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Potato–Soybean Intercropping Increased Equivalent Tuber Yield by Improving Rhizosphere Soil Quality, Root Growth, and Plant Physiology of Potato

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Abstract: Potato–legume intercropping has been confirmed to increase productivity in modern agricultural systems. However, the physiological and ecological mechanisms of potato–soybean intercropping for promoting tuber yield formation in potato remain unclear. Field experiments were conducted in 2022 and 2023 to explore the responses of tuber yield formation, rhizosphere soil quality, root growth, and plant physiology of potato in potato–soybean intercropping. The soil at the experimental site is Cambisols. The treatments included sole cropping potato, sole cropping soybean, and potato–soybean intercropping. Our results indicated that potato –soybean intercropping decreased the water content, increased the total K content and activities of urease and catalase in rhizosphere soil, and enhanced the root mean diameter, root projected area, and root length density in the 0–5 cm and 15–20 cm soil layers of potato. Moreover, potato–soybean intercropping improved the plant photosynthetically active radiation and light transmittance rate of the middle and lower layers as well as the leaf area index, enhanced the leaf chlorophyll b content and ribulose-1,5-diphosphate carboxylase/oxygenase activity, and increased the leaf net photosynthetic rate and organ dry matter accumulation amounts of potato. The changes in the above parameters resulted in an increased tuber weight per plant (19.4%) and commercial tuber number (42.5%) and then enhanced the equivalent tuber yield of potato (38.2%) and land equivalent ratio (1.31 in 2022 and 1.33 in 2023). Overall, potato–soybean intercropping greatly increased the equivalent tuber yield by improving the rhizosphere soil quality, root growth, and plant physiology of potato and then achieved a higher land equivalent ratio.

Keywords: potato–soybean intercropping; equivalent tuber yield; rhizosphere soil quality; root growth; plant physiology

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1. Introduction

Potato (*Solanum tuberosum* L.) is an annual herb in the Solanaceae family, which is the third most important food crop in the world after rice and wheat in terms of human consumption. China is the world's largest potato producer and consumer, with the largest potato planting area and total yield [1]. According to the report from the Food and Agriculture Organization of the United Nations (FAO), the potato planting area and total yield in China reached 4.22 million hectares and 78.24 million tons in 2020, accounting for 25.6% and 21.8% of the world's totals, respectively [2]. In China, the potato planting region can be divided into four dominant producing regions, namely the north single-cropping region, the central plains double-cropping region, the southwest mixed-cropping region, and the south winter-cropping region, according to the climatic and geographical conditions, potato cropping system, and biological characteristics of potato [3]. Among the four dominant producing regions, the southwest mixed-cropping region had the highest potato planting area and total yield, while had the lowest yield per unit area [4]. This is mainly because soil environment deterioration caused by long-term potato monoculture seriously restricted the yield potential of potato [5].

Intercropping refers to the cultivation method of planting two or more crops during the same growing period in the same field, which is of great significance to alleviate land-use conflicts between crops and promote the sustainable development of land resources [6]. In recent years, intercropping has shown more and more advantages. It can effectively improve crop productivity and land-use efficiency. For example, Abbas et al. [7] found that maize intercropped with green gram enhanced maize production and land-use efficiency by reducing weed infestation. Furthermore, it can promote the improvement of the soil environment. Dahmardeh et al. [8] showed that maize intercropped with cowpea increased the soil nitrogen, phosphorous, and potassium contents compared to sole cropping of maize. Furthermore, it can make use of the complementary effect of different niche resources to promote the rooting behavior of crops. For instance, Ramirez-Garcia et al. [9] observed that intercropping showed a slightly greater root intensity compared to sole-cropped barley at a deep soil layer, and intercropped barley roots took up more labeled nitrogen than sole-cropped barley roots from the deep soil layer. Moreover, it can improve nutrient uptake and the utilization of crops by altering interspecific competition. Giving an example, Raza et al. [10] discovered that maize intercropped with soybean increased the accumulation of N, P, and K in each organ of the soybean. Additionally, intercropping can increase the light-use efficiency by improving the ventilation and light conditions of crops. For example, Nyawade et al. [11] indicated that potato intercropped with lima bean and dolichos increased the leaf area index and light interception and then caused an increase in radiation-use efficiency of potato compared to sole cropping potato. In addition, it can change the structure of the microbial community to effectively resist pests and diseases. For instance, Messiha et al. [12] found that potato intercropped with cabbage increased the abundance of antagonistic fluorescent pseudomonads, *Bacillus* spp. and *Serratia* spp., and then decreased the density of the pathogen in the rhizosphere. Furthermore, intercropping can utilize biodiversity to inhibit weed growth. Law et al. [13] reported that red clover intercropped with intermediate wheatgrass reduced the biomass and species richness of weeds.

Leguminous crops have a biological nitrogen fixation function, which can reduce the excessive consumption of soil nutrients by crops and contribute fixed nitrogen to neighboring crops to increase the nitrogen source, and this has significant implications for reducing nitrogen input and mitigating agricultural environmental pollution [14,15]. Many findings have well documented that potato–legume intercropping improved soil quality and plant growth [16–18]. However, the physiological and ecological mechanisms of potato–soybean intercropping in promoting tuber yield formation in potato remain unclear. We hypothesized that potato–soybean intercropping could promote tuber yield formation in potato through the interaction effects above and below ground. The objectives of this study were to (1) evaluate the changes in tuber yield formation in potato under potato–soybean intercropping; (2) assess the responses of rhizosphere soil quality, root growth, and plant physiology of potato in potato–soybean intercropping; and (3) clarify the contributions of the rhizosphere soil quality, root growth, and plant physiology to tuber yield formation in potato.

2. Materials and Methods

2.1. Experimental Site and Materials

Field experiments were conducted in 2022 and 2023 at the Guiyang Experimental Station (26°32′ N, 106°48′ E) of the Guizhou Academy of Agricultural Sciences (Guiyang, China). The site has an elevation of 1139 m above sea level, and the area is classified as having a subtropical humid monsoon climate, and the precipitation and air temperature during the experiment are shown in Figure 1. The soil type at the experimental site is classified as Cambisols in the World Reference Base for Soil Resources (WRB) system [19], with a pH of 7.3, organic matter of 55.5 g kg^{-1}, total N of 1.78 g kg^{-1}, total P of 0.61 g kg^{-1}, total K of 8.73 g kg^{-1}, available N of 64.3 mg kg^{-1}, available P of 333 mg kg^{-1}, and available K of 54.4 mg kg^{-1} in the 0–100 mm soil layer at the start of experiment in 2022. Potato cultivar Yushu-5 and soybean strain Yindou-1 were adapted to local conditions and used in the experiment. Yushu-5 is a fresh-eating potato cultivar widely used in local production with a semi-compact plant type, which was approved by the Chongqing Crop Variety Approval Committee in 2014, and its seed potatoes were provided by Chongqing Agricultural Technology Extension Station (Chongqing, China). Yindou-1, a grain-type spring soybean strain with a compact plant type and determinate podding habit, is suitable for intercropping planting, and its seeds were provided by the Institute of Upland Food Crops, Guizhou Academy of Agricultural Sciences (Guiyang, China).

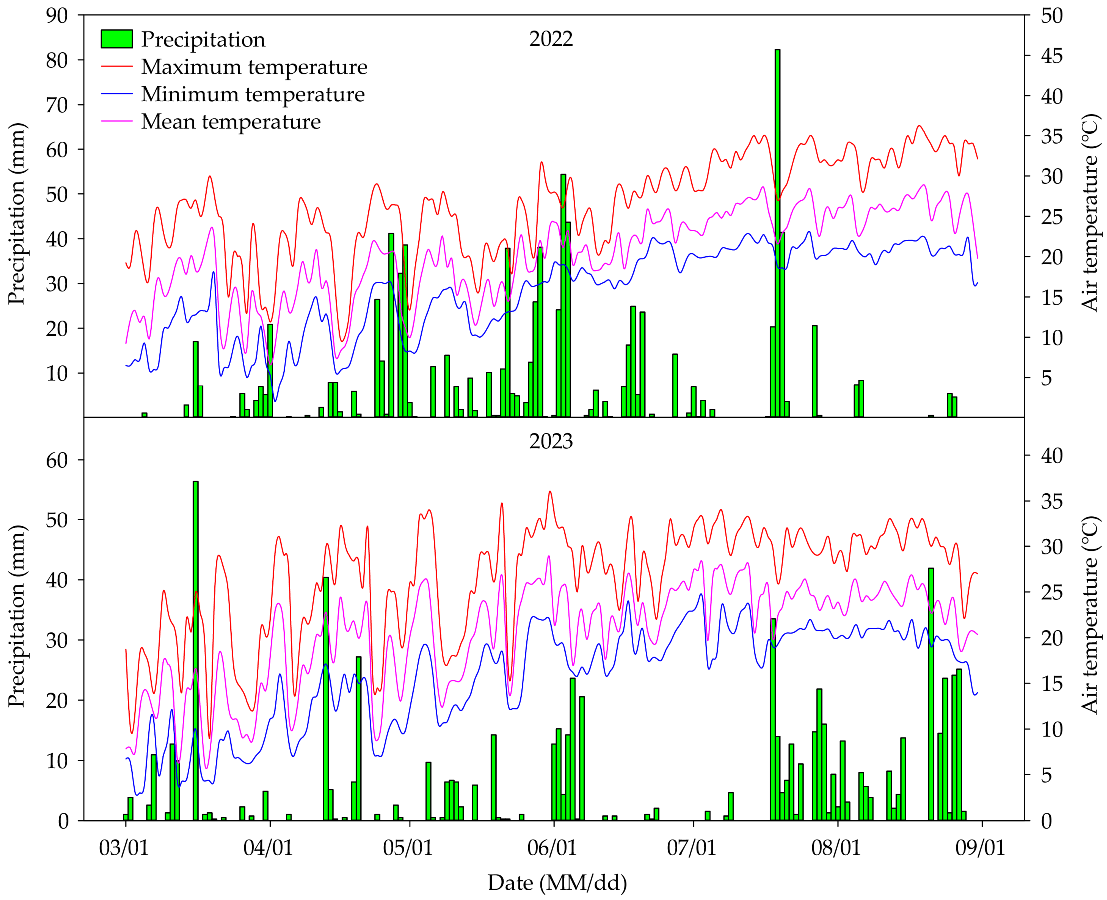

Figure 1. The precipitation, maximum air temperature, minimum air temperature, and mean air temperature during the experiment.

