

<https://doi.org/10.17221/60/2021-SWR>

The influence of *Shewanella oneidensis* MR-1 on the transformation of iron oxides and phosphorus in a red soil

WEIMIN YU, RONGPING WANG*, RONGYUN LINGHU, JIAWEI LIANG, QIQI HU, YULING YAO

National-Regional Joint Engineering Research Center for Soil Pollution Control and Remediation in South China, Guangdong Key Laboratory of Integrated Agro-environmental Pollution Control and Management, Institute of Eco-environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou, P.R. China

*Corresponding author: rpwang@soil.gd.cn

Citation: Yu W., Wang R., Linghu R., Liang J., Hu Q., Yao Y. (2022): The influence of *Shewanella oneidensis* MR-1 on the transformation of iron oxides and phosphorus in a red soil. Soil & Water Res., 17: 59–68.

Abstract: In this study, *Shewanella oneidensis* MR-1, an iron (Fe)-reducing bacterium, was inoculated to a red soil, which was then incubated. Soil samples were taken regularly to analyse the variation of iron oxides and phosphorus (P) fractions. The results showed that the MR-1 inoculation increased the content of the free iron oxides, but decreased the activity of the iron oxides in the soil, and had no significant influence on the amorphous iron oxides. The MR-1 inoculation increased the resin-P and residual-P, decreased the NaHCO₃-extracted inorganic P (NaHCO₃-P_i) and NaOH-extracted inorganic P (NaOH-P_i), but did not significantly influence the diluted HCl-extracted inorganic P (D.HCl-P_i) and concentrated HCl-extracted inorganic P (C.HCl-P_i). The presence of MR-1 influenced the correlation between the free iron oxides and NaOH-P_i. In the CK where deactivated MR-1 was applied, there was a significant positive correlation between the free iron oxides and the NaOH-P_i; in the treatment with the live MR-1 inoculation, there was no correlation between them. In addition, there was a significant positive correlation between the free iron oxides and the C.HCl-P_i, and there was a significant negative correlation between the NaHCO₃-P_i, resin-P, and residual-P. Therefore, the MR-1 inoculation improved the P availability by decreasing the activity of the iron oxides and consequently improved the P use efficiency in the red soil.

Keywords: incubation experiment; iron oxide activity; iron-reducing bacterium; phosphorus fractionation

Phosphorus (P) is an essential nutrient element for plants. According to the statistical data released by the National Bureau of Statistics of China, China's annual phosphate fertiliser output in 2015 was 18 572 000 t, and the equivalent P amount of the applied agricultural phosphate fertiliser was nearly 8 430 600 t. However, the research data show that P use efficiency is extremely low, with most of the P applied to soils being immobilised by Mn/Fe oxides or transformed to unavailable forms through adsorp-

tion and precipitation (Chen et al. 1997). Applying large quantities of phosphate fertiliser to soils not only leads to low P use efficiency, but also aggravates the environmental load (Wang & Liang 2014; Huang et al. 2017; Van der Salm et al. 2017). Therefore, it is of significance to improve the P use efficiency.

Due to strong desilication and ferrallitic weathering, red soils have very high contents of iron oxides, which readily bond with P, resulting in low P availability (de Mello et al. 1998; Rozan et al. 2002; Lu

Supported by the GDAS' Project of Science and Technology Development, Project No. 2021GDASYL-20210302003, by the Guangdong Foundation for Program of Science and Technology Research, Project No. 2020B1212060048, by the Guangdong R&D Programme in Key Fields, Project No. 2020B0202010005, and by the Guangzhou Science and Technology Program Key Projects, Project No. 202103000058.

et al. 2014). It is documented that iron (Fe)-P compounds account for 40–80% of the total content of the different forms of P (Baefan 1963). Therefore, it would be significant to improve the P availability in red soils to improve the P use efficiency.

Soil microbes drive geochemical cycling and the mass and energy exchange between different portions of the global ecosystem (Song et al. 2013). Moreover, soil microbes are also referred to as the converters of biological dark matter in the cycling of soil nutrients (Jansson 2013). It is estimated that each gram of soil may contain several tens of thousands of microbial species and about 10 billion microbes (Song et al. 2013). As these communities perform their respective functions, they provide and maintain a stable soil environment. *Shewanella oneidensis* MR-1 is a Gram-negative facultative anaerobe capable of utilising a broad range of electron acceptors and also the first known Fe-reducing bacterium that oxidises organic matters via Fe(III) reduction to obtain energy for growth (Myers & Nealson 1988). With the reduction of Fe(III) to Fe(II), the P that is strongly fixed by Fe(III) is expected to be released and become bioavailable (Maranguit et al. 2017). For crops that require a flooding period during their growth such as rice, *S. oneidensis* MR-1 can play an important role during the flooding period in providing available P for crop growth and development. In fact, anaerobic microenvironments are ubiquitous in aerobic soils (Kaiser & Bollag 1990). Therefore, *S. oneidensis* MR-1 is expected to play a significant role in the P transformation in aerobic soils as well. The present research was aimed to investigate the influence of *S. oneidensis* MR-1 on the transformation of Fe and P in a red soil. The findings of this study are expected to help improve the P use efficiency in red soils, which is of significant in terms of resource preservation and environmental protection.

