ year⁻¹ of SSP) treatments at the Winchmore fertilizer trial. Bars represent the standard errors of the mean for each treatment ($n = 4$). Different lowercase letters indicate significant differences ($p < .05$) between P treatments for a given growing season

(January and July), while minimum concentrations were noted in spring and autumn (October and March) across the study period (Figure 3c).

On average, acid phosphatase activity was twice the alkaline phosphatase activity in the present study (Table 1). The data also showed that the control treatment exhibited significantly higher acid phosphatase activity, whereas P fertilization (188P and 376P) significantly increased alkaline phosphatase activity. Over the study period, acid phosphatase activity was on average 14% higher in the control compared with P fertilized treatments (188P and 376P) (Table 1, Figure 4a). In contrast, alkaline phosphatase activity was on average 14% and 22% higher under 188P and 376P, respectively, compared with the control treatment (Table 1, Figure 4b). Under P fertilized treatments (188P and 376P), acid and alkaline phosphatase activities were not significantly different (Figure 4a,b). Regardless of P treatment, acid and alkaline phosphatase activities exhibited similar seasonal patterns with higher activity in summer and lower activity in winter (Figure 4a,b).

3.5 | Relationship between Olsen P, microbial biomass P, phosphatase activities, and environmental conditions

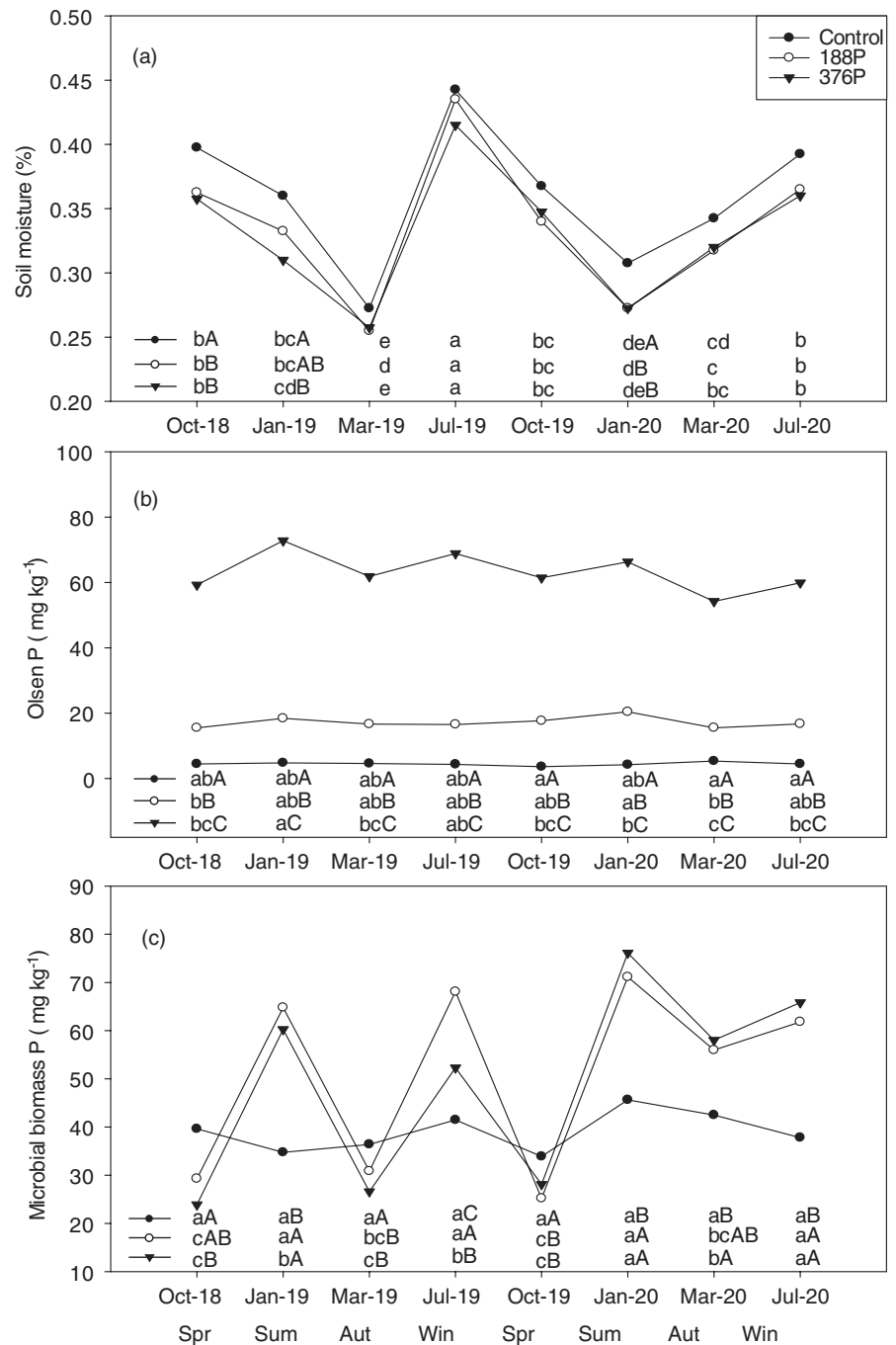
On the basis that Olsen P, microbial biomass P, acid and alkaline phosphatase activity, soil moisture, and temperature were correlated with one another (Table 3), a PCA was carried out and revealed that the data were divided into two principal components (Figure 5). The first component explained 40% of the data variability and was mainly composed by temperature (loading = 0.861), soil moisture (loading = -0.743), alkaline phosphatase activity (loading = 0.770), and acid phosphatase activity (loading = 0.598). While the second component explained another 25% of the data variability and included Olsen P (loading = 0.824) and microbial biomass P (loading = 0.546). Correlation analysis further

	Control		188P		376P	
	July 19	July 20	July 19	July 20	July 19	July 20
Soil pH	5.9aB	6.17aA	5.69bB	6.06bA	5.70bB	6.0bA
Total C	4.14 ns	4.08 ns	4.21 ns	4.15 ns	4.11 ns	4.11 ns
Total N	0.35b	0.36b	0.41a	0.40a	0.40a	0.40a
NH ₄ ⁺ -N	27.92a	26.53a	13.20bB	19.04bA	12.33bB	19.03bA
NO ₃ ⁻ -N	6.11b	4.94b	44.22aA	24.52aB	49.93aA	23.51aB

TABLE 2 Soil pH, total C (g kg⁻¹), total N (g kg⁻¹), NH₄⁺-N (mg kg⁻¹), and NO₃⁻-N (mg kg⁻¹), measured in July 2019 and July 2020 in the control, 188P, and 376P treatments

Note: Soil samples were taken from 0 to 75 mm of the Winchmore fertilizer. Values are means of 4 replicates. Different lowercase letters mean significant differences ($p < .05$) between P treatments for a given sampling date, while different uppercase letters mean significant differences ($p < .05$) between sampling dates for a given P treatment.

FIGURE 3 Temporal changes in soil moisture (a), Olsen P (b), and microbial biomass P (c) in the control, 188P (188 kg ha⁻¹ year⁻¹ of SSP), and 376P (376 kg ha⁻¹ year⁻¹ of SSP) treatments. Soil samples were taken from 0 to 75 mm of the Winchmore fertilizer trial from October 2018 to July 2020. Values are means of four replicates. Lowercase and uppercase letters were used to show significance. Within columns, different lowercase letters indicate significant differences ($p < .05$) between seasons for a given P treatment, while within rows different uppercase letters indicate significant differences ($p < .05$) between P treatments for a given season



showed that microbial biomass P was significantly and positively correlated with alkaline phosphatase activity ($p < .01$), whereas there was a significant negative correlation between Olsen P and acid phosphatase activity in this study ($p < .01$) (Table 3). On the other hand, microbial biomass P and Olsen P were poorly correlated with environmental conditions (soil moisture and soil temperature) in this irrigated grazed pasture system. However, acid and alkaline phosphatase activities were significantly correlated with soil temperature and soil moisture ($p < .01$). High soil temperature enhanced phosphatase activities, while high soil moisture had a

repressive effect on phosphatase activities in this study (Table 3).

