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Exogenous Organic Matter Improves Potato Yield by Regulating the Microbiological Fertility Index

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Abstract: The nutrient availability of carbon (C), nitrogen (N), and phosphorus (P) has been decreasing due to a decline in the biological function of yellow soil, limiting potato yield (PY). Increasing biochar or organic fertilizer input is an effective way to improve soil microbiological fertility. However, indexes to regulate soil microbiological fertility using biochar and organic fertilizer individually or in combination and these indexes' associations with PY remain unclear. In this study, four fertilization strategies were developed using the nutrient balance method: CK (recommended NPK fertilization), BC (NPK + biochar), OF (NPK + organic fertilizer), and BF (NPK + 1/2 biochar + 1/2 organic fertilizer). Using different fertilization strategies, the eco-stoichiometry characteristics of the soil microbial biomass and enzyme activity; the bioavailability of C, N, and P; and the differences in PY were investigated, and the direct and indirect effects of these factors on PY were determined over a two-year period. The results showed that exogenous organic matter input could considerably affect the stoichiometric ratios of soil microbial biomass; C; N; P; the stoichiometric ratios of C-converting, N-converting, and P-converting enzyme activities (expressed as BG+CBH, NAG+LAP, and AP, respectively); and the integrated enzyme index (IEI). The IEI was the highest in BF, followed by OF, BC, and CK. A significant positive correlation was found between the microbial biomass C, N, and P and their corresponding converting enzyme activities ($p < 0.05$). The ln(BG+CBH):ln(NAG+LAP), ln(BG+CBH):lnAP, and ln(NAG+LAP):lnAP ratios were all higher than 1:1, but they approached 1:1 in the order of CK-BC-OF-BF. Compared to soil C and N, P-converting enzyme activity was the primary limiting factor for soil nutrient conversion in the study area. BF was less restricted by P and more balanced in its nutrient ratio. The microbial biomass C:N:P could affect PY in eight ways. (1) Microbial biomass C:N directly decreased PY, and microbial biomass C:P indirectly increased PY. (2) It could decrease C-converting enzyme activity, (3) decrease N availability to increase C-converting enzyme activity, (4) decrease P availability, or (5) decrease P availability to decrease the soil C:P-converting enzyme activity ratio. Microbial biomass N:P indirectly increased PY (6) by increasing the soil C:P-converting enzyme activity ratio, (7) by increasing C-converting enzyme activity, or (8) by increasing N availability to increase C-converting enzyme activity. Thus, BF is an effective strategy for regulating the soil microbiological fertility index; enhancing C, N, and P nutrient conversion; and increasing PY. The input of exogenous organic matter can alter the stoichiometric ratios of soil microbial biomass C, N, and P; the stoichiometric ratios of C-converting, N-converting, and P-converting enzyme activities; and nutrient availability, thus regulating PY. Microbial biomass N:P and soil C:P-converting enzyme activity ratios influence PY the most.

Keywords: biochar; eco-stoichiometry; microbiological fertility; organic fertilizer; PY; structural equation models

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1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth-highest-yield food crop in the world [1]. The potato planting area in Guizhou Province in Southwest China ranks second in China, accounting for 12.64% of the total nationwide [2]. However, the average per-unit yield only ranks 16th in China [3]. One reason for the low potato yield is that the climatic characteristics of Guizhou, where rain and heat coincide and rainfall exceeds evapotranspiration, cause farmland plant biomass to oxidize and decompose very quickly [4]. This, coupled with the long-term application of large amounts of chemical fertilizers, not only fails to compensate for the lack of soil organic matter but also exacerbates the depletion of organic matter [5], ultimately resulting in the decline of the biological function of the loess, a decrease in soil fertility, and the deterioration of the effectiveness of the soil C, N, and P nutrients [6,7]. Increasing the input of exogenous organic matter can improve soil microbial biomass and enzyme activity, affecting nutrient bioavailability and crop yield, and this has attracted global attention [8]. Soil microbial biomass is the living component of soil organic matter and serves as the "source" and "sink" of soil nutrients, primarily N and P. By fixation and mineralization, soil microbial biomass controls the C, N, and P flow in the soil ecosystem [9]. Moreover, soil microbes can also convert organic matter through extracellular enzymes into inorganic forms, significantly altering the soil C:N:P ratio and nutrient availability. Therefore, it is essential to study the eco-stoichiometry characteristics of microbial biomass and enzyme activity under different exogenous organic matter inputs and their relationships to assess the bioavailability of C, N, and P and to reveal the direct and indirect influence of these factors on PY. The findings will be of great value for determining the limiting nutrients of the soil ecosystem in the study area and understanding the mechanism for increasing PY.

Currently, most research on microbial biomass focuses on the microbial biomass C (MBC):N (MBN):P (MBP) ratio and its relationship with the soil C:N:P ratio. Globally, the MBC:MBN:MBP average is 42:6:1 [10], and the soil C:N:P average is 186:13:1 [11]. Allison et al. found that microbial biomass communities with different MBC:MBN:MBP ratios can obtain limiting nutrients from complex substrates by secreting specific extracellular enzymes, thus altering soil enzyme stoichiometry [12]. β-1,4-glucosidase (BG) and cellobiohydrolase (CBH) are both enzymes closely related to C conversion, and β-1,4-acetylglucosaminase (NAG) and leukine aminopeptidase (LAP) are two enzymes closely related to N conversion, whereas alkaline phosphatase (AP) is closely related to P conversion. In recent years, many reports have focused on the effects of chemical fertilizer reduction [13], organic fertilizer increase [14], and replacement of chemical fertilizer with organic fertilizer [15] on soil microbial biomass and enzyme activity. Research has suggested that organic and inorganic fertilizer application can considerably improve soil enzyme activities and microbial biomass C, N, and P contents. However, studies have mainly focused on the effect of chemical fertilizer reduction or its replacement with organic fertilizer on crop yield and soil properties. Little attention has been paid to regulating the strategies for exogenous organic matter input and its effect on soil microbiological fertility, especially the association between microbial biomass C, N, and P stoichiometry and enzyme activity stoichiometry and crop yield. According to previous studies, increasing the input of exogenous organic matter, such as organic fertilizer, can increase soil's microbial activity, considerably improving soil's microbial biomass C, N, and P contents and soil enzyme activity. Based on an appropriate proportion of C, N, and P in the soil, microbes will preferentially convert limiting elements [16]. For example, a low soil MBC:MBN indicates that N is more abundant than C in the soil. In this case, microbes will mineralize soil organic matter to supplement the soil C pool, increasing the restriction of soil C on microbes. If the soil MBC:MBN is high, C is more abundant than N, wherein microbes must assimilate more N to maintain their normal growth and development and may compete with plants for N [17]. According to the concept of soil enzyme stoichiometry, (BG+CBH):(NAG+LAP), (BG+CBH):AP, and (NAG+LAP):AP are often associated with C:N, C:P, and N:P and can be used for assessing the nutrient supply of microbial biomass C, N, and P. Sinsabaugh et al. [18] found that BG, NAG, and AP activities increase gradually with an increase in soil organic matter. The BG:(NAG+LAP):AP ratio is close to 1:1:1, resulting in a balanced ratio of soil C, N, and P [18]. If ln(NAG+LAP):lnAP is above 1:1, the soil P-converting enzyme activity limits the conversion rate of soil nutrients more than N. If ln(BG+CBH):ln(NAG+LAP) and ln(BG+CBH):lnAP are higher than 1:1, the conversion rate of soil nutrients is more limited by the N- and P-converting enzyme activities than by C.

