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Effects of artificial vegetation restoration on the fractions and availability of soil phosphorus in the water-level-fluctuating zone of Three Gorges Reservoir, China

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Abstract

Purpose The water-level-fluctuating zone (WLFZ) is the buffer zone of energy and material exchange between terrestrial and aquatic ecosystems. Artificial vegetation restoration of WLFZ can improve the interception capacity of P pollution. The purpose of this study is to explore the effect of artificial vegetation restoration on the bioavailability of soil phosphorus (P) in the WLFZ.
Material and methods Soil samples from different spatial locations (natural vegetation zone, artificial vegetation restoration zone) and different altitudes of the WLFZ were collected in the Three Gorges Reservoir (TGR) region, Chongqing, China. Soil P fraction, microbial biomass P (MBP), and phosphatase activity were measured.
Results and discussion Artificial vegetation restoration changed the spatial distribution patterns of soil bioavailable P (Bio-P) in the WLFZ. The soil bioavailable inorganic P (Bio-P_i) in the artificial vegetation restoration zone was significantly higher than those at the natural vegetation zone ($p < 0.05$) and its content decreased with the decrease of altitude. The content of bioavailable organic P (Bio-P_o) in the two transects was not significantly different in general, but was different at different altitudes. Phosphodiesterase (PDE) activity was negatively correlated with Bio-P_o in artificial vegetation restoration zone ($p < 0.01$, $R^2 = 0.21$), but significantly positively correlated with in natural vegetation zone ($p < 0.05$, $R^2 = 0.17$); this suggests that the relationship between Bio-P_o and PDE activity was altered by vegetation restoration. Moreover, the factors controlling the bioavailability of P in the WLFZ are discussed.
Conclusion Artificial vegetation restoration and altitude are the control factors of soil P fractions and bioavailability in WLFZ. Vegetation restoration can increase soil TP and Bio-P_i in general but has little effect on Bio-P_o.

Keywords Phosphorus fractions · Bioavailable phosphorus · Vegetation restoration · Three Gorges Reservoir · Water-level fluctuation zone

1 Introduction

The water-level-fluctuating zone (WLFZ) is a transition zone between aquatic and terrestrial ecosystems and is also an active zone for elemental transport and transformation (Hill et al. 2000; Li et al. 2019). The WLFZ plays an important role in controlling soil erosion and relieving ecological stress (Hale et al. 2007; Cheng et al. 2015). Water level fluctuation affects not only the physicochemical properties of the soils in the zone, but also the transport and deposition of materials in the water column, thus

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affecting the biogeochemical cycling of elements at the water-land interface (Tang et al. 2014; Evtimova et al. 2016; Zhu et al. 2022).

Phosphorus (P) regulates the primary productivity of terrestrial and aquatic ecosystems and has an important impact on ecosystem functioning (Lembi et al. 2001; Cleveland et al. 2011). Studies on agricultural, forest, grassland, and wetland ecosystems have shown that drying and rewetting (DRW) conditions altered soil P fractions and increased the amount of labile P in the soil, providing nutrients to vegetation but increasing the risk of its loss with runoff (Bünemann et al. 2013; Brödlin et al. 2019; Khan et al. 2022). Due to the frequent DRW cycle in the WLFZ of the reservoir after dam construction, the contents of labile P in the soil increase (Wang et al. 2021). DRW causes structural disruption of soil aggregates, releasing large amounts of molybdate reactive phosphorus and molybdate unreactive phosphorus bound to the soil matrix (Bünemann et al. 2013). Drastic changes in intracellular osmotic pressure after soil DRW will lead to the death of microorganisms and the release of P from the microorganisms as solutes in organic (P_o) and inorganic (P_i) form, leading to an increase in labile P (Birch 1958; Turner et al. 2003).

The development of hydropower in the Yangtze River basin has led to significant impacts on the water ecosystem (Cheng et al. 2015; Wang et al. 2018, 2020b; Shen et al. 2022). To meet the needs of flood control, power generation, and navigation, the unique scheduling mechanism of the Three Gorges Reservoir (TGR) creates a WLFZ of up to 30 m during the rainy season when flood discharge is maintained at low water levels and during the dry season when water storage is maintained at high water levels (Zhang et al. 2012; Tang et al. 2018). As a result of the anti-seasonal cycle of DRW, the original vegetation in the zone dies due to long-term flooding and habitat transformation, posing a serious threat to the ecology of the reservoir area (Wu et al. 2004). In order to prevent soil erosion and maintain ecosystem stability, extensive vegetation restoration has been carried out in the WLFZ of TGR. The natural vegetation zone vegetation is dominated by herbaceous plants, and the artificial vegetation restoration zone vegetation consists of herbs, trees, and shrubs (Ye et al. 2014). Previous studies have shown that soil microbial biomass of C, N, and P in the WLFZ is significantly increased after vegetation restoration, and that vegetation type has a significant impact on microbial load, usually grassland > cropland and woodland > bare ground (Yang et al. 2017).

The WLFZ is sensitive to natural and human activities and becomes the hotspot of global P cycling (Jeppesen et al. 2009; Vidon et al. 2010). The spatial and temporal distribution of P in the WLFZ of TGR has been extensively studied, but its variability pattern remains controversial (Zhang et al. 2012; Wu et al. 2016; Ye et al. 2019). For example, Wu et al. (2016) suggest that the bioavailable P (Bio-P) in soils in the permanent backwater zone (near the dam) is higher than in the fluctuant backwater zone (away from the dam). However, Ye et al. (2019) found that Bio-P had higher concentration levels in soils in the midstream WLFZ of the reservoir area. Due to periodic reservoir scheduling, soils in the higher altitude WLFZ take about 125 days longer to fall dry than those at lower altitudes. The study on Pengxi River, a tributary of TGR, showed that Bio-P increased with the decrease of altitude, and MBP, OM, and Fe oxides were the main factors affecting Bio-P in the WLFZ (Wang et al. 2020b). Previous studies have focused on natural vegetation zone, and fewer studies have been conducted on the quality changes of artificially restored soils, especially the effect of artificial vegetation restoration on the bioavailability of P in WLFZ soils has rarely been reported.

The long-term anti-seasonal operation of the TGR has led to the degradation of the structure and function of the ecosystem in the WLFZ and thus causing a series of ecological problems, such as the degradation of the original vegetation, the change of soil physical and chemical properties, and the loss of water and soil. In recent years, with the development of many kinds of vegetation restoration measures in the WLFZ of the TGR area, the habitat condition of WLFZ has been well improved, but P pollution is still a major water environmental and ecological problem in the basin (Xue et al. 2020). Therefore, it is of great significance and necessity for deepen understanding the dynamic changes of soil P fractions in the WLFZ. Take two typical transects in the TGR area as examples: natural vegetation zone, artificial vegetation restoration zone; additionally, combined different altitudes and soil depths, soil P was fractioned to study its bioavailability.

