

The effect of molybdenum and boron in soil on the growth and photosynthesis of three soybean varieties

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ABSTRACT

This paper presents a study on growth and photosynthesis response of soybean to Mo and/or B in soil. Pot experiments were set up to examine the effect of Mo and/or B on growth and photosynthesis of three soybean varieties with four treatments (control, +Mo, +B, +[Mo + B]) at various growth stages. The study showed that Mo and/or B increased main length, system volume and dry weight of the roots, aboveground biomass, leaves' photosynthesis rate of soybean. The variation and interaction between Mo and B in soil was explored with regard to their impact on soybean growth and photosynthesis. There were some dissimilarity in growth and photosynthesis in the plants between the supplements of Mo and B in the soil, and the interrelation between Mo and B in plant and was co-supplementary to each other. Therefore, growth and photosynthesis of the soybean with Mo and B treatments were much more improved than those with Mo or B alone. Besides, some genotypic variation was found in three soybean varieties, in which Zhechun III was the most sensitive and 3811 the most tolerant plant to Mo and B.

Keywords: main length of roots; system volume of roots; dry weight of roots; leaf area; aboveground biomass; photosynthesis rate

Molybdenum (Mo) is an essential micronutrient for plants, bacteria and animals and boron (B) is an essential microelement in higher plants. Many soils in the world suffer from a deficiency of microelements such as Mo and B. More than 44.7 million hectares of land lacks in Mo and 33.3 million hectares lacks in B in China (Liu 1996, Liu 2001). Therefore, Mo and B deficiency of soil is a widespread agricultural problem that induces yield and quality losses in many crop species worldwide (Liu 1991, Shorrocks 1997, Liu et al. 2000, Liu 2001). Mo-deficient plants exhibit poor growth and low contents of chlorophyll and ascorbic acid (Marschner 1995, Liu 2002b). Boron deficiency causes inhibition in flower development, low fruit and seed set, male sterility, seed abortion or the formation of damaged embryos, and malformed fruits (Dell and Huang 1997, Liu 2002a). There are still many questions surrounding plant Mo uptake and metabolism; the exact functional of B in the plant is not fully understood (Marschner 1995, Goldbach 1997, Liu et al. 2000, Hale et al. 2001, Liu 2002b).

The soybean belongs to the plant that needs more Mo than most of other plants and is very sensitive to B deficiency. Various studies have been reported that application of Mo or B enhances the yield of soybean that grows in the Mo or B deficient soil (Gupta and Lipsett 1981, Liu 2001, Guertal 2004). The growth and photosynthesis of soybean responding to Mo and/or B fertilization need further systematic study to examine the interactive and conjunctive effect of Mo and B.

It is well known that there is a difference in response to a particular nutrient deficiency among different plants or different genotypes in the plants (Bellaloui and Brown 1998). The ability of a genotype to grow and yield well in soils too deficient in a particular nutrient for a standard genotype has been defined as nutrient efficiency, without inferring any mechanism (Graham 1984). Many studies reveal dramatic differences in a plants response to Mo or B nutrient between species and cultivars of the same species raised under identical conditions (Gupta and Lipsett 1981, Liu 1991, 1996). Little research has been reported to differences among

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different genotypes of soybean in Mo and/or B nutrient in soil.

Therefore, the aim of this study was to determine the effect of Mo and/or B in soil on growth and photosynthesis, interactive effect between Mo and B on soybean and to determine the differences in growth and photosynthesis among three soybean varieties. To achieve this goal, we investigated the main root length, roots system volume, dry weigh, leaf area, above-ground biomass, photosynthesis rates of leaves of three soybean varieties under different treatments of Mo and/or B.

MATERIAL AND METHODS

Plant materials

The soybean, *Glycine max* (L.) Merrill, seeds of three varieties, Zhechun III, Zhechun II and 3811, used for the study were obtained from the seeds store, Zhejiang Academy of Agricultural Science, Hangzhou, China.