China has implemented a series of measures to improve soil fertility for many years, such as organic fertilizer subsidies and straw turnover, to improve the soil organic matter level. The surface soil SOC (soil organic carbon) content in the study area was only 8.47 $g \cdot kg^{-1}$, which was not only lower than the global terrestrial SOC content (25.71 $g \cdot kg^{-1}$) [19] but also lower than China's terrestrial SOC content (17.12 $g \cdot kg^{-1}$) [19]. It was also lower than the average SOC content in Guizhou Province (27.34 $g \cdot kg^{-1}$) [20] and the Karst region of Guangxi (24.23 $g \cdot kg^{-1}$) in the southwestern region of China [21]. However, changes in soil microbial activity are driven by changes in active organic C content and affected by the types of exogenous organic matter. Methods to regulate soil microbiological fertility using biochar and organic fertilizer individually or in combination and their influence on PY need to be determined. Biochar is a C-rich product of biomass pyrolysis at high temperatures in a low-oxygen environment. Rich pores can provide a habitat for microbes and retain nutrients and water, but inert C is dominant and, thus, is not the active C source for soil microbes [22]. Applying organic fertilizer can generally increase the active organic C content in soil and provide energy substances for microbes. Still, its ability to retain nutrients, fix C, and reduce discharge is much weaker than that of biochar [23]. In contrast, applying chemical fertilizer (especially N fertilizer) can facilitate the accumulation of easily oxidized organic C and is superior to biomass C and organic fertilizer in increasing crop yield. Still, it will reduce the content of water-soluble organic C, limiting microbial activity [24]. Therefore, it is hypothesized that biochar and organic fertilizer can complement each other based on recommended fertilization. This is an ideal input strategy to increase soil microbial biomass, stimulate soil enzyme activity, and improve soil nutrient availability.

Given this, four strategies of exogenous organic matter input were developed in this study in dry yellow soil, following the nutrient balance principle, and the PY; soil C, N, and P contents; soil microbial biomass C, N, and P; and activities of extracellular enzymes related to C, N, and P conversion were investigated to determine the following using eco-stoichiometry: (1) the influence of different strategies of exogenous organic matter input on soil microbial biomass C, N, and P stoichiometry; enzyme activity stoichiometry; and C, N, and P bioavailability; (2) the limiting factors for soil nutrient conversion rate in the study area to propose effective fertilization strategies; and (3) the biological mechanism of fertilization strategies influencing PY. The results will be significant for optimizing and upgrading soil fertility and improving PY.

2. Materials and Methods

2.1. Study Area

The study area was located in Tangjiazhai Village (27°47′32″ N, 109°13′8″ E), Chuandong Street, Bijiang District, Tongren City, Guizhou Province, China. This is in the northeast of Guizhou Province and east of Tongren City. This area has a subtropical monsoon humid climate, with an annual average temperature of 16.9 °C, an annual frost-free period of 291 days, an annual rainfall of 1265.4 mm, an annual sunshine of 1171 h, and an altitude of 434 m. It has mountainous yellow soil and silty clay loam soil. According to the United Nations FAO/UNESCO classification [25], the soil in the test site is a sandy clay loam with strong leachability. The gravel content was 3.48%, sand content was 45.15%, sediment content was 20.86%, clay content was 23.58%, and the soil capacity was 1.35 $kg \cdot m^{-3}$. The soil fertility of the study area was low: the soil pH was 6.23, the organic carbon was 8.47 $g \cdot kg^{-1}$, the alkali-hydrolysable N was 10.51 $mg \cdot kg^{-1}$, the available P was 5.42 $mg \cdot kg^{-1}$, rapidly available K was 42.13 $mg \cdot kg^{-1}$.

2.2. Experimental Design

In this study, the potato field experiment was conducted with C, N, and P, and K nutrient inputs. The trial was conducted in farmer fields for two consecutive growing seasons from 2022 to 2023. The crop grown prior to the trial was potatoes in a one-per-year maturity system, which was harvested and left fallow. Four strategies were developed: CK (recommended NPK fertilization as the control), BC (NPK + biochar), OF (NPK + organic fertilizer), and BF (NPK + 1/2 biochar + 1/2 organic fertilizer). Firstly, the amount of pure nutrients of nitrogen, phosphorus, and potassium brought in by biochar at the recommended application rate was calculated according to the nitrogen, phosphorus, and potassium percentage of biochar. Then, the amount of organic fertilizer input was converted according to the principle of C-equivalence between biochar and organic fertilizer. Next, the amount of pure nutrients of nitrogen, phosphorus, and potassium brought in by the application of organic fertilizer was calculated according to the nitrogen, phosphorus, and potassium percentage of organic fertilizer. Finally, the amount of fertilizer supplement was calculated according to the recommended fertilizer amount and the principle of NPK nutrient balance (Table 1). CK: the N fertilizer used was urea (N, 46%), the P fertilizer was heavy superphosphate (P_2O_5, 46%), the K fertilizer was potassium chloride (K_2O, 60%), and the recommended dosage was N at 150 kg·hm^{-2}, P_2O_5 at 135 kg·hm^{-2}, and K_2O at 135 kg·hm^{-2} [26]. BC: the biochar tested was corn stalk C at pH 8.23 with ω (C) = 52%, ω (N) = 0.11%, ω (P_2O_5) = 0.40%, and ω (K_2O) = 0.15%, and the recommended dosage was 2.0 t·hm^{-2}. OF: The organic fertilizer was sheep manure, with ω (C) = 15.7%, ω (N) = 0.75%, ω (P_2O_5) = 0.51%, and ω (K_2O) = 0.42 g·kg^{-1}. The amount of sheep manure added was 6.6 t·hm^{-2} (dry basis) following the corn stalk C-equal amount principle. BF: 1.0 t·hm^{-2} biochar and 3.3 t·hm^{-2} organic fertilizer were input synergistically. The NPK nutrients in BC, OF, and BF were the same as those in CK, and they were supplemented with CK fertilizer when insufficient. A randomized block trial design was adopted and repeated three times using the potato variety "Nongyin No. 2". The plot area was 30 m^2 with twelve plots covering a total of 360 m^2. The plant spacing was 30 × 50 cm. Biochar and organic fertilizers were applied to the ridge once when the potato was sown (during the third week of February each year). The fertilizer dosage and field management were the same as those of ordinary production fields, in which all P and K fertilizers were used as the basal fertilizer, 50% N fertilizer was used as the basal fertilizer, and 50% N fertilizer was used as the topdressing. The remaining 50% of the nitrogen fertilizer was spread in four equal portions around the roots of potato plants on 15 March, 15 April, 15 May, and 15 June each year, after which the soil was turned over and covered.