Here, we made the following hypotheses: (1) artificial vegetation restoration would influence the change of soil P fraction and then affect its bioavailability, and (2) vegetation restoration could affect soil phosphatase activity and thus affect P cycle.

2 Materials and methods

2.1 Study sites and sampling

The study site is located in the WLFZ on the right bank of the Yangtze River in Qingxi Town, Fuling, Chongqing (29° 48′ N, 107° 28′ E).The climate is humid subtropical monsoon, with an average temperature of 18.1 °C and an average precipitation of 1072 mm. The regional soil type is mainly yellow brown soil (Ye et al. 2014). Two representative transects were selected: (1) artificial vegetation restoration zone and (2) natural vegetation zone. There are little effects of human activities on the natural vegetation zone, and the dominant species of plants are the annual plant *Echinochloa crus-galli*, perennials *Acorus gramineus* Soland, and *Cynodon dactylon*. The artificial vegetation restoration zone is about 5 km away from the natural vegetation zone. At the altitude of 165–175 m a.s.l., where mainly planted native plants, such as *Morus alba* and *Salix matsudana* Koidz. The regions of below the 165 m a.s.l., the submersion time is relatively long, approximately 7–8 months of each year. Here, annual *Polypogon fugax* and *Cynodon dactylon* were planted. The WLFZ is relatively flat above 170 m a.s.l., the slope of the middle and lower part is 20° and 25°, and the lighting conditions and flooding gradient are basically the same.

In the summer of 2022, July (during the low water level of the TGR) soil samples were collected along each transect at different depths (0–10, 10–30, 30–50 cm) at four altitudes of 145, 155, 165, and 175 m a.s.l (Fig. 1). Within each plot, three 1 m × 1 m soil sampling subplots were made and then mixed into one composite sample, totaling 24 samples. Soil samples were collected using foil sampler. The specific operation is inserting the foil sampler into the soil and extracting intact cores from sides of the quantitative soil pits. Fresh soil samples were sealed in polythene bags and stored at 4 °C and transported to the laboratory immediately.

2.2 Laboratory analysis

Soil pH was measured from suspension (soil:water, 1:2.5) using a combination pH electrode. The bulk weight (BD) was determined by the cutting ring method. Soil particle size was measured using a laser particle size analyzer (Mastersizer 2000; Malvern, UK); each sample was pretreated with 10% H_2O_2 and 10% HCl to remove organic matter and carbonate. The particle size of the samples was summarized as coarse sand (200–2000 μm), fine sand (20–200 μm), silt (2–20 μm), and clay (0.0–2 μm). Soil moisture content (MC) was measured by drying at 105 °C to a constant weight. Soil porosity is determined using the pycnometer method, soil porosity $(\%) = (1 - \text{BD soil specific gravity}^{-1}) \times 100$.

Referring to the kit instruction offered by Shanghai Enzyme-linked Biotechnology Co., Ltd, the activity of phosphatase activity was measured. The activity of alkaline phosphatase (ALP), acid phosphatase (ACP), phosphodiesterase (PDE), and phytase (PAE) in the samples was calculated from the standard curves by measuring the absorbance at 450 nm with the spectrophotometric method of enzyme standardization.

Soil MBP was determined by chloroform fumigation (Brookes et al. 1982). Five grams (dry weight) of fresh soil was weighed into a Petri dish and placed in a vacuum desiccator together with 50 ml of ethanol-free chloroform and evacuated to vacuum. The vacuum desiccator was incubated in the dark for 24 h at room temperature and the chloroform was removed. The P of the supernatant was determined by ICP-OES by extracting MBP with 0.5 M

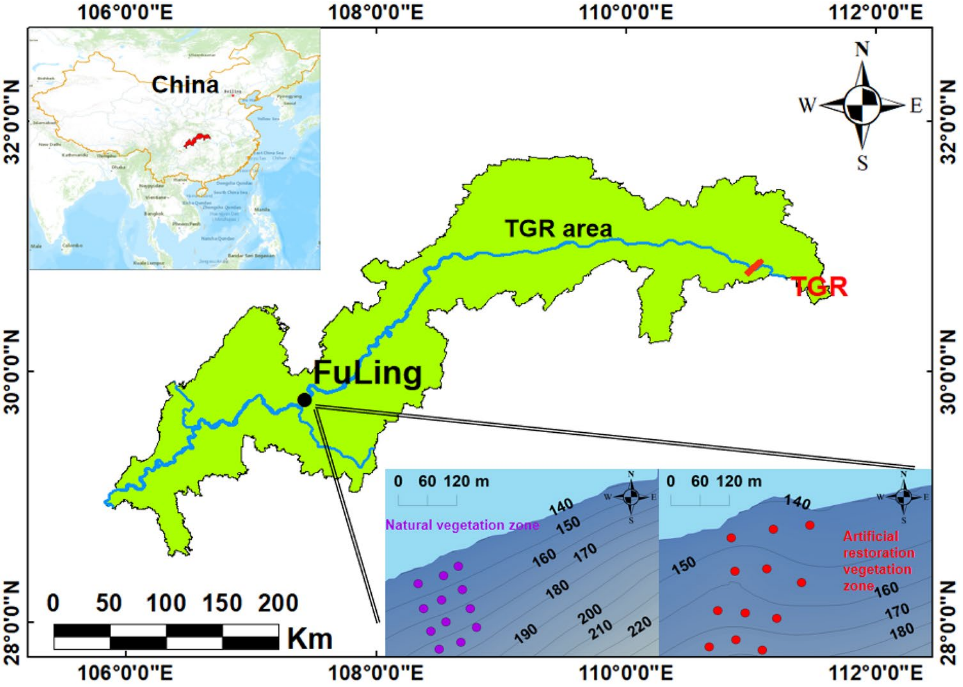

Fig. 1 The sampling sites (red and purple dots) in the water-level-fluctuation zone of Three Gorges Reservoir, China

$NaHCO_3$ at a soil to water ratio of 1:10 and shaking for 30 min. Unfumigated soils of the same control were also extracted as described above. The P content in the fumigated soil was subtracted from the corresponding P content in the unfumigated soil and divided by 0.4 to calculate the MBP.