4 | DISCUSSION

4.1 | Long-term P fertilizer effects on organic soil P cycling

Phosphorus fertilization in agroecosystems has been recommended to enhance soil P availability and increase primary productivity (Haygarth et al., 2013; Simpson

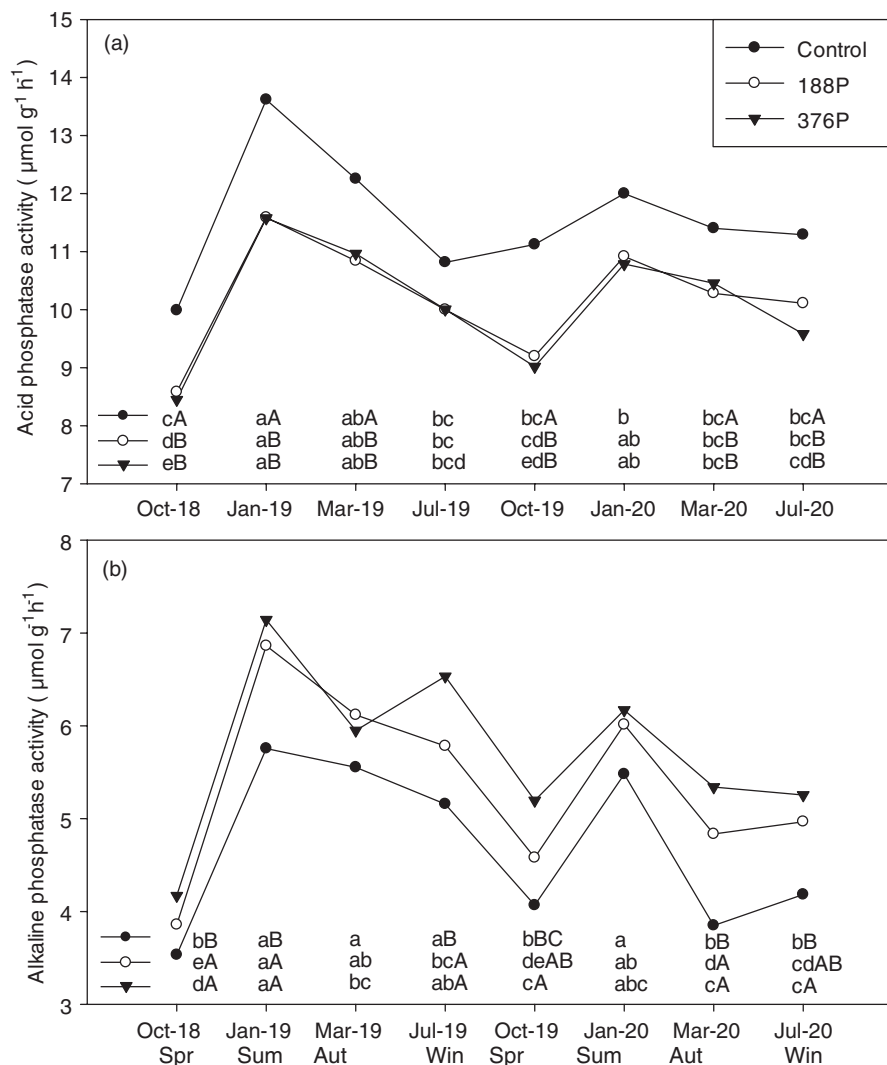


FIGURE 4 Temporal changes in acid (a) and alkaline phosphatase activities (b) in the control, 188P (188 kg ha⁻¹ year⁻¹ of SSP), and 376P (376 kg ha⁻¹ year⁻¹ of SSP) treatments. Soil samples were taken from 0 to 75 mm of the Winchmore fertilizer trial from October 2018 to July 2020. Values are means of 4 replicates. Lowercase and uppercase letters were used to show significance. Within columns, different lowercase letters indicate significant differences (*p* < .05) between seasons for a given P treatment, while within rows different uppercase letters indicate significant differences (*p* < .05) between P treatments for a given season

TABLE 3 Coefficients of correlation analysis (Pearson's and Spearman's) between soil biological and biochemical properties and environmental conditions (*n* = 96)

	Olsen P	MBP ^a	Acid P ^b	Alk P ^c	Soil moisture	Soil temperature
Olsen P	1	0.206*	-0.362**	0.482**	-0.196	0.067
MBP ^a	0.206*	1	0.176	0.389**	-0.017	-0.047
Acid P ^b	-0.362**	0.176	1	0.382**	-0.306**	0.529**
Alk P ^c	0.482**	0.389**	0.382**	1	-0.304**	0.459**
Soil moisture	-0.196	-0.017	-0.306**	-0.304**	1	-0.735**
Soil temperature	0.067	-0.047	0.529**	0.459**	-0.735**	1

*Significant difference at *p* < .05; **significant difference at *p* < .01.

^aMicrobial biomass phosphorus.

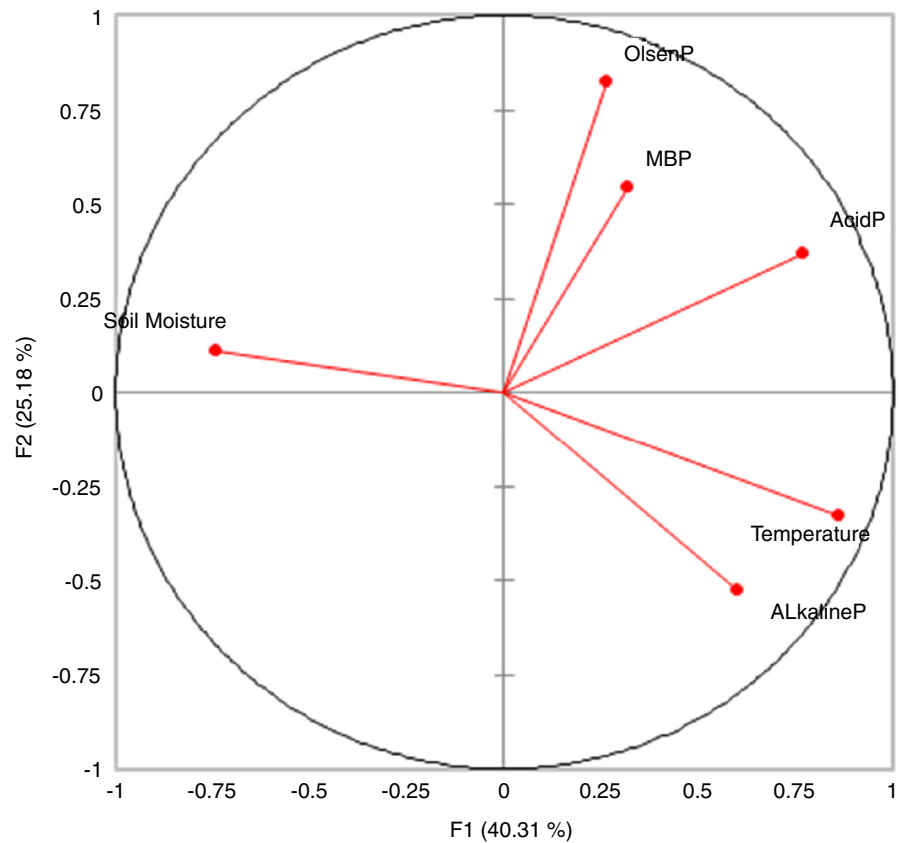
^bAcid phosphatase activity.

^cAlkaline phosphatase activity.

et al., 2011). As expected, long-term P inputs significantly increased Olsen P concentrations under 376P and 188P compared with the control. The average concentrations of Olsen P over the entire study period were 63.1, 17.2, and 4.5 mg kg⁻¹ for 376P, 188P, and the control, respectively.