Table 1. Fertilization amounts for different treatments/kg·hm^{-2}.

Nutrient	CK	BC	OF	BF
N	150	2 (148)	50 (100)	26 (124)
P_2O_5	135	8 (127)	34 (101)	21 (114)
K_2O	135	3 (132)	28 (107)	15 (120)

The numbers outside the brackets indicate the amount of NPK pure nutrients introduced by biochar or organic fertilizer, and the numbers inside the brackets indicate the amount of chemical fertilizer supplement.

2.3. Sample Collection and Analysis

With the border row in each plot removed during the potato harvesting time (late June to early July), five potato plants with similar growth statuses and no diseases or insect pests were collected in each plot along an "S"-shaped distribution. Rhizosphere soil samples were collected by shaking the root and were mixed into treatment samples. One portion of soil samples was air-dried and stored to detect soil nutrients. The other portion was stored in a refrigerator at 4 °C to determine the soil microbial biomass and enzyme activity.

In addition, five whole plants collected in each plot were tested for seeds, and potato tubers were weighed and graded as large tubers (>150 g), medium tubers (75–150 g), and small tubers (<75 g). The number of missing plants and variant plants in the plot were investigated. The actual final harvest plants in the plot were determined, the entire harvest was taken as the yield, and the commodity potato rate was calculated.

Soil nutrients and microbial biomass were determined. Soil organic carbon (SOC) was determined using the potassium dichromate oxidation method [27]. Soil total N (TN) was determined using a Kjeldahl nitrogen analyzer (KDN-812, Shanghai, China) after digestion with concentrated sulfuric acid [28]. Soil total P (TP) was detected via Mo–Sb colorimetry using an EdgeLight UV754 spectrophotometer (Shanghai, China) [28]. Microbial biomass C, N, and P was determined by the chloroform fumigation–K_2SO_4 extraction method [29].

Soil extracellular enzyme activity was determined. Five essential soil extracellular enzymes were selected: BG, CBH, NAG, LAP, and AP. All soil extracellular enzymes were extracted and cultured according to the method by Saiya-Cork [30], and their activities were excited at 365 nm and measured at 450 nm using a multifunctional microplate reader (Tecan/Spark, Männedorf, Switzerland) with 96-well microplates. See Table S1 for the corresponding reaction substrates. The enzyme activity stoichiometric ratio was expressed as ln(BG+CBH):ln(NAG+LAP):lnAP.

The integrated enzyme index (*IEI*) was calculated in four steps [31]:

(1) Selection of factors: Five key extracellular enzymes related to soil C, N, and P cycles were selected: BG, CBH, NAG, LAP, and AP.

(2) Determination of membership degree ($IEI(x_i)$): The membership degree of extracellular enzymes was calculated using a single-factor evaluation model, and the measured value of extracellular enzyme activity was converted into a value between 0 and 1 to achieve dimensional normalization of the index.

$$IEI(x_i) = (x_{ij} - x_{i\,min})/(x_{i\,max} - x_{i\,min}) \tag{1}$$

Here, x_{ij} represents soil enzyme activity, and $x_{i\,max}$ and $x_{i\,min}$ represent the maximum and minimum soil enzyme *i* activity, respectively.

(3) Determination of weight (W_i): This was determined by correlation coefficients between different enzyme activities. The calculation equation is as follows:

$$W_i = C_i/C. \tag{2}$$

C_i is the average correlation coefficient between the individual enzyme activity and other enzyme activities, and C is the sum of all averaged correlation coefficients.

(4) *IEI*

An ascending distribution function was used to calculate the *IEI*:

$$IEI = \sum_{i=1}^{n} w_i \times IEI(x_i) \tag{3}$$

where the *IEI* is the integrated enzyme index, w_i represents the weight of soil enzyme *i*, and $IEI(x_i)$ represents the membership degree of enzyme *i*.

The commodity potato rate (*CPR*) was calculated as follows:

$$CPR/\% = m_1/m \times 100\% \tag{4}$$

where m_1 is the fresh weight of large and medium tubers, and *m* is the total fresh weight of the tubers.

2.4. Statistical Analysis

First, Microsoft Excel 2010 was used for data processing, and *IEI* was calculated using Equation (3). One-way ANOVA and homogeneity of variance tests were carried out for the soil extracellular enzyme activity and the eco-stoichiometric ratio among groups using the SPSS 27.0 software package. Then, based on the soil microbiological fertility index, a linear regression model was established with extracellular enzyme activity as the dependent variable and microbial biomass as the independent variable, and $p < 0.05$ was considered statistically significant. Limiting factors of soil C, N, and P conversion were explored based on the enzyme activity stoichiometric ratio. Finally, the structural equation model (SEM) was used as a generalized conceptual model to assess the direct and indirect influence pathways of the soil microbiological fertility index on PY. The SEM considered the soil microbial biomass characteristics (i.e., MBC, MBN, MBP, MBC:MBN, MBC:MBP, and MBN:MBP), extracellular enzyme activity characteristics (i.e., BG+CBH, NAG+LAP, AP, ln(BG+CBH):ln(NAG+LAP), ln(BG+CBH):lnAP, ln(NAG+LAP):lnAP), and C, N, and P bioavailability characteristics (i.e., MBC:SOC, MBN:TN, and MBP:TP). To fit the model and reduce the SEM complexity, we removed the insignificant effects of factors using the backward stepwise selection procedure for the full model. At each step of this procedure, the insignificant path with the highest p value was removed sequentially from the model. The reduced model fit was evaluated at each step using Fisher's C statistic and the AUC value. A reduced model was accepted at each step to provide a good fit to the data if the Fisher's C statistic test was insignificant ($p > 0.05$). Finally, the best model with the lowest AUC value was chosen.