MATERIAL AND METHODS

Soil and bacterial strain. The experimental soil samples were acquired from Zhanjiang City (Xuwen County, Guangdong Province, China). The soil was naturally air-dried in a well-ventilated place, passed through a 2-mm nylon sieve, and then sealed for later use. The basic physicochemical properties were as follows: pH_{H₂O} 5.1, organic matter 1.96% (Lu 1999), NaHCO₃-extractable P 104 mg/kg (Olsen et al. 1965), alkali-hydrolysable N 69.0 mg/kg (Lu 1999), NH₄OAC-extractable potassium 358 mg/kg (Lu 1999), and

1 mol/L HNO₃-extractable potassium 154 mg/kg (Lu 1999). A liquid culture of *S. oneidensis* MR-1, which is a facultative anaerobic bacterium, was used in the experiment. The microbial culture was provided by the microbial remediation team at the Guangdong Institute of Eco-environment Science & Technology.

Experimental design and laboratory analyses. For the experiment, 50 g of air-dried soil was added to a 250-mL polyethylene bottle. The bacterial strain *S. oneidensis* MR-1 was inoculated at 5×10^7 CFU/g soil. Then, the soil-water content was adjusted to 120% of the field water capacity. After the liquid and soils were mixed thoroughly, the mixture was cultivated for 35 days in a biochemical incubator at a constant temperature of 25 °C. Two treatments were set up for the incubation experiment: One was CK where *S. oneidensis* MR-1 autoclaved at 120 °C for 30 min was added to the soil, and the other was MR-1 where the live *S. oneidensis* MR-1 was inoculated to the soil. Each treatment was set up in triplicate, with samples collected on day 0, 2, 4, 7, 14, 21, 28, and 35, during the incubation period. Then, the collected soil samples were air-dried and sieved through a 10-, 60-, or 100-mesh (i.e., 2.0-, 0.25-, and 0.15-mm, respectively) nylon sieves to determine of the related properties.

The soil pH and redox potential (Eh) were measured under the condition that the ratio of soil to water was 1 : 2.5. The free iron oxide in the soil was extracted using the dithionite-citrate-bicarbonate (DCB) method, and then its concentration was measured using phenanthroline colorimetry (Lu 1999). The amorphous iron oxide was extracted using an ammonium oxalate buffer solution, and its concentration was also measured using phenanthroline colorimetry (Lu 1999). The soil P was fractionated into: resin-P, NaHCO₃ extracted inorganic (NaHCO₃-P_i) and organic P (NaHCO₃-P_o), NaOH extracted inorganic (NaOH-P_i) and organic P (NaOH-P_o), concentrated HCl extracted inorganic (C.HCl-P_i) and organic P (C.HCl-P_o), diluted HCl extracted inorganic P (D.HCl-P_i), and residual P according to Tiessen and Moir (1993). Briefly, dry soil, distilled water, and a strip of anion exchange resin membrane were put in a centrifuge tube and shaken. The resin-P was recovered with HCl. The soil residue was extracted with an NaHCO₃ solution. A portion of the NaHCO₃ extract was used to determine of NaHCO₃-P_i after precipitating the extracted organic matter. The other portion of the NaHCO₃ extract was digested to determine the total P, and NaHCO₃-P_o was calculated as the differ-

<https://doi.org/10.17221/60/2021-SWR>

ence between the total P and $\text{NaHCO}_3\text{-P}_i$. The soil residue was then extracted with the NaOH solution. Similarly, NaOH-P_i was determined after a portion of the extract was acidified to precipitate the extracted organic matter, and NaOH-P_o was calculated as the difference between the total P of the extract and NaOH-P_i . The soil residue was extracted with diluted HCl (1 mol/L) and D.HCl-P_i was determined using the supernatant. The soil residue was extracted with concentrated HCl. The supernatant was used to determine C.HCl-P_i , and C.HCl-P_o was the difference between the total P of the extract and C.HCl-P_i . The final soil residue was digested to determine the residual P. Of the obtained fractions, resin-P , $\text{NaHCO}_3\text{-P}_i$, and $\text{NaHCO}_3\text{-P}_o$ are labile P forms, NaOH-P_i and NaOH-P_o are moderately stable P forms, and C.HCl-P_i , C.HCl-P_o , D.HCl-P_i , and residual P are stable P forms.

Statistical analyses. Statistical analyses were conducted using IBM SPSS Statistics 20, correlations were determined using Pearson's correlation analysis, and the graphs were drawn using Origin (Ver. 8.5.1).

RESULTS

Changes in soil pH and Eh. The soil pH increased from 5.1 for the first seven days of the incubation and then continuously decreased to approximately 4.2 in both the CK and MR-1 treatments (Figure 1). In contrast, the soil Eh decreased for the first several days and then continuously increased. During incubation, the soil pH was significantly higher while the soil Eh was significantly lower in the MR-1 treatment than in the CK one.

