学 位 論 文 の 要 旨

論文題目： Different shoot and root responses to low phosphorus availability in Japanese cultivars of maize and soybean
（日本のトウモロコシとダイズの品種における地上部と根部の異なる低リン応答性）

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Introduction:

Low phosphorus (P) availability in agricultural soils severely impacts crop productivity worldwide. Over-applicating P fertilizers is not a viable solution to overcome P deficiency because such P is a non-renewable resource. Plants have evolved morphological, physiological, and biochemical responses to P deficiency. However, these morphological, physiological, and biochemical responses to P deficiency are species- and genotype-specific. Therefore, assessing the genotypic variability of crop genotypes under low P conditions and developing P-efficient crop genotypes are crucial to keeping the momentum of sustainable agriculture. Phosphorus efficient genotypes are advanced in either P acquisition efficiency (PAE) or P use efficiency (PUE). Strategies related to PAE and PUE are equally essential to improve the P efficiency of crops. Maize (*Zea mays* L.) and soybean (*Glycine max* L.) are important food crops with divergent root traits. Maize, a typical monocot, has a fibrous root system, whereas soybean, a typical dicot, is a tap-root crop. These crop species are essential in diversified cropping systems like intercropping or rotations. Accordingly, genotype strategies could be combined with agronomic strategies to enhance P efficiency jointly in the cropping system.

Research Objectives:

The study aimed to evaluate (1) genotypic variability of Japanese core collections of maize and soybean in response to low P availability, (2) different shoot and root responses of selected Japanese cultivars of maize and soybean, (3) acid phosphatase (ACP) activity and rhizosphere acidification of selected Japanese cultivars of maize and soybean, and (4) to compare different shoot and root responses to low P availability between two species.

Research Methodology:

The study comprised two preliminary screenings of Japanese core collections of maize (86 cultivars) and soybean (94 cultivars) under low P in hydroponic conditions and a pot experiment with Regosols for 30 days. During preliminary screening, soybean and maize cultivars were exposed to low P (50 μM) and (2 μM), respectively. Based on preliminary screening results, ten cultivars of each species were selected for further evaluation under soil conditions. The pot experiment had two P supply rates: low P (10 mg P kg^{-1} dry soil) and high P (50 mg P kg^{-1} dry soil). At harvest in both experiments, the shoot and roots were separated. Shoot dry weight (SDW), root dry weight (RDW), total root length (TRL), root-to-shoot ratio (RRS), and specific root length (SRL) were evaluated. All dried shoot and root samples were ground and digested for P determination using the HNO_3 and H_2O_2 digestion methods. In addition, at the harvest of the pot experiment, root systems were carefully lifted out of the soil with minimal damage, and rhizosphere soil samples were collected to evaluate ACP activity and rhizosphere acidification. PUE (dry weight per unit P uptake) was calculated as SDW divided by shoot P content.

Results and Discussion:

Genotypic variability of core collections of maize and soybean in response to low P:

Based on the preliminary screening results, maize and soybean core collections were clustered into 4 groups. Cluster analysis of soybean and maize revealed that soybean cluster III and maize cluster II characterized the highest Cluster mean for SDW, RDW, and TRL, indicating the availability of promising genotypes for the performance under low P stress in these two cluster groups. This study found that traits such as shoot and root biomass, root length, and shoot and root P contents were highly correlated under low P availability. The positive correlation between root dry weight and shoot and root P contents confirmed that genotypes with enhanced root growth under low P conditions could explore more nutrients.

Plasticity of the shoot and root growth responses:

Among the tested cultivars, except the maize cultivar JMC 76 and soybean cultivar GmJMC033, all other cultivars reduced the shoot biomass drastically under low P stress. Their relative shoot growths under low P stress compared to high P were 83% and 81%, respectively. P deficiency caused an increase in RRS in almost all cultivars due to decreased shoot growth and increased carbon allocation from the shoot to the roots. However, we found differences in RDW, TRL, and SRL among different cultivars in both species under low P. In maize at low P, RDWs were either significantly decreased (JMC 8, JMC 13, and JMC 80) or not significantly different compared to high P among the tested cultivars. TRLs were either significantly increased (JMC 76), decreased (JMC 80), or not significantly different relative to high P.

Contrary to maize, soybean RDWs were almost significantly increased, and TRLs were either significantly increased (GmJMC040 and GmJMC085) or not significantly different compared to high P. These results imply that different root responses to P deficiency are genotype-specific. Furthermore, the above responses of some of the cultivars of the two species were distinct under low P, indicating their low P tolerance. In maize, the cultivars JMC 57, JMC 76, JMC 8 and JMC 58, and in soybean, the cultivars GmJMC033, GmJMC040 and GmJMC085 showed distinct modifications in root morphology, including high RRS, SRL, and TRL to produce comparatively greater shoot biomass under low P by increasing P acquisition.