SPSS 27.0 was used for one-way ANOVA, Pearson correlation analysis, and regression analysis, and Origin 2018 was used for plotting. Structural equations were constructed based on the piecewiseSEM package of R (V.4.2.1).

3. Results

3.1. Influence of Different Exogenous Organic Matter Inputs on Soil Microbial Biomass Stoichiometric Ratio and C, N, and P Bioavailability

Microbial biomass C, N, and P (MBC, MBN, MBP) are the reservoir pools of active soil nutrients. The microbial biomass C:N:P ratio reflects whether nutrients meet the needs of microbial growth and determines the activation degree of soil C, N, and P. BC, OF, and BF significantly decreased MBC:MBN and MBC:MBP compared with CK, but significantly increased MBN:MBP (Figure 1a). As shown in Figure 1a, biochar plus organic fertilizer was observed to have the greatest influence on soil microbial biomass C:N:P, while biochar alone had the least influence on soil microbial biomass C:N:P.

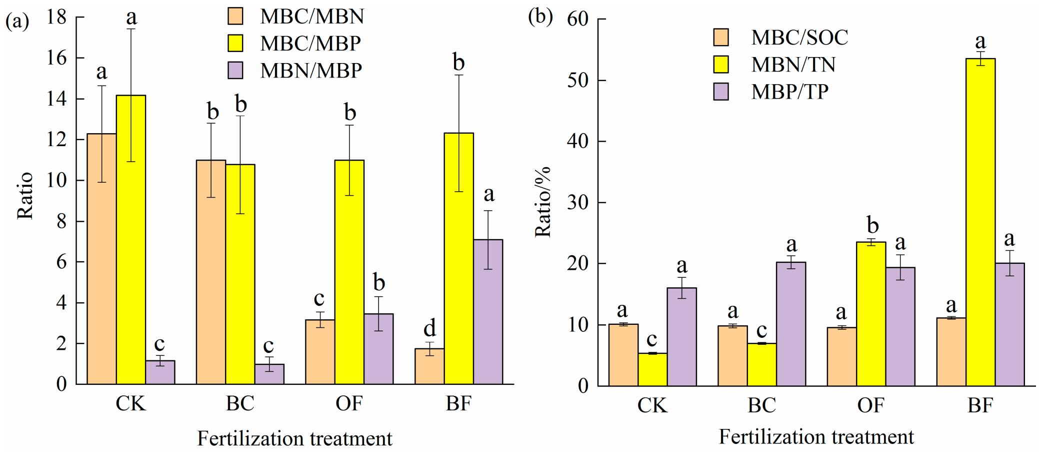

Figure 1. Differences in (**a**) the soil microbial biomass stoichiometric ratio and (**b**) C, N, and P bioavailability with different inputs of exogenous organic matter. Different lowercase letters on the column indicate significant differences between treatments ($p < 0.05$).

MBC:SOC and MBN:TN indicate the soil C, N, and P bioavailability to some extent. Compared with CK, different input strategies of exogenous organic matter did not significantly alter soil MBC:SOC or MBP:TP but significantly increased soil MBN:TN ($p < 0.05$). MBN:TN was the highest in BF, followed by OF, and the lowest in BC (Figure 1b). In addition, although exogenous organic matter input did not significantly alter soil MBP:TP, MBP:TP increased by 20.80–26.11% compared with using CK.

3.2. Influence of Different Inputs of Exogenous Organic Matter on Soil Enzyme Activities

Different inputs of exogenous organic matter significantly influenced extracellular enzyme activities related to C, N, and P conversion ($p < 0.05$). The activities were the highest in BF, followed by OF, BC, and CK. The C-converting enzyme activities (BG+CBH) in BF, BC, and OF were 2.6, 1.6, and 1.2 times that in CK, respectively (Figure 2a). The N-converting enzyme activities (NAG+LAP) were 2.2, 1.9, and 1.1 times that in CK, respectively, and there was no significant difference between BC and CK (Figure 2b). The P-converting enzyme activities (AP) were 2.0, 1.7, and 1.3 times that in CK (Figure 2c).

IEI comprehensively reflects the activities of all soil extracellular enzymes and can objectively show the changes in soil extracellular enzyme activities. As shown in Figure 2d, *IEI* was significantly different with different exogenous organic matter ($p < 0.05$): BF (67.0) > OF (38.3) > BC (21.2) > CK (14.6).