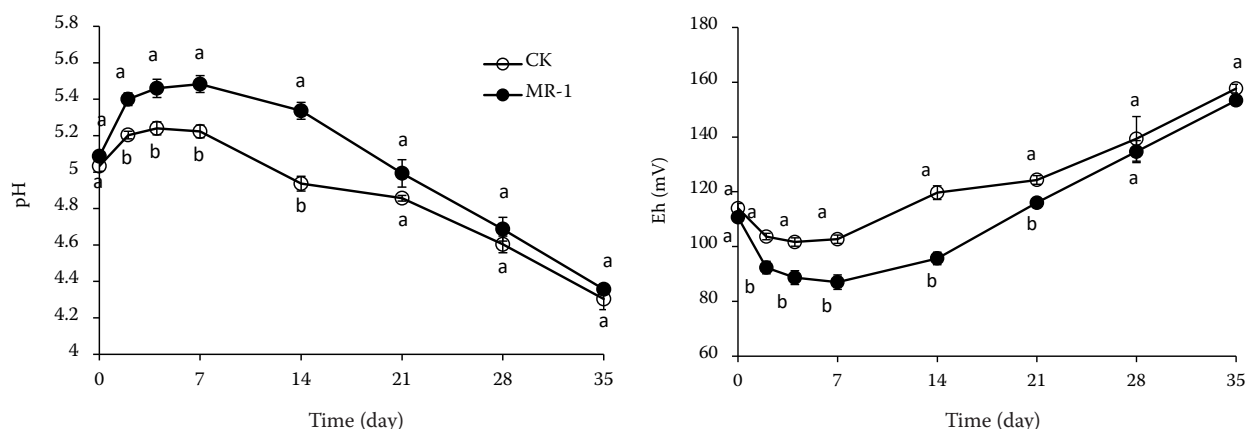


Figure 1. Changes in the soil pH and redox potential (Eh) in the CK treatment (deactivated *Shewanella oneidensis* MR-1 was added) and the MR-1 treatment (alive *S. oneidensis* MR-1 was inoculated) during incubation; error bars are standard errors ($n = 3$)

different letters indicate significant differences between the treatments for the same sampling time

Changes in iron oxides. As important minerals in subtropical soils, iron oxides can determine the colours and certain properties of the soils, and are characterised by high activity and a highly variable range of contents. Of the iron oxides, amorphous iron oxides are of special interest due to their important roles in chemical processes.

Figure 2A shows the changes in the contents of the free iron oxides. In the two treatments, the free iron oxide content increased with time. In the CK treatment, the free iron oxide content increased rapidly (by 6 g/kg) in the first four days of the experiment, then decreased, and then increased again. In the MR-1 treatment, the content of the free iron oxides decreased in the first four days, but increased sharply (by 5.6 g/kg) over the next three days, and then increased slowly. At the end of the incubation, the free iron oxide content in the CK treatment increased by approximately 10% compared with that at the beginning of incubation, while that in the MR-1 treatment increased by approximately 11%. There were no significant differences in the free iron oxide content between the two treatments during the entire incubation period.

Figure 2B shows the changes in the content of the amorphous iron oxides. After two days of incubation, the amorphous iron oxide content in both treatments decreased by close magnitudes. From day 2 to 4, the amorphous iron oxide content in the CK treatment decreased further while that in the MR-1 treatment increased. After 7 days of incubation, the amorphous iron oxide content in both treatments began to decline again. During the 35-day incubation period,

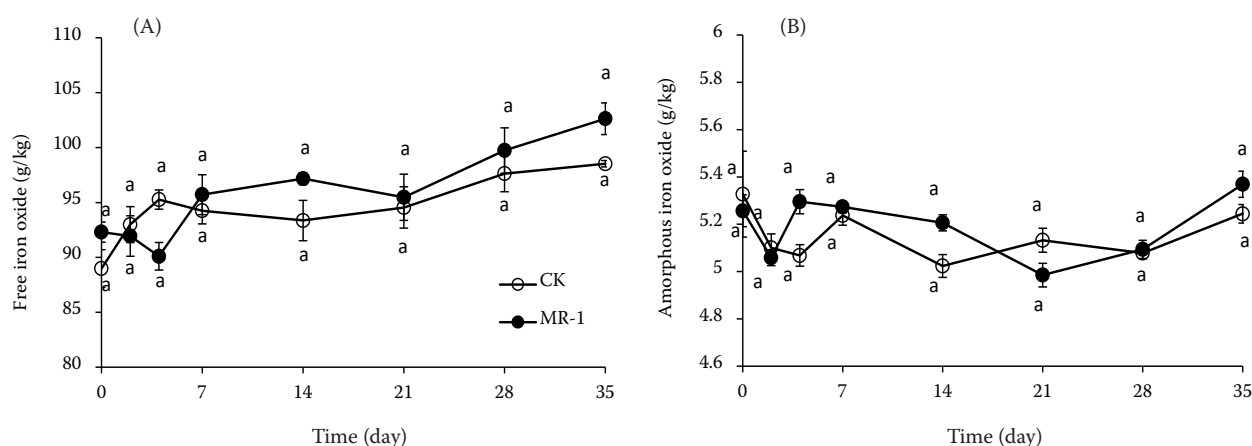


Figure 2. Changes in the free iron oxide (A) and amorphous iron oxide (B) contents in the CK treatment (deactivated *Shewanella oneidensis* MR-1 was added) and the MR-1 treatment (live *S. oneidensis* MR-1 was inoculated) during incubation different letters indicate significant differences between the treatments for the same sampling time

the amorphous iron oxide content in the two treatments did not show large changes, but only small fluctuations. There were no significant differences in the amorphous iron oxide content between the two treatments during the entire incubation period. This indicates that the inoculation of *S. oneidensis* MR-1 did not have a significant influence on the amorphous iron oxide content in the soil.

The activity of iron oxides is quantified as the ratio (percentage) of the amorphous iron oxide content to the free iron oxide content in the soil. Table 1 shows the changes in the iron oxide activity in the two treatments. The iron oxide activity decreased slightly during incubation in both treatments. The activity changes indicate the gradual ageing of the free iron oxides in soils with time, regardless of whether the soils were inoculated with *S. oneidensis* MR-1 or not.