2.2. Experimental Design

Experimental treatments included sole cropping potato (SCP), sole cropping soybean (SCS), and potato–soybean intercropping (PSI). For the SCP treatment, the plot size was 12.5 m^2 (5 m long and 2.5 m wide) with row spacing of 50 cm, hill spacing of 25 cm, and consisted of five potato planting rows. For the SCS treatment, the plot size was 12.5 m^2 (5 m long and 2.5 m wide) with row spacing of 50 cm, hill spacing of 25 cm, and consisted of five soybean planting rows. For the PSI treatment, the plot size was 31.5 m^2 (5 m long and 6.3 m wide) with a planting pattern of two rows of potato intercropped with two rows of soybean, potato row spacing of 40 cm, soybean row spacing of 40 cm, distance between adjacent potato and soybean rows of 50 cm, potato hill spacing of 25 cm, soybean hill spacing of 25 cm, and consisted of eight potato planting rows and six soybean planting rows. Field configurations of all treatments were selected based on typical agricultural practices of potato and soybean in Southwest China, and detailed experimental treatments are shown in Figure 2A–C. All treatments were organized in a random block design with six replicates, of which three replicates were used for sampling, and another three replicates were used for yield measurement. Potatoes were sown according to the uniform specification of one seed potato per hill on 1 March 2022 and 5 March 2023 and harvested on 24 June 2022 and 7 July 2023, respectively. Soybean was sown on 8 April 2022 and 31 March 2023, thinned at the five-leaf stage to a uniform specification of two plants per hill, and harvested on 8 August 2022 and 20 July 2023, respectively. Detailed growing periods of potato and soybean are shown in Figure 2D.

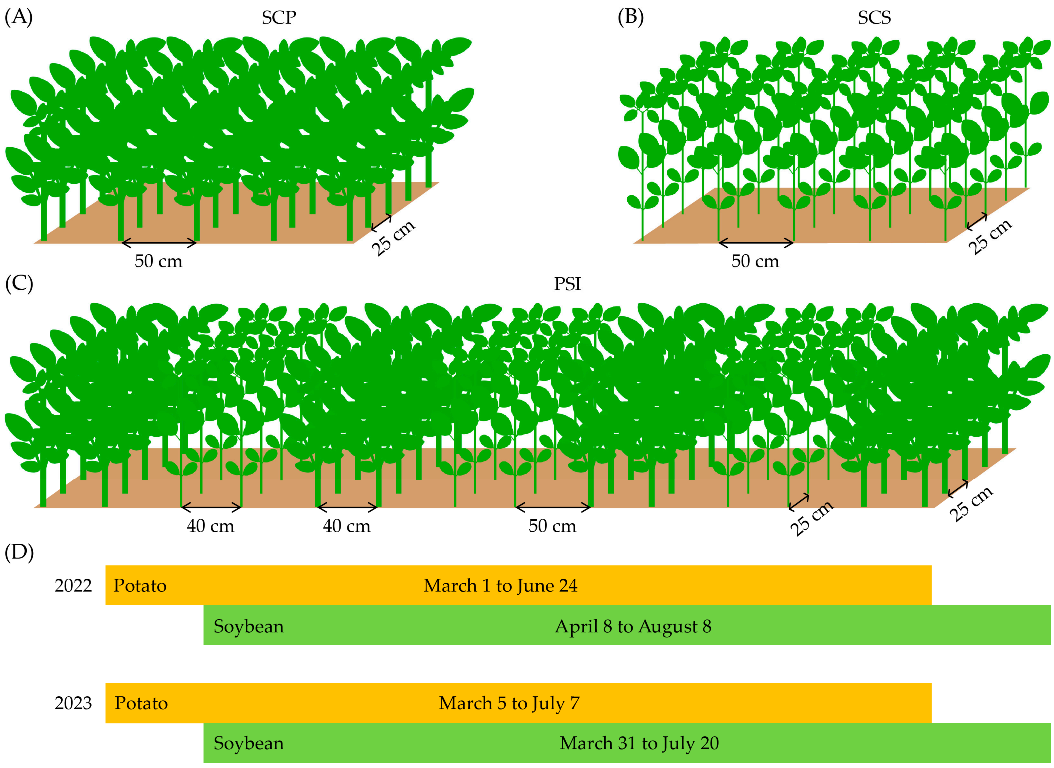

Figure 2. Schematic layout diagram of field experimental treatments (**A**–**C**) and growing periods (from sowing to harvesting) of potato and soybean (**D**). SCP: sole cropping potato; SCS: sole cropping soybean; PSI: potato–soybean intercropping.

For potato, a compound fertilizer (Kailin brand containing 16% N, 8% P_2O_5, and 21% K_2O, Guizhou Kailin Group Co., Ltd., Guiyang, China) was used as a basal fertilizer at a dose of 450 kg ha^{-1} at the sowing time, and urea (Chi brand containing 46.2% N, Guizhou Chitianhua Tongzi Chemical Co., Ltd., Zunyi, China) was used as additional fertilizer at a dose of 300 kg ha^{-1} at the seedling stage. For soybean, a compound fertilizer (Kailin brand containing 16% N, 8% P_2O_5, and 21% K_2O, Guizhou Kailin Group Co., Ltd., Guiyang, China) was used as a basal fertilizer at a dose of 300 kg ha^{-1} at the sowing time. Phoxim (Yiqichu brand granules containing 3% effective constituent, Leshan Xinlu Chemical Co., Ltd., Leshan, China) was used mixed with the basal fertilizer at a dose of 12 kg ha^{-1} to control underground pests. Imidacloprid (Guoguang-Bike brand wettable powder containing 10% effective constituent, Jiangsu Kangpeng Agrochemical Co., Ltd., Taizhou, China) and carbendazim (Guoguang brand wettable powder containing 50% effective constituent, Sichuan Guoguang Agrochemical Co., Ltd., Chengdu, China) were, respectively, diluted 500 times with water and applied via foliar spraying at the seedling stage of potato and soybean to prevent insects and diseases. Artificial weeding was performed at the seedling stage of potato and the branching stage of soybean.

2.3. Rhizosphere Soil Analysis

At the tuber swelling stage and maturity stage, three potato plants were selected randomly from the middle strip of each plot and uprooted with a small hoe. The loose soil on the surface of the roots was shaken off gently by hands, and the soil that tightly adhered to the roots was collected carefully with a brush as rhizosphere soil. Then, rhizosphere soils of three plants in each plot were mixed as a composite sample and sieved through a 2 mm mesh to remove impurities. The soil samples were divided into three subsamples evenly, of which one subsample was immediately used to measure the physical properties, one subsample was naturally air-dried and stored at room temperature for the determination of the chemical properties, and another subsample was immediately frozen in liquid nitrogen (Guizhou Saipulun Technology Co., Ltd., Guiyang, China) and then stored in a refrigerator (Haier DW/BD-55W151EU1, Qingdao Haier Special Electric Freezer Co., Ltd., Qingdao, China) at −20 °C for the measurement of enzyme activities.

2.3.1. Soil Physical Properties

The soil physical properties were determined according to the method described by Lv and Li [20], with slight modification. An empty aluminum box with a 40 mm diameter and 25 mm depth was placed in an oven (Jiangdong DHG-9240A, Suzhou Jiangdong Precision Instrument Co., Ltd., Suzhou, China) at 105 °C for 2 h and weighed as M_0 after cooling at room temperature. The aluminum box was filled with soil samples and weighed as M_1. Then, the aluminum box filled with soil samples was placed in the oven at 105 °C for 6 h and weighed as M_2 after cooling at room temperature. The soil water content (WC) and bulk density (BD) were calculated using the following formulas:

$$\mathrm{WC} = (\mathrm{M}_1 - \mathrm{M}_2)/(\mathrm{M}_2 - \mathrm{M}_0) \times 100\%$$

$$\mathrm{BD} = (\mathrm{M}_2 - \mathrm{M}_0)/\mathrm{V}$$

where V is the volume of the aluminum box.