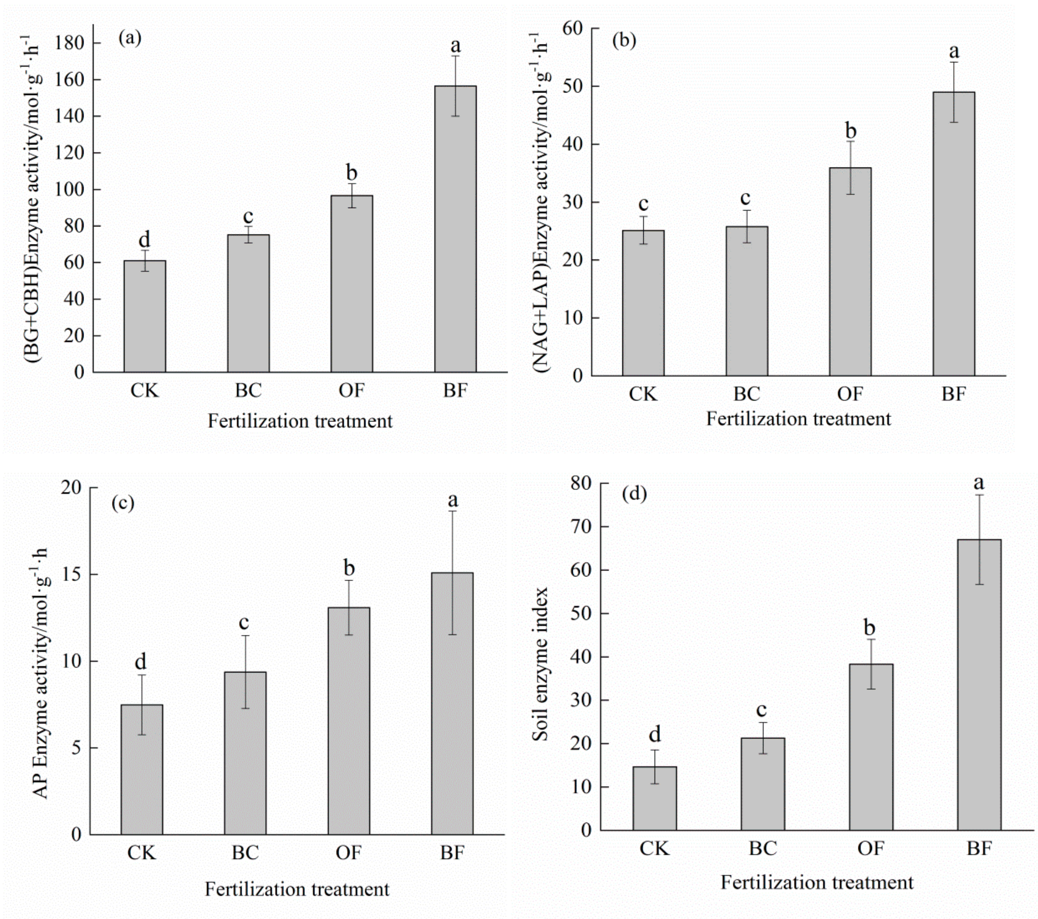

Figure 2. Changes in (**a**–**c**) extracellular enzyme activities and (**d**) the IEI with different inputs of exogenous organic matter. BG+CBH represents the sum of the activities of enzymes BG and CBH related to soil C conversion, NAG+LAP represents the sum of the activities of enzymes NAG and LAP related to N conversion, and AP represents the enzymes related to P conversion. Different lowercase letters on the column indicate significant differences between treatments ($p < 0.05$).

3.3. Correlations between Soil Extracellular Enzyme Activities and Microbial Biomass C, N, and P

Significant linear positive correlations were found between BG+CBH and MBC, between NAG+LAP and MBN, and between AP and MBP (Figure 3a–c, respectively), with coefficients of determination of 0.74, 0.84, and 0.62, respectively, suggesting that increases in MBC, MBN, and MBP will significantly enhance the activities of enzymes related to soil C, N, and P. According to the fitting equation, the activities of BG+CBH, NAG+LAP, and AP increased by 0.856, 0.194, and 0.788 mol·g^{-1}·h^{-1}, respectively, with every 1 mg·kg^{-1} increase in MBC, MBN, and MBP.

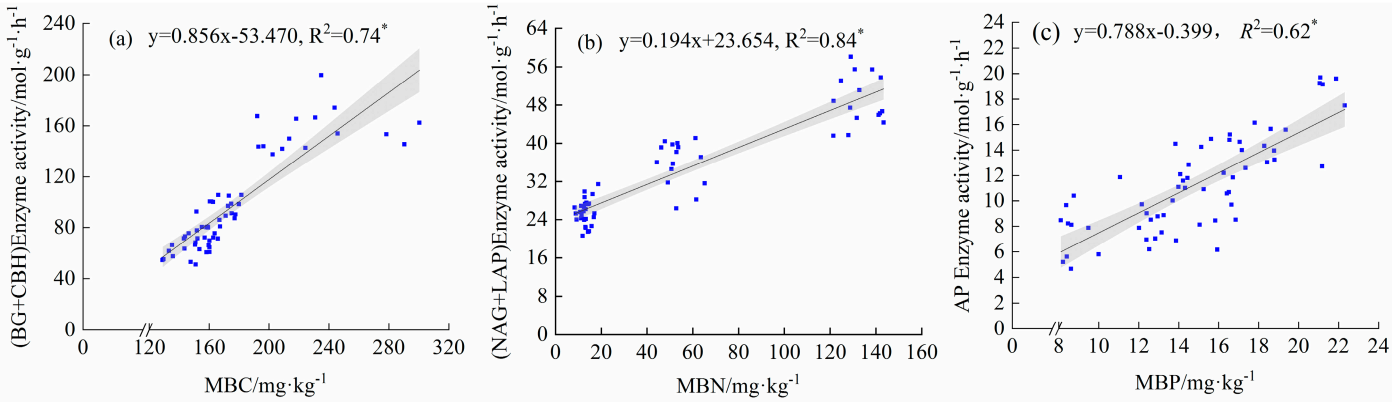

Figure 3. Regression analysis of (**a**) C-converting enzyme activity and C microbial biomass, (**b**) N-converting enzyme activity and N microbial biomass, and (**c**) P-converting enzyme activity and P microbial biomass P. BG+CBH represents the sum of the activities of enzymes BG and CBH related to soil C conversion, NAG+LAP represents the sum of the activities of enzymes NAG and LAP related to N conversion, and AP represents an enzyme associated with P conversion. * $p < 0.05$.

3.4. Stoichiometric Relationships of Soil Extracellular Enzymes

Ln(BG+CBH):ln(NAG+LAP), ln(BG+CBH):lnAP, and ln(NAG+LAP):lnAP showed linear positive correlations in the four treatments, with all above 1:1 (Figure 4a–c, respectively). The ratios of Ln(BG+CBH):ln(NAG+LAP) (Figure 4a) and ln(BG+CBH):lnAP (Figure 4b) being above 1:1 suggest that the soil nutrient conversion rate was limited by the activities of enzymes related to soil N and P conversion compared to C. The ln(NAG+LAP):lnAP ratio above 1:1 (Figure 4c) indicated that the soil nutrient conversion rate was limited by the activity of soil P-converting enzyme compared to N. Ln(BG+CBH):ln(NAG+LAP) was closer to 1:1 than ln(BG+CBH):lnAP, indicating that the soil nutrient conversion rate was more limited by the activities of enzymes related to P conversion than those related to N. In addition, the soil enzyme activity stoichiometric ratios gradually approached 1:1 in the order of CK-BC-OF-BF, indicating that nutrients most strongly limited CK. At the same time, BF was less limited by N or P than BC and OF, with a more balanced nutrient ratio.