Changes in inorganic P and residual P. The resin-P is the most bioavailable of the variable P forms in the soil. In the MR-1 treatment, the resin-P content first increased and then continuously decreased (Figure 3A). Similarly, the resin-P content increased and then de-

creased in the CK treatment, but with much smaller magnitudes. The resin-P content was significantly higher in the MR-1 treatment than in the CK one for the entire incubation period, and the maximum resin-P content in the MR-1 treatment (97.2 mg/kg) was 35% higher than that in the CK one (71.9 mg/kg), indicating that the inoculation of *S. oneidensis* MR-1 increased the resin-P content in the soil.

The $\text{NaHCO}_3\text{-P}_i$ content in the MR-1 treatment decreased rapidly in the first four days and then increased (Figure 3B), while that in the CK treatment increased with time. It was significantly higher in the CK treatment than in the MR-1 treatment for the entire incubation period. The NaOH-P_i content did not change much in the CK treatment during the incubation period, while that in the MR-1 treatment first decreased then increased (Figure 3C). In the first seven days, the NaOH-P_i content in the MR-1 treatment decreased by approximately 12 mg/kg, indicating that part of the NaOH-P_i had been transformed into other forms of P due to the presence of *S. oneidensis* MR-1. In the subsequent two weeks, the content of NaOH-P_i increased, indicating that

Table 1. Iron oxide activity changes in the CK treatment (deactivated *Shewanella oneidensis* MR-1 was added) and in the MR-1 treatment (live *S. oneidensis* MR-1 was inoculated) during incubation of the red soil

Treatment	Iron oxide activity (%)							
	day 0	day 2	day 4	day 7	day 14	day 21	day 28	day 35
CK	6.0	5.5	5.3	5.8	5.4	5.3	5.2	5.3
MR-1	5.7	5.5	5.9	5.5	5.4	5.2	5.1	5.2

Values are means ($n = 3$)

<https://doi.org/10.17221/60/2021-SWR>

other forms of P had been transformed into NaOH-P_i. In the later stage of the experiment, the NaOH-P_i content remained stable. As can be seen from Figure 3D, the D.HCl-P_i content remained almost unchanged regardless of whether *S. oneidensis* MR-1 was inoculated or not.

Figure 3E shows the variation in the C.HCl-P_i content (also referred to as stable inorganic P). The C.HCl-P_i content decreased by approximately 70 mg/kg in the first four days in both treatments and then did not change much for the rest of the incubation period, indicating that the inoculation of *S. onei-*

