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Nodule Formation and Nitrogen Use Efficiency Are Important for Soybean to Adapt to Water and P Deficit Conditions

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Abstract: Drought stress and phosphorus (P) deficit decrease soybean P and nitrogen (N) accumulation, which limits soybean productivity. Therefore, soybean traits related to N and P uptake and/or their efficient utilization are important for soybean adaptation to P- and water-deficit conditions. We hypothesize that increasing soybean nodulation to enhance N and P uptake, and/or improving N and P use efficiency (PUE and NUE) are important for the adaptation of soybean to drought and low P conditions. To test this hypothesis, we selected four genotypes with different nodule dry weight (DW) and yield performance for a pot experiment under two water treatments [well-watered (WW) and cycle water stress (WS)] and three P levels [0 (P0, low), 60 (P60, mid), and 120 (P120, high) mg P kg^{-1} dry soil on top 40 cm]. Our study showed that P deficit and water stress significantly decreased soybean P and N accumulation, which limited seed yield under both WS and WW conditions. P addition increased soybean nodule dry weight (DW), thus increasing N and P uptake. Increasing nodule DW required high water use, and while there was no relationship found between nodule DW and yield under WS, a positive relationship under WW was shown. Partitioning more dry matter to seed could improve NUE and PUE. P addition did not change soybean NUE, which is important to yield determination under WS and P0 but has no effect on yield under WW. We conclude that increasing nodule formation improved soybean N and P uptake, which diminished the yield loss under WS and improved yield performance under WW. While high NUE reflects efficient utilization of N, which can improve yield under drought stress and low P availability, and does not impair the yield under WW. We propose that NUE and nodules are important traits for breeders to improve the tolerance to water- and P-deficit conditions.

Keywords: water- and P-deficit; nodule dry weight; N and P uptake; N and P use efficiency; harvest index; water use efficiency; seed yield

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Citation: Jin, Y.; He, J.; Zhu, Y.; Siddique, K.H.M. Nodule Formation and Nitrogen Use Efficiency Are Important for Soybean to Adapt to Water and P Deficit Conditions. *Agriculture* **2022**, *12*, 1326. https://doi.org/10.3390/agriculture12091326

Academic Editors: Othmane Merah, Purushothaman Chirakkuzhyil Abhilash, Magdi T. Abdelhamid, Hailin Zhang and Bachar Zebib

Received: 22 July 2022
Accepted: 25 August 2022
Published: 28 August 2022

1. Introduction

Soybean is one of the most important oil crops worldwide. Drought is the main abiotic factor restricting soybean yield [1–4], while low availability of phosphorus (P) is the main nutrition factor related to seed yield potential [5,6]. Developing soybean cultivars with high seed yield under both water- and P-deficit conditions is urgently needed to cope with climate change [7,8] and P shortage [9,10]; however, revealing the underlying mechanism related to the water- and P-deficit adaptation is a prerequisite to achieving this.

Previous studies showed that the seed yield and N and P accumulation were significantly reduced under water stress in soybean [6,11]; while P deficit also led to the reduction of soybean yield and N and P accumulation [11]. These results indicate that N and P uptake is limited by water and P shortage, which results in a decrease in yield. Therefore, traits related to soybean P and N uptake would be important for yield performance under water- and P-deficit conditions. Recent studies found that changes to root morphology and architecture can increase the ability and/or efficiency of soybean P and N uptake [5,6,12–14]. For legumes, their nodulation, which is associated with biological N fixation, also plays important roles in N accumulation [15]. Further, plant nodules can increase plant P uptake because nodules mobilize insoluble P [16]. However, increasing soybean nodulation would increase investment, which may not necessarily yield favorable performance under drought conditions, and the relationship between the nodulation in soybean and P and N accumulation and yield performance under different water and P levels is not known.

Due to the low availability of P and N under water- and P-deficit conditions, how to effectively use the P and N available is also important to crop yield performance. Under natural conditions, NUE and PUE play important roles in plant adaptation to N and P deficits [17]. For rice, N use efficiency (NUE) is tightly correlated with productivity under drought stress [18]. While under P-limited conditions, P use efficiency (PUE) is critical to common bean environmental adaptation [19]. These results indicate that PUE and NUE may be essential water- and P-deficit tolerance [20,21]. Both the P and N use efficiency, defined as the seed yield per unit P and N uptake, were varied in crops [22–25]. A high supply of nutrition always results in low nutrition use efficiency [20,21], but a recent study found that selection for high yield could increase the N use efficiency independently of N addition [26]. However, the changes of the P and N use efficiency in soybean under different P and water levels and their roles in yield performance are not known.