Although this increase in P availability concurred with a significant increase (1.75-fold) in dry matter compared with the control, the dry matter was not statistically different between 188P and 376P treatments. This suggested a greater risk of inorganic P accumulation and P transfer

FIGURE 5 Loading plot from the results of principal component analysis (PCA) showing the relationships between soil properties and environmental conditions at the Winchmore fertilizer trial. The two principal components explained 65% of the data variability. Arrows indicate the factor loading of each variable with the principal component. AcidP, acid phosphatase activity; AlkalineP, alkaline phosphatase activity; MBP, microbial biomass P



in drainage under the 376P treatment, especially under irrigation. Previous studies combining data on pasture production and bioavailable P have pointed out that Olsen P under the 376P treatment was considerably above the agronomic optimum (Edmeades et al., 2006; Nguyen & Goh, 1992b). Furthermore, work involving sequential P fractionation revealed a higher accumulation of inorganic P forms to a depth of 500 mm under 376P treatment compared with the control and 188P treatments (Tian et al., 2017).

Most of the soil chemical properties investigated in this study were significantly affected by the long-term P applications in this grazed pasture system, except total C. Lower soil pH was observed under 188P and 376P treatments, which could be ascribed to soil acidification because of the application of superphosphate fertilizer (Horsnell, 1985). Although our data showed that pastures were grass-dominant over the whole study period because of a lack of grazing over the March to September 2018 period (McDowell et al., 2021), historical data over the last 13 years (2005–2017) indicated that the content of white clover was 1.8-fold higher under P fertilized treatments compared with the control (McDowell et al., 2021). Legumes are known to fix atmospheric N and uptake more cations than anions, which may have also contributed to lowering the soil pH under the P fertilized treatments (de Klein et al., 1997; Tang & Rengel, 2003).

Total C was unchanged after 65 years of contrasted P inputs to this grazed pasture, although dry matter and thus inputs to the system, in the form of plant detritus and root turnover, were much higher under 188P and 376P treatments compared with the control. Past research in the same site has revealed a faster soil organic matter turnover under the P fertilized treatments yielding, in the long run, a similar total C content across P treatments (Condrón et al., 2012). This accelerated organic matter mineralization along with greater N inputs (plant and animal returns), probably resulted in the higher concentrations of total N and NO_3^- -N observed in our study under 188P and 376P treatments (Curtin et al., 2019; Tate et al., 1991). Conversely, slower soil organic matter mineralization (Scott et al., 2012; Wakelin et al., 2017) and nitrification rates (Tate et al., 1991) together with N immobilization (Curtin et al., 2019) may explain the lower concentrations of NO_3^- -N and the higher concentrations of NH_4^+ -N found under the control treatment. However, without further data, we cannot confirm this conclusion.

In the present study, although microbial biomass P was increased by the long-term P applications (average: 50 mg kg^{-1}) compared with the control (average: 39 mg kg^{-1}), microbial biomass P under 188P and 376P was similar, which contrasted our hypothesis. Both total N and the concentrations of NO_3^- -N were statistically similar under P fertilized treatments in our study.

Additionally, Wakelin et al. (2017) found that available C was not significantly different under 188P and 376P treatments. Therefore, similar availability of C and N could have generated similar P immobilization by the microbial biomass despite P availability being 3.6-fold higher under 376P compared with 188P. Besides P, soil microbial biomass is limited by the availability of C and N (Cleveland & Liptzin, 2007; Heuck et al., 2015; Liu et al., 2012). This is driven by the fact that C:N:P stoichiometry plays a key role in regulating microbial biomass transformations and dynamics in soil systems (Griffiths et al., 2012; Maaroufi & De Long, 2020). Massey et al. (2016) found that long-term P applications under a grassland system in Ireland had no impact on microbial biomass P. They attributed this result to similar C availability across P treatments caused by the continual biomass removal. Similarly, under a cut and carry system, microbial biomass P was irresponsive to a range of P applications ($0\text{--}30\text{ kg P ha}^{-1}\text{ year}^{-1}$) in a grazed pasture, which was ascribed to lower availabilities of N and C (Randall et al., 2019).

Our results showed that acid and alkaline phosphatase activities exhibited opposite trends in response to long-term P inputs. While acid phosphatase activity was inhibited by P applications, alkaline phosphatase enzymes showed higher activity under P fertilized treatments compared with the control. These findings concur with data from other studies showing that P applications decreased acid phosphatase activity (Lemanowicz, 2011; Randall et al., 2019). However, a closer look at the response of alkaline phosphatase activity to P applications in the literature reveals contradictory results. While P applications decreased alkaline phosphatase enzymes in intensive cropping systems (Liu et al., 2020; Saha et al., 2008), organically managed agroecosystems showed higher alkaline phosphatase activity (Liu et al., 2010; Sakurai et al., 2008). This suggests that alkaline phosphatase activity is impacted by soil organic matter inputs and C turnover (Allison & Vitousek, 2005; Luo et al., 2019).

In this grazed pasture system, plant litter, root turnover, and dung are expected to be higher under P fertilized treatments compared with the control owing to 1.75-fold higher dry matter under these treatments. Plant and root cells contain a large amount of organic P in the form of phospholipids, nucleic acids, and phospho-esters (Alamgir & Marschner, 2013; Noack et al., 2012), while organic P accounts for up to 15% of total P in animal dung (Arnuti et al., 2020; McDowell & Stewart, 2005). Higher inputs of plant residues and excreta in the P fertilized treatments are expected to result in higher organic P returns compared with control (Simpson et al., 2011; Stutter et al., 2015). Additionally, soil P bioavailability was high under P fertilized treatments, which may have induced C-limitation for soil microbes (Griffiths et al., 2012).

Therefore, to satisfy their C demand, soil microorganisms needed to dephosphorylate organic P, thereby exhibiting higher levels of alkaline phosphatase activity (Spohn et al., 2015; Spohn & Kuzyakov, 2013a). Correlation analysis results showed a significant and positive correlation between microbial biomass P and alkaline phosphatase activity ($p < .01$), which is consistent with the findings of Sakurai et al. (2008). Furthermore, in the same study site, Wakelin et al. (2017) highlighted that C cycling was faster under P fertilized treatments compared with the control because soil microbes are driven by C demand rather than P (Heuck et al., 2015; Spohn & Kuzyakov, 2013b).

It has been suggested that acid phosphatase activity is mostly derived from plant roots (Dick et al., 1983; McLachlan, 1980; Yadav & Tarafdar, 2001) and may be more sensitive to P inputs (Adams & Pate, 1992; Tadano & Sakai, 1991). Under adequate and high P conditions, plants do not invest in the synthesis of acid phosphatase enzymes to mobilize organic P (Speir & Cowling, 1991). This explains the significantly lower acid phosphatase activity found under 188P and 376P compared with the control. This is supported by the negative and significant correlation found between acid phosphatase activity and Olsen P, which is consistent with Colvan et al. (2001).

The activity of acid and alkaline phosphatase enzymes can be affected by soil pH (Dick et al., 2000). Acid phosphatase enzyme activity was on average 2-fold higher compared with alkaline phosphatase enzyme activity, which is consistent with previous studies under acidic soils (Eivazi & Tabatabai, 1977; Skujins et al., 1962). Soil pH (0–75 mm) was significantly lower under the P fertilized treatments compared with the control suggesting that acid phosphatase activity would be higher under the P fertilized treatments. However, our results showed that alkaline phosphatase activity was higher in P fertilized treatments, whereas acid phosphatase activity was higher in the control. Hence, differences in acid and alkaline phosphatase activities in this grazed pasture were not attributed to changes in soil pH in response to long-term P inputs. Taking together, our results support, from a long-term field trial, the difference in origin and nutrient demand between acid and alkaline phosphatase enzymes, where acid phosphatases are derived from plant roots and repressed by P availability, whereas alkaline phosphatase enzymes are released by soil microorganisms and depend on C availability.