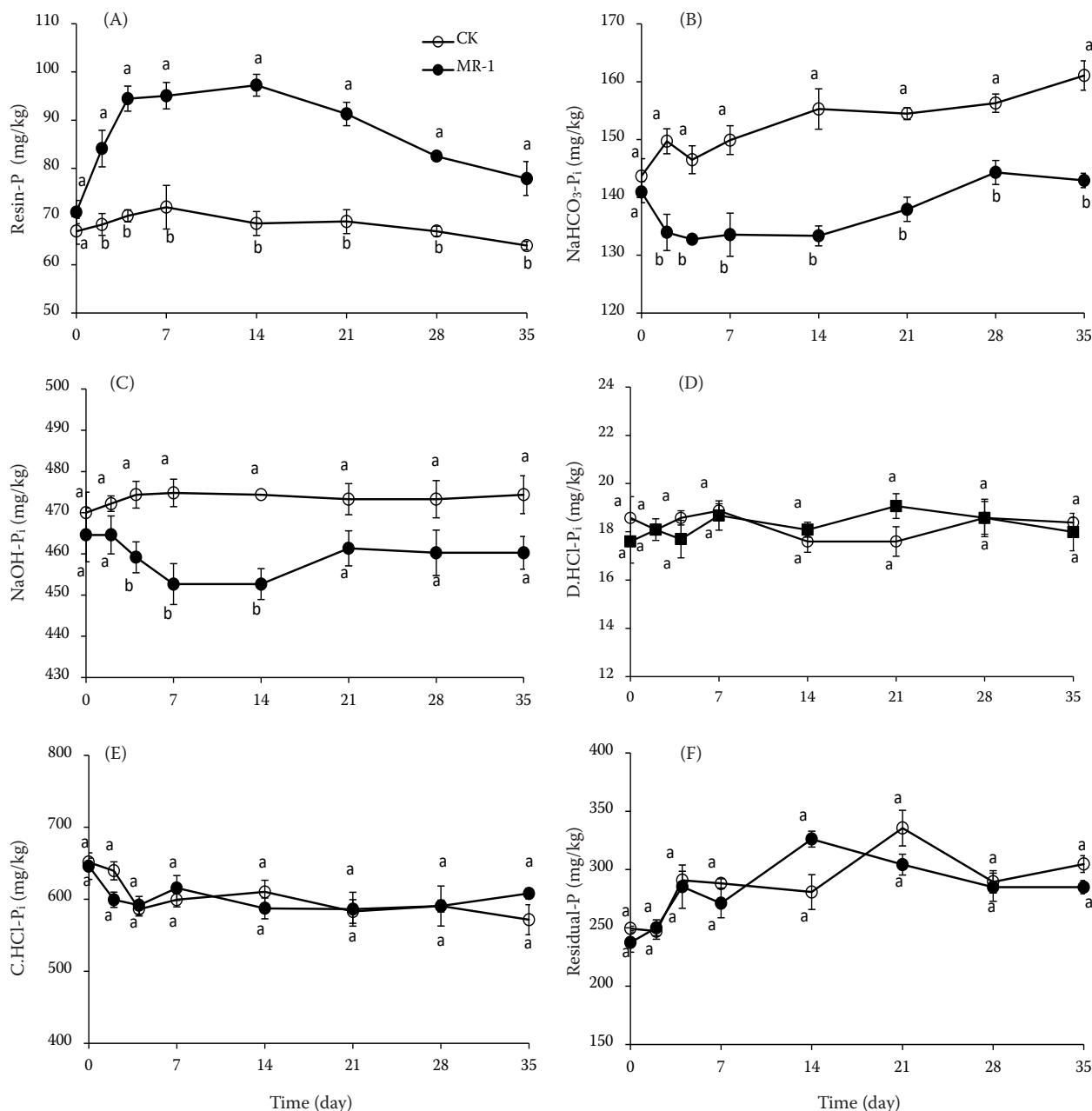


Figure 3. Changes in the resin-P (A), NaHCO₃-P_i (B), NaOH-P_i (C), D.HCl-P_i (D), C.HCl-P_i (E), and residual-P (F) contents in the CK treatment (deactivated *Shewanella oneidensis* MR-1 was added) and the MR-1 treatment (live *S. oneidensis* MR-1 was inoculated) during incubation

different letters indicate significant differences between the treatments for the same sampling time; NaHCO₃-P_i – NaHCO₃ extracted inorganic P; NaOH-P_i – NaOH extracted inorganic P; D.HCl-P_i – diluted HCl extracted inorganic P; C.HCl-P_i – concentrated HCl extracted inorganic P

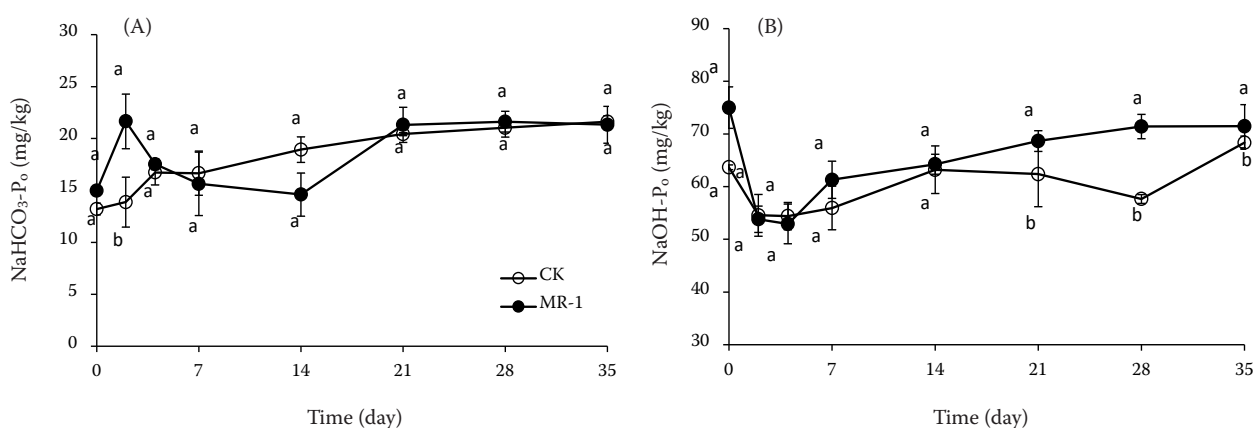


Figure 4. Changes in the $\text{NaHCO}_3\text{-P}_o$ (A) and NaOH-P_o (B) contents in the CK treatment (deactivated *Shewanella oneidensis* MR-1 was added) and the MR-1 treatment (live *S. oneidensis* MR-1 was inoculated) during incubation. Different letters indicate significant differences between the treatments for a same sampling time; $\text{NaHCO}_3\text{-P}_o$ – NaHCO_3 extracted organic P; NaOH-P_o – NaOH extracted organic P.

densis MR-1 only influenced the C.HCl-P_i content for a short time. The residual-P is the most stable P fraction in the soil, and can hardly be utilised by plants. There were no significant differences in the residual-P between the two treatments, and it tended to increase with time in both treatments (Figure 3F). Of the six inorganic P fractions, the C.HCl-P_i content was the highest (> 550 mg/kg), while the D.HCl-P_i content was the lowest (< 20 mg/kg).

Changes in organophosphorus. The $\text{NaHCO}_3\text{-P}_o$ content was very low (10–25 mg/kg) in the soil (Figure 4A). In the CK treatment, the $\text{NaHCO}_3\text{-P}_o$ content increased slightly with time. In the MR-1 treatment, the $\text{NaHCO}_3\text{-P}_o$ content decreased by 41.5% in the first 14 days, increased over the next seven days, and did not change much afterwards. The NaOH-P_o content decreased by 9 mg/kg in the CK treatment and by 22 mg/kg in the MR-1 treatment in the first four days of incubation (Figure 4B), indicating that the inoculation of *S. oneidensis* MR-1 to the red soil may have driven the transformation of NaOH-P_o into other forms of P.