This study aimed to evaluate how soybean nodulation under different P and water levels influences soybean N and P uptake and yield performance. We also investigated the role of N and P use efficiency in soybean productivity under water- and P-deficit conditions. We hypothesized that (1) the root nodules dry weight is coordinated with P and N accumulation to achieve high yield under conditions of scarcity and abundance of P and N; and (2) that high P and N use efficiency plays a more important role in yield performance when water and/or P were lacking. This study may assist with obtaining a better understanding of the underlying mechanism of soybean adaptation to water- and P-deficit conditions.

2. Materials and Methods

2.1. Materials and Treatments

Two soybean cultivars [Zhonghuang 30 (ZH) and Jindou 21 (J21)] and two landraces [Bailudou (B) and Huangsedadou (HD)] with contrasting yield performance and nodulation were studied in a pot experiment at Lanzhou University in Yuzhong County, Gansu Province, China. We used large cylindrical pots (1.05 m tall, 0.16 m wide) containing 18.6 kg soil (loess soil:vermiculite (*v:v*) = 3:1) obtained from a field near the experimental station, with one seed sown per pot. There were 72 pots in total in our study. The pots were placed in a rainout shelter that could be closed when it rained, while other conditions remained similar to the ambient conditions. The mixed soil had a pot capacity of 30.4%, a pH of 8.3, and contained available P at about 2 mg kg^{-1}. There were 3 P level treatments: 0 (P0, low), 60 (P60, mid), and 120 (P120, high) mg P kg^{-1} dry soil mixed in the top 0.4 m of soil, and two water treatments: well-watered (WW, soil water content maintained above 85% pot capacity) and water stress (WS, drought cycles, each pot rewatered to 100% pot capacity when its soil water content reached 35% pot capacity). Pot capacity was determined by watering the soil until free draining and then allowing it to drain for 24 h before weighing. Pots were weighed every four days to determine how much water needed to be added. There were three replications for each treatment.

2.2. Yield Determination

Plants were harvested at physiological maturity (136–147 days after sowing). Yellowed leaves were collected before they dropped. After removing the shoots at soil level, soil was washed over a 0.2 mm sieve to collect the roots, separating the root nodules. Leaves, stems, roots, pods, and nodules were oven-dried at 80 °C for at least 48 h and then weighed. Shoot dry weight (DW) included leaves, stems, and pods. Grain yield (GY) was determined after shelling pods. The water use (WU) of each pot was calculated as the total water added during the whole growth period minus the residual water after harvest. Water use efficiency (WUE) was calculated as GY/WU, and harvest index (HI) was calculated as GY/shoot DW.

2.3. P and N Use Efficiency

Samples were ground in a mill (ZM200, Retsch, GmbH, Düsseldorf, Germany) before determining the N and P contents of each part. As the nodule weight was quite low for some treatments, we mixed the nodules and roots uniformly to determine root N and P contents. About 0.2 g subsamples of each part were digested in H_2SO_4–H_2O_2, with N concentration calculated using the Kjeldahl method, and the P concentration determined using molybdenum-antimony anti-spectrophotometry method: measured the absorbance at the wavelength of 700 nm after the digesting solution developed color [27]. Total N and P uptake (TN and TP) were the sum of total N and P accumulation in each organ. N and P use efficiencies (NUE and PUE) were calculated as TN (or TP)/GY.

2.4. Data Analysis

All variables passed the normal distribution test, so we undertook a three-way analysis of variance to determine how genotype, P application and water treatment influenced each variable. Correlations and coefficients among traits were undertaken using Pearson's regression for p-value < 0.05. We used principal component analysis to investigate variable coordination and determine each treatment's score as principal component 1 (PC1) and PC2. All analysis was performed in R software (version 4.1.2, R Core Team, 2021).

3. Results

Water stress and P deficit decreased soybean yield performance. Under WS, soybean yield increased with P supply while water stress reduced seed yield more than P deficit. Under WW conditions, the mid P (P60) and high P (P120) treatments had similar yields. The new soybean cultivar ZH produced the lowest yields for P60 and P120 under WW conditions but the highest yields for P60 and P120 under WS and P0 under WW conditions. (Figure 1; Table 1).