The soil P fractions are determined by the modified Hedley sequential P fraction method (Tiessen and Moir 1993). Briefly, after drying, grinding, and passing through a 100-mesh sieve, 0.5 g of soil was weighed into a centrifugal tube, extracted by successive additions of different reagents (H_2O, 0.5 M $NaHCO_3$, 0.1 M NaOH, 1 M HCl) at a soil to water ratio of 1:60, shaken for 16 h, centrifuged, and passed through a 0.45-μm filter membrane. The extracts were digested with potassium persulfate at 121 °C to determine the total P (TP). The phosphate in each extract was determined using the molybdenum blue colorimetric method and the P_o in each extraction state was the difference between TP and P_i. The extracted P fractions were designated as H_2O-P, $NaHCO_3$-P, NaOH-P, and HCl-P. Bioavailable phosphorus (Bio-P) is considered to be the bioavailable fractions of soil P and is also more readily released into water (Cross and Schlesinger 1995).

In this study, the equations for Bio-P_i and Bio-P_o are shown below (Wang et al. 2020a).

$$\mathrm{Bio}-\mathrm{P}_\mathrm{i}=\mathrm{H_2O}-\mathrm{P}_\mathrm{i}+\mathrm{NaHCO_3}-\mathrm{P}_\mathrm{i}+\mathrm{NaOH}-\mathrm{P}_\mathrm{i} \tag{1}$$

$$\mathrm{Bio}-\mathrm{P}_\mathrm{o}=\mathrm{H_2O}-\mathrm{P}_\mathrm{o}+\mathrm{NaHCO_3}-\mathrm{P}_\mathrm{i}+\mathrm{NaOH}-\mathrm{P}_\mathrm{o} \tag{2}$$

$$\mathrm{Bio}-\mathrm{P}=\mathrm{Bio}-\mathrm{P}_\mathrm{i}+\mathrm{Bio}-\mathrm{P}_\mathrm{o} \tag{3}$$

2.3 Statistical analyses

Statistical analyses of the data were carried out using SPSS. One-way ANOVA was carried out to test differences P fractions and phosphatase activities among the altitudes and transects. The unary linear regression was conducted to determine the relationship among phosphatase activity and P fractions. Pearson correlation was used to explain the relationship between P fractions and particle size.

3 Results and discussion

3.1 Physicochemical properties of soil samples

As shown in Table 1, soil pH in the WLFZ ranged from 7.37 to 8.75, with little variation overall, all being weakly alkaline. Natural vegetation zone was generally higher than artificial vegetation restoration zone, but the difference did not reach a significant level. Soil BD ranged from 1.01 to 1.52 g cm^{-3}. Porosity ranged from 33.88 to 64.02%. MC ranges from 5.14 to 31.08%, with lower altitude soils (145 m, 155 m) subject to frequent periodic inundation and higher water content than higher altitude soils (165, 175 m). Soil median particle size ranged from 5.05 to 55.61 μm, with the mean median grain particle increasing with elevation in both sections (Fig. S1). Due to periodic water level fluctuations, fine-grained suspended particulate matter is more likely to be deposited in the WLFZ at lower altitude (Tang et al. 2018).

3.2 Distribution of P fractions in WLFZ soil

Artificial vegetation restoration had a significant effect on P fractions in the WLFZ, which varied with elevation (Fig. 2). Overall, inorganic P is the main fractions of soil P in the WLFZ (152.23 to 614.91 mg/kg). The contents of H_2O-P_i, $NaHCO_3$-P_i, NaOH-P_i, and HCl-P_i were 0.20 to 7.29 mg kg^{-1}, 0.15 to 55.55 mg kg^{-1}, 0.09 to 100.38 mg kg^{-1}, and 130.32 to 631.49 mg kg^{-1}. The TP content of artificial vegetation restoration zone was significantly higher than that of natural vegetation zone (508.92 ± 62.63 mg kg^{-1}, 490.06 ± 120.72 mg kg^{-1}, $p < 0.05$, Fig. 2a).

H_2O-P_i is weakly adsorbed P, a status of P present in soil porewater and physically adsorbed on the surface of fine soil particles. $NaHCO_3$-P_i is potentially active inorganic P, more stable than H_2O-P_i. At each altitude, the contents of H_2O-P_i and $NaHCO_3$-P_i in the artificial vegetation restoration zone soil were higher than those in the natural vegetation zone (Fig. S1). The NaOH-P_i is metal oxide-bound inorganic P, which is easily converted to labile P and released into the water column under anaerobic conditions. At 155 m a.s.l., NaOH-P_i contents in the artificial vegetation restoration zone were higher than that in the natural vegetation zone, but the result was opposite at other altitudes. HCl-P_i is Ca-bound inorganic P, which is mainly found in rock-forming minerals and can be converted to soil Bio-P over a longer time scale through weathering and dissolution processes. In this study, HCl-P_i was the main component (44–100%) of the soil P pool in the WLFZ. The effects of artificial vegetation restoration measures and variations of altitude on HCl-P_i were not significant, indicating that its source was mainly soil minerals, which is consistent with previous results in the TGR area (Zhang et al. 2012). HCl-P_i is refractory P that is slow to participate in the P cycle, and on the other hand, its content is relatively high, and it is not sensitive to vegetation restoration and periodic DRW cycle. The Bio-P_i content of artificial vegetation restoration zone soil was significantly higher than that of natural vegetation zone at each

Table 1 Soil chemical and physical properties at different altitudes in WLFZ

Vegetation type	Altitude (m)	Depth (cm)	BD (%)	Porosity (g cm$^{3\ -1}$)	MC (%)	pH
Artificial vegetation restoration zone	145	0–10	18.93	1.26	53.38	7.41
	145	10–30	26.38	1.36	46.56	7.86
	145	30–50	20.95	1.34	61.77	7.85
	155	0–10	23.65	1.28	48.53	7.77
	155	10–30	22.67	1.26	50.86	7.37
	155	30–50	22.69	1.01	64.02	7.68
	165	0–10	23.48	1.35	50.15	7.85
	165	10–30	27.97	1.42	41.44	8.1
	165	30–50	19.13	1.4	41.91	7.93
	175	0–10	19.1	1.05	58.6	7.91
	175	10–30	18.31	1.16	35.08	7.46
	175	30–50	13.38	1.4	41.58	7.54
Natural vegetation zone	145	0–10	21.56	1.21	45.46	7.58
	145	10–30	21.42	1.35	45.26	7.71
	145	30–50	27.96	1.36	40.42	8.06
	155	0–10	23.18	1.33	45.37	8.05
	155	10–30	26.59	1.23	44.28	7.85
	155	30–50	27.61	1.2	49.88	8.07
	165	0–10	26.16	1.41	40.43	7.69
	165	10–30	25.8	1.31	46.21	7.95
	165	30–50	21.72	1.1	51.4	8.13
	175	0–10	5.14	1.34	49.77	8.75
	175	10–30	31.08	1.29	45.78	8.31
	175	30–50	19.33	1.52	33.88	7.79

altitude, except for 155 m a.s.l. (85.81 ± 30.51 mg kg^{-1}, 51.81 ± 28.28 mg kg^{-1}, $p < 0.05$, Fig. 2b). Possible reasons for the above phenomenon are as follows: (1) the vegetation cover after the artificial vegetation restoration reduced the amount of soil erosion and P loss, and (2) the vegetation restoration has facilitated the transformation of different fractions of P in the soil of the WLFZ, making the P fractions migrate in a direction more conducive to plant growth and uptake.