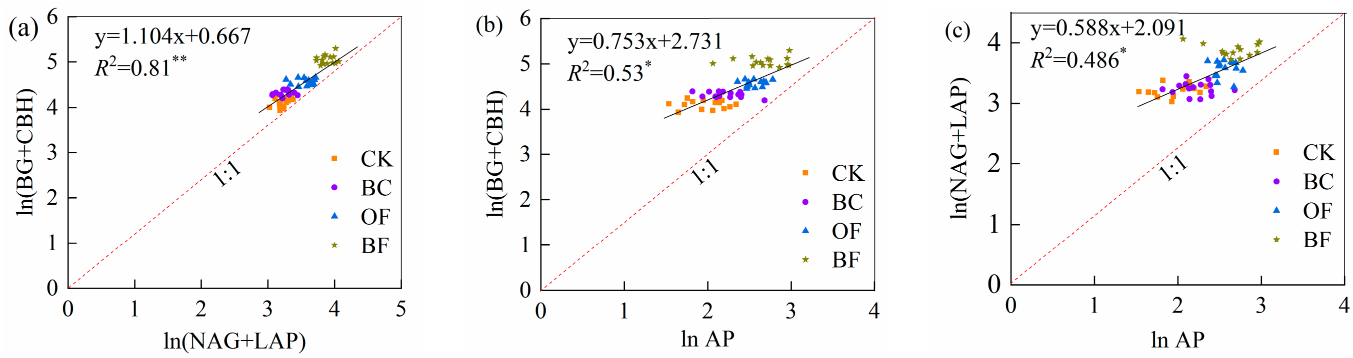

Figure 4. Stoichiometric relationships between (**a**) soil C- and N-converting enzyme activities, (**b**) C- and P-converting enzyme activities, and (**c**) N- and P-converting enzyme activities. Ln(BG+CBH) represents the natural logarithm of the sum of the activities of enzymes BG and CBH related to soil C conversion, ln(NAG+LAP) represents the natural logarithm of the sum of the activities of enzymes NAG and LAP related to N conversion, and ln(AP) represents the natural logarithm of enzyme AP associated with P conversion. The red dotted line indicates an enzyme activity ratio of 1:1, and the black solid line shows the trend line of the enzyme activity ratio. The ratio above the dotted line is greater than 1:1, that below the dotted line is less than 1:1, and that near the dotted line is close to 1:1. * $p < 0.05$; ** $p < 0.001$.

3.5. Influence of Different Exogenous Organic Matter Inputs on PY

Different exogenous organic matter inputs had different effects on PY. Specifically, OF and BF significantly increased PY ($p < 0.05$). BC had no significant influence on PY (Figure 5a). The CPR was maintained between 36.9% and 65.5%, and it was the highest (65.5%) in BF, which increased by 28.62%, 21.11%, and 8.90% over those in CK, BC, and OF, respectively (Figure 5b).

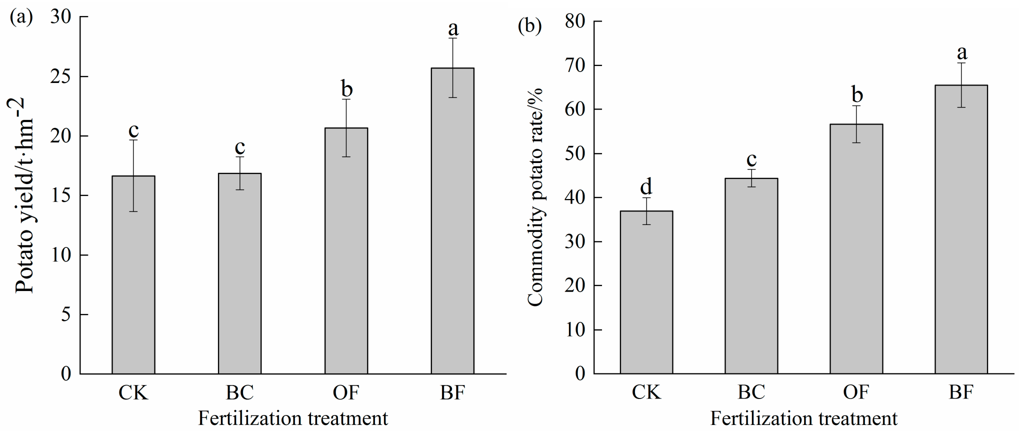

Figure 5. Differences in (**a**) PY and (**b**) CPR from different exogenous organic matter inputs. Different lowercase letters on the column indicate significant differences between treatments ($p < 0.05$).

3.6. Influence of the Soil Microbiological Fertility Index on PY

As shown by the optimal structural equation (Fisher's C = 20.59, df = 26, p = 0.76), soil MBC:MBP, MBC:MBN, MBN:MBP, MBP:TP, MBN:TN, EC:EP, and BG+CBH contributed to 79% of the change in PY (Figure 6a). MBC:MBP accounted for 18% of the change in MBP:TP. MBN:MBP and MBP:TP accounted for 84% of the change in EC:EP. MBN:MBP and MBC:MBP accounted for 74% of the change in MBN:TN. In addition, MBC:MBP, MBN:TN, and MBN:MBP accounted for 88% of the change in BG+CBH (Figure 6a).

As shown in Figure 6a, EC:EP (Ln(BG+CBH):LnAP) had a direct positive influence [standardized effect (SE) = 0.77)] on PY. BG+CBH had a direct positive influence (SE = 0.25) on PY. MBP:TP had a direct positive influence (SE = 0.56) on PY or had a significant negative influence on PY via EC:EP (SE = −0.59). Moreover, MBC:MBN had a significant negative correlation with PY (SE = −0.30). MBC:MBP had four pathways of indirect influence on PY. (1) It negatively and indirectly influenced PY via MBP: TP (SE = −0.24); (2) it positively and indirectly influenced PY via MBP:TP and EC:EP (SE = 0.25); (3) it negatively and indirectly influenced PY via BG+CBH (SE = −0.03); (4) it negatively and indirectly influenced PY via MBN:TN and BG+CBH (SE = −0.02). MBN:MBP had three pathways of indirect influence on PY. (1) It positively and indirectly influenced PY via EC:EP (SE = 0.32); (2) it positively and indirectly influenced PY via MBN:TN and BG+CBH (SE = 0.08); (3) it positively and indirectly influenced PY via BG+CBH (SE = 0.15). In general, soil MBN:MBP and EC:EP had the most influence on PY compared with soil enzyme activities, while soil MBP:TP had the most indirect influence on PY (Figure 6b).