The water and P interaction significantly affected shoot DW, HI, WU, and WUE (Figure 2; Table 1). Similarly, total P and N uptake and PUE differed among water treatments and P levels, but NUE was not affected by P level (Figure 3; Table 1). The genotypes also differed for shoot DW, HI, WU, WUE, total P, N uptake, PUE, and NUE, and their response to water treatments (except for NUE, with no genotype × water treatment interaction) (Table 1). The ZH cultivar had the lowest shoot DW, WU, and P and N accumulation among genotypes in the same treatment (except for P and N accumulation at P120 under WS), but the highest HI, WUE, PUE, and NUE (except for PUE at P60 and P120 under WW condition) (Figures 2 and 3). Water stress and P deficit also affected soybean root DW and nodule formation. Genotype ZH had no nodule and the lowest root DW in all treatments (Figure 4; Table 1).

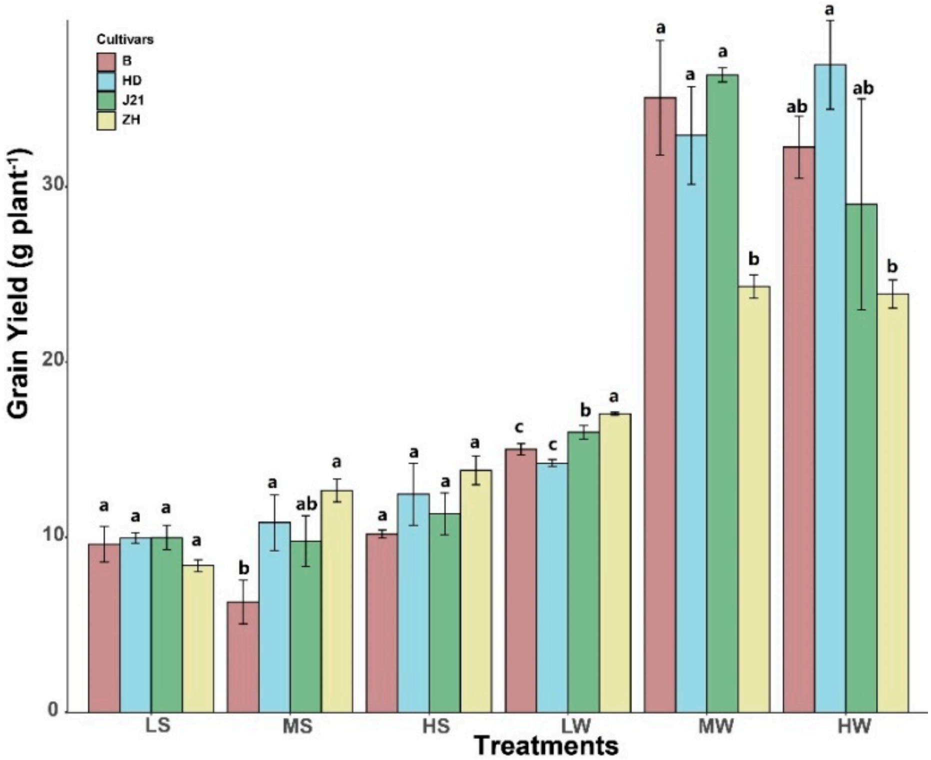

Figure 1. Yield performance of four soybean genotypes [B (Bailudou), HD (Huangsedadou), J21 (Jindou 21), and ZH (Zhonghuang)] under two water treatments [S (cycle water stress), W (well-watered)] and three P levels [L, low P supply (P0), M, mid P supply (P60), H, high P supply (P120)]. The letters under each group of bars indicate different combinations of P and water treatment, with the first letter indicating P level and the second letter representing water treatments. Values are means plus one standard error of the mean ($n = 3$).

Table 1. Significance of 11 traits (see Figures 1–5) of four soybean genotypes under two water treatments (cycle water stress and well-watered) and 3 P levels (low P supply, mid P supply, high P supply). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; blank cells indicate no significance.