In the WLFZ of the TGR, Ca-P was formed and released due to the reduction and dissolution of Fe–P during the flooding period, and the mineralization of soil organic P was intensified during the drying period, which resulted in the massive depletion of soil organic P (Ma et al. 2008). This explains why the content of organic P in the WLFZ soil is significantly lower than that of inorganic P in this study (Fig. S1). The content of H_2O-P_o, $NaHCO_3$-P_o, NaOH-P_o, and HCl-P_o ranged from 0 to 13.17 mg kg^{-1}, 2.06 to 41.75 mg kg^{-1}, 0.97 to 51.08 mg kg^{-1}, and 0 to 121.90 mg kg^{-1}. H_2O-P_o and $NaHCO_3$-P_o were both labile organic P (Gao et al. 2022; Bauke et al. 2022), easily migrated and mineralized in the soil and entered the water column under flooding conditions, with no significant pattern of variation between altitudes and transects (Fig. S2). NaOH-P_o is bioavailable P_o and HCl-P_o is mainly Ca-bound organic P (Wang et al 2020a; Bauke et al. 2022). The contents of NaOH-P_o in artificial vegetation restoration zone decreased with the decreasing of altitude, while the content of HCl-P_o in natural vegetation zone increased with the decreasing of altitude, showing an opposite variation pattern in transects along altitude, which may be related to the change of the response relationship between phosphatase activity and organic P in vegetation restoration transects. There was no significant difference in Bio-P_o contents between the two transects overall, but the distribution along altitude showed a certain pattern (Fig. 2c, f). At low altitudes (145 m, 155 m), the soil Bio-P_o contents in artificial vegetation restoration zone were lower than that in natural vegetation zone, while at high altitudes (155 m, 165 m) it was the opposite (Fig. 2f). The content of soil Bio-P_o in artificial vegetation restoration zone decreased with the decreasing of altitudes, while no significant change was found in natural vegetation zone, indicating that the enhancement of DRW cycle in the soil after vegetation restoration led to the enhancement of Bio-P_o mineralization, and this distribution pattern is different from that in the study of Pengxi River (Gao et al. 2022). In terms of distribution along depth, while each form P_i did not vary significantly from P_o (Fig. S3).

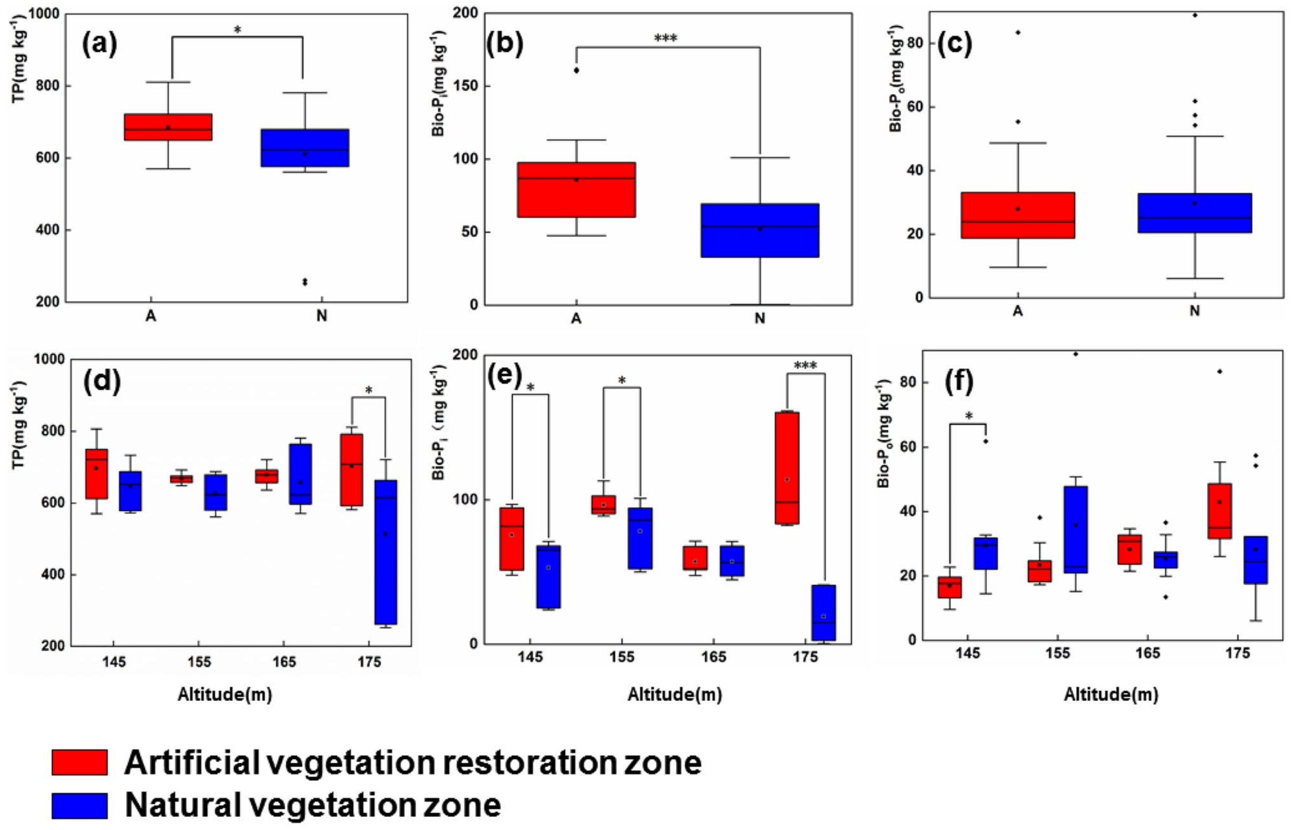

Fig. 2 Box plot of P content in different transects and altitudes. Lower and upper box boundaries represent the quartiles (25% and 75% quantiles, respectively), the square is the mean value, and the solid lines are the median. Asterisks indicate significant difference in P content between the two transects (*, $p < 0.05$; ***, $p < 0.001$). A, artificial vegetation zone; N, natural vegetation zone

Studies have shown that particle size is an important factor controlling the distribution patterns of P fractions, and that as particle size decreases, Bio-P content of the soil/sediment increases (Zhang et al. 2012). In this study, the soil median particle size increased with altitudes in both transects (Fig. 3), and Bio-P and Bio-P_i showed a significant positive correlation (Table 2, $p < 0.05$), which is consistent with the findings of Wang et al. (2020b).