Plant growth condition

Seeds of the soybean were disinfected with 10% (w/v) H₂O₂ for 20 minutes and washed thoroughly with distilled water and sown in seedbeds filled with a mixture of perlite and vermiculite (1/1, v/v) in a greenhouse under natural light and air conditions, 25°C, 80% relative humidity. The germinated soybean seedlings were selected for uniformity when the first trifoliolate leaf completely outspread and transferred to plastic growth pots (35 cm diameter and 35 cm tall, a hole 2 cm drilled at bottom for drain purpose) in a netted-greenhouse, a special greenhouse chamber, with glass roof and wire-netted sides for natural air and light conditions. To facilitate plant removal, the pots were lined with perforated plastic bags; there were four plants in each pot. The pots were moved and rearranged daily to receive a random distribution of growth condition in the netted-greenhouse. The plants were watered with 200–400 ml deionised water per pot, increased as the plant grew, and done each morning to avoid water stress.

Soil, 5 kg per pot, was topsoil of 0–20 cm deep collected from a field in Jiangshan, Zhejiang Province, China (28°45'N, 118°38'E). The soil belongs to subtropical alluvial red soils. The freshly collected soil was screened with an 8-mm sieve to remove the stones, coarse plant roots and residues then air-dried prior to further the pot experiment. The screened and air-dried soil was ground to pass through a 2-mm sieve for chemical analysis. The physico-chemical characteristics of the soil were

analysed as: pH 5.96, organic C 18.2 g/kg, cation exchange capacity (CEC) 39.4 mmol/kg, total N 0.53 g/kg, hydrolytic N 22.8 mg/kg, total P 2.3 g/kg, available P 60.4 mg/kg, available K 147.9 mg/kg, effective Mo 0.134 mg/kg, hot water soluble (HWS) B 0.20 mg/kg.

Mo and B treatments

The experiment was run for 110 days with four treatments (CK, +Mo, +B, +[Mo + B]). CK is the control without application of Mo/B fertilizers and it is in the condition of Mo and B deficiency; three treatments (+Mo, +B and +[Mo + B]) were applied with various amounts of Mo and/or B fertilizers. +Mo is the adequate Mo treatment containing 0.0185 g Ammonium Heptamolybdate, (NH₄)₆Mo₇O₂₄·4 H₂O; +B the adequate B treatment containing 0.08 g borax (Na₂B₄O₇·10 H₂O), and +[Mo + B] is the adequate Mo and B treatment containing 0.0185 g Ammonium Heptamolybdate and 0.08 g borax.

Sampling and plant growth analysis

Each treatment consisted of four replicates in a randomised block design including twenty-eight in total and was sampled at six growth stages. Four sampling pots were selected randomly from the same treatment at the first five growth stages except for eight pots in the harvest maturity stage for sufficient plant sampling. Six growth stages were adopted (c.f. Fehr et al. 1971): V5 (5-trifolia stage), R1 (initiation of flowering stage), R3 (early podding stage), R4 (peak of podsetting stage), R7 (physiological maturity stage) and R8 (harvest maturity stage). Main root length, root system volume, leaf area, biomass of roots and the aboveground parts were measured at V5, R1, R4 and R8 stages. The photosynthesis rates of the soybean leaves were measured at V5, R1, R3 and R7.

When sampling, the roots of the soybean plants were freed from soil by immersing the pot in a bucket of water for 5 minutes to avoid damage to the roots. The soil was subjected to careful washing under a gentle water flow. Root system volume in ml was measured by the water displacement method. The main root length of soybean was measured with a ruler. Leaf area per plant was determined using a method of regression relationship between leaf weight and leaf area (Zhang 1992). Subsequently, the roots and shoots were separated from each other. The roots and the aboveground parts (stems, leaves, flowers, pods and seeds) were dried separately at 60°C for 48 hours for biomass determination.

Photosynthesis analysis

Photosynthetic rates of soybean leaf were measured with the second expanded leaflet on the main stem (one leaf per plant, eight plants per treatment) at V5, R1, R3 and R7. Measurements were made between 11:00 and 13:00 hour at photosynthetic light saturation with a LI-6200 portable photosynthesis system (LiCor Inc., Lincoln, NE).

Statistical analysis

The data obtained were analysed by a statistical analysis system program (SAS 1990) using an analysis of variance (ANOVA). All values shown in the tables and graphs represent the means of four replicates. Error bars indicate SES. *LSD* was used to compare means among treatments.