	GY	Shoot DW	HI	WU	WUE	TP	TN	PUE	NUE	Root DW	Nodule DW
Genotypes (G)		***	***	***	***	***	***	***	***	***	***
P	***	***	***	***		***	***	***		***	***
Water (W)	***	***		***	***	***	***	***	***	***	***
G × P		*		**			*	**			***
G × W	***	***		***		***	***			***	***
P × W	***	***	***	***	**	***	***	**		*	***
G × P × W	**		**	*	***	*	**				***

PC1 and PC2 captured 64% and 22.7% of the total variation in 11 traits for the four genotypes under WS, and 65.8% and 23.2% of total variation under WW, respectively (Figure 5). PC1 mainly represented resource acquisition, while PC2 mainly represented resource use efficiency. GY was mainly correlated with PC2 under WS (Figure 5A): GY related to HI ($r = 0.37$, $p < 0.05$) but not Shoot DW ($p > 0.05$), and other resource use efficiency related traits (WUE: $r = 0.61$; NUE: $r = 0.64$), with a weaker but significant relationship with resource accumulation related traits (TP: $r = 0.48$; TN: $r = 0.46$) (Figure S1A). While under WW and GY mainly determined by PC1 (Figure 5B): GY was determined by shoot DW ($r = 0.82$, $p < 0.001$) rather than HI ($p > 0.05$), with yield variations mainly associated with resource acquisition traits (WU, TP, TN, GY, root DW, and nodule DW). GY negatively correlated with PUE ($r = -0.52$, $p < 0.01$) and had no relationship with NUE and WUE ($p > 0.05$) under WW conditions (Figure S1B). A significant negative correlation occurred between shoot DW and HI, WU and WUE, and TP and PUE under both WS and WW, while TN and NUE had a weak correlation (r = 0.39 under WS and r = 0.49 under WW, respectively) (Figure 5 and Figure S1). Under WS and WW, nodule DW and root DW positively correlated with resource acquisition traits (WU, TP, and TN), negatively correlated with PUE (Figure 5 and Figure S1). Nodule DW and root DW negatively correlated to HI and WUE under WS, but had no relationship with yield (Figure 5 and Figure S1). Under WS, ZH at P60 and P120, with the highest WUE, NUE, and HI, produced the highest yields. In contrast, under WW, ZH at three P levels and the other three cultivars (J21, B, and HD) at P0 had the lowest resource acquisition, resulting in the lowest yields (Figure 5).