2.3.2. Soil Chemical Properties and Enzyme Activities

The measurements of the soil chemical properties and enzyme activities were outsourced to Guizhou Wela Technology Co., Ltd. (Guiyang, China). Briefly, the organic matter (OM) content was assayed using a potassium dichromate thermal dilution method. The total N (TN) content was measured using a semi-micro Kjeldahl distillation method after boiling with concentrated sulfuric acid. The total P (TP) content was analyzed using molybdenum–antimony–D-isoascorbic acid colorimetry after melting with NaOH solution. The total K (TK) content was assayed using flame photometry after melting with NaOH solution. Additionally, the urease (UE) activity was assayed using indophenol blue colorimetry, and one unit of enzyme activity (U) was defined as 1 μg of NH_3-N generated by 1 g of soil sample per day. The polyphenol oxidase (PPO) activity was determined using pyrogallol colorimetry, and one unit of enzyme activity (U) was defined as 1 mg of purple gallic acid produced by 1 g of soil sample per day. The catalase (CAT) activity was determined using ultraviolet spectrophotometry, and one unit of enzyme activity (U) was defined as 1 μmol of H_2O_2 degraded by 1 g of soil sample per day. The sucrase (SC) activity was determined using 3,5-dinitrosalicylic acid colorimetry, and one unit of enzyme activity (U) was defined as 1 mg of reducing sugar produced by 1 g of soil sample per day. The nitrate reductase (NR) activity was assayed using phenol disulfonic acid colorimetry, and one unit of enzyme activity (U) was defined as 1 μmol of NO_2-N generated by 1 g of soil sample per day.

2.4. Root Analysis

2.4.1. Root Growth Parameters

At the tuber swelling stage and maturity stage, six potato plants were selected randomly from the middle strip of each plot and uprooted with a small hoe. The roots were cut off with scissors and then washed clean with distilled water. Three roots were scanned using an Epson Perfection V800 photo scanner (Seiko Epson Corp., Nagano, Japan) and then analyzed using WinRHIZO Pro 2016d software (Regent Instruments Inc., Québec, QC, Canada) to obtain the root total length (RTL), mean diameter (RMD), volume (RV), and projected area (RPA), according to the method described by Sanada and Agehara [21]. Another three roots were used to measure the root activity (RA) using the kit with the 2,3,5-triphenyltetrazolium chloride (TTC) reduction method produced by Beijing Leagene Biotechnology Co., Ltd. (Beijing, China) following the instructions of the manufacturer.

2.4.2. Root Distribution

Three potato plants were selected randomly from the middle strip of each plot at the tuber swelling stage and maturity stage, and the aboveground part of each selected plant was cut off with a sickle. The root–soil samples of the 0–5, 5–10, 10–15, 15–20, and 20–25 cm soil layers were collected using a soil auger with a 10 cm radius and 5 cm length and then placed in a 400-mesh nylon bag. The roots were washed clean with distilled water, and we removed debris carefully. The root total length (RTL) was measured using the WinRHIZO plant root analysis system (Regent Instruments Inc., Québec, QC, Canada), and the root length density (RLD) was calculated using the following formula described by de Moraes et al. [22]:

$$RLD = RTL/V$$

where V is the volume of the root–soil sample.

2.5. Plant Analysis

2.5.1. Photosynthetically Active Radiation (PAR) and Light Transmittance Rate (LTR)

According to the method described by Kara [23], with slight modification, at the tuber swelling stage and maturity stage, the PAR of the potato population top layer (15 cm above the top of plant), upper layer (15 cm below the top of plant), middle layer (middle of plant), and lower layer (15 cm above the base of plant) in the middle strip of each plot was measured using an HM-G10 plant canopy measuring instrument (Shandong Hengmei Electronic Technology Co., Ltd., Weifang, China) from 11:00 to 13:00 on a sunny day. The LTR was calculated using the following formula:

$$LTR = PAR_i/PAR_0 \times 100\%$$

where PAR_i is the PAR of the upper layer, middle layer, and lower layer, and PAR_0 is the PAR of the top layer.

2.5.2. Leaf Area Index (LAI)

According to the method described by Huang et al. [24], with slight modification, three potato plants were selected randomly from the middle strip of each plot at the tuber swelling stage and maturity stage. Green leaves of each selected plant were cut off with scissors, and some round green leaves were obtained with a hole puncher with a 6 mm diameter. Then, the fresh weights of the round green leaves (FW_1) and other green leaves (FW_2) were measured using an electronic balance (XingYun JA203H, Changzhou Xingyun Electronic Equipment Co., Ltd., Changzhou, China). The LAI was calculated using the following formula:

$$LAI = [N_1 \times S_1 \times (FW_1 + FW_2) \times N]/(FW_1 \times S)$$

where N_1 is the number of round green leaves in each plant, S_1 is the area of each round green leaf, N is the number of potato plants in each plot, and S is the occupied area of potato plants in each plot.

2.5.3. Net Photosynthetic Rate (P_n), Chlorophyll Content, and Photosynthetic Enzyme Activities

At the tuber swelling stage and maturity stage, three potato plants were selected randomly from the middle strip of each plot, and the third functional leaf from the top of each plant was labeled to investigate the P_n using a Li-6400 photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) equipped with a 6400-02B LED leaf chamber, according to the method described by Okamoto et al. [25], with slight modification. The measurements were conducted from 8:30 to 11:30 on a sunny day under a light intensity of 1000 μmol m^{-2} s^{-1}, temperature of 25 °C, CO_2 concentration of 400 μmol mol^{-1}, flow rate of 500 mL min^{-1}, and relative humidity of 75%.

At the tuber swelling stage and maturity stage, three potato plants were selected randomly from the middle strip of each plot, and the third functional leaf from the top of each plant was used to measure the chlorophyll content and photosynthetic enzyme activities using the kit produced by Beijing Solarbio Science and Technology Co., Ltd. (Beijing, China) following the instructions of the manufacturer. In brief, the contents of chlorophyll a (Chl-a), chlorophyll b (Chl-b), and the total chlorophyll (Chl-T) were assayed using the colorimetric method of ethanol extraction. The ribulose-1,5-diphosphate carboxylase/oxygenase (Rubisco) activity was assayed using ultraviolet spectrophotometry, and one unit of enzyme activity (U) was defined as 1 nmol of NADH being oxidized by 1 g of leaf sample per minute in the 25 °C reaction system. The sucrose phosphate synthetase (SPS) activity was determined using visible spectrophotometry, and one unit of enzyme activity (U) was defined as 1 μg of sucrose generated by 1 g of leaf sample per minute.

2.5.4. Dry Matter Accumulation

According to the method described by Tiwari et al. [26], with slight modification, three potato plants were selected randomly from the middle strip of each plot at the tuber swelling stage and maturity stage, and the plants were uprooted with a small hoe. Every organ (root, culm, leaf, and tuber) of each sampled plant was separated and placed in an oven for 30 min at 105 °C to terminate biochemical reactions in the samples and then dried to constant weight at 80 °C. The dry weight of each organ was measured with an electronic balance, and the dry matter accumulation amount (DA) was converted according to the number of potato plants and the occupied area of potato plants in each plot.

2.6. Yield, Productivity, and Benefit Analysis

At the maturity stage, five potato plants were selected randomly from the middle strip of each plot to determine the plant height (PH), culm diameter (CD), tuber number per plant (TNPP), tuber weight per plant (TWPP), and commercial tuber number (CTN, weight of single tuber was greater than or equal to 70 g). Potatoes and soybeans of each replicate in different treatments were hand-harvested, and the actual tuber yield of potato (ATY) and actual grain yield of soybean (AGY) were measured, respectively. The equivalent tuber yield of potato (ETY) and equivalent grain yield of soybean (EGY) were converted according to the occupied area of potato and soybean plants in each plot, respectively. The land equivalent ratio (LER) was calculated using the following formula described by Abbas et al. [7]:

$$\mathrm{LER} = \mathrm{ATY}_2/\mathrm{ATY}_1 + \mathrm{AGY}_2/\mathrm{AGY}_1$$

where ATY_1 and ATY_2 are the actual tuber yields of potato under sole cropping and intercropping treatments, respectively, and AGY_1 and AGY_2 are the actual grain yields of soybean under sole cropping and intercropping treatments, respectively.

The total economic benefit (TEB) was calculated according to the market prices of each crop, in which the market prices of potato and soybean are 2 and 7.5 CNY kg^{-1}, respectively.

2.7. Statistical Analysis

Two-way analysis of variance (ANOVA) with a fixed-effects model was performed using DPS v7.05 software (Hangzhou Ruifeng Information Technology Co., Ltd., Hangzhou, China), and the means were tested using the least significant difference at the 0.05 level ($LSD_{0.05}$). The sampling stage and soil depth were fixed factors. The multiple stepwise regression equation based on stepwise regression analysis was used to select the most important physiological and ecological indexes affecting tuber yield formation in potato. Figures were drawn using SigmaPlot 12.5 software (Aspire Software Intl., Ashburn, VA, USA).

3. Results

3.1. Rhizosphere Soil Physicochemical Properties and Enzyme Activities

From the tuber swelling stage to the maturity stage, the WC and BD gradually increased, the TN and TK contents gradually decreased, and the OM and TP contents were almost constant in the same treatment in both years (Table 1). The year had significant effects on the TP and TK, while it had no significant effects on the WC, BD, OM, and TN in both stages. The treatment had significant effects on all soil physicochemical properties in both stages. The interaction between the year and treatment only had a significant effect on the BD at the tuber swelling stage. The contents of OM, TN, TP, and TK under PSI treatment were higher than those under SCP treatment in all years and stages, while the WC and BD were exactly the opposite. Compared to SCP treatment, the PSI treatment increased the contents of OM, TN, TP, and TK (mean of two years) by 6.37%, 17.7%, 90.8%, and 9.96% at the tuber swelling stage and 7.72%, 18.5%, 80.7%, and 15.4% at the maturity stage, respectively. However, the mean WC and BD of the two years under PSI treatment were decreased by 19.6% and 14.2% at the tuber swelling stage and 26.1% and 24.8% at the maturity stage, respectively, compared with SCP treatment.