RESULTS

Mo and B on root growth of soybean

Roots of plant are the most sensitive organs to a deficiency or surplus of nutrition elements in the soil. Under Mo and B fitness or deficiency, the fast root growth responses had been exhibited (Figure 1 and Table 1). Mo and/or B cause elongation of the main root, enlarging of root volume and increasing of root dry weight (biomass). Among the effect of the treatments on promoting root growth of three soybean varieties as compared to CK (control, Mo/B deficiency), the effect by +[Mo + B] (Mo and B treatment) was the highest, then +B (B treatment), and +Mo (Mo treatment) the lowest. By comparison of temporal changes in the root growth at four growth stages, the stage from R1 to R4 had the greatest increase of main root length, volume and dry weight of the root. Because the soybean needed more nutrition in those stages the fast root growth was very important to absorbing nutrition. Some genetic variation in the response to Mo and/or B was found among three soybean varieties. In CK, the main root length, volume and dry weight of root of 3811 was the highest, then Zhechun II, the third Zhechun III; however, in +Mo and/or +B, Zhechun III was the highest, then Zhechun II and 3811.

Mo and B on leaf area of soybean

There was significant ($P < 0.05$) or very significant ($P < 0.01$) differences in leaf area between Mo and/or B of the three treatments and the control (Figure 2). +[Mo + B] had the largest leaf area at

Table 1. The response of volume and dry weight of soybean roots to Mo and B with four treatments at four growth stages

Characteristics of root growth	Treatment	Soybean varieties											
		Zhechun III				Zhechun II				3811			
		V5	R1	R4	R8	V5	R1	R4	R8	V5	R1	R4	R8
Volume (cm ³)	CK	0.13 ± 0.04	0.17 ± 0.03	0.24 ± 0.04	0.27 ± 0.04	0.15 ± 0.02	0.19 ± 0.03	0.26 ± 0.03	0.28 ± 0.03	0.16 ± 0.02	0.20 ± 0.02	0.27 ± 0.03	0.31 ± 0.03
	+Mo	0.20 ± 0.03*	0.25 ± 0.01*	0.32 ± 0.02*	0.36 ± 0.02*	0.20 ± 0.03*	0.25 ± 0.05*	0.36 ± 0.05*	0.39 ± 0.05*	0.18 ± 0.03	0.24 ± 0.02*	0.33 ± 0.04*	0.35 ± 0.02*
	+B	0.35 ± 0.01**	0.40 ± 0.05**	0.47 ± 0.04**	0.50 ± 0.05**	0.24 ± 0.02*	0.32 ± 0.02*	0.46 ± 0.02**	0.48 ± 0.02**	0.17 ± 0.01	0.24 ± 0.01*	0.35 ± 0.02*	0.38 ± 0.03*
	+ [Mo + B]	0.40 ± 0.05**	0.45 ± 0.02**	0.51 ± 0.03**	0.54 ± 0.04**	0.25 ± 0.03*	0.35 ± 0.03*	0.49 ± 0.03**	0.53 ± 0.06**	0.19 ± 0.04	0.26 ± 0.02*	0.37 ± 0.02*	0.42 ± 0.02*
Dry weight (g)	CK	0.10 ± 0.03	0.15 ± 0.03	0.22 ± 0.02	0.26 ± 0.02	0.11 ± 0.02	0.19 ± 0.04	0.25 ± 0.03	0.28 ± 0.03	0.12 ± 0.01	0.17 ± 0.02	0.25 ± 0.03	0.29 ± 0.02
	+Mo	0.15 ± 0.03*	0.20 ± 0.01*	0.34 ± 0.01*	0.38 ± 0.02*	0.14 ± 0.02	0.22 ± 0.03	0.32 ± 0.02*	0.37 ± 0.02*	0.13 ± 0.03	0.21 ± 0.03*	0.31 ± 0.04*	0.35 ± 0.03*
	+B	0.17 ± 0.02*	0.22 ± 0.02*	0.38 ± 0.03*	0.43 ± 0.03*	0.16 ± 0.02*	0.24 ± 0.02*	0.36 ± 0.04*	0.40 ± 0.04*	0.15 ± 0.02	0.23 ± 0.02*	0.34 ± 0.02*	0.38 ± 0.02*
	+ [Mo + B]	0.19 ± 0.01*	0.25 ± 0.02*	0.40 ± 0.02*	0.45 ± 0.04*	0.17 ± 0.02*	0.26 ± 0.03*	0.38 ± 0.03*	0.42 ± 0.02*	0.16 ± 0.01	0.24 ± 0.02*	0.36 ± 0.03*	0.41 ± 0.04*