3.2.1 MBP in WLFZ soil

Soil MBP is the labile fractions of soil organic P and is dominated by nucleic acids, phospholipids and is generally highly associated with $NaHCO_3$-P (Khan and Rainer 2012). Compared with other organic P in the soil, MBP is more easily to be mineralized and absorbed by plants, becoming an important source of soil Bio-P (Oehl et al. 2001; George et al. 2010). In this study, MBP ranged from 2.54 to 57.60 mg kg^{-1}, accounting for 0.45 to 13.74% of TP (Fig. 4a). In the two transects, the highest MBP content was found at 165 m a.s.l., and the content of MBP decreased with the decreasing of altitude (Fig. 4b). Previous studies have demonstrated that the soil MBP content within the TGR area exhibits variation based on the presence of different vegetation covers, however, the spatial and temporal distribution of MBP in the region does not follow a consistent pattern (Jia et al. 2016; Ren et al. 2018). As the soil in lower altitudes experienced frequent DRW cycle, a large amount of water-soluble P was released after the lysis of cells, which will also affect the absorption of available P by vegetation, and the MBP content in the two sections shows a similar variation trend along the altitude. This finding is different from previous reports (Jia et al. 2016; Yang et al. 2017).

The contents of MBP in artificial vegetation restoration zone were significantly lower than that in natural vegetation zone at each altitude ($p < 0.05$, Fig. 4a), which was contrary to the dynamic variation of Bio-P_i (Fig. 2e). The soil MBP content was significantly positively correlated with NaOH-P_o and Bio-P_o in artificial vegetation restoration zone ($p < 0.01$, Fig. 5a; $p < 0.01$, Fig. 5b), but not in natural vegetation zone ($p > 0.05$, Fig. 5a, b), indicating that MBP became the component of NaOH-P_o and Bio-P_o in the WLFZ soil after vegetation restoration. There was no correlation between MBP component and $NaHCO_3$-P and NaOH-P_i,

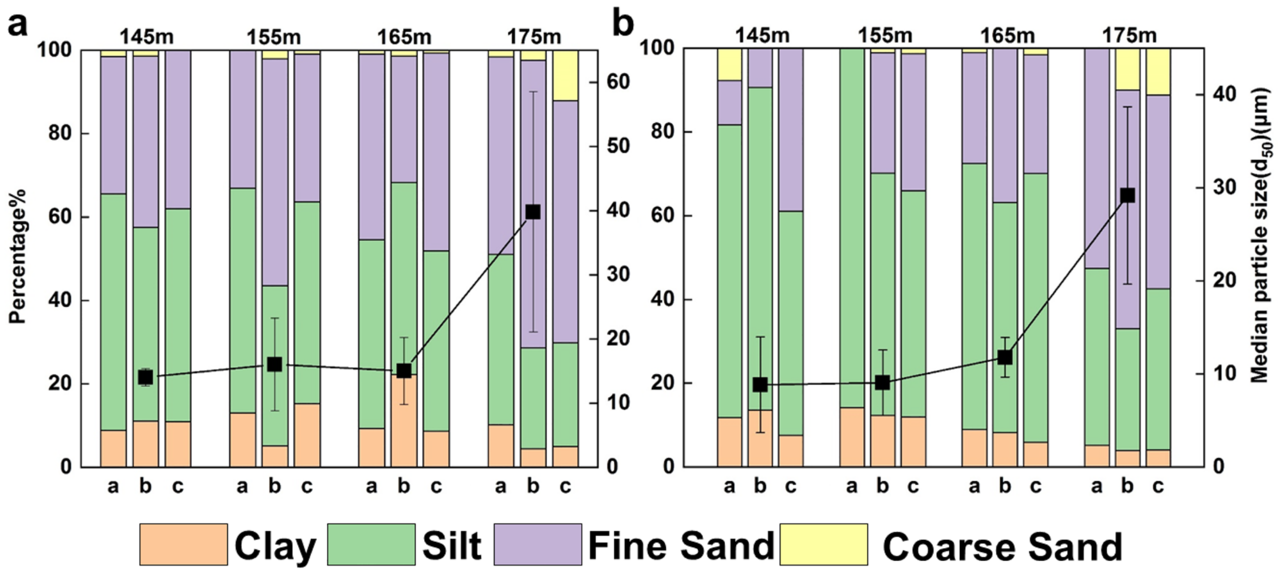

Fig. 3 Particle size of the samples at different transects **a** artificial vegetation restoration zone and **b** natural vegetation zone. The black squares represent the median particle size. a: 0–10 cm, b: 10–30 cm, and c: 30–50 cm

which was different from previous studies (Ren et al. 2018). Numerous studies have shown that both plant uptake and litter accumulation may lead to transformation of soil MBP (Chen et al. 2003; Cleveland et al. 2007). The dynamic balance between vegetation nutrient and soil nutrient was affected by vegetation type, changed the transformation relationship between MBP and Bio-P_o, which resulted in the decrease of soil MBP content in the WLFZ after artificial vegetation restoration.

3.2.2 Phosphatase activity of WLFZ soil

Soil phosphatase is a kind of hydrolase that catalyzes and accelerates mineralization of soil organic P, and it is an important index to measure the mineralization rate of organic P and the bioavailability of P (Nannipieri et al. 2011; Burns et al. 2013). Soil phosphatase activities in the WLFZ are shown in Fig. S4; the activity of ALP, ACP, PDE, and PAE was 1.71 to 2.60 μmol·(g·h) $^{-1}$, 0.53 to 0.76 μmol·(g·h) $^{-1}$, 4.35 to 6.58 μmol·(g·h) $^{-1}$, and 1.74 to 1.89 μmol·(g·h) $^{-1}$. Generally, ALP and PAE activities were similar, ACP activity was the lowest, and PDE activity was the highest.