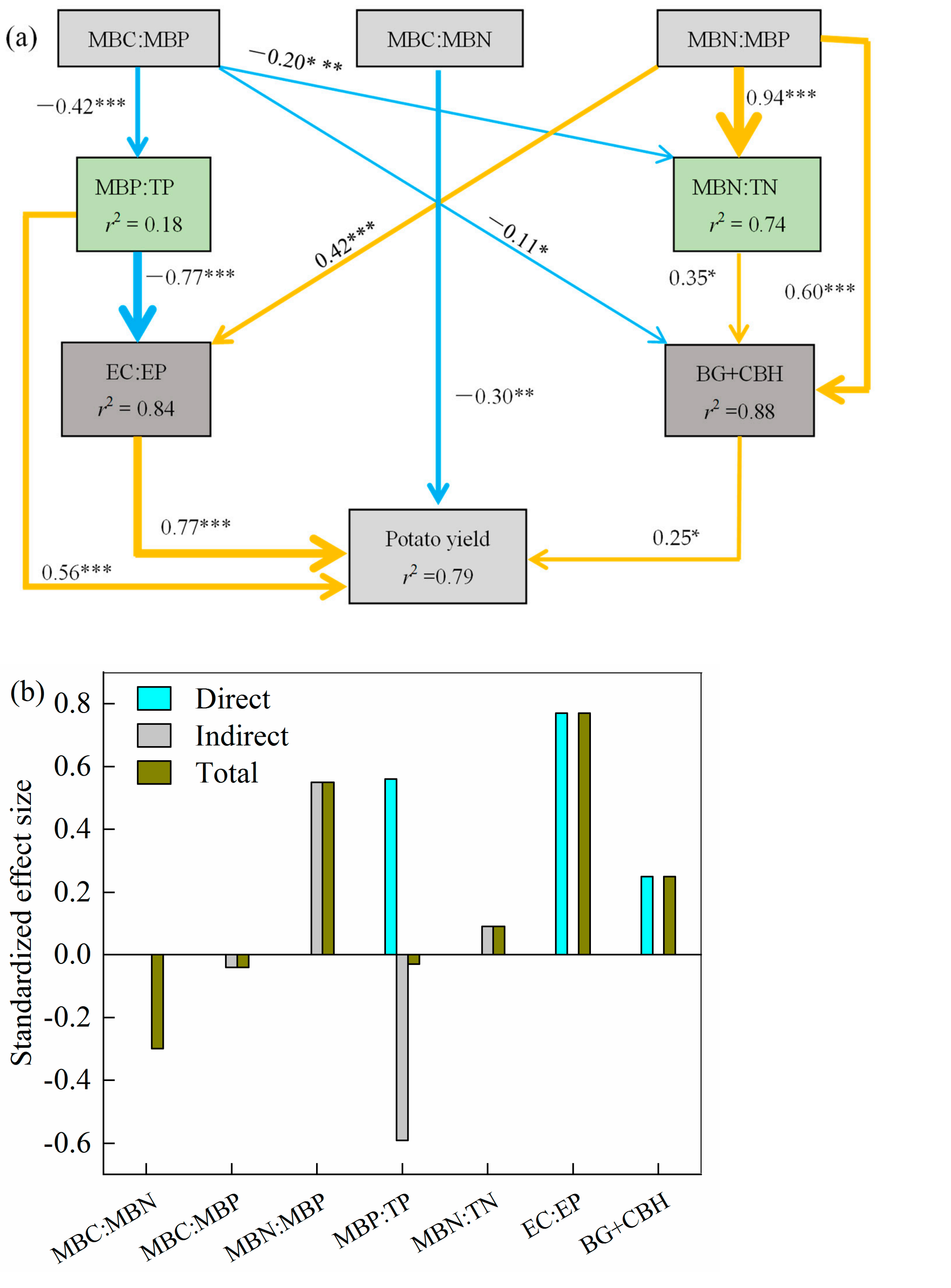

Figure 6. Model of optimal pathways for PY (**a**). The model was supported by the data (Fisher's C = 20.59, *df* = 26, p = 0.76). The number adjacent to the arrow line is the standardized coefficient that shows the variance explained by the variable. The width of the line is proportional to the strength of factor loading (values are also provided). The yellow and blue lines indicate the positive and negative effects, respectively. (**b**) The standardized direct, indirect, and total effect sizes of the soil microbiological fertility index were calculated by summing the direct and indirect effects derived from the best pathway. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. MBC:MBN, soil microbial biomass C:N; MBC:MBP, soil microbial biomass C:P; MBN:MBP, soil microbial biomass N:P; MBP:TP, soil microbial biomass P:total P; MBN:TN, soil microbial biomass N:total N; BG+CBH represents the sum of the activities of the enzymes BG and CBH related to soil C conversion; EC:EP, soil C:P-converting enzyme activities, i.e., ln(BG+CBH): lnAP. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

4. Discussion

4.1. Differences in Microbial Biomass Stoichiometric Ratios and C, N, and P Bioavailability with Different Inputs of Exogenous Organic Matter

The soil MBC:MBN ratio characterizes the microbial community structure in the soil. Generally, C:N is between 7 and 12 in fungi and between 3 and 6 in bacteria [32]. Our results showed that MBC:MBN decreased in the order of CK-BC-OF-BF, with mean values of 12.27, 10.99, 3.17, and 1.74, respectively (Figure 1a). The type of exogenous organic matter can significantly alter the ratio of bacteria to fungi in the overall community structure of soil, and in this study, MBC:MBN changed the most with synergistic input of biochar and organic fertilizer, consistent with previous research results [33,34]. In particular, MBN:MBP in BF (approximately 7:1) increased considerably over that in CK (Figure 1a) and was slightly higher than the global average (6:1) [10], suggesting that soil N is abundant, but P is relatively limited in BF. In this case, microbes need to assimilate more P to maintain their normal growth and development, manifested by the enhanced P fixation capacity, which may generally produce competition with plants for P. Therefore, N fertilizer should be reduced, and P fertilizer should be supplemented in future production.