Table 1. Effects of potato–soybean intercropping on rhizosphere soil physicochemical properties and enzyme activities in potato.

Stage	Year	Treatment	WC (%)	BD (g cm^{-3})	OM (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	TK (g kg^{-1})	UE (U g^{-1})	PPO (U g^{-1})	CAT (U g^{-1})	SC (U g^{-1})	NR (U g^{-1})
TSS	2022	SCP	27.09 a	0.83 a	39.43 b	1.50 b	0.18 b	8.21 b	18.97 b	248.94 b	145.03 b	2.60 a	0.10 b
		PSI	22.84 a	0.75 b	41.85 a	1.95 a	0.38 a	9.33 a	39.40 a	685.38 a	186.87 a	3.04 a	0.41 a
	2023	SCP	28.44 a	0.87 a	38.65 b	1.61 a	0.34 b	9.52 b	23.29 b	252.32 b	119.17 b	3.78 b	0.30 b
		PSI	21.82 b	0.71 b	41.20 a	1.72 a	0.61 a	10.17 a	46.40 a	490.08 a	172.13 a	5.51 a	0.44 a
	Mean	SCP	27.76 a	0.85 a	39.04 b	1.56 b	0.26 b	8.87 b	21.13 b	250.63 b	132.10 b	3.19 b	0.20 b
		PSI	22.33 b	0.73 b	41.53 a	1.83 a	0.49 a	9.75 a	42.90 a	587.73 a	179.50 a	4.28 a	0.43 a
	Source of variation												
	Year		ns	ns	ns	ns	***	***	*	**	**	***	***
	Treatment		*	***	***	*	***	**	***	***	***	**	***
	Year × treatment		ns	**	ns	ns	ns	ns	ns	**	ns	*	**
MS	2022	SCP	33.09 a	1.19 a	39.92 a	1.49 b	0.17 b	7.61 b	19.92 b	412.47 b	146.82 b	3.64 b	0.20 b
		PSI	25.53 b	0.92 b	42.03 a	1.85 a	0.38 a	8.89 a	53.77 a	889.33 a	195.80 a	4.91 a	0.48 a
	2023	SCP	36.53 a	1.20 a	38.33 b	1.46 a	0.36 b	8.61 b	24.73 b	298.95 b	124.35 b	4.22 b	0.30 b
		PSI	25.92 b	0.88 b	42.26 a	1.65 a	0.58 a	9.82 a	57.27 a	598.15 a	178.67 a	7.02 a	0.48 a
	Mean	SCP	34.81 a	1.19 a	39.13 b	1.48 b	0.27 b	8.11 b	22.11 b	355.71 b	135.59 b	3.93 b	0.25 b
		PSI	25.72 b	0.90 b	42.15 a	1.75 a	0.48 a	9.35 a	55.52 a	743.74 a	187.24 a	5.97 a	0.48 a
	Source of variation												
	Year		ns	ns	ns	ns	***	***	ns	***	**	***	*
	Treatment		***	***	**	**	***	***	***	***	***	***	***
	Year × treatment		ns	ns	ns	ns	ns	ns	ns	***	ns	**	*

Data are the mean of three replicates, and different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. TSS: tuber swelling stage; MS: maturity stage; SCP: sole cropping potato; PSI: potato–soybean intercropping; WC: water content; BD: bulk density; OM: organic matter; TN: total N; TP: total P; TK: total K; UE: urease; PPO: polyphenol oxidase; CAT: catalase; SC: sucrase; NR: nitrate reductase. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

The activities of UE, PPO, CAT, SC, and NR gradually increased from the tuber swelling stage to the maturity stage in the same treatment in both years (Table 1). The year had significant effects on soil enzyme activities, except for the UE activity at the maturity stage. The treatment had significant effects on all soil enzyme activities in both stages. The interaction between the year and treatment had significant effects on the PPO, SC, and NR activities, while it had no significant effects on the UE and CAT activities in both stages. PSI treatment increased the activities of UE, PPO, CAT, SC, and NR in all years and stages compared with SCP treatment. The mean UE, PPO, CAT, SC, and NR activities of the two years under PSI treatment were 2.03, 2.35, 1.36, 1.34, and 2.16 times greater at the tuber swelling stage and 2.51, 2.09, 1.38, 1.52, and 1.90 times greater at the maturity stage than those under SCP treatment, respectively.

3.2. Root Growth and Distribution

The RTL, RMD, RV, RPA, and RA gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years (Table 2). The treatment had significant effects on RTL, RMD, RV, RPA, and RA, while the year and interaction between the year and treatment had no significant effects on RTL, RMD, RV, RPA, and RA in both stages. The RTL, RMD, RV, RPA, and RA under PSI treatment were higher than those under SCP treatment in all years and stages. For the mean of two years, compared with SCP treatment, the PSI treatment increased the RTL, RMD, RV, RPA, and RA by 35.2%, 58.1%, 80.9%, 69.3%, and 65.8% at the tuber swelling stage and 39.7%, 87.5%, 160%, 82.5%, and 74.0% at the maturity stage, respectively.

Table 2. Effects of potato–soybean intercropping on root growth and distribution in potato.

Stage	Year	Treatment	RTL (cm)	RMD (mm)	RV (cm^3)	RPA (cm^2)	RA ($\mu g\ g^{-1}\ h^{-1}$)	RLD ($dm\ dm^{-3}$)				
								0–5 cm	5–10 cm	10–15 cm	15–20 cm	20–25 cm
TSS	2022	SCP	391.49 b	0.73 b	2.30 b	32.35 b	127.41 b	13.09 b	11.82 b	6.99 b	2.72 b	1.18 b
		PSI	540.11 a	1.17 a	4.12 a	52.07 a	208.02 a	31.26 a	29.03 a	22.72 a	9.77 a	5.72 a
	2023	SCP	399.82 b	0.84 b	2.37 b	29.94 b	132.36 b	14.42 b	12.71 b	10.07 b	3.58 b	2.35 b
		PSI	529.43 a	1.30 a	4.33 a	53.35 a	222.57 a	28.19 a	25.52 a	22.67 a	15.19 a	9.58 a
	Mean	SCP	395.65 b	0.78 b	2.34 b	31.15 b	129.89 b	13.76 b	12.27 b	8.53 b	3.15 b	1.77 b
		PSI	534.77 a	1.24 a	4.22 a	52.71 a	215.30 a	29.73 a	27.28 a	22.70 a	12.48 a	7.65 a
	Source of variation											
		Year	ns	ns	ns	ns	ns	ns	ns	ns	**	ns
		Treatment	***	***	***	***	***	***	***	***	***	***
		Year × treatment	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
MS	2022	SCP	380.27 b	0.64	1.37 b	26.12 b	114.00 b	12.03 b	9.71 b	5.22 b	1.59 b	0.79 b
		PSI	530.64 a	1.10	3.63 a	47.36 a	202.06 a	27.16 a	23.19 a	15.36 a	7.58 a	4.74 a
	2023	SCP	366.64 b	0.60	1.56 b	27.46 b	117.33 b	12.32 b	10.71 b	4.27 b	2.01 b	0.94 b
		PSI	512.38 a	1.24	4.01 a	50.40 a	200.34 a	24.02 a	21.62 a	14.83 a	6.66 a	5.03 a
	Mean	SCP	373.45 b	0.62	1.47 b	26.79 b	115.66 b	13.76 b	10.21 b	4.74 b	1.80 b	0.86 b
		PSI	521.51 a	1.17	3.82 a	48.88 a	201.20 a	29.73 a	22.41 a	15.09 a	7.12 a	4.88 a
	Source of variation											
		Year	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Treatment	***	***	***	***	***	***	***	***	***	***
		Year × treatment	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Data are the mean of three replicates, and different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. TSS: tuber swelling stage; MS: maturity stage; SCP: sole cropping potato; PSI: potato–soybean intercropping; RTL: root total length; RMD: root mean diameter; RV: root volume; RPA: root projected area; RA: root activity; RLD: root length density. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

The RLD gradually decreased with an increasing soil depth, and the RLD of each soil layer gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years (Table 2). The treatment had significant effects on the RLD of each soil layer in both stages. The year and interaction between the year and treatment only had a significant effect on the RLD in the 15–20 cm soil layer at the tuber swelling stage. Compared to SCP treatment, the PSI treatment increased the RLD of each soil layer in all years and stages. The mean RLD of two years in the 0–5, 5–10, 10–15, 15–20, and 20–25 cm soil layers under PSI treatment were 2.16, 2.22, 2.66, 3.96, and 4.33 times greater at the tuber swelling stage and 2.10, 2.19, 3.18, 3.97, and 5.66 times greater at the maturity stage than those under SCP treatment, respectively.

3.3. Plant Light Environment

The PAR gradually decreased from the top layer to lower layer, and the PAR of each layer gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years (Table 3). The year only had significant effects on the PAR of the top and upper layers at the maturity stage. The treatment had significant effects on the PAR of each layer, except for the lower layer at the maturity stage. The interaction between the year and treatment only had a significant effect on the PAR of the upper layer at the maturity stage. The PAR of each layer among treatments was in the order of PSI > SCP in all years and stages. Compared to SCP treatment, the PSI treatment increased the PAR of the top, upper, middle, and lower layers (mean of two years) by 7.37%, 67.7%, 124%, and 190% at the tuber swelling stage and 5.72%, 20.1%, 51.1%, and 11.6% at the maturity stage, respectively.