4.2 | Effects of seasonal conditions on organic soil P cycling

The present data showed that the control treatment exhibited relatively stable Olsen P and microbial biomass P

concentrations throughout the study period, whereas significant seasonal variations in these soil properties were observed under P fertilized treatments. Higher P application rates and total P under P fertilized treatments, especially 376P, can explain the higher variations of Olsen P concentrations during the study period. Higher plant P demand, plant returns, and microbial and micro-faunal activities under P fertilized treatments could have also contributed to the seasonal variations observed (Nguyen & Goh, 1992b; Smith et al., 2012; Tian et al., 2019). Our results revealed that dry matter and soil fertility were higher under P fertilized treatments compared with the control. Furthermore, previous investigations under the same study site reported that microbial activity was higher under P fertilized treatments compared with the control (Wakelin et al., 2017), while the population and biomass of earthworms were significantly greater under 376P treatment compared with the other treatments (Fraser et al., 1994).

Microbial biomass P in 188P and 376P treatments followed similar seasonal trends being higher in summer and winter and lower in spring and autumn. Higher microbial biomass P in summer could be attributed to warmer conditions and adequate soil moisture stimulating plant growth and enhancing inputs of root exudates into the soil (Chen et al., 2003; Perrott et al., 1992; Shi et al., 2020). Plant rhizodeposits would have been higher under P fertilized treatments as a result of higher plant biomass compared with the control. These conditions might have then promoted higher microbial P immobilization under P fertilized treatments in comparison with the control. Microbial biomass P was also higher in winter in our study. Under pasture systems, an accumulation of microbial and organic P has been described in winter (Chen et al., 2003; Perrott et al., 1992; Scott & Condon, 2003; Tate et al., 1991). The storage of labile organic P and P in the microbial biomass has been suggested to be driven by low temperatures leading to lower microbial activity and plant P demand as well as potential changes in the microbial community composition (Perrott et al., 1990, 1992; Sarathchandra et al., 1989). In a pot experiment with no water limitation, Sarathchandra et al. (1989) simulated winter conditions (lower temperature) in soil cores from a highly productive pastoral system and investigated biological and biochemical soil properties. They found that C, N, and P accumulated in the microbial biomass in winter and related that to the shift in microbial population towards more fungi able to degrade root residues accumulated in winter. In a seasonal study, Chen et al. (2003) observed an increased microbial biomass P during winter in a grassland soil, which was suggested to be derived from grass root litter returns. Provided that dry matter under P fertilized treatments

was on average 1.75-fold higher than the control, higher root residues are expected under these treatments. Higher root residues may have increased the population of fungi, thereby promoting higher microbial P immobilization under P fertilized treatments compared with the control. Nevertheless, an assessment of soil microbial diversity along with other soil chemical properties (total and available N and C, microbial biomass N and C) across seasons and P treatments is required to confirm this hypothesis. Decreases in microbial biomass P noticed in spring and autumn could be explained by the adequate environmental conditions and higher pasture P demand, thereby promoting microbial P release to meet plant uptake (Perrott et al., 1992). Plant production in our study site was maximum in summer but also higher in spring and autumn, especially under P fertilized treatments. Although the season had a significant effect on microbial biomass P, correlation analysis results revealed that microbial biomass P was weakly correlated with soil temperature and soil moisture. This suggested that microbial P dynamics in this grazed pasture system were not only affected by environmental factors but by other factors, including plant P demand, plant residue returns, microbial activity, and microbial community composition, all of which have been affected by the long-term P fertilization.

In contrast to microbial biomass P, acid and alkaline phosphatase enzyme activities followed similar seasonal trends being higher in summer and lower in winter regardless of P treatment. In their global meta-analysis, Margalef et al. (2017) pointed out that soil moisture and temperature were among the main factors driving phosphatase activity across different biomes. Ge et al. (2017) showed that increasing temperature enhanced the activity of phosphatase enzymes in the rhizosphere of rice, while Wu et al. (2015) found that warming accelerated C turnover, shifted microbial community composition, and increased phosphatase activity in a meadow. Recent data from forest ecosystems and grasslands have shown that drought decreased acid phosphatase activity, whereas high rainfall and prolonged waterlogging decreased the activity of alkaline phosphatase enzymes because of anaerobic conditions (Sun et al., 2020; Zhang et al., 2020; Zuccarini et al., 2020). In the current study, higher soil temperature during the spring–summer period concurred with a maximum activity of acid and alkaline phosphatase enzymes as well as plant biomass, while minimum acid and alkaline phosphatase activities and plant growth were found in winter along with the highest levels of soil moisture. Furthermore, acid and alkaline phosphatase enzyme activities were significantly positively correlated with temperature but significantly negatively correlated with soil moisture. Our findings

agree with previous investigations in temperate pastoral and silvopastoral systems showing an enhanced organic P mineralization in the spring–summer period to meet increased plant P demand but a build-up of organic P in winter because of lower microbial activity and plant growth (Chen et al., 2003; Scott & Condron, 2003; Speir & Cowling, 1991; Tate et al., 1991).

Under controlled environments, P fertilization has been found to have a more prominent effect on acid and alkaline phosphatase enzyme activities than soil moisture or temperature (Randall et al., 2020; Sun et al., 2018). However, field studies conducted in intensively managed agroecosystems and grasslands showed that seasonal changes in soil moisture and temperature had a more significant impact on alkaline phosphatase enzyme activity compared with P fertilization (Shi et al., 2013, 2020). Several authors have pointed out the possible combined effects of soil moisture and temperature on phosphatase enzyme activity (Arenberg & Arai, 2019; Criquet et al., 2004; Margalef et al., 2021), which are more likely to happen under field conditions than in controlled environments. In Mediterranean shrubland, warming increased organic P cycling through phosphatase enzymes, but only when water was not a limiting factor (Zuccarini et al., 2020). The study carried out by Zuccarini et al. (2020) stressed that optimal conditions of both soil moisture and temperature were critical for organic P mineralization. In the irrigated pasture system investigated in the current study, it is suggested that adequate soil moisture (irrigation) and high soil temperature in summer enhanced soil microbial activity and promoted plant growth, hence higher acid and alkaline phosphatase activities were observed across all P treatments (Chen et al., 2008; Zuccarini et al., 2020). In contrast, excessive water and cold soil temperatures during winter reduced plant growth and inhibited the activity of phosphatase enzymes (Harrison, 1979; Sun et al., 2020). Collectively, the findings of this study indicate that environmental conditions (soil moisture and temperature) controlled seasonal changes in plant (acid) and microbial (alkaline) phosphatase activities and suggest that under adequate soil moisture conditions, global warming is expected to accelerate organic P mineralization regardless of soil P status (Zuccarini et al., 2020). Therefore, in the context of climate change, with increasing temperature and more frequent droughts and flooding events, both soil moisture and temperature need to be integrated into models predicting soil organic P mineralization. Nevertheless, more field studies on soil moisture and temperature need to be carried out under different biomes and soil P fertility to disentangle the combined effects of these climatic variables on organic soil P cycling through phosphatase enzymes (Margalef et al., 2021).

5 | CONCLUSIONS

Phosphorus applications for more than 65 years to a grazed pasture system increased plant dry matter and P and N availability, but with no effect on total C. This indicates the positive effect of P fertilization on soil fertility and C turnover. Increasing Olsen P concentrations through P fertilization (188P and 376P) did not concur with an increase in microbial biomass P, thereby emphasizing the critical role of C:N:P stoichiometry in controlling microbial biomass transformations in soil systems. Long-term P fertilization decreased the activity of acid phosphatases but increased the activity of alkaline phosphatases. This supports, from a field perspective, the difference in origin and nutrient demand between acid and alkaline phosphatase enzymes. Our findings suggest that acid phosphatases are derived from plant roots and repressed by P availability, whereas alkaline phosphatase enzymes are released by soil microorganisms and are dependent on C availability. Soil moisture and temperature controlled seasonal changes in the activity of both plant and microbes derived phosphatase enzymes. This result stresses the need to integrate both climatic variables in models dedicated to predicting organic P mineralization, especially under future climate change scenarios.