MBC:SOC, MBN:TN, and MBP:TP represent the soil C, N, and P bioavailability, respectively, and the higher the ratios, the higher the soil C, N, and P activities [35]. In this study, synergistic input of biochar and organic fertilizer considerably increased the N bioavailability (Figure 1b). The abundant biochar pores can provide a habitat for microbes and fix nutrients and water. Organic fertilizer is an abundant C source. The synergistic input of biochar and organic fertilizer enhanced MBN fixation and organic N mineralization, which is the possible reason for the sharp increase in MBN:TN in BF.

4.2. Changes in Soil Extracellular Enzyme Activities with Different Inputs of Exogenous Organic Matter

Previous studies on enzyme activity have mainly focused on the relationship between enzyme activity and soil properties, land use patterns [36], and the dynamic change in enzyme activity with crop growth period or season [37]. However, little attention has been paid to quantifying the correlation between extracellular enzyme activity and MBC, MBN, and MBP. Enzymes originate from microbes, and enzyme activity affects microbial activity. Thus, determining their relationship is important for understanding the biological mechanism of nutrient conversion. In this study, the activities of enzymes related to soil C, N, and P conversion had linear positive correlations with MBC, MBN, and MBP, respectively (Figure 3a–c), suggesting that the activities of enzymes converting C, N, and P increased considerably with increases in MBC, MBN, and MBP. Compared with C- and N-converting enzyme activities, P-converting enzyme activity declined, indicating that the mineralization capacity of soil organic P was insufficient. However, exogenous organic matter significantly stimulated AP activity, especially in BF, which was 2.0 times that in CK, followed by BC and OF, which were 1.3 and 1.7 times that in CK, respectively. This is because AP activity is closely related to pH [38], and biochar or organic fertilizer increased the pH of acidic yellow soil in the study area, contributing to the enzymatic reaction of AP. Zhu et al. [39] argued that organic matter can compete with P for adsorption sites of iron–aluminum oxides, and the increase in pH can reduce the amorphous phase in iron–aluminum oxides. Increasing soil pH and organic matter can directly or indirectly affect the population and quantity of microbes releasing enzymes, reduce the P fixation of soil, and promote P conversion. In this study, biochar had a high pH (8.23), while organic fertilizer was rich in inactive organic matter, which may be the reason for the high AP activity of the soil.

In addition to responding to substrate variation by adjusting or altering their C:N:P functional group structure, soil microbes can adjust the proportion of extracellular enzymes to adapt to substrate changes [40]. Globally, soil BG:(NAG+LAP) is 1.41, BG:AP is 0.62, and (NAG+LAP):AP is 0.44 [18]. In this study, BG:(NAG+LAP) was 1.13–2.33, which is not considerably different from the global average. Moreover, BG:AP was 3.97–7.97, which is much higher than the global average, suggesting that the soil C-converting enzyme activity was strong in this study area. The C decomposition and conversion speed was also high, which was consistent with prior results [41] suggesting that the plant biomass in farmland is quickly oxidized and decomposed due to the climate characteristics of rain and heat over the same period in subtropical areas. Our results showed that the soil nutrient conversion rate was considerably limited by the soil P-converting enzyme activity, mainly because P is primarily fixed in zonal yellow soil. Thus, the P availability declined. Previous studies have shown that increasing the exogenous organic matter input can provide a C source and energy for microbes, improve microbial activity, enhance microbial homeostasis, and enhance soil P conversion and utilization [42]. These may be the reasons for the improved soil P bioavailability in this study with the input of exogenous organic matter (Figure 1b).

4.3. Biological Mechanism of Increased PY with the Input of Exogenous Organic Matter

The results showed that the input of exogenous organic matter significantly increased PY (Figure 5a) because the increase in exogenous organic matter can regulate PY by altering the stoichiometric ratio of microbial biomass C, N, and P, the stoichiometric ratio of enzyme activity, and the bioavailability of C, N, and P (Figure 6a). Compared with CK, BC, OF, and BF could increase PY the most. The following mechanism is suggested. The honeycomb pore structure of biochar can immobilize water and nutrients, and organic fertilizer is a rich active C source. Thus, the complementary advantages of the two provide a good "living bed" and nutritional conditions for soil microbes, which directly or indirectly regulate the activity of soil extracellular enzymes. Thus, the stoichiometric ratio of enzyme activity is closer to the appropriate value (Figure 4a–c), and soil C, N, and P nutrients are more balanced, which is also one of the biological mechanisms for BF maximizing PY. Moreover, we found that MBN:MBP and ln(BG+CBH):lnAP had the most influence on PY, while MBP:TP had the most indirect influence on PY (Figure 6b). Therefore, the microbiological fertility indexes related to soil N and P conversion were key limiting factors for PY and, especially, for P. These findings are useful for examining the coupling relationship between soil microbial metabolism and enzyme activity and its internal mechanism, improving the understanding of the microbiological fertility index, and improving the mechanism to improve crop yields.

5. Conclusions

Increasing the input of exogenous organic matter can considerably alter the stoichiometric ratio of soil microbial biomass and the stoichiometric ratio of enzyme activity, thereby improving soil N and P bioavailability. The activities of extracellular enzymes related to C, N, and P conversion positively correlate with the changes in microbial biomass C, N, and P ($p < 0.05$).

Soil nutrient conversion was most restricted by P-converting enzyme activity in the study area. BF was less restricted by P, with a more balanced nutrient proportion and higher IEI and PY, which could be used as a recommended fertilization strategy to increase PY. In actual production, however, reducing N and supplementing P appropriately is needed to balance N and P nutrients and alleviate P restriction.

The stoichiometric ratio of soil microbial biomass involved eight mechanisms that influence PY: one direct and seven indirect ways. Therefore, the indirect influence of the stoichiometric ratios of soil microbial biomass and extracellular enzyme activities on PY should not be ignored, especially soil MBN:MBP, MBP:TP, and ln(BG+CBH):lnAP, which function as a bridge. In future research and PY influence model predictions, attention should be paid to the critical role of eco-stoichiometry of soil microbial biomass and enzyme activity. In addition, this study was a short-term field trial on a small area, focusing only on soil microbiological fertility indicators and potato yield, and the relationship between the two. The nutrient utilization and economic benefits of nitrogen, phosphorus, and potassium (NPK) fertilizers should be considered in follow-up studies to provide more data support for the recommended fertilizer application in the study area.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14030571/s1, Table S1: Names, functions, and substrates of soil extracellular enzymes.

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