Table 3. Effects of potato–soybean intercropping on plant photosynthetically active radiation (PAR), light transmittance rate (LTR), and leaf area index (LAI) in potato.

Stage	Year	Treatment	PAR (μmol m^{-2} s^{-1})				LTR (%)			LAI
			Top	Upper	Middle	Lower	Upper	Middle	Lower	
TSS	2022	SCP	1022.80 a	495.40 b	256.40 b	113.40 b	48.82 b	25.22 b	11.20 b	5.36 b
		PSI	1117.80 a	814.40 a	592.40 a	369.80 a	73.46 a	54.01 a	33.80 a	8.50 a
	2023	SCP	1079.40 a	501.80 b	271.80 b	145.40 b	46.69 b	25.19 b	13.46 b	5.60 b
		PSI	1138.20 a	857.40 a	589.00 a	380.00 a	75.50 a	52.12 a	33.43 a	7.73 a
	Mean	SCP	1051.10 b	498.60 b	264.10 b	129.40 b	47.76 b	25.21 b	12.32 b	5.48 b
		PSI	1128.00 a	835.90 a	590.70 a	374.90 a	74.48 a	53.06 a	33.62 a	8.11 a
	Source of variation									
	Year		ns	ns	ns	ns	ns	ns	ns	ns
	Treatment		*	***	***	***	***	***	***	***
	Year × treatment		ns	ns	ns	ns	ns	ns	ns	ns
MS	2022	SCP	750.00 b	342.80 b	96.80 b	53.20 a	45.71 b	12.90 b	7.10 a	4.81 a
		PSI	814.00 a	468.60 a	150.20 a	64.40 a	57.54 a	18.45 a	7.91 a	5.74 a
	2023	SCP	835.20 a	455.60 a	105.20 b	65.60 a	54.47 a	12.60 b	7.88 a	5.09 a
		PSI	861.80 a	490.20 a	155.00 a	68.20 a	57.21 a	18.04 a	7.90 a	5.96 a
	Mean	SCP	792.60 b	399.20 b	101.00 b	59.40 a	50.09 b	12.75 b	7.49 a	4.95 a
		PSI	837.90 a	479.40 a	152.60 a	66.30 a	57.38 a	18.24 a	7.90 a	5.85 a
	Source of variation									
	Year		***	**	ns	ns	ns	ns	ns	ns
	Treatment		*	**	***	ns	*	***	ns	ns
	Year × treatment		ns	*	ns	ns	ns	ns	ns	ns

Data are the mean of three replicates, and different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. TSS: tuber swelling stage; MS: maturity stage; SCP: sole cropping potato; PSI: potato–soybean intercropping. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

The LTR gradually decreased from the upper layer to the lower layer, and the LTR of each layer gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years (Table 3). The treatment had significant effects on the LTR of each layer, except for the lower layer at the maturity stage. The year and interaction between the year and treatment had no significant effects on the LTR of each layer in both stages. PSI treatment increased the LTR of each layer in all years and stages compared with SCP treatment. The mean LTR of two years in the upper, middle, and lower layers were 1.56, 2.11, and 2.73 times greater at the tuber swelling stage and 1.15, 1.43, and 1.06 times greater at the maturity than those under SP treatment, respectively.

From the tuber swelling stage to the maturity stage, the LAI gradually decreased in the same treatment in both years (Table 3). The treatment had a significant effect on the LAI at the tuber swelling stage, while it had no significant effect on the LAI at the maturity stage. The year and interaction between the year and treatment had no significant effect on the LAI in both stages. The LAI under PSI treatment was higher than that under SCP treatment at the tuber swelling stage, while no significant difference was observed among PSI and SCP treatments at the maturity stage in both years. For the mean of two years, compared with SCP treatment, the PSI treatment increased the LAI by 48.0% and 18.3% at the tuber swelling stage and maturity stage, respectively.

3.4. Leaf Photosynthetic Capacity

The Chl-a (Figure 3A,B), Chl-b (Figure 3C,D), and Chl-T (Figure 3E,F) contents gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years. The year only had significant effects on the Chl-a and Chl-b contents at the tuber swelling stage. The treatment had a significant effect on the chlorophyll content, except for the Chl-a content at the maturity stage. The interaction between the year and treatment had no significant effect on the chlorophyll content in both stages. At the tuber swelling stage, the Chl-a, Chl-b, and Chl-T contents among treatments were in the order of PSI > SCP in both years. However, there were no significant differences in the Chl-a, Chl-b, and Chl-T contents among the treatments at the maturity stage in both years. The Chl-a, Chl-b, and Chl-T contents (mean of two years) under PSI treatment were 1.42, 1.31, and 1.38 times greater at the tuber swelling and 1.19, 1.22, and 1.20 times greater at the maturity stage than those under SCP treatment, respectively.

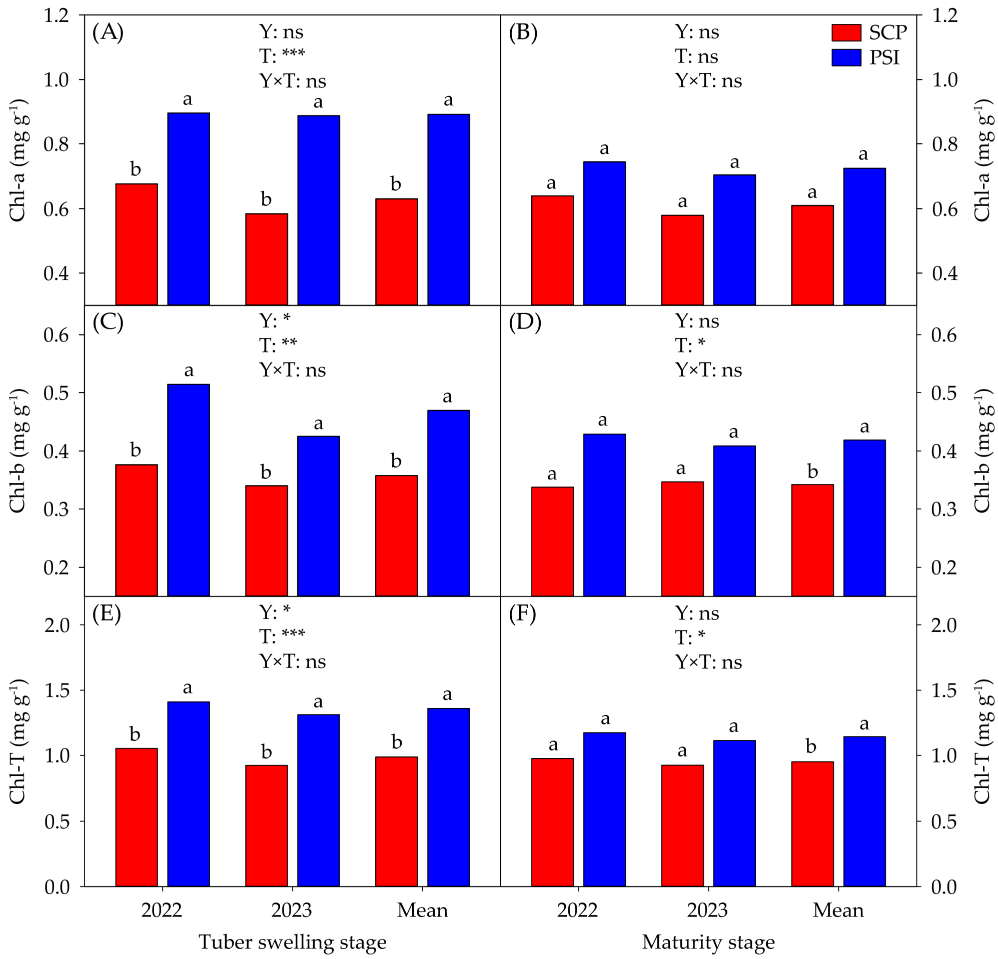

Figure 3. Effects of potato–soybean intercropping on leaf chlorophyll a (Chl-a, (**A**,**B**)), chlorophyll b (Chl-b, (**C**,**D**)), and total chlorophyll (Chl-T, (**E**,**F**)) contents in potato. Data are the mean of three replicates, and different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. SCP: sole cropping potato; PSI: potato–soybean intercropping; Y: year; T: treatment. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

From the tuber swelling stage to the maturity stage, the Rubisco (Figure 4A,B) and SPS (Figure 4C,D) activities gradually decreased in the same treatment in both years. The treatment had significant effects on the Rubisco and SPS activities, while the year and interaction between the year and treatment had no significant effects on the Rubisco and SPS activities in both stages. The Rubisco and SPS activities under PSI treatment were higher than those under SCP treatment in all years and stages. The mean Rubisco and SPS activities of two years under PSI treatment were increased by 47.4% and 17.9% at the tuber swelling stage and 32.0% and 10.2% at the maturity stage, respectively, compared with SCP treatment.