ACKNOWLEDGEMENTS

We express our acknowledgements to AgResearch Ltd. for providing some historical data and arranging for sampling on the trial. We would like to thank Dr Alister Metherell from Ravensdown Limited for reviewing a previous draft of the manuscript. The authors also express their gratitude to Lincoln Lloyd and Geoff Farrar for facilitating access to the trial as well as the Fertiliser Association of New Zealand for funding this trial. Special thanks to all technicians and staff who have been working and maintaining the Winchmore fertilizer trial over the years. This research was supported by Mohammed VI Polytechnic University of Benguerir and the Office Cherifien des Phosphates (OCP). Richard W. McDowell was supported by the Our Land and Water National Science Challenge (contract C10X1507 from the Ministry of Business, Innovation and Employment). Open access publishing facilitated by Lincoln University, as part of the Wiley - Lincoln University agreement via the Council of Australian University Librarians.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

- Adams, M. A., & Pate, J. S. (1992). Availability of organic and inorganic forms of phosphorus to lupins (*Lupinus* spp.). *Plant and Soil*, 145, 107–113. <https://doi.org/10.1007/BF00009546>
- Alamgir, M., & Marschner, P. (2013). Changes in phosphorus pools in three soils upon addition of legume residues differing in carbon/phosphorus ratio. *Soil Research*, 51, 484. <https://doi.org/10.1071/SR12378>
- Allison, S. D., & Vitousek, P. M. (2005). Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biology and Biochemistry*, 37, 937–944. <https://doi.org/10.1016/j.soilbio.2004.09.014>
- Arenberg, M. R., & Arai, Y. (2019). Chapter three – Uncertainties in soil physicochemical factors controlling phosphorus mineralization and immobilization processes. In D. L. Sparks (Ed.), *Advances in agronomy* (pp. 153–200). Academic Press.
- Arnuti, F., Denardin, L. G., Nunes, P. A., Alves, L. A., Cecagno, D., de Assis, J., Schaidhauer, W. D., Anghinoni, I., Chabbi, A., & PCF, C. (2020). Sheep dung composition and phosphorus and potassium release affected by grazing intensity and pasture development stage in an integrated crop-livestock system. *Agronomy*, 10, 1162. <https://doi.org/10.3390/agronomy10081162>
- Blakemore L. C., Searle P. L., & Daly B. (1987). *Methods for chemical analysis of soils*. New Zealand soil bureau scientific report 80. NZ soil bureau, Lower Hutt.
- Boitt, G., Simpson, Z. P., Tian, J., Black, A., Wakelin, S. A., & Condon, L. M. (2018). Plant biomass management impacts on short-term soil phosphorus dynamics in a temperate grassland. *Biology and Fertility of Soils*, 54, 397–409. <https://doi.org/10.1007/s00374-018-1269-6>
- Brookes, P. C., Powlson, D. S., & Jenkinson, D. S. (1982). Measurement of microbial biomass phosphorus in soil. *Soil Biology and Biochemistry*, 14, 319–329. [https://doi.org/10.1016/0038-0717\(82\)90001-3](https://doi.org/10.1016/0038-0717(82)90001-3)
- Chen, C. R., Condon, L. M., Davis, M. R., & Sherlock, R. R. (2003). Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. *Forest Ecology and Management*, 177, 539–557. [https://doi.org/10.1016/S0378-1127\(02\)00450-4](https://doi.org/10.1016/S0378-1127(02)00450-4)
- Chen, C. R., Condon, L. M., & Xu, Z. H. (2008). Impacts of grassland afforestation with coniferous trees on soil phosphorus dynamics and associated microbial processes: A review. *Forest Ecology and Management*, 255, 396–409. <https://doi.org/10.1016/j.foreco.2007.10.040>
- Chen, X., Daniell, T. J., Neilson, R., O'Flaherty, V., & Griffiths, B. S. (2014). Microbial and microfaunal communities in phosphorus limited, grazed grassland change composition but maintain homeostatic nutrient stoichiometry. *Soil Biology and Biochemistry*, 75, 94–101. <https://doi.org/10.1016/j.soilbio.2014.03.024>
- Cleveland, C. C., & Liptzin, D. (2007). C:N:P stoichiometry in soil: Is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry*, 85, 235–252.
- Colvan, S., Syers, J., & O'Donnell, A. (2001). Effect of long-term fertiliser use on acid and alkaline phosphomonoesterase and phosphodiesterase activities in managed grassland. *Biology and Fertility of Soils*, 34, 258–263. <https://doi.org/10.1007/s003740100411>
- Condon, L. M. (2003). Phosphorus—Surplus and deficiency. In P. Schjønning, S. Elmholt, & B. T. Christensen (Eds.), *Managing soil quality—Challenges in modern agriculture* (pp. 69–84). CABI.
- Condon, L. M., Black, A., & Wakelin, S. A. (2012). Effects of long-term fertiliser inputs on the quantities of organic carbon in a soil profile under irrigated grazed pasture. *New Zealand Journal of Agricultural Research*, 55, 161–164. <https://doi.org/10.1080/00288233.2012.662898>
- Criquet, S., Ferre, E., Farnet, A. M., & Le Petit, J. (2004). Annual dynamics of phosphatase activities in an evergreen oak litter: Influence of biotic and abiotic factors. *Soil Biology and Biochemistry*, 36, 1111–1118. <https://doi.org/10.1016/j.soilbio.2004.02.021>
- Curtin, D., Beare, M. H., Qiu, W., & Tregurtha, C. S. (2019). Nitrogen cycling in soil under grass-clover pasture: Influence of long-term inputs of superphosphate on N mineralisation. *Soil Biology and Biochemistry*, 130, 132–140. <https://doi.org/10.1016/j.soilbio.2018.12.003>
- Dalal, R. C. (1977). Soil organic phosphorus. In N. C. Brady (Ed.), *Advances in agronomy* (pp. 83–117). Academic Press.
- de Klein, C. A. M., Monaghan, R. M., & Sinclair, A. G. (1997). Soil acidification: A provisional model for New Zealand pastoral systems. *New Zealand Journal of Agricultural Research*, 40, 541–557. <https://doi.org/10.1080/00288233.1997.9513277>
- Dick, W. A., Cheng, L., & Wang, P. (2000). Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biology and Biochemistry*, 32, 1915–1919. [https://doi.org/10.1016/S0038-0717\(00\)00166-8](https://doi.org/10.1016/S0038-0717(00)00166-8)
- Dick, W. A., Juma, N. G., & Tabatabai, M. A. (1983). Effects of soils on acid phosphatase and inorganic pyrophosphatase of corn roots. *Soil Science*, 136, 19–25.
- Edmeades, D. C., Metherell, A. K., Waller, J. E., Roberts, A. H. C., & Morton, J. D. (2006). Defining the relationships between pasture production and soil P and the development of a dynamic P model for New Zealand pastures: A review of recent developments. *New Zealand Journal of Agricultural Research*, 49, 207–222. <https://doi.org/10.1080/00288233.2006.9513711>
- Eivazi, F., & Tabatabai, M. A. (1977). Phosphatases in soils. *Soil Biology and Biochemistry*, 9, 167–172. [https://doi.org/10.1016/0038-0717\(77\)90070-0](https://doi.org/10.1016/0038-0717(77)90070-0)
- Fraser, P. M., Haynes, R. J., & Williams, P. H. (1994). Effects of pasture improvement and intensive cultivation on microbial biomass, enzyme activities, and composition and size of earthworm populations. *Biology and Fertility of Soils*, 17, 185–190. <https://doi.org/10.1007/BF00336320>
- Frossard, E., Condon, L. M., Oberson, A., Sinaj, S., & Fardeau, J. C. (2000). Processes governing phosphorus availability in temperate soils. *Journal of Environmental Quality*, 29, 15–23. <https://doi.org/10.2134/jeq2000.00472425002900010003x>
- Ge, T., Wei, X., Razavi, B. S., Zhu, Z., Hu, Y., Kuzyakov, Y., Jones, D. L., & Wu, J. (2017). Stability and dynamics of enzyme activity patterns in the rice rhizosphere: Effects of plant growth and temperature. *Soil Biology and Biochemistry*, 113, 108–115. <https://doi.org/10.1016/j.soilbio.2017.06.005>
- Griffiths, B. S., Spilles, A., & Bonkowski, M. (2012). C:N:P stoichiometry and nutrient limitation of the soil microbial biomass in a grazed grassland site under experimental P limitation or excess. *Ecological Processes*, 1, 6. <https://doi.org/10.1186/2192-1709-1-6>