The values are means ± SE (n = 4)

*indicates significantly different ($P < 0.05$) from control, ** very significantly different ($P < 0.01$) from control treatment by LSD

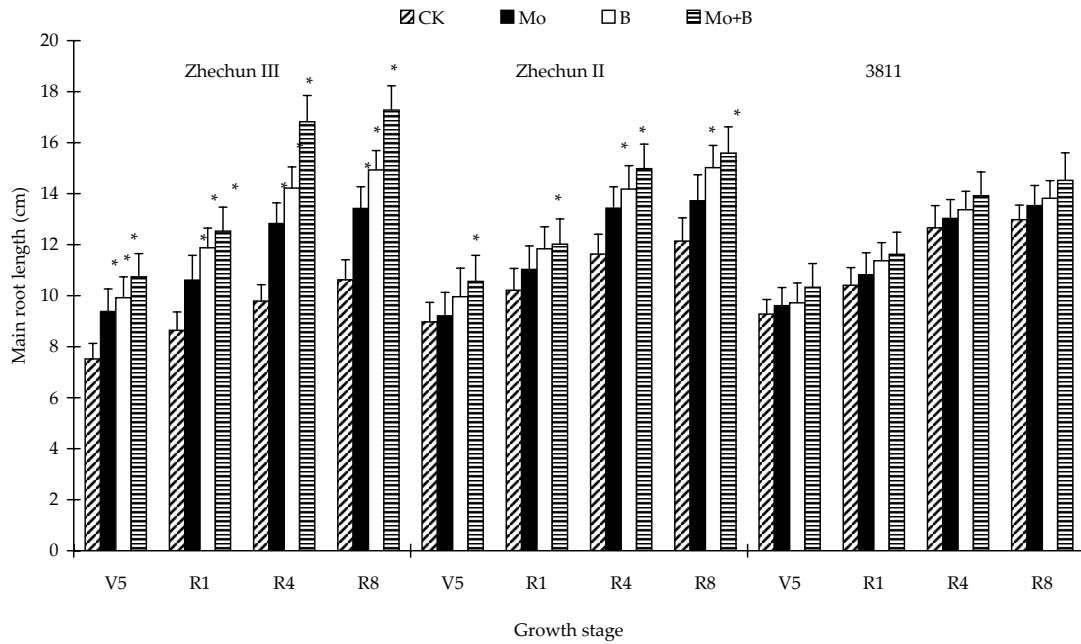


Figure 1. The main root length of three soybean varieties under Mo and B at various levels: CK (control, without Mo/B fertilizer); +Mo, 0.0185 g $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4 \text{H}_2\text{O}$; +B, 0.08 g $\text{Na}_2\text{B}_4\text{O}_7 \cdot 10 \text{H}_2\text{O}$; +[Mo + B], 0.0185 g $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4 \text{H}_2\text{O}$ and 0.08 g $\text{Na}_2\text{B}_4\text{O}_7 \cdot 10 \text{H}_2\text{O}$; four growth stages are shown: 5-trifolia stages (V5), initiation of flowering stages (R1), peak of podsetting stages (R4), harvest maturity (R8); the values are means \pm SE ($n = 4$) *indicates significantly different ($P < 0.05$) from control treatment by LSD

different growth stages, while +B had larger leaf area than +Mo. Due to the requirement of more photosynthesis products to fit fast growth of the reproduction organs, the fastest increasing stage of leaf area was from R1 to R4. A comparison of

leaf area among three varieties in the various treatments reveals that Zhechun III has the greatest increase, 3811 the smallest in CK; however, the result is contrary in other treatments (+Mo, +B and +[Mo + B]).