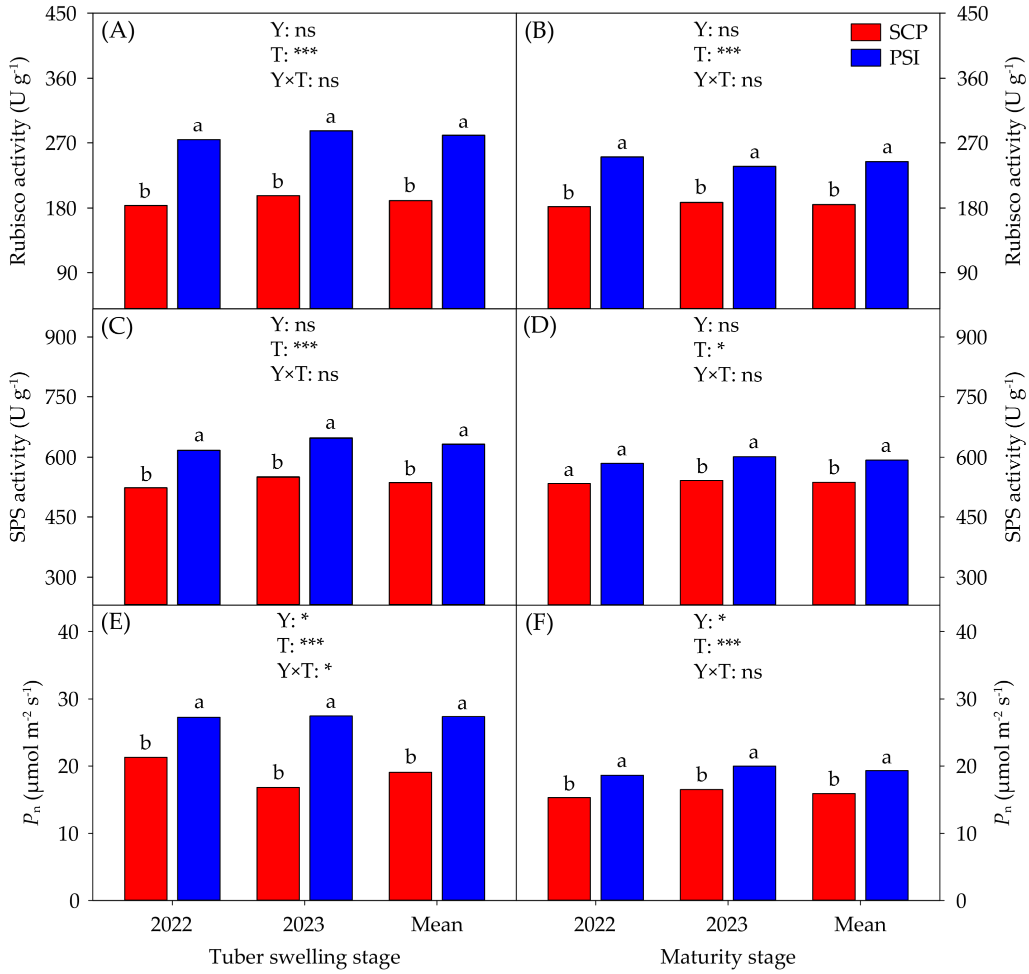

Figure 4. Effects of potato–soybean intercropping on leaf ribulose-1,5-diphosphate carboxylase/oxygenase (Rubisco) activity (**A**,**B**), sucrose phosphate synthetase (SPS) activity (**C**,**D**), and net photosynthetic rate (P_n, (**E**,**F**)) in potato. Data are the mean of three replicates, and different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. SCP: sole cropping potato; PSI: potato–soybean intercropping; Y: year; T: treatment. ns, *, and *** indicate not significant and significant at the 0.05 and 0.001 levels, respectively.

As shown in Figure 4E,F, the P_n gradually decreased from the tuber swelling stage to the maturity stage in the same treatment in both years. The year and treatment had a significant effect on the P_n in both stages. The interaction between the year and treatment had a significant effect on the P_n at the tuber swelling stage, while it had no significant effect on P_n at the maturity stage. The P_n under PSI treatment was higher than that under SCP treatment in all years and stages. For the mean of two years, compared with SCP treatment, the PSI treatment increased the P_n by 43.7% and 21.4% at the tuber swelling stage and maturity stage, respectively.

3.5. Organ Dry Matter Accumulation

From the tuber swelling stage to the maturity stage, the DA of the root (Figure 5A,B), culm (Figure 5C,D), and leaf (Figure 5E,F) gradually decreased, while the DA of the tuber (Figure 5G,H) gradually increased in the same treatment in both years. The order of DA among organs was leaf > culm > tuber > root at the tuber swelling stage and tuber > culm > leaf > root at the maturity stage in all treatments, years, and stages, respectively. The treatment had a significant effect on the DA of each organ in both stages. The year had significant effects on the DA of the leaf at the tuber swelling stage and the DA of the root and tuber at the maturity stage. The interaction between the year and treatment had significant effects on the DA of the root, culm, and leaf at the tuber swelling stage and the DA of culm at the maturity stage. The DA of each organ under PSI treatment was higher than that under SCP treatment in all years and stages. Compared to SCP treatment, the PSI treatment increased the DA by 37.9% for root, 37.4% for culm, 32.5% for leaf, and 35.9% for tuber at the tuber swelling stage and 33.7% for root, 31.0% for culm, 26.4% for leaf, and 35.1% for tuber at the maturity stage, respectively.

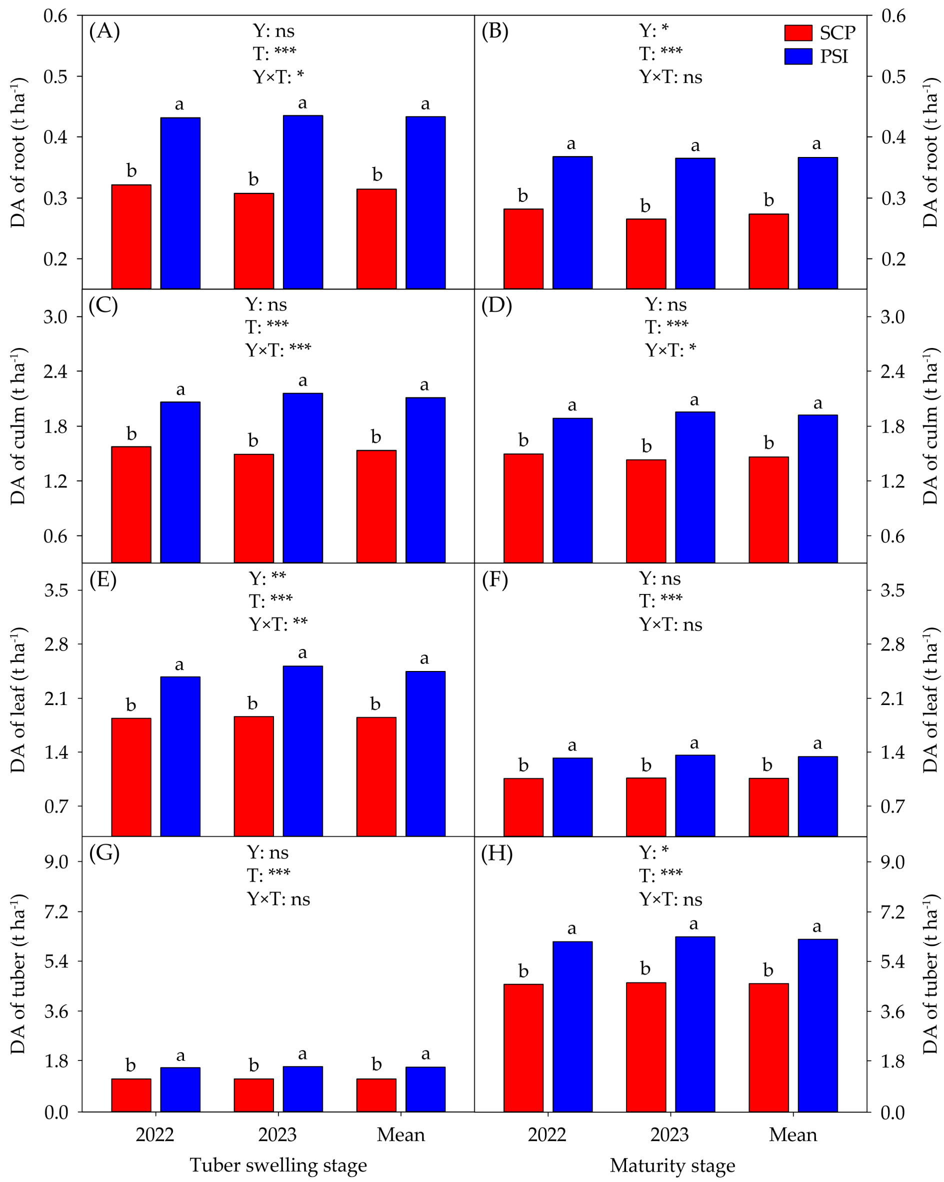

Figure 5. Effects of potato–soybean intercropping on dry matter accumulation amounts (DAs) of root (**A**,**B**), culm (**C**,**D**), leaf (**E**,**F**), and tuber (**G**,**H**) in potato. Data are the mean of three replicates, and

different lowercase letters in the same year within a stage indicate significant differences among treatments at the 0.05 level. SCP: sole cropping potato; PSI: potato–soybean intercropping; Y: year; T: treatment. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

3.6. Yield, LER, and TEB

As shown in Table 4, the year only had a significant effect on the CTN, the treatment had significant effects on the CD, TWPP, CTN, ATY, ETY, and TEB, and the interaction between the year and treatment had no significant effects on the PH, CD, TNPP, TWPP, CTN, ATY, ETY, and TEB. There were no significant differences in the PH and TNPP among treatments in both years. The CD, TWPP, CTN, and ETY among treatments were in the order of PSI > SCP, while the ATY and TEB under PSI treatment were lower than those under SCP treatment in both years. Compared to SCP treatment, the CD, TWPP, CTN, and ETY (mean of two years) under PSI treatment were increased by 12.2%, 19.4%, 42.5%, and 38.2%, respectively, while the ATY and TEB (mean of two years) under PSI treatment were decreased by 21.0% and 7.39%, respectively. Additionally, the LER under PSI treatment was greater than 1 in both years, which was 1.31 in 2022 and 1.33 in 2023.