Correlation between the iron oxides and P fractions. In both the CK and MR-1 treatment, the pH was significantly and negatively correlated with the Eh, with both correlation coefficients being -0.99 ($P < 0.01$), and the pH was significantly and negatively correlated with the $\text{NaHCO}_3\text{-P}_i$, with correlation coefficients of -0.86 ($P < 0.01$) and -0.90 ($P < 0.01$), respectively (Tables 2 and 3). In contrast, the Eh was significantly and positively correlated with the $\text{NaHCO}_3\text{-P}_i$, with correlation coefficients of 0.88

($P < 0.01$) and 0.90 ($P < 0.01$) for the CK and MR-1 treatments, respectively. For the CK treatment, the pH was significantly and negatively correlated with the $\text{NaHCO}_3\text{-P}_o$ ($P < 0.05$), whereas the Eh was significantly and positively correlated with the $\text{NaHCO}_3\text{-P}_o$ ($P < 0.05$). For the MR-1 treatment, the pH was significantly and negatively correlated with the free iron oxide ($P < 0.01$), but significantly and positively correlated with the resin-P ($P < 0.05$); the Eh was significantly and positively correlated with the free iron oxide ($P < 0.01$), but significantly and negatively correlated with the resin-P ($P < 0.05$). There was no significant correlation between the pH and the free iron oxide and resin-P in the CK treatment, and there was no significant correlation between the Eh and the free iron oxide and resin-P in the CK treatment either. In both the CK and MR-1 treatments, the resin-P was significantly and negatively correlated with the $\text{NaHCO}_3\text{-P}_i$, with a correlation coefficient of -0.79 ($P < 0.05$) and -0.81 ($P < 0.01$), respectively. This indicates that the increase in the resin-P content may be primarily due to the transformation of $\text{NaHCO}_3\text{-P}_i$. In the CK treatment, the free iron oxide was significantly and negatively correlated with the NaOH-P_i . However, such a correlation was not observed in the MR-1 treatment. In both the CK and MR-1 treatments, the residual-P was significantly and negatively correlated with the C.HCl-P_i , indicating that the increase in the residual-P may be primarily due to the transformation of C.HCl-P_i . There was also a significant positive correlation between the NaOH-P_o and $\text{NaHCO}_3\text{-P}_i$.

<https://doi.org/10.17221/60/2021-SWR>

Table 2. Correlation coefficients between the contents of the amorphous iron oxide, free iron oxide, and the phosphorus fractions in the CK treatment where deactivated *Shewanella oneidensis* MR-1 was applied

	pH	Eh	Amorphous iron oxide	Free iron oxide	Resin-P	NaHCO ₃ -P _i	NaOH-P _i	D.HCl-P _i	C.HCl-P _i	Residual-P	NaHCO ₃ -P _o	NaOH-P _o
pH	1	-0.99**	0.24	-0.58	0.60	-0.86**	-0.05	0.20	0.45	-0.44	-0.79*	-0.59
Eh		-0.22		0.59	-0.62	0.88**	0.06	-0.19	-0.46	0.44	0.79*	0.62
Amorphous iron oxide			1	-0.32	-0.44	0.32	-0.13	0.5	0.25	-0.16	-0.29	0.4
Free iron oxide				1	0	0.28	0.81**	0.08	-0.88**	0.61	0.83**	0.07
Resin-P					1	-0.79*	0.08	0.01	-0.16	0.19	-0.12	-0.72*
NaHCO ₃ -P _i						1	0.26	-0.2	-0.2	0.23	0.57	0.89**
NaOH-P _i							1	0.02	-0.82**	0.56	0.69*	0.27
D.HCl-P _i								1	0.02	-0.29	-0.26	-0.33
C.HCl-P _i									1	-0.88**	-0.87**	-0.17
Residual-P										1	0.81**	0.29
NaHCO ₃ -P _o											1	0.43
NaOH-P _o												1

Eh – redox potential; NaHCO₃-P_i – NaHCO₃ extracted inorganic P; NaOH-P_i – NaOH extracted inorganic P; D.HCl-P_i – diluted HCl extracted inorganic P; C.HCl-P_i – concentrated HCl extracted inorganic P; NaHCO₃-P_o – NaHCO₃ extracted organic P; NaOH-P_o – NaOH extracted organic P; * and ** indicate significant at 0.05 and 0.01, respectively

Table 3. Correlation coefficients between the contents of the amorphous iron oxide, free iron oxide, and the phosphorus fractions in the MR-1 treatment where live *Shewanella oneidensis* MR-1 was inoculated

	pH	Eh	Amorphous iron oxide	Free iron oxide	Resin-P	NaHCO ₃ -P _i	NaOH-P _i	D.HCl-P _i	C.HCl-P _i	Residual-P	NaHCO ₃ -P _o	NaOH-P _o
pH	1	-0.99**	-0.12	-0.80**	0.74*	-0.90**	-0.29	-0.09	-0.03	-0.09	-0.51	-0.58
Eh		1	0.12	0.80**	-0.74*	0.90**	0.29	0.09	0.03	0.09	0.51	0.58
Amorphous iron oxide			1	0.15	-0.07	0.01	-0.05	-0.62	0.45	-0.11	-0.24	0.04
Free iron oxide				1	-0.36	0.63	-0.04	0.34	-0.17	0.41	-0.02	0.59
Resin-P					1	-0.81**	-0.64	0.25	-0.43	0.56	-0.85**	-0.52
NaHCO ₃ -P _i						1	0.69*	0.07	0.25	-0.16	0.70*	0.84**
NaOH-P _i							1	-0.2	0.37	-0.37	0.86**	0.57
D.HCl-P _i								1	-0.45	0.39	-0.15	0.13
C.HCl-P _i									1	-0.77*	0.46	0.4
Residual-P										1	-0.63	0
NaHCO ₃ -P _o											1	0.51
NaOH-P _o												1