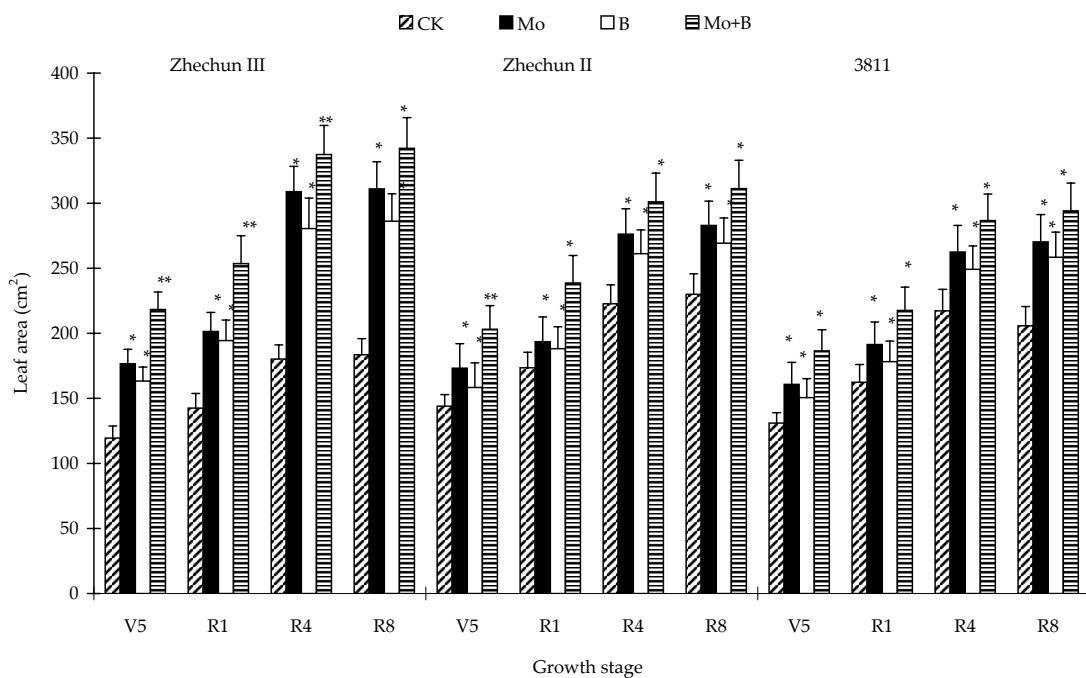


Figure 2. The leaf area of soybean at the various treatments and growth stages under effect of Mo and B; LSD (* or **) are as described in Table 1; the values are means \pm SE ($n = 4$)