Table 4. Effects of potato–soybean intercropping on tuber yield of potato, land equivalent ratio (LER), and total economic benefit (TEB).

Year	Treatment	PH (cm)	CD (mm)	TNPP	TWPP (g)	CTN	ATY (t ha^{-1})	ETY (t ha^{-1})	LER	TEB (10^4 CNY ha^{-1})
2022	SCP	88.79 a	8.76 b	6.40 a	618.27 b	3.60 b	33.06 a	33.06 b		6.61 a
	PSI	90.21 a	9.71 a	7.00 a	746.79 a	5.41 a	26.08 b	45.63 a	1.31	6.09 b
2023	SCP	90.52 a	8.70 b	6.40 a	632.01 b	4.40 b	32.68 a	32.68 b		6.54 a
	PSI	90.04 a	9.88 a	7.00 a	745.56 a	6.00 a	25.85 b	45.24 a	1.33	6.09 a
Mean	SCP	89.66 a	8.73 b	6.40 a	625.14 b	4.00 b	32.87 a	32.87 b		6.57 a
	PSI	90.13 a	9.79 a	7.00 a	746.18 a	5.70 a	25.97 b	45.44 a	1.32	6.09 b
Source of variation										
Year		ns	ns	ns	ns	**	ns	ns		ns
Treatment		ns	***	ns	***	***	***	***		*
Year × treatment		ns	ns	ns	ns	ns	ns	ns		ns

Data are the mean of three replicates, and different lowercase letters in the same year within a column indicate significant differences among treatments at the 0.05 level. SCP: sole cropping potato; PSI: potato–soybean intercropping; PH: plant height; CD: culm diameter; TNPP: tuber number per plant; TWPP: tuber weight per plant; CTN: commercial tuber number; ATY: actual tuber yield; ETY: equivalent tuber yield. ns, *, **, and *** indicate not significant and significant at the 0.05, 0.01, and 0.001 levels, respectively.

3.7. Stepwise Regression Analysis

As shown in stepwise regression analysis (Table 5), the ETY was mainly closely related to WC, TK, UE, CAT, RMD, RPA, and RLD in the 0–5 cm and 15–20 cm soil layers, PAR and LTR for the middle and lower layers, as well as the LAI, P_n, Chl-b, Rubisco, DA of each organ, TWPP, and CTN.

Table 5. Stepwise regression analysis of equivalent tuber yield (y) with rhizosphere soil quality, root growth, and plant physiology in potato.

Independent Variable	Multiple Stepwise Regression Equation	R	F	p	Statistic
Rhizosphere soil properties	$y = -52.47 + 0.38a_1 + 4.80a_2 - 0.10a_3 + 0.26a_4$	0.9997	1194.02	0.0001	1.23
Root growth and distribution	$y = 15.17 + 9.26b_1 + 0.16b_2 + 0.85b_3 - 0.66b_4$	0.9967	113.92	0.0013	1.55
Plant light environment	$y = -1.23 - 0.70c_1 + 1.16c_2 + 7.15c_3 - 12.94c_4 + 7.49c_5$	0.9993	301.94	0.0033	2.32
Leaf photosynthetic capacity	$y = 1.00 - 0.61d_1 + 41.57d_2 + 0.15d_3$	0.9634	17.24	0.0094	1.63

Table 5. *Cont.*

Independent Variable	Multiple Stepwise Regression Equation	*R*	*F*	*p*	Statistic
Organ dry matter accumulation	$y = -3.05 + 143.63e_1 - 20.36e_2 + 9.69e_3 + 3.53e_4$	0.9995	690.91	0.0001	0.63
Agronomic traits	$y = -39.76 + 0.13f_1 - 1.67f_2$	0.9981	652.51	0.0001	2.01

a_1: water content; a_2: total K; a_3: urease; a_4: catalase; b_1: root mean diameter; b_2: root projected area; b_3: root length density in 0–5 cm soil layer; b_4: root length density in 15–20 cm soil layer; c_1: photosynthetically active radiation of middle layer; c_2: photosynthetically active radiation of lower layer; c_3: light transmittance rate of middle layer; c_4: light transmittance rate of lower layer; c_5: leaf area index; d_1: net photosynthetic rate; d_2: chlorophyll b; d_3: ribulose-1,5-diphosphate carboxylase/oxygenase; e_1: dry matter accumulation amount of root; e_2: dry matter accumulation amount of culm; e_3: dry matter accumulation amount of leaf; e_4: dry matter accumulation amount of tuber; f_1: tuber weight per plant; f_2: commercial tuber number.

4. Discussion

Soil's physical properties include the soil texture, structure, aeration, and other characteristics, which have a direct effect on the growth rate and distribution of roots [27]. Our results discovered that PSI treatment decreased the WC and BD of potato rhizosphere soil compared to SCP treatment (Table 1), which was consistent with a previous study on a potato–legume intercropping system [17]. This finding might be attributed to the improvement of soil aeration induced by the interpenetration of roots into soil between different neighboring crops [17]. Soil's chemical properties participate in the processes of soil formation, development, and nutrient cycling, which are essential for maintaining soil fertility and quality [28,29]. In this study, we demonstrated that PSI treatment increased the OM, TN, TP, and TK contents of potato rhizosphere soil compared to SCP treatment (Table 1), which was consistent with previous research on potato intercropped with broad bean and buckwheat [30]. Different from our results, Liu et al. [31] reported that potato intercropped with tartary buckwheat significantly reduced the soil total N, total P, and available N contents. One reason for this discrepancy might be the difference in the sampling environment, i.e., potato rhizosphere soil was investigated in this study, while mixed soil from five random points in each plot was investigated in the previous research. Another explanation might be related to the difference in the sampling stage, i.e., two growth stages of potato were measured in our study, while three growth stages of tartary buckwheat were measured in the previous study. Soil enzymes catalyze a series of biochemical processes in soil, including the degradation of plant and microbial residues, the synthesis of organic compounds, nutrient cycling, and energy conversion, and soil enzyme activities are often used as evaluation indicators of the soil metabolic capacity [32,33]. Our results showed that the activities of UE, PPO, CAT, SC, and NR in potato rhizosphere soil under PSI treatment were higher than those under SCP treatment (Table 1). Similarly, numerous studies have proved that intercropping had positive effects on the soil enzyme activities. For instance, Ilakiya et al. [34] indicated that elephant foot yam intercropped with cluster bean, radish, Amaranthus, and fenugreek increased the activities of urease, dehydrogenases, acid phosphatase, and alkali phosphatase in elephant foot yam rhizosphere soil. Curtright and Tiemann [35] confirmed that intercropping enhanced the soil's extracellular enzyme activities involving carbon, nitrogen, phosphorous, oxidation, and general activities through a meta-analysis. Khan et al. [36] demonstrated that pepper intercropped with garlic increased the activities of catalase, sucrase, urase, and alkaline phosphatase in pepper rhizosphere soil. The changes in the potato rhizosphere soil quality parameters under PSI treatment might be closely related to the nitrogen fixation of soybean and complementary use of resources among different species in intercropping systems [37,38]. These results imply that potato–soybean intercropping can create a healthy soil environment for potato growth and development.

The plasticity of crop roots in intercropping systems is an important feature for plant adaptation to the changes in soil nutrients and temporal and spatial resources [39]. In this study, the RTL, RMD, RV, and RPA of potatoes under PSI treatment were higher than those under SCP treatment (Table 2), which was in agreement with a previous finding of Liu et al. [40], who reported that the root surface area, root total length, and root volume of intercropped alfalfa were significantly higher than those of sole-cropped alfalfa. Similar, Bargaz et al. [41] found that wheat intercropped with soybean significantly increased the root length and root surface area of wheat, regardless of P sufficiency or P deficiency. The root activity is a physiological index that objectively reflects the vital movement of roots, and it is crucial to maintain the health of soil ecology in intercropping systems [42,43]. In this study, the higher RA of potatoes under PSI treatment was discovered compared to SCP treatment (Table 2). Similar, a previous study showed that maize intercropped with soybean significantly increased the root activity of maize and soybean [44]. In the present study, PSI treatment increased the RLD of potatoes in each soil layer compared to SCP treatment (Table 2), which was similar to a study by Dube et al. [45], who demonstrated that the maize and cowpea roots in maize–cowpea intercropping systems showed significantly higher RLDs than sole cropping maize and cowpea. These increases in the RTL, RMD, RV, RPA, RA, and RLD of potatoes under PSI treatment could be explained by the following two possibilities: The first was that the higher rhizosphere soil quality under PSI treatment provided more adequate nutrients for the root growth and distribution of potato [46]. The second was that the interspecific interaction under PSI treatment promoted the root growth and distribution of potato compared to the intraspecific competition under SCP treatment [47]. Interestingly, our results discovered that the most obvious increment in the RLD (333% at the tuber swelling stage and 466% at the maturity stage) under PSI treatment was showed in the 20–25 cm soil layer (Table 2), suggesting that potato intercropped with soybean is more inclined to promote root growth of potato in deep soil. Likewise, Chen et al. [48] confirmed that maize intercropped with soybean changed the spatial distribution of maize roots with different root architectures and increased the proportion of maize roots in deep soil. Therefore, potato–soybean intercropping can promote root growth and distribution by improving the rhizosphere soil quality of potato.