Eh – redox potential; NaHCO₃-P_i – NaHCO₃ extracted inorganic P; NaOH-P_i – NaOH extracted inorganic P; D.HCl-P_i – diluted HCl extracted inorganic P; C.HCl-P_i – concentrated HCl extracted inorganic P; NaHCO₃-P_o – NaHCO₃ extracted organic P; NaOH-P_o – NaOH extracted organic P; * and ** indicate significant at 0.05 and 0.01, respectively

<https://doi.org/10.17221/60/2021-SWR>

DISCUSSION

It is known that red soils have high contents of iron oxides, and iron oxides influence the transformation of soil nutrients. For example, iron oxides together with oxyacid roots (e.g., H_2PO_4^-) are able to change such soil physicochemical processes as absorption, desorption, sedimentation, and dissolution, thus influencing the availability of soil nutrients (Parfitt 1989, Borggaard et al. 1990). Due to the special water management regimes, the redox potential in red paddy soils changes periodically, affecting the redox transformation of Fe. Previous studies have mainly been focused on the relationship between the iron oxides and P fractions in lowland paddy soils (Sun et al. 2008; Tang et al. 2014). Few studies have been conducted on their relationship in upland soils. In the present research, *S. oneidensis* MR-1, an Fe-reducing bacterium, was inoculated to an upland red soil. It was found that the free iron oxide content in the soil inoculated with *S. oneidensis* MR-1 was higher than that in the CK treatment, and that the activity of iron oxides decreased during incubation. The research data show that waterlogging increases the activity of iron oxides because the soil Eh decreases under waterlogging conditions, which is favourable for the transformation of Fe(III) to Fe(II) (Sah et al. 1989; Krairapanond et al. 1993; Su et al. 2001). In the present research, the soil Eh increased with time during the incubation without waterlogging. Therefore, the iron oxide activity did not increase.

The content of various P fractions in the soil is influenced by a variety of factors (Negassa & Leinweber 2009). According to the P fractionation method used in the present research, resin-P is the most bioavailable fraction among all P fractions. When the P in soil solution is depleted due to plant uptake, this fraction of P will replenish the soil solution quickly. In terms of availability, $\text{NaHCO}_3\text{-P}_i$ is second only to the resin-P (Zhang et al. 2009). Our results show that when the soil was inoculated with *S. oneidensis* MR-1, the resin-P increased, while the $\text{NaHCO}_3\text{-P}_i$ decreased. There was a significant negative correlation between the resin-P and $\text{NaHCO}_3\text{-P}_i$ (correlation coefficient of -0.81 and $P < 0.05$), indicating that the increase in the resin-P may be due to the transformative use of $\text{NaHCO}_3\text{-P}_i$ by *S. oneidensis* MR-1.

In red soils, P readily complexes with Fe and becomes unavailable (Mozaffari & Sims 1994, Nash & Halliwell 1999). The higher the content of free iron

oxides in the soil, the more P is fixed (Guo et al. 2012). In this study, the NaOH-P_i and residual-P were the prevalent P fractions, accounting for 40–45% of the total P. The free iron oxide content was positively correlated with that of NaOH-P_i . Such a relationship was also reported by Guo et al. (2012). Phosphorite is the major component of D.HCl-P in red soils (Zhang et al. 2009). In the present work, the D.HCl-P content was extremely low and remained stable during the incubation, which may be because the soil was acidic (Linghu et al. 2016). Of the P fractions, resin-P and $\text{NaHCO}_3\text{-P}_i$ changed greatly during the entire incubation period while the other fractions obviously changed at the early stage of the incubation, but were relatively stable in the later stages. The bacterial strain *S. oneidensis* MR-1 influenced the P availability by driving the transformation of Fe. In addition, when *S. oneidensis* MR-1 absorbs P from the available forms, the P becomes unavailable and organic.

CONCLUSION

S. oneidensis MR-1 inoculation increased the free iron oxide content in the soil and decreased the iron oxide activity. In addition, the *S. oneidensis* MR-1 inoculation increased the resin-P and residual-P, reduced the $\text{NaHCO}_3\text{-P}_i$, C.HCl-P_i, $\text{NaHCO}_3\text{-P}_o$ and NaOH-P_o , and had no significant influence on the D.HCl-P_i in the soil. The increase in the resin-P was mainly due to the transformation of $\text{NaHCO}_3\text{-P}_i$, while the increase in the residual-P was mainly due to the transformation of C.HCl-P_i. Inoculation of *S. oneidensis* MR-1 to red soils can increase the P bioavailability.

REFERENCES

- Baefan C. (1963): The content of iron phosphate in the paddy soils of southern China and their significance to the phosphorus nutrition of rice plant. *Acta Pedologica Sinica*, 11: 361–369.
- Borggaard O., Jørgensen S., Moberg J., Raben-Lange B. (1990): Influence of organic matter on phosphate adsorption by aluminium and iron oxides in sandy soils. *European Journal of Soil Science*, 41: 443–449.
- Chen X., Yu W., Shen S. (1997): Changes of soil phosphorus pool under low-input phosphorus fertilization system II. Soil available phosphorus and the composition of soil inorganic phosphorus. *Acta Pedologica Sinica*, 34: 81–88.