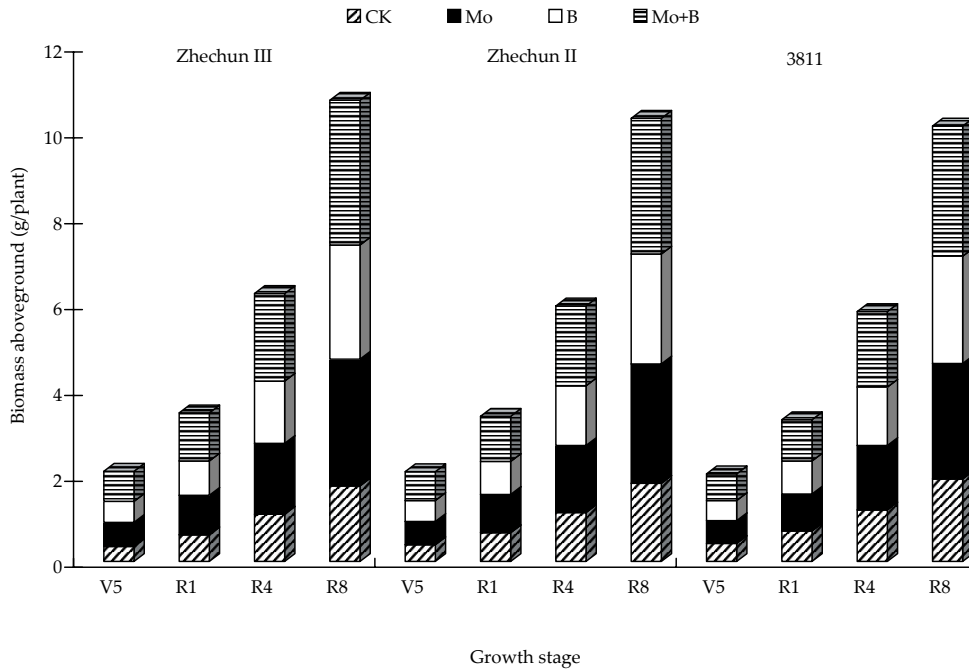


Figure 3. The aboveground biomass of soybean (including stems, leaves, flowers and pods) at various treatments and growth stages under Mo/B effect; the values are means \pm SE ($n = 4$)

Mo and B on aboveground biomass

The results suggest that Mo and/or B significantly ($P < 0.05$) promoted accumulation of aboveground biomass of soybean in +Mo and +B and very significantly ($P < 0.01$) in +[Mo + B] (Figure 3) compared to CK. Therefore, the best promoting effect on above-

ground biomass was observed in +[Mo + B]. The effect on biomass in +Mo was greater than that in +B. Unlike the temporal change of the root growth and leaf area, the accumulation of aboveground biomass varied in the different treatments. The greatest accumulation stages were from V5 to R1, R4 to R8, R4 to R8 and R1 to R4 in the treatments

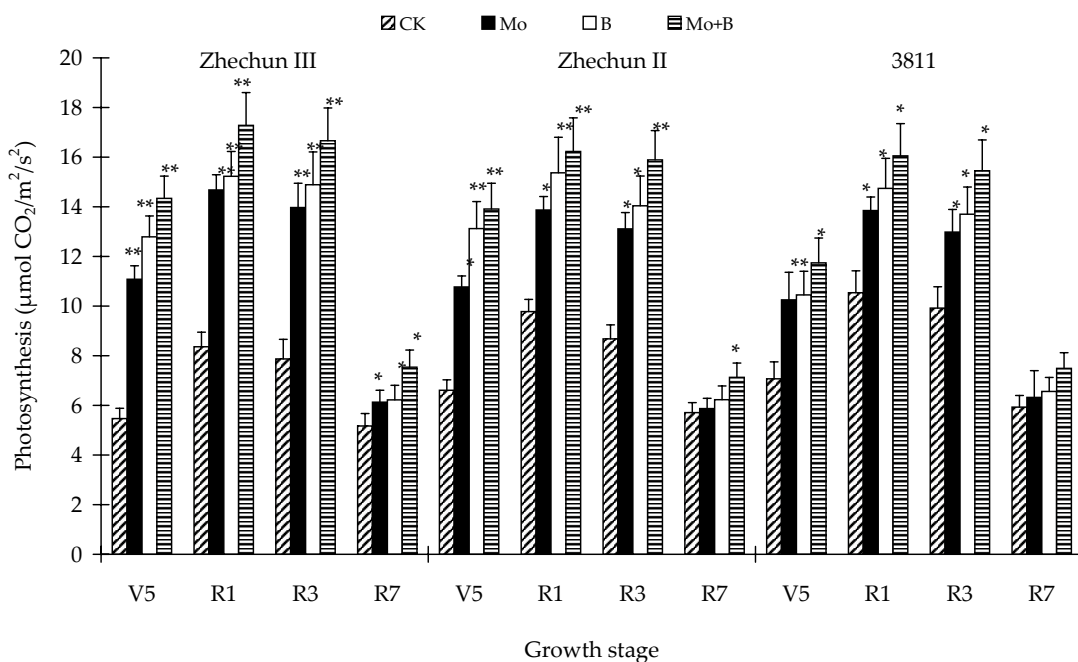


Figure 4. The photosynthesis rates of soybean leaves under Mo and B effect in the treatments and growth stages (V5, R1, R3 the early podding stage and R7 the physiological maturity stage); LSD (* or **) is as described in Table 1; the values are means \pm SE ($n = 4$)

CK, +Mo, +B and +[Mo + B], respectively. In CK (low Mo/B), the increases of biomass accumulation between stages reduced with growth stages from V5 to R8. For example, the increases of Zhechun II are 71.8%, 70.2%, 59.7% at R1, R4 and R8 respectively, relative to their previous stages. As Mo/B deficiency inhibits growth of the soybean, more inhibition will occur with prolonged time (Liu 2000). The difference in changes of aboveground biomass with regard to the various Mo/B treatments in three soybean varieties was similar to that of root growth and leaf area.