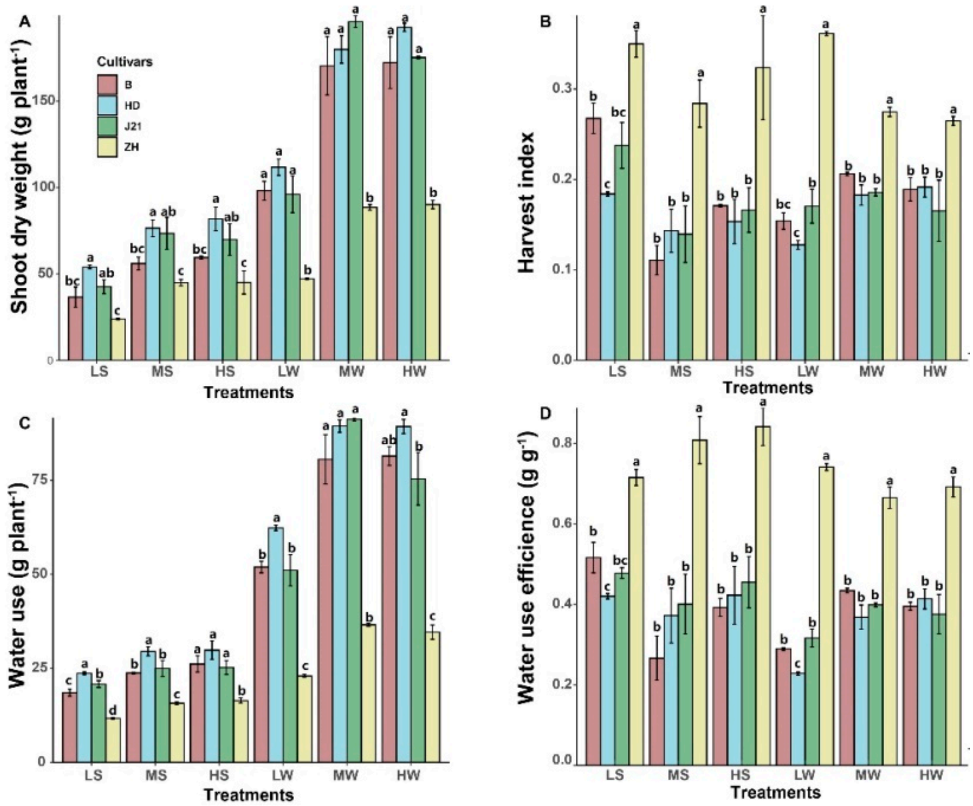

Figure 2. Shoot dry weight (**A**), harvest index (**B**), water use during the whole growth period (**C**), water use efficiency for grain yield (**D**) of four soybean genotypes [B (Bailudou), HD (Huangsedadou), J21 (Jindou 21), and ZH (Zhonghuang)] under two water treatments [S (cycle water stress), W (well-watered)] and three P levels [L, low P supply (P0), M, mid P supply (P60), H, high P supply (P120)]. The letters under each group of bars indicate different combinations of P and water treatments (as per Figure 1). Values are means plus one standard error of the mean (n = 3).

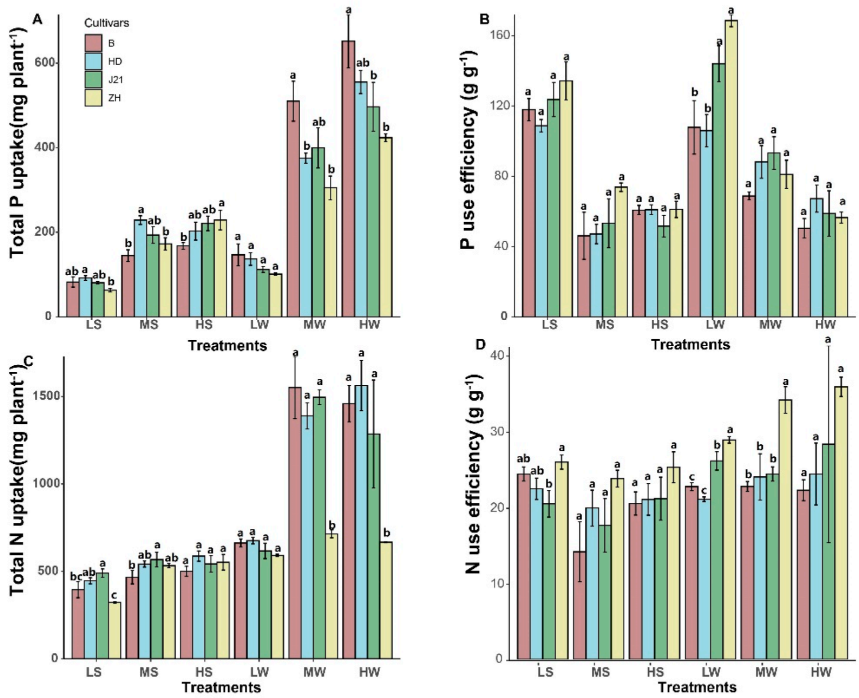

Figure 3. Total P uptake during whole growth period (**A**), P use efficiency for grain yield (**B**), total N uptake during whole growth period (**C**), N use efficiency for grain yield (**D**) of four soybean genotypes [B (Bailudou), HD (Huangsedadou), J21 (Jindou 21), and ZH (Zhonghuang)] under two water treatments [S (cycle water stress), W (well-watered)] and three P levels [L, low P supply (P0), M, mid P supply (P60), H, high P supply (P120)]. The letters under each group of bars indicate different combinations of P and water treatments (as per Figure 1). Values are means plus one standard error of the mean (n = 3).