- de Mello J.W.V., Barron V., Torrent J. (1998): Phosphorus and iron mobilization in flooded soils from Brazil. *Soil Science*, 163: 122–132.
- Guo H., Zhou J., Luo X., Wang W., Wu X. (2012): Phosphorus fractions of latosols developed from different parent materials in rubber plantation of Hainan province. *Chinese Journal of Tropical Crops*, 33: 1724–1730.
- Huang J., Xu C., Ridoutt B.G., Wang X., Ren P. (2017): Nitrogen and phosphorus losses and eutrophication potential associated with fertilizer application to cropland in China. *Journal of Cleaner Production*, 159: 171–179.
- Jansson J.K. (2013): Microbiology: The life beneath our feet. *Nature*, 494: 40–41.
- Kaiser J.P., Bollag J.M. (1990): Microbial activity in the terrestrial subsurface. *Experientia*, 46: 797–806.
- Krairapanond A., Jugsujinda A., Patrick W. (1993): Phosphorus sorption characteristics in acid sulfate soils of Thailand: Effect of uncontrolled and controlled soil redox potential (Eh) and pH. *Plant and Soil*, 157: 227–237.
- Linghu R., Wang R., Liang J., Liao X., Zhan Z., Wu Y. (2016): Effects of iron reducing bacteria on the transformation of phosphorus in vegetable red soils. *Journal of Agro-Environment Science*, 9: 1742–1749.
- Lu R. (1999): *Agricultural Chemistry Analysis of Soil*. Beijing, China Agricultural Science and Technology Press. (in Chinese)
- Lu S.G., Malik Z., Chen D.P., Wu C.F. (2014): Porosity and pore size distribution of Ultisols and correlations to soil iron oxides. *Catena*, 123: 79–87.
- Maranguit D., Guillaume T., Kuzyakov Y. (2017): Effects of flooding on phosphorus and iron mobilization in highly weathered soils under different land-use types: Short-term effects and mechanisms. *Catena*, 158: 161–170.
- Mozaffari M., Sims J.T. (1994): Phosphorus availability and sorption in an Atlantic coastal plain watershed dominated by animal-based agriculture. *Soil Science*, 157: 97–107.
- Myers C.R., Nealson K.H. (1988): Bacterial manganese reduction and growth with manganese oxide as the sole electron acceptor. *Science*, 240: 1319–1321.
- Nash D.M., Halliwell D.J. (1999): Fertilisers and phosphorus loss from productive grazing systems. *Australian Journal of Soil Research*, 37: 403–429.
- Negassa W., Leinweber P. (2009): How does the Hedley sequential phosphorus fractionation reflect impacts of land use and management on soil phosphorus: A review. *Journal of Plant Nutrition and Soil Science*, 172: 305–325.
- Olsen S.R., Cole V., Watanabe F.S., Dean L.B. (1965): Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. Washington, D.C., USDA.
- Parfitt R. (1989): Phosphate reactions with natural allophane, ferrihydrite and goethite. *European Journal of Soil Science*, 40: 359–369.
- Rozan T.F., Tallefert M., Trouwborst R.E., Glazer B.T., Ma S.F., Herszage J., Valdes L.M., Price K.S., Luther G.W. (2002): Iron-sulfur-phosphorus cycling in the sediments of a shallow coastal bay: Implications for sediment nutrient release and benthic macroalgal blooms. *Limnology and Oceanography*, 47: 1346–1354.
- Sah R., Mikkelsen D., Hafez A. (1989): Phosphorus behavior in flooded-drained soils. II. Iron transformation and phosphorus sorption. *Soil Science Society of America Journal*, 53: 1723–1729.
- Song C., Wu J., Lu Y., Shen Q., He J., Huang Q., Jia Z., Leng S., Zhu Y. (2013): Advances of soil microbiology in the last decade in China. *Advances in Earth Science*, 28: 1087–1105.
- Su L., Lin X., Zhang Y., Yang Y. (2001): Effects of flooding on iron transformation and phosphorus adsorption-desorption properties in different layers of the paddy soils. *Journal of Zhejiang University (Agricultural & Life Sciences)*, 27: 124–128.
- Sun L., Qu D., Wei Y. (2008): Effect of illumination on iron oxide reduction in anaerobic paddy soils. *Acta Pedologica Sinica*, 45: 628–634.
- Tang B., Yang S., Wang D., Rao W., Zhang Y., Wang D., Zhu Y. (2014): Effect of sulfur on the species of Fe and As under redox condition in paddy soil. *Environmental Science*, 35: 3851–3861.
- Tiessen H., Moir J.O. (1993): Characterization of available P by sequential extraction. In: Carter M.R. (ed): *Soil Sampling and Methods of Analysis*. Boca Raton, CRC Press: 75–86.
- Van der Salm C., Van Middelkoop J.C., Ehlert P.A.I. (2017): Changes in soil phosphorus pools of grasslands following 17 yrs of balanced application of manure and fertilizer. *Soil Use Manage*, 33: 2–12.
- Wang L., Liang T. (2014): Effects of exogenous rare earth elements on phosphorus adsorption and desorption in different types of soils. *Chemosphere*, 103: 148–155.
- Zhang L., Wu N., Wu Y., Luo P., Liu L., Chen W., Hu H. (2009): Soil phosphate form fraction scheme. *Chinese Journal of Applied Ecology*, 20: 1775–1782. (in Chinese)

Received: April 21, 2021

Accepted: December 13, 2021

Published online: January 10, 2022