Both ALP and ACP are belonged to phosphomonoesterase, ALP is mainly released by microorganisms, while ACP is mainly produced by plants, and they have different adaptations to soil pH, catalyzing the hydrolysis of phosphate monoester in soil organic P to release phosphate molecules (Dinkelaker et al. 1992; Nannipieri et al. 2011). PDE can catalyze the hydrolysis of phospholipids and nucleic acids in soil organic P to release phosphomonoester, and the

Table 2 Relationship between soil P fraction and particle size

	d (0.5)	0.0–2 μm	2–20 μm	20–200 μm	200–2000 μm
TP (mg kg^{-1})	−0.079	0.108	−0.092	0.139	−0.359
H_2O-P_i (mg kg^{-1})	0.428*	0.3	0.021	−0.052	−0.213
H_2O-P_o (mg kg^{-1})	−0.234	0.324	0.563**	−0.566**	−0.205
$NaHCO_3$-P_i (mg kg^{-1})	0.197	0.470*	0.052	−0.137	−0.165
$NaHCO_3$-P_o (mg kg^{-1})	0.184	−0.028	0.155	−0.125	−0.055
NaOH-P_i (mg kg^{-1})	0.332	0.437*	0.049	−0.128	−0.153
NaOH-P_o (mg kg^{-1})	0.176	0.103	0.138	−0.169	0.053
HCl-P_i (mg kg^{-1})	−0.27	−0.163	−0.024	0.122	−0.241
HCl-P_o (mg kg^{-1})	−0.082	0.051	−0.475*	0.461*	−0.246
Bio-P_i (mg kg^{-1})	0.29	0.450*	0.049	−0.13	−0.162
Bio-P_o (mg kg^{-1})	0.141	0.095	0.226	−0.232	−0.023

Pearson correlation tests were used. *, $p < 0.05$, $n = 24$; **, $p < 0.01$, $n = 24$, significant correlation. Two-tail test was used in correlation analysis

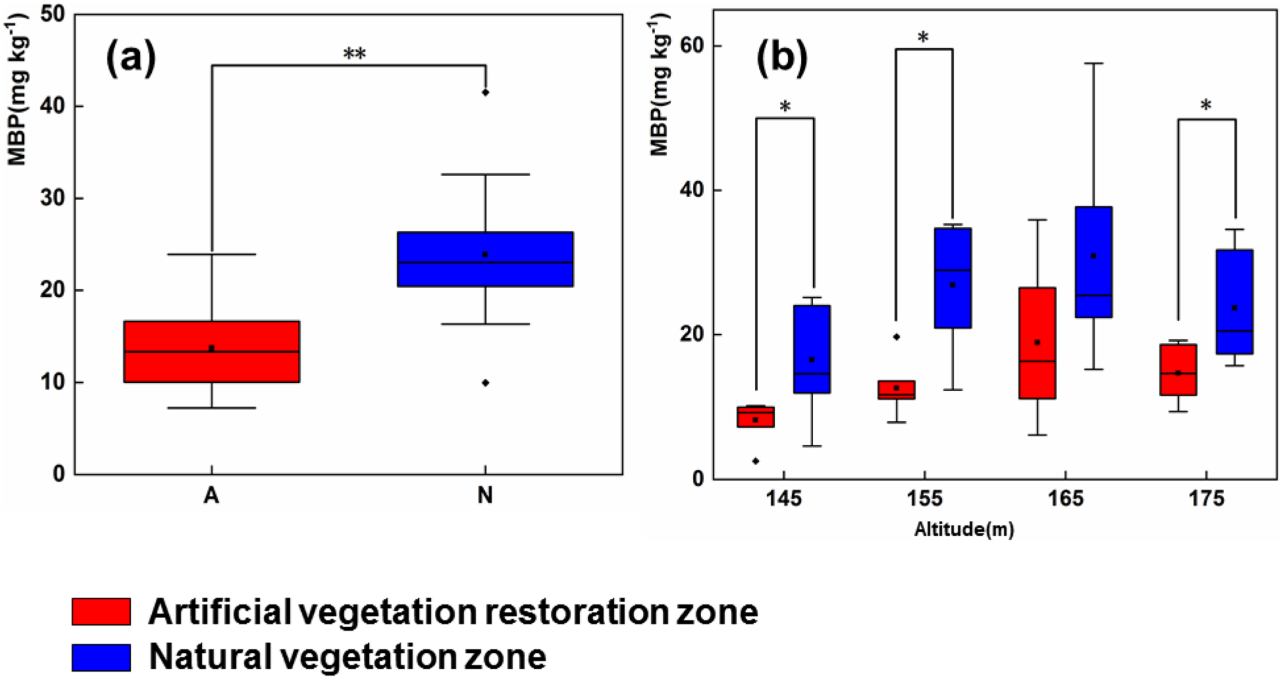

Fig. 4 Distribution of MBP content in **a** transect and **b** altitude. Lower and upper box boundaries represent the quartiles (25% and 75% quantiles, respectively), the square is the mean value, and the solid lines are the median. Asterisks indicate significant difference in P content between the two transects (*, $p < 0.05$; **, $p < 0.01$). A, artificial vegetation zone; N, natural vegetation zone

hydrolyzed products can be further hydrolyzed by ALP and ACP (Turner and Haygarth 2005; Spohn et al. 2013). PAE catalyzes the degradation of soil phytic acid to myo-inositol phosphates or inorganic P and is a specific phosphomonoesterase. Numerous studies have shown that soil pH is an important factor affecting enzyme activity (Dinkelaker

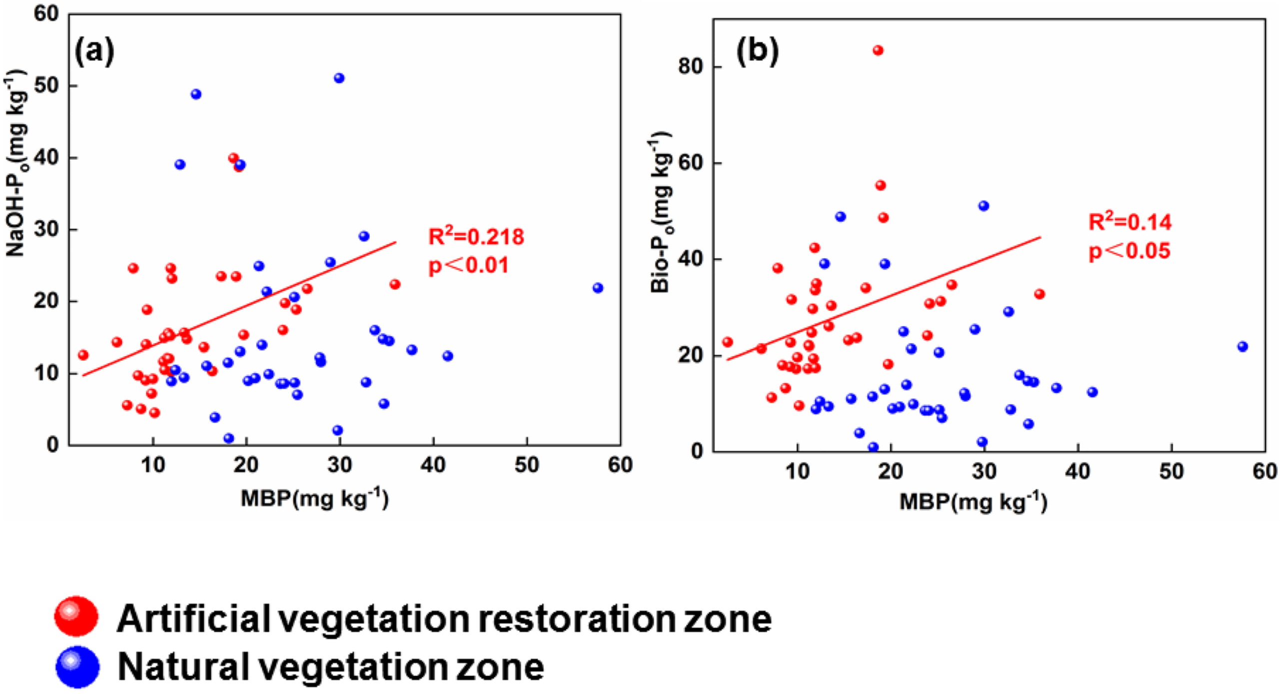

Fig. 5 Relationships between MBP and the content of **a** NaOH-P_o and **b** Bio-P_o