- Harrison, A. F. (1979). Variation of four phosphorus properties in woodland soils. *Soil Biology and Biochemistry*, *11*, 393–403. [https://doi.org/10.1016/0038-0717\(79\)90053-1](https://doi.org/10.1016/0038-0717(79)90053-1)
- Haygarth, P. M., Bardgett, R. D., & Condon, L. M. (2013). Nitrogen and phosphorus cycles and their management. In P. J. Gregory & S. Nortcliff (Eds.), *Soil conditions and plant growth* (pp. 132–159). Blackwell Publishing Ltd.
- He, Z. L., Wu, J., O'Donnell, A. G., & Syers, J. K. (1997). Seasonal responses in microbial biomass carbon, phosphorus and Sulphur in soils under pasture. *Biology and Fertility of Soils*, *24*, 421–428. <https://doi.org/10.1007/s003740050267>
- Heuck, C., Weig, A., & Spohn, M. (2015). Soil microbial biomass C:N:P stoichiometry and microbial use of organic phosphorus. *Soil Biology and Biochemistry*, *85*, 119–129. <https://doi.org/10.1016/j.soilbio.2015.02.029>
- Horsnell, L. (1985). The growth of improved pastures on acid soils. 1. The effect of superphosphate and lime on soil pH and on the establishment and growth of phalaris and lucerne. *Australian Journal of Experimental Agriculture*, *25*(149), 149. <https://doi.org/10.1071/EA9850149>
- Hynd, P. (2019). *Animal nutrition: From theory to practice*. Csiro Publishing.
- Ikoyi, I., Fowler, A., & Schmalenberger, A. (2018). One-time phosphate fertilizer application to grassland columns modifies the soil microbiota and limits its role in ecosystem services. *Science of the Total Environment*, *630*, 849–858. <https://doi.org/10.1016/j.scitotenv.2018.02.263>
- Katsalirou, E., Deng, S., Gerakis, A., & Nofziger, D. L. (2016). Long-term management effects on soil P, microbial biomass P, and phosphatase activities in prairie soils. *European Journal of Soil Biology*, *76*, 61–69. <https://doi.org/10.1016/j.ejsobi.2016.07.001>
- Lemanowicz, J. (2011). Phosphatases activity and plant available phosphorus in soil under winter wheat (*Triticum aestivum* L.) fertilized minerally. *Polish Journal of Agronomy*, *4*, 12–15.
- Liu, E., Yan, C., Mei, X., He, W., Bing, S. H., Ding, L., Liu, Q., Liu, S., & Fan, T. (2010). Long-term effect of chemical fertilizer, straw, and manure on soil chemical and biological properties in Northwest China. *Geoderma*, *158*, 173–180. <https://doi.org/10.1016/j.geoderma.2010.04.029>
- Liu, J., Ma, Q., Hui, X., Ran, J., Ma, Q., Wang, X., & Wang, Z. (2020). Long-term high-P fertilizer input decreased the total bacterial diversity but not *phoD*-harboring bacteria in wheat rhizosphere soil with available-P deficiency. *Soil Biology and Biochemistry*, *149*, 107918. <https://doi.org/10.1016/j.soilbio.2020.107918>
- Liu, L., Gundersen, P., Zhang, T., & Mo, J. (2012). Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biology and Biochemistry*, *44*, 31–38. <https://doi.org/10.1016/j.soilbio.2011.08.017>
- Luo, G., Sun, B., Li, L., Li, M., Liu, M., Zhu, Y., Guo, S., Ling, N., & Shen, Q. (2019). Understanding how long-term organic amendments increase soil phosphatase activities: Insight into *phoD*- and *phoC*-harboring functional microbial populations. *Soil Biology and Biochemistry*, *139*, 107632. <https://doi.org/10.1016/j.soilbio.2019.107632>
- Lynch, P. B. (1966). *Conduct of field experiments*. New Zealand Department of Agriculture.
- Maaroufi, N. I., & De Long, J. R. (2020). Global change impacts on forest soils: Linkage between soil biota and carbon-nitrogen-phosphorus stoichiometry. *Frontiers in Forests and Global Change*, *3*, 16. <https://doi.org/10.3389/ffgc.2020.00016>
- MacDonald, G. K., Bennett, E. M., & Taranu, Z. E. (2012). The influence of time, soil characteristics, and land-use history on soil phosphorus legacies: A global meta-analysis. *Global Change Biology*, *18*, 1904–1917. <https://doi.org/10.1111/j.1365-2486.2012.02653.x>
- Margalef, O., Sardans, J., Fernández-Martínez, M., Molowny-Horas, R., Janssens, I. A., Ciais, P., Goll, D., Richter, A., Obersteiner, M., Asensio, D., & Peñuelas, J. (2017). Global patterns of phosphatase activity in natural soils. *Scientific Reports*, *7*, 1–13. <https://doi.org/10.1038/s41598-017-01418-8>
- Margalef, O., Sardans, J., Maspons, J., Molowny-Horas, R., Fernández-Martínez, M., Janssens, I. A., Richter, A., Ciais, P., Obersteiner, M., & Peñuelas, J. (2021). The effect of global change on soil phosphatase activity. *Global Change Biology*, *27*, 5989–6003. <https://doi.org/10.1111/gcb.15832>
- Margenot, A. J., Nakayama, Y., & Parikh, S. J. (2018). Methodological recommendations for optimizing assays of enzyme activities in soil samples. *Soil Biology and Biochemistry*, *125*, 350–360. <https://doi.org/10.1016/j.soilbio.2017.11.006>
- Marschner, P., Crowley, D., & Rengel, Z. (2011). Rhizosphere interactions between microorganisms and plants govern iron and phosphorus acquisition along the root axis – Model and research methods. *Soil Biology and Biochemistry*, *43*, 883–894. <https://doi.org/10.1016/j.soilbio.2011.01.005>
- Massey, P. A., Creamer, R. E., Whelan, M. J., & Ritz, K. (2016). Insensitivity of soil biological communities to phosphorus fertilization in intensively managed grassland systems. *Grass and Forage Science*, *71*, 139–152. <https://doi.org/10.1111/gfs.12163>
- McDowell, R., Moss, R. A., Gray, C. W., Smith, L. C., & Sneath, G. (2021). Seventy years of data from the world's longest grazed and irrigated pasture trials. *Scientific Data*, *8*, 53. <https://doi.org/10.1038/s41597-021-00841-x>
- McDowell, R. W., & Condon, L. M. (2012). Phosphorus and the Winchmore trials: Review and lessons learnt. *New Zealand Journal of Agricultural Research*, *55*, 119–132. <https://doi.org/10.1080/00288233.2012.662899>
- McDowell, R. W., Monaghan, R. M., & Carey, P. L. (2003). Potential phosphorus losses in overland flow from pastoral soils receiving long-term applications of either superphosphate or reactive phosphate rock. *New Zealand Journal of Agricultural Research*, *46*, 329–337. <https://doi.org/10.1080/00288233.2003.9513561>
- McDowell, R. W., & Stewart, I. (2005). Phosphorus in fresh and dry dung of grazing dairy cattle, deer, and sheep. *Journal of Environmental Quality*, *34*, 598–607. <https://doi.org/10.2134/jeq2005.0598>
- McLachlan, K. D. (1980). Acid phosphatase activity of intact roots and phosphorus nutrition in plants. 1. Assay conditions and phosphatase activity. *Australian Journal of Agricultural Research*, *31*, 429–440. <https://doi.org/10.1071/ar9800429>
- Morel, C., Tiessen, H., & Stewart, J. W. B. (1996). Correction for P-sorption in the measurement of soil microbial biomass P by CHCl_3 fumigation. *Soil Biology and Biochemistry*, *28*, 1699–1706. [https://doi.org/10.1016/S0038-0717\(96\)00245-3](https://doi.org/10.1016/S0038-0717(96)00245-3)