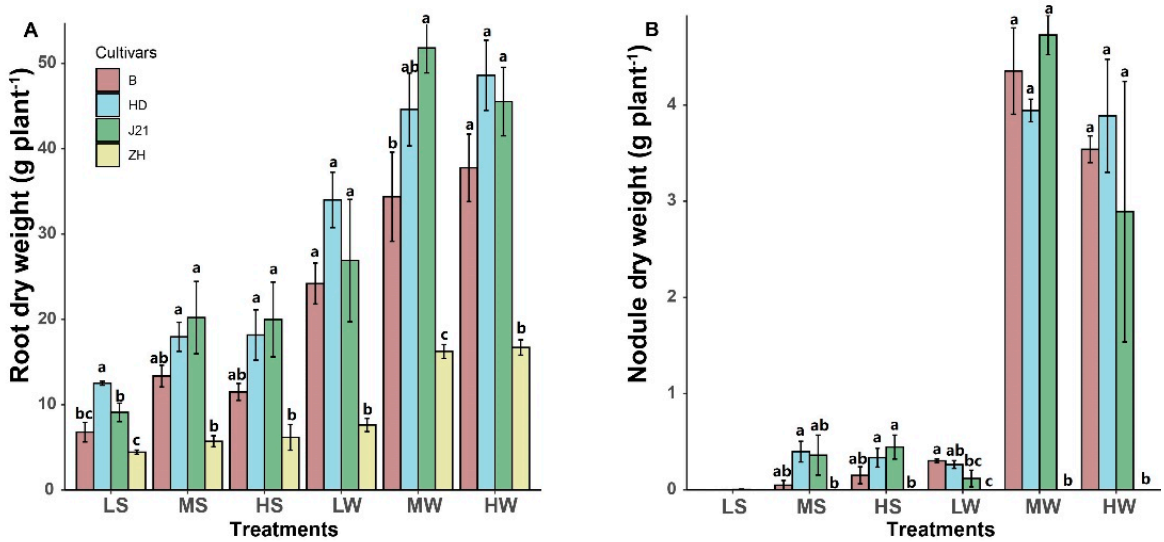

Figure 4. The root traits: root dry weight (**A**), nodule dry weight (**B**) of four genotypes under two water treatments and three P levels of four soybean genotypes [B (Bailudou), HD (Huangsedadou), J21 (Jindou 21), and ZH (Zhonghuang)] under two water treatments [S (cycle water stress), W (well-watered)] and three P levels [L, low P supply (P0), M, mid P supply (P60), H, high P supply (P120)]. The letters under each group of bars indicate different combinations of P and water treatments (as per Figure 1). Values are means plus one standard error of the mean (n = 3).