Mo and B on photosynthesis rates

The photosynthesis rate in the soybean leaves varies in four treatments. It was the lowest in CK and the highest in +[Mo + B] (Figure 4). It is noticed that the photosynthesis rate of soybean leaves in +B was greater than that in +Mo. The response of three plant varieties to the Mo/B treatments varies at different growth stages. For example, in comparison to CK, photosynthesis rates of Zhechun III soybean leaves in +[Mo + B], +B and +Mo increased some 162.16%, 133.82% and 102.56% at V5; 106.7%, 82.18% and 75.6% at R1; 111.69%, 89.2% and 77.56% at R3; and 46.7%, 20.31% and 18.57% at R7, respectively. This indicates that the difference in photosynthesis rate among four treatments reduces with time. Zhechun II and 3811 soybean varieties possess similar characteristics. The photosynthesis rates of soybean leaves were higher at R1 stages and followed by R3, V5 and R7. The change of photosynthesis rates in three soybean varieties under Mo/B effect was similar to that of the root growth.

DISCUSSION

The most rapid response to B deficiency in higher plants is the cessation of root elongation through limiting cell enlargement and cell division (Marschner 1995, Dell and Huang 1997, Goldbach 1997, Liu 2002a). We demonstrated in this study that the growth of main root length, roots system volume and dry weight are enhanced with Mo or B and the extent of increase with B treatment are better than those with Mo treatment (Figure 1 and Table 1). There was no previous study on the direct effect of Mo on the root growth of the plant, but our research exhibited that Mo treatment apparently enhanced the growth of the main root length, roots system volume and dry weight of soybean. From previous knowledge on physiological function (Gupta and Lipsett 1981, Marschner 1995, Liu 2000), we postulate that Mo

indirectly affects the growth of plant roots through enhancing nitrogenase activity, nitrate reductase activity and growth of the nodule of the soybean roots, and promoting hormone synthesis that can be transported to roots. On the other hand, Mo plays a key role in nitrogen metabolism through some important Mo-enzymes (Stallmeyer et al. 1999, Liu 2000, Liu and Yang 2001) and B that indirectly involves nitrogen metabolism (Goldbach 1997, Liu et al. 2000). Consequently, we found that an increase of leaf area and aboveground biomass in the Mo treatment is greater than that in the B treatment compared to the control (Figures 2, 3, 5 and Table 4).

No previous experimental result showed a direct effect on photosynthesis of the plant from Mo or B (Gupta and Lipsett 1981, Dell and Huang 1997), but Mo and B can be indirectly associated with photosynthesis rates of soybean according to our recent study (Liu 2000). Liu (2000) found that B enhanced photosynthesis efficiency of soybean by membrane maintenance and photosynthesis products translocation and Mo did by chlorophyll stability and enlarging leaf area for photosynthesis. Some studies demonstrated that B excess or deficiency resulted in a decrease of photosynthesis rates in *Cucurbita pepo*, citrus and sunflower leaves (Lovatt and Bates 1984, Kastori et al. 1995, Papadakis et al. 2004), but Sage et al. (1989) reported that photosynthesis in *Streptanthus morrisonii* leaves are unaffected by high boron and Zhao and Oosterhuis (2003) found that in the field study, neither soil nor foliar B treatment improved cotton photosynthesis due to sufficient soil B for plant growth (0.2 and 0.3 mg/kg at two study sites). Gupta et al. (1991) also observed that treatment with 2 mg/kg Mo (soil dry weight) resulted in a decrease in photosynthesis of 22% in the soybean leaves. The results (Figure 4) clearly showed that photosynthesis rates of the soybean leaves remarkably increased with Mo or B, and photosynthesis rate for adequate B treatment was greater than that of an adequate Mo treatment.