et al. 1992; Turner and Haygarth 2005). In this study, the soil in WLFZ is weakly alkaline, which may explain the lower ACP activity. In general, vegetation restoration can increase soil phosphatase activity (Fu et al. 2020; Zhang et al. 2021), but our results show that there is no significant difference in soil phosphatase activity at different altitudes between the two transects (Fig. S4). This finding may be related to that P is not a limiting nutrient for the productivity of soil in WLFZ of TGR, which is consistent with the study of Ren et al. (2018). Although the artificial vegetation restoration had no significant effect on phosphatase activity, the PDE activity increased with the decreasing of altitude. Gao et al. (2022) found that soil phosphatase activity in the WLFZ of Pengxi River, a tributary of the TGR, was affected by plant and microbial biomass and increased with the increasing of altitude, which was contrary to the results of this study. Frequent DRW cycling cannot only intensify soil Bio-P mineralization, but also lead to the dissolution of reducing metal ions, thus promoting or inhibiting phosphatase activity (Pulford and Tabatabai 1988; Wang et al. 2021). The vegetation restoration in the WLFZ may further enhance these effects, resulting in higher soil phosphatase activity at lower altitudes compared to higher altitudes.

Soil orthophosphate absorbed by plants to maintain growth, and organic P mineralized to provide nutritional support when inorganic P deficiency. Therefore, the level of soil phosphatase activity directly affects the turnover of organic P (Turner and Haygarth 2005; Li et al. 2021; Wang et al. 2021). The activity of PDE was the highest in the two transects; one possible explanation is that the soil organic P in this study were mainly phosphodiesters. The H_2O-P_i was significantly negatively correlated with the PDE activity in artificial vegetation restoration zone ($p < 0.05$, Fig. 7a) and natural vegetation zone ($p < 0.05$, Fig. 7a). H_2O-P_i is the most easily uptaked and utilized P fractions in soil by plants, which indicates that when the soil inorganic P contents in the WLFZ are low, plants and microorganisms will be prompted to secrete phosphatase and raise the PDE activity to promote the process of organic P mineralization.

There is a significant correlation between soil P content and enzyme activity, but due to the wide range of soil enzyme sources and the heterogeneity of soil physicochemical properties, the correlation between P fractions and enzyme activity is currently difficult to establish (Adams et al. 1992; Allison et al. 2007). On the one hand, the production of phosphatase promoted by microorganisms usually leads to depletion of organic P (Nannipieri et al. 2011); on the other hand, lower concentrations of easily degradable substrates may inhibit enzyme activity (Turner and Haygarth 2005; Boitt et al. 2018; Wang et al. 2021). The soil Bio-P_o content in artificial vegetation restoration zone and natural vegetation zone was different at each altitude, but not significant (Fig. 2f), indicating that the inhibition of PDE activity had no relation with substrate concentration. Phosphodiester in soil must be sequentially hydrolyzed by PDE and phosphomonoesterase to release inorganic phosphate for plant uptake and utilization (Turner and Haygarth 2005). In natural vegetation zone, PDE activity was positively correlated with NaOH-Po and Bio-Po ($p < 0.05$, Fig. 7f; $p < 0.05$, Fig. 7i), while the distribution of soil phosphatase activity and Bio-P did not change regularly along altitude (Fig. S4). After the artificial vegetation restoration, the original vegetation pattern in the WLFZ was changed, and the distribution of soil microbial community along altitude also succession correspondingly. There was a significant negative correlation between PDE activity and NaOH-P_o and Bio-P_o ($p < 0.05$, Fig. 7e; $p < 0.01$,

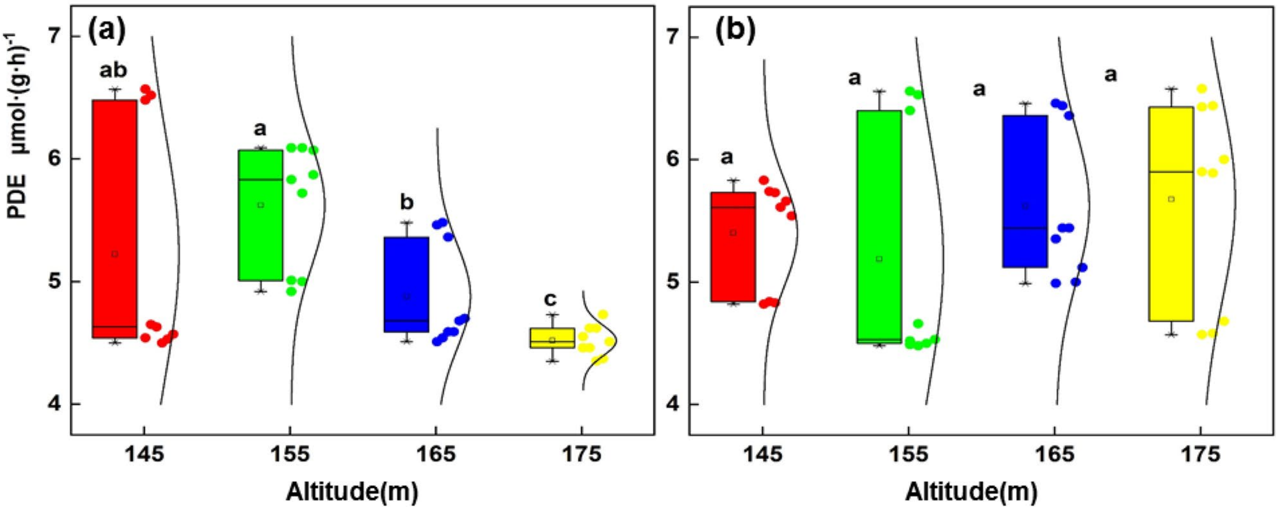

Fig. 6 Distribution of PDE activity along altitude in **a** artificial vegetation restoration zone and **b** natural vegetation zone. Different lowercase letters represent significant differences between different altitudes ($p < 0.05$)