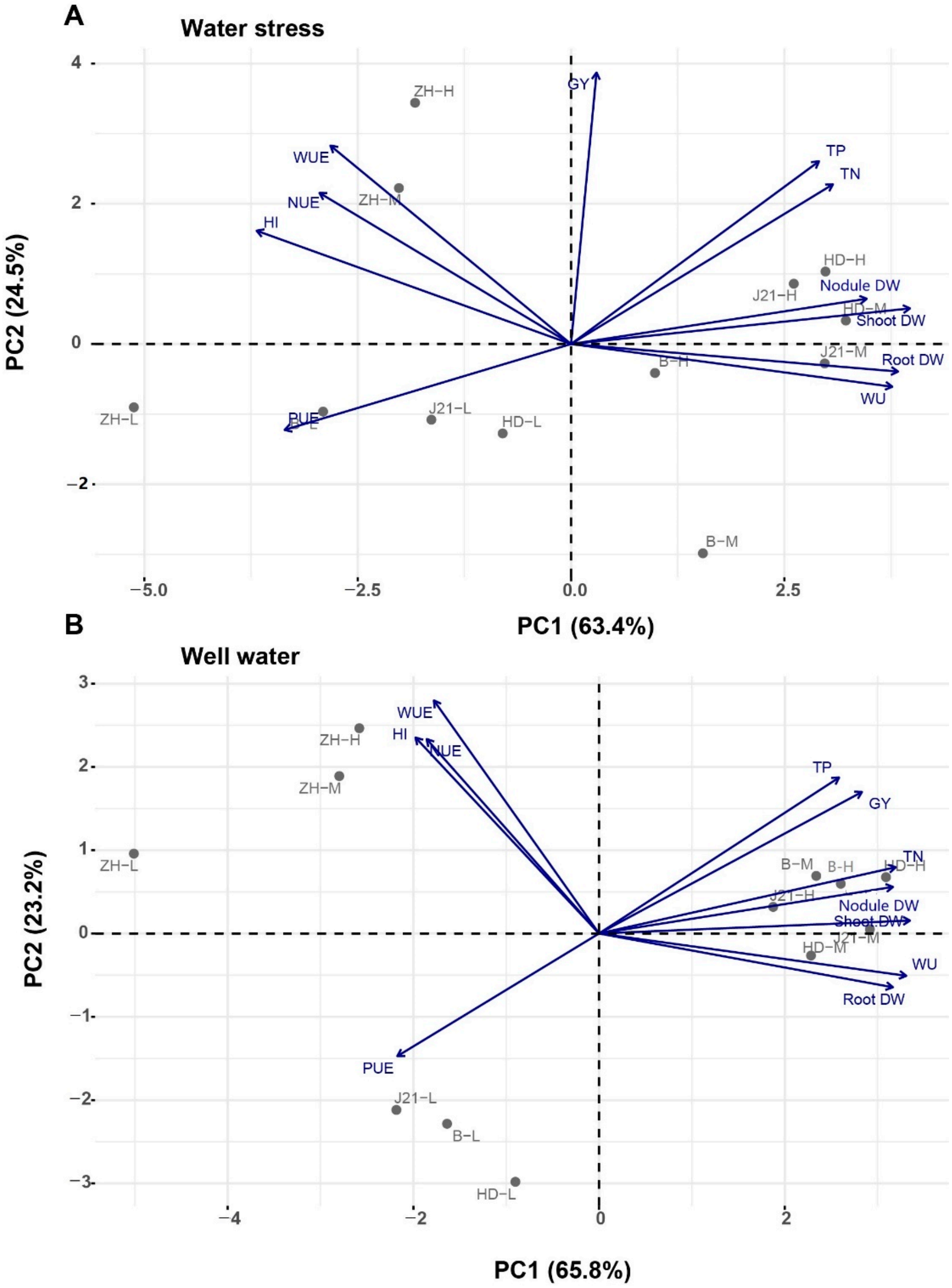

Figure 5. Principal component analysis of 11 traits in four soybean genotypes [B (Bailudou), HD (Huangsedadou), J21 (Jindou 21), and ZH (Zhonghuang)] under two water treatments [cycle water stress (**A**) and well-watered (**B**)]. The 11 traits (vectors indicated by blue arrows) and each genotype with different P level were loaded on the first and second axes. The letters indicating traits are same as Figure 5; the letters after each genotype indicate P level [L, low P supply (P0), M, mid P supply (P60), H, high P supply (P120)].

4. Discussion

4.1. Interaction of P Supply and Water Treatment on Soybean Yield Performance

Similar to previous studies, drought stress and P deficiency significantly impaired soybean productivity [2,3,28,29]. In our study, soybean yield under WS and P0 decreased by about two-thirds and one half of that under WW and P supply, respectively, indicating the soybean yield was more dependent on the water than the P application. P application significantly reduced the adverse effects of water deficit on soybean yield, as reported elsewhere [5,6,11,28]. First, P addition maintained high soybean HI when under WS although the seed yield significantly reduced under WS. This was consistent with previous studies which found that maintaining high HI would be important for crop yield performance under water stress [2,19]. In addition, P supply maintained WUE even with increasing water use and higher WUE is essential to crop drought stress tolerance [2,29]. The P supply can increase Rubisco, modifying the relationship between photosynthates and stomatal conductance, thereby increasing WUE [30]. Finally, P supply significantly increased N and P uptake. The TN and TP positively correlated with GY both under WW and WS, indicated that the limitation of N and P under drought stress and low P availability is one of main reasons decreasing soybean yield. In past studies, researchers found that P addition increased root length, adventitious root density, and root dry weight, which enhanced soybean N and P uptake [5,12,13]. Similarly, in this study, P addition significantly increased root DW which significantly correlated with N and P accumulation. In addition, we found that soybean nodulation also played an important role in soybean N and P accumulation.

4.2. The Relationships between the Nodulation in Soybean and P and N Accumulation and Yield Performance under Different Water and P Levels

Soybean nodulation is affected by both water and P availability [31,32]. Our study showed that water stress and low P availability greatly inhibited nodule DW, restricting the ability of soybean to fix atmospheric nitrogen and acquire P [16]. P addition significantly increased soybean nodule DW, increasing N and P accumulation, and under WW there was a significantly positive correlation between GY and nodule DW. The three soybean cultivars with nodules have significantly higher seed yield than ZH under water and P supply conditions, indicating the important roles of nodule formation in yield performance in different soybean cultivars under varied environments. While under WS, despite P addition stimulating soybean nodulation and increased N and P uptake, we failed to find a significant relationship between nodule DW and GY. This may be because increasing nodule DW means more carbon investment and water use, which lead to a decrease in HI and WUE, thus being detrimental to seed yield under drought conditions. Indeed, it was similar to increasing root DW to enhance soybean N and P uptake, which also decreased HI and WUE, and had no relationship with GY under WS. This indicated that increasing soybean root and nodules investment to improve N and P uptake to increase yield under water deficit conditions is not an economical approach, while improving soybean to effectively use N and P would be more important to soybean yield determination.