The effect of Mo and B on the plant has been investigated in a number of studies (Li et al. 1997, Du et al. 1999, Liu 2000, 2001, Garcia et al. 2001, Li et al. 2002, Deng and Zhang 2003), but most of these studies were concerned only with crop yield. As the result of a supplement of Mo and B, the crop yield markedly increased, especially in Mo/B deficiency soil, when compared with a supplement of Mo or B alone. Almost all of those studies were not referred to the interactive and combined effect of Mo and B in growth and physiology. According to the results obtained in this study, main root length, roots system volume, dry weight of roots, aboveground biomass and photosynthesis rates of leaves with Mo and

B increased greater than that with Mo or B alone. This indicated that the interaction between Mo and B is positively correlated and co-supplementary. From the interrelated researches up to now, Mo is absorbed from the soil solution by roots mainly as MoO_4^{2-} and HMoO_4^- with active entry into cells and B is absorbed from the soil solution by roots mainly as H_3BO_3 with passive entry into cells (Bellaloui et al. 1999, Liu et al. 2000, Liu and Yang 2001). BO_3^{3-} , MoO_4^{2-} and HMoO_4^- are very weak anions, and thus Mo and B are not competitive in the process of entry into the cells, which may result in the co-supplementary effect of Mo and B. Further study on the mechanism of the interaction between Mo and B in plant and soil needs to be carried out.

Many studies reported that a large genotypic variation of growth, physiology and quality in response to B (Liu and Yang 1999, Liu 2000, 2001, Karabal et al. 2003) and Mo (Gupta and Lipsett 1981, Liu 2000, 2001). Three soybean varieties in our experiment exhibited some genotypic variation in response to Mo and B. Zhechun III is more sensitive than Zhechun II and 3811. Under low Mo and B, most indices of the growth and physiological characteristics in our results are low, but they became higher with Mo and B. The sensitivity of Zhechun III is just contrary to 3811 and Zhechun II is in between. The mechanism behind genotypic variations has yet explained, some hypothesis had been formulated to different genotypic response to Mo or B. It may be a difference in cell wall composition (Marschner 1995), membrane permeability (Hu and Brown 1997) or activities of total antioxidant systems (Liu 2000). Studies of genotypic variation in response to Mo and B at molecular level have begun to appear in the literature in the last few years. Genetic control of B efficiency has been reported for many species (Rerkasem and Jamjod 1997, Yang and Romheld 1999). Boron efficiency genes in *Brassica napus* have been mapped (Xu et al. 2001) and a membrane protein, with homology to bicarbonate transporters in animals, shown to be responsible for B transport has been identified in *Arabidopsis thaliana* (Takano et al. 2002). Genetic control of molybdenum cofactor that is related to Mo efficiency (Savidov et al. 1997) has also been reported for some plants (Pan et al. 2000, Xiong et al. 2001). Further research is needed to clarify the particular process of all genetic control to the genotypic variations in response to Mo and/or B.

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ABSTRAKT

Vliv molybdenu a bóru v půdě na růst a fotosyntézu tří odrůd sóje

Byla studována závislost růstu a fotosyntézy rostlin sóje na obsahu Mo a B v půdě. V nádobových pokusech byly sledovány čtyři varianty (kontrola, +Mo, +B, +[Mo + B]) tří odrůd v několika růstových fázích. Mo i B zvyšoval průměrnou výšku rostlin, objem a hmotnost kořenového systému i nadzemní části a rychlost fotosyntézy listů. Hodnocena byla také variabilita a interakce v působení Mo a B. Mezi účinkem Mo a B v půdě na růst a rychlost fotosyntézy

sóji byly významné rozdíly, přičemž obě živiny se vzájemně doplňovaly. To znamená, že růst a fotosyntéza byly u varianty +[Mo + B] zvýšeny mnohem výrazněji než u variant +Mo nebo +B. Prokázány byly také odrůdové rozdíly, přičemž odrůda Zhechun III byla nejcitlivější a odrůda 3811 byla ovlivněna nejméně.

Klíčová slova: délka hlavních kořenů; objem kořenového systému; hmotnost sušiny kořenů; listová plocha; hmotnost sušiny nadzemní biomasy; rychlost fotosyntézy

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