- Murphy, J., & Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, 27, 31–36. [https://doi.org/10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)
- Nannipieri, P., Giagnoni, L., Landi, L., & Renella, G. (2011). Role of phosphatase enzymes in soil. In E. Bünemann, A. Oberson, & E. Frossard (Eds.), *Phosphorus in action: Biological processes in soil phosphorus cycling* (pp. 215–243). Springer.
- Nguyen, M. L., & Goh, K. M. (1992a). Status and distribution of soil Sulphur fractions, total nitrogen and organic carbon in camp and non-camp soils of grazed pastures supplied with long-term superphosphate. *Biology and Fertility of Soils*, 14, 181–190. <https://doi.org/10.1007/BF00346059>
- Nguyen, M. L., & Goh, K. M. (1992b). Nutrient cycling and losses based on a mass-balance model in grazed pastures receiving long-term superphosphate applications in New Zealand: 1. Phosphorus. *The Journal of Agricultural Science*, 119, 89–109. <https://doi.org/10.1017/S0021859600071586>
- Nguyen, M. L., Rickard, S. D., & McBride, S. D. (1989). Pasture production and changes in phosphorus and Sulphur status in irrigated pastures receiving long-term applications of superphosphate fertiliser. *New Zealand Journal of Agricultural Research*, 32, 245–262. <https://doi.org/10.1080/00288233.1989.10423460>
- Noack, S. R., MJ, M. L., Smernik, R. J., TM, M. B., & Armstrong, R. D. (2012). Crop residue phosphorus: Speciation and potential bio-availability. *Plant and Soil*, 359, 375–385. <https://doi.org/10.1007/s11104-012-1216-5>
- Pavinato, P. S., Cherubin, M. R., Soltangheisi, A., Rocha, G. C., Chadwick, D. R., & Jones, D. L. (2020). Revealing soil legacy phosphorus to promote sustainable agriculture in Brazil. *Scientific Reports*, 10, 15615. <https://doi.org/10.1038/s41598-020-72302-1>
- Perrott, K., Sarathchandra, S., & Waller, J. (1990). Seasonal storage and release of phosphorus and potassium by organic matter and the microbial biomass in a high producing pastoral soil. *Soil Research*, 28, 593. <https://doi.org/10.1071/SR9900593>
- Perrott, K. W., Sarathchandra, S. U., & Dow, B. W. (1992). Seasonal and fertilizer effects on the organic cycle and microbial biomass in a hill country soil under pasture. *Soil Research*, 30, 383–394. <https://doi.org/10.1071/sr9920383>
- Phelps, L. N., & Kaplan, J. O. (2017). Land use for animal production in global change studies: Defining and characterizing a framework. *Global Change Biology*, 23, 4457–4471. <https://doi.org/10.1111/gcb.13732>
- Randall, K., Brennan, F., Clipson, N., Creamer, R., Griffiths, B., Storey, S., & Doyle, E. (2019). Soil bacterial community structure and functional responses across a long-term mineral phosphorus (pi) fertilisation gradient differ in grazed and cut grasslands. *Applied Soil Ecology*, 138, 134–143. <https://doi.org/10.1016/j.apsoil.2019.02.002>
- Randall, K. C., Brennan, F., Clipson, N., Creamer, R. E., Griffiths, B. S., Storey, S., & Doyle, E. (2020). An assessment of climate induced increase in soil water availability for soil bacterial communities exposed to long-term differential phosphorus fertilization. *Frontiers in Microbiology*, 11, 682.
- Richardson, A. E. (1994). Soil microorganisms and phosphorus availability. In C. E. Pankhurst, B. M. Doube, V. V. S. R. Gupta, & P. R. Grace (Eds.), *Soil biota: Management in sustainable farming systems* (pp. 50–62). CSIRO.
- Richardson, A. E. (2001). Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. *Functional Plant Biology*, 28, 897–906.
- Richardson, A. E., Lynch, J. P., Ryan, P. R., Delhaize, E., Smith, F. A., Smith, S. E., Harvey, P. R., Ryan, M. H., Veneklaas, E. J., Lambers, H., Oberson, A., Culvenor, R. A., & Simpson, R. J. (2011). Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil*, 349, 121–156. <https://doi.org/10.1007/s11104-011-0950-4>
- Richardson, A. E., & Simpson, R. J. (2011). Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Plant Physiology*, 156, 989–996. <https://doi.org/10.1104/pp.111.175448>
- Ross, D. J., Speir, T. W., Kettles, H. A., & Mackay, A. D. (1995). Soil microbial biomass, C and N mineralization and enzyme activities in a hill pasture: Influence of season and slow-release P and S fertilizer. *Soil Biology and Biochemistry*, 27, 1431–1443. [https://doi.org/10.1016/0038-0717\(95\)00069-Q](https://doi.org/10.1016/0038-0717(95)00069-Q)
- Saha, S., Prakash, V., Kundu, S., Kumar, N., & Mina, B. L. (2008). Soil enzymatic activity as affected by long term application of farm yard manure and mineral fertilizer under a rain-fed soybean-wheat system in N-W Himalaya. *European Journal of Soil Biology*, 44, 309–315. <https://doi.org/10.1016/j.ejsobi.2008.02.004>
- Sakurai, M., Wasaki, J., Tomizawa, Y., Shinano, T., & Osaki, M. (2008). Analysis of bacterial communities on alkaline phosphatase genes in soil supplied with organic matter. *Soil Science & Plant Nutrition*, 54, 62–71. <https://doi.org/10.1111/j.1747-0765.2007.00210.x>
- Sarathchandra, S. U., Perrott, K. W., & Littler, R. A. (1989). Soil microbial biomass: Influence of simulated temperature changes on size, activity and nutrient-content. *Soil Biology and Biochemistry*, 21, 987–993. [https://doi.org/10.1016/0038-0717\(89\)90034-5](https://doi.org/10.1016/0038-0717(89)90034-5)
- Scott, J. T., & Condron, L. M. (2003). Dynamics and availability of phosphorus in the rhizosphere of a temperate silvopastoral system. *Biology and Fertility of Soils*, 39, 65–73. <https://doi.org/10.1007/s00374-003-0678-2>
- Scott, J. T., Stewart, D. P. C., & Metherell, A. K. (2012). Alteration of pasture root carbon turnover in response to superphosphate and irrigation at Winchmore New Zealand. *New Zealand Journal of Agricultural Research*, 55, 147–159. <https://doi.org/10.1080/00288233.2012.662896>
- Sharpley, A. N., McDowell, R. W., & Kleinman, P. J. A. (2001). Phosphorus loss from land to water: Integrating agricultural and environmental management. *Plant and Soil*, 237, 287–307. <https://doi.org/10.1023/A:1013335814593>
- Shi, Y., Lalande, R., Hamel, C., Ziadi, N., Gagnon, B., & Hu, Z. (2013). Seasonal variation of microbial biomass, activity, and community structure in soil under different tillage and phosphorus management practices. *Biology and Fertility of Soils*, 49, 803–818. <https://doi.org/10.1007/s00374-013-0773-y>
- Shi, Y., Ziadi, N., Hamel, C., Bélanger, G., Abdi, D., Lajeunesse, J., Lafond, J., Lalande, R., & Shang, J. (2020). Soil microbial biomass, activity and community structure as affected by mineral phosphorus fertilization in grasslands. *Applied Soil Ecology*, 146, 103391. <https://doi.org/10.1016/j.apsoil.2019.103391>
- Simpson, R. J., Oberson, A., Culvenor, R. A., Ryan, M. H., Veneklaas, E. J., Lambers, H., Lynch, J. P., Ryan, P. R., Delhaize, E.,