4.3. How NUE and PUE Influences Soybean Yield Performance?

Our study showed that water treatment significantly affected PUE and NUE, while P addition did not change NUE but decreased PUE. NUE, but not PUE, was significantly correlated with yield performance under WS, while under WW, PUE was negatively correlated with GY but NUE had no relationship with GY. This demonstrated the importance of NUE for plant adaption under resource scarcity conditions, which was consistent with previous findings [17,18,26]. Nutrition use efficiency depends on crops' ability to uptake, assimilate, store, and remobilize nutrition [33]. In our study, NUE and PUE were tightly correlated with HI, suggesting that plants that partitioned more dry matter to seed could improve NUE and PUE [26,33]. The negative correlation between TN and NUE and TP and PUE indicated that more uptake of N and P result in low NUE and PUE. This may be because increased N and dry matter distributed to seed increased NUE and PUE, resulting in less N and C being directed to vegetative organs (e.g., root and leaves), thus limiting the N and P uptake. Water stress likely limited the capacity for plant vegetative organs' N and P uptake and C and N assimilation, resulting in a low-cost efficiency of distribution and much more N and P being directed to the vegetative organs. Our results revealed lower correlation coefficients between nodule DW and TN, TP, and shoot DW under WS than WW; thus, more N distribution to seeds than other organs with higher resource uptake would be important for yield formation under WS. Further, higher distribution of C, N, and P to other organs, such as leaves and roots, increased water use and the risk of drought stress and impaired yield performance under WS, especially during the reproductive period [2,34]. In contrast, conserving water use would benefit yield performance under water stress conditions [35].

The PUE in our study did not affect yield, possibly due to the lower P contents compared with C and N in seed. Indeed, the role of P is mainly to participate in C and N assimilation and transport; thus, TP would be more critical for yield determination than PUE under low P [36]. Alternatively, this trend may be due to genetic differences between the four genotypes and should be tested with more genotypes. However, PUE remains important for seed production under WS as it tightly correlated with HI and NUE because P influences C and N transport and allocation to seed.

However, some soybean traits related to high PUE and NUE may restrict yield potential when resources are not limited. For example, cultivar ZH had no nodules and the lowest root DW, which increased NUE, PUE, HI, and WUE, and yield performance under WS and P0, but restricted P and N accumulation and shoot DW, limiting its yield potential under sufficient water and P. Therefore, PUE was negatively correlated with yield under WW. The NUE had no significant relationship with yield under WW, this may be because soybean redistributes N from other senescent organs to seed or other new organs to increase NUE [37], weakening the negative relationship of NUE and TN. As a result, there was a weak trade-off between TN and NUE under WS and WW. However, this assumption still needs to be proven in the future. These results demonstrated the important role of NUE in soybean drought adaptation and low P availability, which helps to effectively utilize N to produce more yield under low water availability, and does not impair productivity when water is abundant.

5. Conclusions

In summary, this study showed that P supply increases nodule formation, and thus improves N and P uptake, which decreases the adverse effects of water deficit and increases yield under high water availability. Increasing the allocation of N and P could improve PUE and NUE, while P addition did not affect soybean NUE, an important contributor to yield performance under water shortage and does not influence yield potential under well water conditions. Our study helps us understand the importance of nodule formation and NUE for soybean adaptation to water- and P-deficit conditions, and we suggest that they can be used as important reference traits for further breeding under these conditions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture12091326/s1, Figure S1, the correlation matrix of 11 functional traits under WS and WW.

Author Contributions: The listed authors contributed to this work as described in the following: Conceptualization, Y.J. and J.H.; Funding acquisition, J.H.; Investigation, Y.J., J.H. and Y.Z.; Methodology, Y.J.; formal analysis, Y.J.; Writing-the original draft, Y.J.; Writing—review and editing, Y.J., J.H., Y.Z. and K.H.M.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (32060427), China Postdoctoral Science Foundation funded project (2020M681634).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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