Solar radiation is a key factor affecting plant growth and development, dry matter accumulation, and yield formation in intercropping systems [49]. In this study, the PAR and LTR of potatoes in the upper layer, middle layer, and lower layer under PSI treatment were higher than those under SCP treatment in both stages (Table 3). Similarly, previous studies found that intercropped maize intercepted more PAR energy than sole-cropped maize [50], and maize intercropped with peanut observably increased the LTR of the ear layer in maize [51]. These increases in the PAR and LTR of potatoes under PSI treatment might be due to the intercropped crops with compact or semi-compact plant types providing more space for potato plants to intercept solar radiation. The LAI determines the amount of solar radiation intercepted and directly affects leaf photosynthetic capacity of crops [52]. Our results showed that the PSI treatment increased the LAI of potatoes compared to SCP treatment in both stages (Table 3), which was in agreement with a previous study by Umesh et al. [53], who discovered that sorghum intercropped with lablab and cowpea significantly increased the LAI of sorghum. This increase in the LAI of potatoes under PSI treatment may be attributed to the development and expansion of the potato leaf being promoted by an increasing PAR and LTR. These findings imply that potato–soybean intercropping can improve the light environment of the potato plant. Chlorophyll is essential for the photosynthesis of crops, and Chl-a and Chl-b are important pigments that absorb light energy during photosynthesis of crops [54]. In the present study, the Chl-a, Chl-b, and Chl-T contents of potatoes under PSI treatment were higher than those under SCP treatment in both stages (Figure 3A–F), which was similar to a study by Yao et al. [54], who demonstrated that maize intercropped with soybean significantly increased the Chl-a, Chl-b, and Chl-T contents of soybean. These increases in the Chl-a, Chl-b, and Chl-T contents of potatoes under PSI treatment might be related to the improvement of the light environment in the potato plant promoting the synthesis of chlorophyll in the potato leaf. Photosynthetic enzymes play an important role in the photosynthesis of crops. Rubisco is a key enzyme in photosynthetic carbon assimilation [55]. SPS is a key enzyme involved in the synthesis of the initial photosynthesis product sucrose and has a feedback regulation effect on the photosynthesis of crops [56,57]. In our study, the Rubisco and SPS activities of potatoes under PSI treatment were higher than those under SCP treatment in both stages (Figure 4A–D). Similarly, Nasar et al. [58] discovered that maize intercropped with soybean significantly increased the Rubisco activity of maize leaf. Luo et al. [59] found that sweet potato intercropped with maize increased the SPS activity of sweet potato. These increments in Rubisco and SPS activities of potatoes under PSI treatment also might be attributed to the improvement of the light environment in the potato plant. The P_n is an index that directly reflects the leaf photosynthetic capacity of crops, and it was increased under PSI treatment compared to SCP treatment in both stages in our study (Figure 4E,F). A similar result for P_n was also confirmed by previous reports about maize–peanut [51] and maize–soybean [58] intercropping systems. These findings imply that potato–soybean intercropping can increase the photosynthetic capacity by increasing the chlorophyll content and photosynthetic enzyme activities of potato leaf. Thus, potato–soybean intercropping enhances the photosynthetic capacity of the potato leaf by improving the light environment of the potato plant.

Dry matter is the main product of photosynthesis, which provides the material basis for the yield formation of crops [51]. It is necessary to study the dry matter accumulation of various organs in crops in intercropping systems to obtain high yield of crops. In our study, the DAs of the root, culm, leaf, and tuber in potatoes under PSI treatment were greater than those under SCP treatment (Figure 5A–H), which might be attributed to the improvement of the plant light environment in potato. Similarly, previous studies have pointed out that potato intercropped with maize notably increased the dry matter accumulation amounts of shoot and tuber in potato during the whole growth period of potato [60]. This result suggests that potato–soybean intercropping can increase dry matter accumulation of each organ in potato. Our results showed that the CD, TWPP, CTN, and ETY of potatoes under PSI treatment were higher than those under SCP treatment (Table 4). Similarly, previous studies have shown that intercropping promoted plant growth and tuber development of potato [61]. The increases in the CD, TWPP, CTN, and ETY of potatoes could be explained by the following two reasons: The first is that the potatoes could take advantage of more resources in the neighboring open spaces before soybean sowing. The second is that the potatoes presented more competitiveness than soybean during the symbiotic period, so the potatoes could capture more nutrients for plant growth and tuber development. However, in the present study, the ATY of potatoes under PSI treatment was lower than that under SCP treatment (Table 4), which was mainly because intercropping with a 2:2 row ratio configuration resulted in a lower planting density for potato compared with sole cropping. Our study found that the LER of the PSI treatment was greater than 1 (Table 4), suggesting that potato–soybean intercropping increased the system yield without increasing the cultivated area. In other words, potato–soybean intercropping increased the land-use efficiency. Furthermore, our study showed that the ETY was mainly closely related to the WC, TK, UE, CAT, RMD, RPA, and RLD in the 0–5 cm and 15–20 cm soil layers, the PAR and LTR for the middle and lower layers, as well as the LAI, P_n, Chl-b, Rubisco, DA of each organ, TWPP, and CTN (Table 5). Taken together, as shown in Figure 6, potato–soybean intercropping can promote potato growth and development by improving the rhizosphere soil quality and plant light environment and then lead to an increase in the ETY and LER. The physiological and ecological interactions between potato and soybean contributed to the increased potato yield and could be explained by the following three possibilities: The first is that soybean supplemented nitrogen for potato growth and development through nitrogen fixation [37]. Additionally, the complementary use of resources among different species in intercropping systems promoted potato growth and development [38]. Furthermore, the reproduction and growth of beneficial soil microbes in intercropping systems created a favorable condition for the growth and development of potato [62].

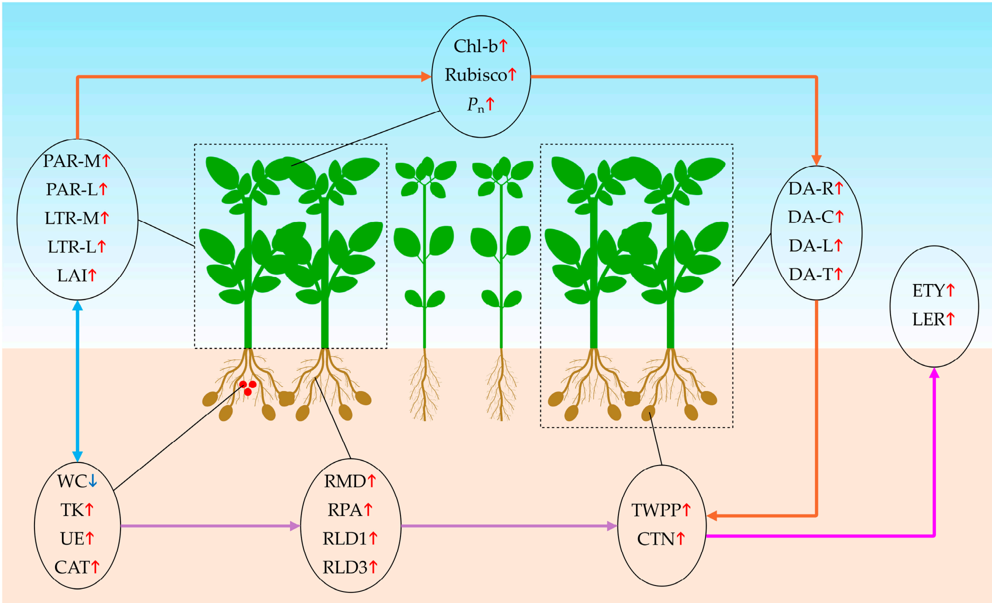

Figure 6. Conceptual diagram of mechanism for potato–soybean intercropping to increase equivalent tuber yield by improving rhizosphere soil quality, root growth, and plant physiology of potato. The red and blue arrows next to parameters indicate increase and decrease, respectively. WC: water content; TK: total K; UE: urease; CAT: catalase; RMD: root mean diameter; RPA: root projected area; RLD1: root length density in 0–5 cm soil layer; RLD3; root length density in 15–20 cm soil layer; PAR-M: photosynthetically active radiation of middle layer; PAR-L: photosynthetically active radiation of lower layer; LTR-M: light transmittance rate of middle layer; LTR-L: light transmittance rate of lower layer; LAI: leaf area index; P_n: net photosynthetic rate; Chl-b: chlorophyll b; Rubisco: ribulose-1,5-diphosphate carboxylase/oxygenase; DA-R: dry matter accumulation amount of root; DA-C: dry matter accumulation amount of culm; DA-L: dry matter accumulation amount of leaf; DA-T: dry matter accumulation amount of tuber; TWPP: tuber weight per plant; CTN: commercial tuber number; ETY: equivalent tuber yield; LER: land equivalent ratio.

5. Conclusions

In this study, potato–soybean intercropping promoted potato growth and development by improving the rhizosphere soil quality and plant light environment and then increased the equivalent tuber yield of potato and land equivalent ratio. Our findings provide a valuable insight for the physiological and ecological mechanisms of productivity increase in potato–soybean intercropping. Future studies will be focused on the study of optimal row ratio and bandwidth configurations in potato–soybean intercropping to promote the practical application of this planting technology.

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