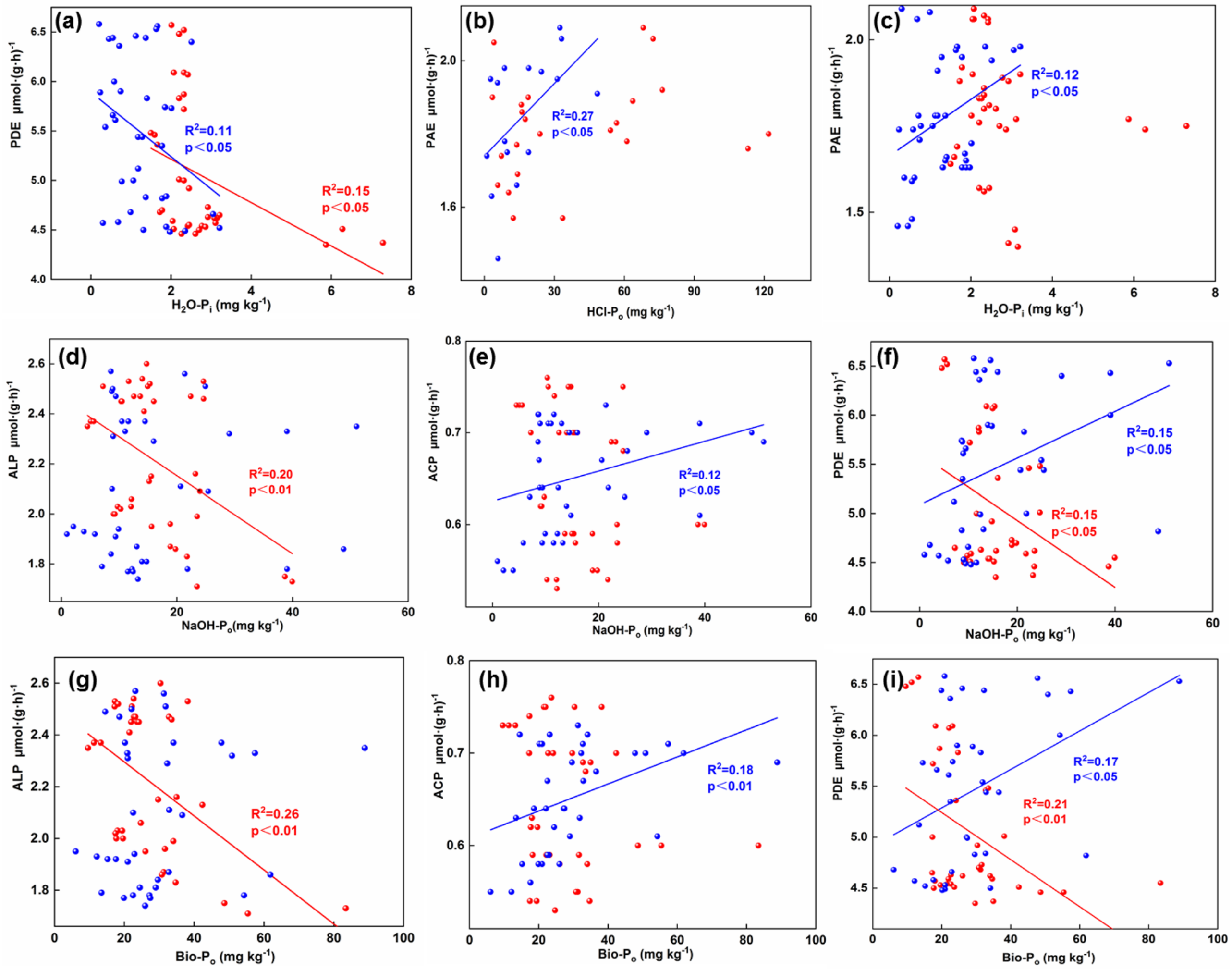

Fig. 7 Relationships between soil P fractions and phosphatase activity

Fig. 7h); the distribution of Bio-P$_o$ and PDE activity showed an opposite pattern along altitude (Fig. 2f, Fig. 6a). Soil phosphomonoesterase (ALP, ACP) activity and Bio-Po in the two transects revealed the same correlation as PDE and Bio-Po, through the indirect influence of PDE and phosphomonoesterase (Fig. 7). The evidence presented indicates that artificial vegetation restoration has enhanced the response of PDE activity to the DRW cycle. Moreover, it has influenced the distribution pattern of Bio-P$_o$ across different altitudes. Furthermore, a notable positive correlation between MBP and Bio-P$_o$ was observed ($p < 0.01$, Fig. 5a; $p < 0.05$, Fig. 5b), providing further support for this perspective.

Previous studies have shown that soil phytate chelates with metal cations such as Ca^{2+}, Mg^{2+}, and Zn^{2+} and can release inorganic P through phytase catalyzed hydrolysis to provide P sources for plant growth (Perkins and Underwood 2001; Zhu et al. 2017). HCl-P$_o$ is a resistant organic P containing phytic (He et al. 2006). In this study, soil PAE activity in natural vegetation zone had a significant positive correlation with HCl-P$_o$ ($p < 0.05$, Fig. 7b). In the artificial vegetation restoration zone, PAE activity and HCl-P$_o$ distribution along the altitude are not regular, and there is no significant correlation between them. One possible explanation is that the vegetation restoration years in the WLFZ is short, and phytase mineralization of organic P is not fully established. Unfortunately, our study was insufficient to investigate the relationship between enzyme activity and P fractions on the vegetation restoration years.

4 Conclusion

The study showed that the TP and Bio-P$_i$ contents in the WLFZ of TGR were significantly increased after artificial vegetation restoration, and the distribution of Bio-P$_i$ was mainly affected by particle size. The variation in Bio-P$_o$

content was not significantly different between the transects in general, but the distribution was different between different altitudes. Artificial vegetation restoration exerts an impact on the mineralization of soil OP within the WLFZ, thereby altering the biological bioavailability of phosphorus (P). Furthermore, this effect varies with altitude due to the influence of the DRW cycle. This change may protect water from the threat of eutrophication in the WLFZ. Artificial vegetation restoration resulted in a significant decrease in MBP content and an increase in PDE activity, and both showed regular changes along the altitude gradient. The PDE activity mainly controls the soil Bio-P_o mineralization, but the mechanism of action in the two transects is different. Through these studies, vegetation restoration can be better selected to improve the ecological function of WLFZ wetlands at different altitudes, providing a new perspective for understanding the soil P cycle in the WLFZ.

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Declarations

Conflict of interest The authors declare no competing interests.

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