- Smith, F. A., Smith, S. E., Harvey, P. R., & Richardson, A. E. (2011). Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. *Plant and Soil*, 349, 89–120. <https://doi.org/10.1007/s11104-011-0880-1>
- Simpson, R. J., Richardson, A. E., Nichols, S. N., & Crush, J. R. (2014). Pasture plants and soil fertility management to improve the efficiency of phosphorus fertiliser use in temperate grassland systems. *Crop & Pasture Science*, 65, 556–575. <https://doi.org/10.1071/CP13395>
- Skujins, J. J., Braal, L., & McLaren, A. D. (1962). Characterization of phosphatase in a terrestrial soil sterilized with an electron beam. *Enzymologia (Netherlands) Superseded by Molecular and Cellular Biochemistry*, 25, 125–133.
- Smith, L., Moss, R., Morton, J., Metherell, A. K., & Fraser, T. J. (2012). Pasture production from a long-term fertiliser trial under irrigation. *New Zealand Journal of Agricultural Research*, 55, 105–117. <https://doi.org/10.1080/00288233.2012.662897>
- Speir, T. W., & Cowling, J. C. (1991). Phosphatase activities of pasture plants and soils: Relationship with plant productivity and soil P fertility indices. *Biology and Fertility of Soils*, 12, 189–194. <https://doi.org/10.1007/BF00337200>
- Spohn, M., & Kuzyakov, Y. (2013a). Distribution of microbial- and root-derived phosphatase activities in the rhizosphere depending on P availability and C allocation – Coupling soil zymography with ¹⁴C imaging. *Soil Biology and Biochemistry*, 67, 106–113. <https://doi.org/10.1016/j.soilbio.2013.08.015>
- Spohn, M., & Kuzyakov, Y. (2013b). Phosphorus mineralization can be driven by microbial need for carbon. *Soil Biology and Biochemistry*, 61, 69–75. <https://doi.org/10.1016/j.soilbio.2013.02.013>
- Spohn, M., Treichel, N. S., Cormann, M., Schloter, M., & Fischer, D. (2015). Distribution of phosphatase activity and various bacterial phyla in the rhizosphere of *Hordeum vulgare* L. depending on P availability. *Soil Biology and Biochemistry*, 89, 44–51. <https://doi.org/10.1016/j.soilbio.2015.06.018>
- Stutter, M. I., Shand, C. A., George, T. S., Blackwell, M. S. A., Dixon, L., Bol, R., MacKay, R. L., Richardson, A. E., Condon, L. M., & Haygarth, P. M. (2015). Land use and soil factors affecting accumulation of phosphorus species in temperate soils. *Geoderma*, 257–258, 29–39. <https://doi.org/10.1016/j.geoderma.2015.03.020>
- Sun, D., Bi, Q., Li, K., Dai, P., Yu, Y., Zhou, W., Lv, T., Liu, X., Zhu, J., Zhang, Q., Jin, C., Lu, L., & Lin, X. (2018). Significance of temperature and water availability for soil phosphorus transformation and microbial community composition as affected by fertilizer sources. *Biology and Fertility of Soils*, 54, 229–241. <https://doi.org/10.1007/s00374-017-1252-7>
- Sun, F., Song, C., Wang, M., Lai, D. Y. F., Tariq, A., Zeng, F., Zhong, Q., Wang, F., Li, Z., & Peng, C. (2020). Long-term increase in rainfall decreases soil organic phosphorus decomposition in tropical forests. *Soil Biology and Biochemistry*, 151, 108056. <https://doi.org/10.1016/j.soilbio.2020.108056>
- Tabatabai, M. A. (1994). Soil enzymes. In S. H. Mickelson & J. M. Bigham (Eds.), *Methods of soil analysis: Part 2—Microbiological and biochemical properties* (pp. 775–833). Soil Science Society of America.
- Tadano, T., & Sakai, H. (1991). Secretion of acid phosphatase by the roots of several crop species under phosphorus-deficient conditions. *Soil Science & Plant Nutrition*, 37, 129–140. <https://doi.org/10.1080/00380768.1991.10415018>
- Tan, H., Barret, M., Mooij, M. J., Rice, O., Morrissey, J. P., Dobson, A., Griffiths, B., & O’Gara, F. (2013). Long-term phosphorus fertilisation increased the diversity of the total bacterial community and the *phoD* phosphorus mineraliser group in pasture soils. *Biology and Fertility of Soils*, 49, 661–672. <https://doi.org/10.1007/s00374-012-0755-5>
- Tang, C., & Rengel, Z. (2003). Role of plant cation/anion uptake ratio in soil acidification. In Z. Rengel (Ed.), *Handbook of soil acidity* (pp. 57–81). CRC Press.
- Tate, K. R., Speir, T. W., Ross, D. J., Parfitt, R. L., Whale, K. N., & Cowling, J. C. (1991). Temporal variations in some plant and soil P pools in two pasture soils of widely different P fertility status. *Plant and Soil*, 132, 219–232. <https://doi.org/10.1007/BF00010403>
- Tian, J., Boitt, G., Black, A., Wakelin, S., Chen, L., Cai, K., & Condon, L. (2019). Mass balance assessment of phosphorus dynamics in a fertilizer trial with 57 years of superphosphate application under irrigated grazed pasture. *Nutrient Cycling in Agroecosystems*, 114, 33–44. <https://doi.org/10.1007/s10705-019-09992-1>
- Tian, J., Boitt, G., Black, A., Wakelin, S., Condon, L. M., & Chen, L. (2017). Accumulation and distribution of phosphorus in the soil profile under fertilized grazed pasture. *Agriculture, Ecosystems and Environment*, 239, 228–235. <https://doi.org/10.1016/j.agee.2017.01.022>
- Vance, C. P., Uhde-Stone, C., & Allan, D. L. (2003). Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *The New Phytologist*, 157, 423–447. <https://doi.org/10.1046/j.1469-8137.2003.00695.x>
- Wakelin, S. A., Condon, L. M., Gerard, E., Dignam, B. E. A., Black, A., & O’Callaghan, M. (2017). Long-term P fertilisation of pasture soil did not increase soil organic matter stocks but increased microbial biomass and activity. *Biology and Fertility of Soils*, 53, 511–521. <https://doi.org/10.1007/s00374-017-1212-2>
- Watanabe, F. S., & Olsen, S. R. (1965). Test of an ascorbic acid method for determining phosphorus in water and NaHCO₃ extracts from soil. *Soil Science Society of America Journal*, 29, 677–678. <https://doi.org/10.2136/sssaj1965.03615995002900060025x>
- Wei, K., Bao, H., Huang, S., & Chen, L. (2017). Effects of long-term fertilization on available P, P composition and phosphatase activities in soil from the Huang-Huai-Hai plain of China. *Agriculture, Ecosystems and Environment*, 237, 134–142. <https://doi.org/10.1016/j.agee.2016.12.030>
- Wu, J., Xiong, J., Hu, C., Shi, Y., Wang, K., & Zhang, D. (2015). Temperature sensitivity of soil bacterial community along contrasting warming gradient. *Applied Soil Ecology*, 94, 40–48. <https://doi.org/10.1016/j.apsoil.2015.04.018>
- Yadav, R., & Tarafdar, J. (2001). Influence of organic and inorganic phosphorus supply on the maximum secretion of acid phosphatase by plants. *Biology and Fertility of Soils*, 34, 140–143. <https://doi.org/10.1007/s003740100376>
- Zhang, H., Shi, L., Lu, H., Shao, Y., Liu, S., & Fu, S. (2020). Drought promotes soil phosphorus transformation and reduces phosphorus bioavailability in a temperate forest. *Science of the Total Environment*, 732, 139295. <https://doi.org/10.1016/j.scitotenv.2020.139295>

Zuccarini, P., Asensio, D., Ogaya, R., Sardans, J., & Peñuelas, J. (2020). Effects of seasonal and decadal warming on soil enzymatic activity in a P-deficient Mediterranean shrubland. *Global Change Biology*, 26, 3698–3714. <https://doi.org/10.1111/gcb.15077>

SUPPORTING INFORMATION

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How to cite this article: Touhami, D., Condon, L. M., McDowell, R. W., & Moss, R. (2022). Effects of long-term phosphorus fertilizer inputs and seasonal conditions on organic soil phosphorus cycling under grazed pasture. *Soil Use and Management*, 00, 1–17. <https://doi.org/10.1111/sum.12830>