A few differences existed among the low P-tolerant maize cultivars: JMC 57, JMC 76, JMC 8, and

JMC 58 under low P in their modifications, especially in RRS and SRL. The maize cultivars JMC 76, JMC 8 and JMC 58 produced a similar amount of biomass with reduced metabolic cost of soil exploration compared to the cultivar JMC 57. In the case of low P-tolerant soybean cultivars: GmJMC033, GmJMC040 and GmJMC085, GmJMC085 showed remarkable responses with regards to RDW, TRL and SRL compared to the other two cultivars under low P conditions. Thus, soybean cultivar GmJMC085 produced greater biomass with reduced metabolic cost of soil exploration than soybean cultivar GmJMC033. Besides, genotypes with reduced metabolic costs of soil exploration are imperative to improve P acquisition under low P stress. In addition, the maize cultivars JMC 13, JMC 71, and soybean, the cultivars GmJMC064, GmJMC059 and GmJMC106 were P-inefficient due to poor modification in root growth. Our results highlighted that compared to low P-sensitive genotypes of both species, low P-tolerant genotypes could modify their root system by increasing RRS, TRL, and SRL to acquire P to cope with P deficiency.

P accumulation and PUE:

Shoot P concentrations were significantly lower in low P treatment in maize and soybean cultivars except for GmJMC059 and GmJMC106. The notable genotypic variation in shoot P concentrations could be found under both species' high P but not the low P. The shoot and root P concentrations were lower in P-tolerant cultivars than in P-sensitive cultivars, e.g., in maize cultivars JMC 57 and JMC 71 and the soybean cultivars GmJMC085 and GmJMC106. Therefore, the genotypes with poor biomass and high tissue P concentrations were considered poor performers under low P conditions. However, P deprivation caused a significant increase in the PUE in both maize and soybeans. The notable genotypic variation in PUE could be found in maize and soybean cultivars under low P, indicating that some cultivars efficiently utilized acquired P more than others under low P conditions.

ACP and rhizosphere acidification:

The amelioration in ACP activity of rhizosphere soil of maize under low P condition seemed distinct in all cultivars. However, it was not prominent in P-sensitive soybean cultivars GmJMC064, GmJMC059, and GmJMC106 under low P. It further indicates that ACP activity under low P depends on plant species, and compared to maize, soybean resulted in weak ACP activity in rhizosphere soil. The soybean cultivars GmJMC040, GmJMC085, and GmJMC033 are among the cultivars that showed higher ACP activity under low P, indicating that low P-tolerant cultivars of soybean are characterized by high ACP activity in rhizosphere soil. These variations are imperative for future breeding ventures in producing P-efficient genotypes.

Compared to maize cultivars, the reduction in rhizosphere pH was noticeable among the soybean cultivars under low P. Among the low P-tolerant maize cultivars, only JMC 76 significantly reduced rhizosphere soil pH and the low P-tolerant soybean cultivars, GmJMC033 and GmJMC085, significantly dropped down the rhizosphere soil pH under low P conditions However, our results highlighted that maize cultivars showed low P tolerance; JMC 76, JMC 57, JMC 58 and JMC 8 highly depended on root morphological traits rather than physiological traits. Further, the soybean cultivar GmJMC085, characterized by well-defined morphological and physiological responses under P deficiency, indicated that low P tolerance was due to both responses in soybean.

Contrasting responses of maize and soybean under low P stress:

Maize seems more responsive to P under high P conditions than soybeans. It drastically reduced the shoot P growth under low P stress than soybean reduced. Both species were characterized by high RRS, sustained TRL, and SRL under P deficiency. In contrast, maize had significantly higher TRL and SRL than soybean, indicating that contrasting root traits evolved in efficient P acquisition. The possible reasons for the higher TRL and SRL in maize would be aerenchyma formation, root hair proliferation, and enhanced or sustained lateral rooting to maximize soil exploration at minimum metabolic cost. However, the high P uptake efficiency of soybeans is supported by the fineness of the root system. Under low P stress, both species significantly improved the PUE, whereas soybean resulted in higher PUE than maize under both P conditions.

Furthermore, maize enhanced the ACP activity notably more than soybean under P-impoverished conditions, which can facilitate mobilizing sparingly available P in soils. Therefore, significant variation among species and genotypes in the same species exists regarding the root traits under low P stress. Hence, further exploiting genotypic variation is needed for better crop performance under low P stress.

Conclusions:

We observed significant genotypic variation in selected cultivars of Japanese core collections of maize and soybean under low and sufficient P conditions. The results showed that the plasticity of the root system characterized by high RRS, SRL and TRL contributes to the differences among genotypes. Their distinct modifications in morphological and physiological traits are crucial in considering future breeding ventures to produce more P-efficient crop genotypes. Among the tested maize cultivars, JMC 76, JMC 57, JMC 58 and JMC 8 and under the tested soybean cultivars GmJMC033, GmJMC040, and GmJMC085 showed distinctive root modification under low P stress, showing their low P tolerance. Further, identifying their quantitative trait loci (QTLs) would be more beneficial in understanding the genetic basis for their adaptations under low P stress. These genotypic adaptations could be combined with agronomic strategies to enhance the overall P use efficiency in diversified cropping systems like intercropping.